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A Survey of Gross Stomach Morphology in New World Cricetinae (Rodentia, Muroidea), with Comments on Functional Interpretations

BY
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INTRODUCTION

The dental battery of muroid rodents has received more attention from a comparative aspect than have other sections of the alimentary tract. Among earlier works, the studies of Toepfer (1891), Tullberg (1899) and Bensley (1902) are notable exceptions to the inattention usually accorded to posterior segments of the gut; however, they sampled relatively few species of Muroidea. More recently, Vorontsov (1957, 1962, 1967) has greatly extended the number of muroid species examined and demonstrated substantial variation in different sectors of the digestive system. Such comprehensive knowledge of this morphological variation provides a framework for comparative physiological studies of digestion which may lend insight to dietary differences between various species. Furthermore, a comparative approach often discloses additional characters useful in assessing phyletic relationships.

The diverse modifications recorded for the stomachs of muroid rodents are particularly striking and applicable to both systematic and functional problems. In view of Vorontsov's limited representation of New World forms, a survey of gross gastric morphology was undertaken in a group of New World rodents, the Cricetinae. The results of that survey, together with a discussion of possible functional interpretations, form the subject of the present report.

ACKNOWLEDGMENTS

A number of people have contributed to this study. Various stages of the manuscript have been critically read and commented upon by Drs. D. M. Lay and E. T. Hooper and fellow graduate students D. G. Huckaby and J. A. Lackey. Their efforts and suggestions are sincerely appreciated. Special thanks are due Dr. D. J. Klingener of the University of Massachusetts for reading the manuscript and initially suggesting the problem.

The collection and facilities of the University of Michigan Museum of Zoology were freely opened to me by Drs. Hooper and Lay. Many specimens used in the study were obtained from other institutions and I wish to thank the curators of those collections who made the samples available: Dr. G. G. Musser, the American Museum of Natural History; Dr. R. H. Baker, The Museum, Michigan State University; Drs. L. de la Torre and K. Liem, the Field Museum of Natural History, Chicago; Dr. C. O. Handley, the U.S. National Museum; and Dr. S. R. Humphrey, the Florida State Museum, University of Florida. Peter Dalby of Michigan State University made special effort to provide examples of certain Argentinian species, and Dr. G. L. Forman at Rockford College, Illinois kindly supplied the sample of *Neotoma phenax* from his private collection. I am also grateful to Philip Hershkovitz of the Field Museum of Natural History for verifying the identification of fluid specimens contained there.

I am indebted to Martha B. Lackey, the Museum of Zoology staff artist, who gave expert advice on preparation of the drawings and plates.

Financial support for a portion of this study was provided by a Title IV N.D.E.A. Fellowship which I held while a graduate student at the University of Massachusetts.

MATERIALS AND METHODS

This study samples 145 species of 38 genera of New World cricetines. In addition, several species of Old World cricetines were studied for comparative purposes. The majority of specimens examined are contained in the University of Michigan Museum of Zoology, but others are in the American Museum of Natural History (AMNH), Field Museum of Natural History, Chicago (FMNH), Florida State Museum (UF/FSM), Museum of Michigan State University (MSU), and the U.S. National Museum (USNM). The number and locality of specimens examined are listed below and grouped alphabetically by genera under three headings: "South American cricetines," "neotomine-peromyscines," and "Old World cricetines." The assignment of genera to the two New World assemblages follows Hooper and Musser (1964b). I have generally used the specific nomenclature of Hall and Kelson (1959) for North American forms and of Cabrera (1961) for South American forms. In many instances, however, the use of a specific name observes the judgment of a later reviser.

South American cricetines

Abrothrix longipilis: Chile, Malleco Prov., 4 (MSU).
A. mimus: Bolivia, La Paz, 5 (AMNH).
Akodon aerosus: Peru, San Martin, 1 (FMNH).
A. arenicola: Argentina, Buenos Aires, 2.
A. arviculoides: Brazil, Rio de Janeiro, 2 (FMNH).
A. azarae: Argentina, Buenos Aires, 2.
A. benefactus: Argentina, Buenos Aires, 2.
A. boliviensis: Bolivia, La Paz, 3 (AMNH).
A. cursor: Argentina, Misiones, 4 (FMNH).
A. dayi: Bolivia, Cochabamba, 2 (FMNH).
A. jelskii: Bolivia, La Paz, 4; Peru, Puno, 1 (FMNH).
A. obscurus: Argentina, Buenos Aires, 5 (MSU).
A. olivaceous: Chile, Malleco Prov., 8 (MSU).
A. urichi: Trinidad, San Rafael, 1 (FMNH).
A. xanthorhinus: Chile, Magallanes, 1.
Calomys callosus: Brazil, Matto Grosso, 1 (FMNH).
C. laucha: Argentina, Buenos Aires, 2.
C. sorellus: Peru, Huanuco, 1 (FMNH).
Chilomys instans: Ecuador, Pichincha, 3 (AMNH).
Daptomys venezuelae: Venezuela, Sucre, 2 (AMNH).
Eligmodontia typus: Argentina, Neuquen, 4.
Euneomys chinchilloides: Chile, Malleco Prov., 3 (MSU).
Holochilus braziliensis: Argentina, Buenos Aires, 5 (MSU).
Irenomys tarsalis: Chile, Malleco Prov., 3 (MSU).
Neacomys guianae: Venezuela, Aragua, 4.

N. spinosus: Colombia, Meta, 1 (FMNH); Peru, Huanuco, 1 (FMNH).
Nectomys squamipes: British Guiana, Demara, 1 (FMNH).
Neotomys ebriosus: Bolivia, La Paz, 1 (AMNH).
Neusticomys monticolus: Ecuador, Pichincha, 2 (AMNH); El Oro, 2 (AMNH).
Notiomys valdivianus: Chile, Malleco Prov., 1 (MSU).
Nyctomys sumichrasti: Guatemala, Solola, 3.
Oryzomys albigularis devius: Costa Rica, San Jose, 1; Panama, Chiriqui, 1.
O. a. meridensis: Venezuela, Tachira, 1 (FMNH).
O. alfaroi: Mexico, Oaxaca, 2.
O. bicolor: Colombia, Vaupes, 2 (FMNH).
O. caliginosus: Costa Rica, Cartago, 2.
O. capito laticeps: Trinidad, San Rafael, 3 (FMNH).
O. c. talamancae: Costa Rica, Puntarenas, 1; Panama, Canal Zone, 1.
O. concolor: Colombia, Vaupes, 3 (FMNH).
O. fulvescens: Costa Rica, San Jose, 2.
O. longicaudatus: Chile, Coquimba, 1.
O. melanotis: Mexico, San Luis Potosi, 2.
O. nigripes: Brazil, Sao Paulo, 5 (FMNH); Argentina, Buenos Aires, 1.
O. palustris: Costa Rica, Guanacaste, 2.
Otonyctomys hatti: Guatemala, Peten, 2 (UF/FSM).
Oxymycterus misionalis: Argentina, Misiones, 1 (FMNH).
O. platensis: Argentina, Buenos Aires, 1.
O. quaestor: Brazil, Rio de Janeiro, 2 (FMNH).
O. rutilans: Argentina, Buenos Aires, 2.
Phyllotis andium: Peru, Huanuco, 2 (FMNH).
P. griseoflavus: Argentina, La Pampa, 2.
P. osilae: Bolivia, La Paz, 5 (AMNH).
Podoxomys roraimae: Brazil, Amazonas, 5 (AMNH).
Reithrodon physodes: Argentina, Tierra del Fuego, 1; Buenos Aires, 1 (MSU).
Rheomys hartmanni: Costa Rica, San Jose, 3.
R. thomasi: Guatemala, Huehuetenango, 1.
R. underwoodi: Costa Rica, Alajuela, 2; Panama, Chiriqui, 1.
Rhipidomys latimanus: Venezuela, Carapas, 1 (AMNH).
R. leucodactylus: Peru, Ayacucho, 1 (AMNH); Cuzco, 1 (FMNH).
R. mastacalis: Brazil, Goyaz, 3 (AMNH).
R. macconnelli: Brazil, Amazonas, 10 (AMNH).
Scapteromys tumidus: Argentina, Buenos Aires, 1; Uruguay, Canelones, 4 (AMNH).
Sigmodon fulviventer: New Mexico, Hidalgo Co., 1.
S. hispidus: Costa Rica, Puntarenas, 3.
S. leucotis: Mexico, Durango, 8 (MSU).
S. ochrognathus: Texas, Brewster Co., 3.
Thomasomys aureus: Peru, Cuzco, 1 (FMNH).
T. baeops: Ecuador, Tungurahua, 4 (AMNH).
T. cinereus: Colombia, Huila, 4 (FMNH).
T. hylophilus: Venezuela, Tachira, 2 (FMNH).
T. ischyurus: Ecuador, Cotopaxi, 3 (AMNH).
T. paramorum: Ecuador, Napo Pastaza, 2 (AMNH).
T. rhoadsi: Ecuador, El Oro, 2 (AMNH).
Zygodontomys brevicauda: Costa Rica, Puntarenas, 3.
Z. lasiurus: Brazil, Matto Grosso, 1 (FMNH).

neotomine-peromyscines

Baiomys musculus: Mexico, Guerrero, 3.
B. taylori: Mexico, Sinaloa, 2.

Nelsonia neotomodon: Mexico, Durango, 1 (MSU).
Neotoma albigula: Arizona, Pima Co., 3.
N. alleni: Mexico, Colima, 3.
N. angustapalata: Mexico, Tamaulipas, 1.
N. cinerea: Montana, Carbon Co., 3.
N. floridana: Kansas, Douglas Co., 2.
N. fuscipes: California, Monterrey Co., 2.
N. goldmani: Mexico, Nuevo Leon, 1.
N. lepida: California, Los Angeles Co., 2.
N. mexicana: Arizona, Cochise Co., 3; Mexico, Chiapas, 4.
N. micropus: Oklahoma, Cimarron Co., 3.
N. phenax: Mexico, Sinaloa, 1.
N. stephani: Arizona, Greenlee Co., 1.
Neotomodon alstoni: Mexico, Morelos, 3.
Ochrotomys nuttalli: Texas, Nacodoches Co., 2; Florida, Alachua Co., 2.
Onychomys leucogaster: Nebraska, Custer Co., 2.
O. torridus: Arizona, Pima Co., 2.
Ototylomys phyllotis: Guatemala, Peten, 2; Costa Rica, Guanacaste, 1.
Peromyscus aztecus: Mexico, Hidalgo, 1.
P. banderanus: Mexico, Guerrero, 2.
P. boylei: Arizona, Cochise Co., 5.
P. californicus: California, Alameda Co., 3; Monterrey Co., 2.
P. crinitis: California, Los Angeles Co., 2.
P. difficilis: Mexico, Aguacalientes, 3.
P. eremicus: Mexico, Sinaloa, 3.
P. eva: Mexico, Baja California Sur, 1.
P. evides: Mexico, Guerrero, 1; Michoacan, 1.
P. floridanus: Florida, Alachua Co., 2.
P. furvus: Mexico, Hidalgo, 2; Puebla, 2.
P. gossypinus: Florida, Alachua Co., 3.
P. grandis: Guatemala, Huehuetenango, 3.
P. guardia: Mexico, Baja California Norte, 4.
P. guatemalensis: Mexico, Chiapas, 3; Guatemala, Huehuetenango, 4.
P. interparietalis: Mexico, Baja California Norte, 4.
P. latirostris: Mexico, San Luis Potosi, 1.
P. lepturus: Mexico, Oaxaca, 3.
P. leucopus: Michigan, Washtenaw Co., 5; Mexico, Campeche, 3.
P. lophurus: Guatemala, Huehuetenango, 3.
P. maniculatus: Michigan, Washtenaw Co., 5.
P. megalops auritus: Mexico, Guerrero, Puerto Chico, 2.
P. m. auritus: Mexico, Guerrero, Xochipala, 3 (MSU).
P. m. megalops: Mexico, Oaxaca, 2.
P. m. melanurus: Mexico, Oaxaca, near Juchatengo, 3 (MSU).
P. m. melanurus: Mexico, Oaxaca, near San Gabriel Mixtepec, 9.
P. melanocarpus: Mexico, Oaxaca, 1.
P. melanophrys: Mexico, Oaxaca, 1.
P. melanotis: Mexico, Jalisco, 3.
P. merriami: Mexico, Sonora, 1.
P. mexicanus angelensis: Mexico, Oaxaca, 2 (AMNH).
P. m. gymnotis: Mexico, Chiapas, 5; Guatemala, Esquintla, 5.
P. m. mexicanus: Mexico, Chiapas, 5; Veracruz, 5.
P. m. saxatilis: Nicaragua, Matagalpa, 5.
P. m. teapensis: Mexico, Tabasco, 1.
P. m. totontepecus: Mexico, Veracruz, 1; Oaxaca, 4 (AMNH).
P. nudipes: Costa Rica, Cartago, 3; Panama, Chiriqui, 5.

P. oaxacensis: Mexico, Chiapas, 3.
P. ochraventer: Mexico, Tamaulipas, 5.
P. perfulvus: Mexico, Jalisco, 1.
P. pectoralis: Mexico, Nuevo Leon, 3.
P. pirrensis: Panama, Darien, 3 (USNM).
P. polionotus: Florida, Lake Co., 4.
P. stephani: Mexico, Sonora, 3.
P. thomasi: Mexico, Guerrero, 3.
P. truei: Mexico, Oaxaca, 3.
P. yucatanicus: Mexico, Campeche, 3; Yucatan, 2.
P. zarhynchus: Mexico, Chiapas, 3.
Reithrodontomys brevirostris: Costa Rica, Cartago, 1.
R. creper: Costa Rica, San Jose, 3.
R. fulvescens: Mexico, Guerrero, 3.
R. gracilis: Mexico, Campeche, 5.
R. humulis: Florida, Alachua Co., 2.
R. megalotis: Mexico, Oaxaca, 4.
R. mexicanus: Costa Rica, Puntarenas, 5.
R. microdon: Mexico, Oaxaca, 1.
R. montanus: Nebraska, Cherry Co., 2; Colorado, Washington Co., 1.
R. sumichrasti: Mexico, Chiapas, 5; Panama, Chiriqui, 3.
Scotinomys teguina: Costa Rica, Puntarenas, 3.
S. xerampelinus: Costa Rica, Cartago, 3.
Tylomys nudicaudus: Mexico, Chiapas, 2.

Old World cricetines

Cricetulus barabensis: Tuvinskaya, A.S.S.R., 2.
C. griseus: China, Peking, 3.
Cricetus cricetus: Kazakhstan S.S.R., Ural'sk Krai, 2.
Mesocricetus branti: Gruzinskaya S.S.R., Tbilsi, 1; Armyanskaya S.S.R., Yerevan, 1.
Phodopus sungorus: U.S.S.R., Krasnoyarskii Krai, 2.

The whole carcasses (mostly adults) listed above are preserved in 70% alcohol or 10% formalin. Stomachs were removed for observation by severing the posterior end of the esophagus and the anterior of the duodenum. Excised stomachs were bisected along a plane horizontal with the longitudinal body axis, and the contents washed out and usually saved. This plane of section provided the most information for illustrative purposes. Figured stomachs thus appear in conventional anatomical position with the ventral half cut away. Anatomical observations were made with a Bausch and Lomb stereozoom microscope (10×–40×). I prepared the semidiagrammatic drawings.

The descriptive terminology employed attempts to minimize confusion between the gross anatomical structure of the stomach and particular glandular types found within it. In describing the human stomach, for instance, the terms cardia, fundus, and pylorus serve to delineate external features of the stomach as well as to classify the three kinds of gastric glands contained internally. These terms may be misleading, however, when applied to a stomach with a greatly reduced glandular epithelium as obtains in many of these rodents. Anatomical terms used in the descriptions are illustrated in Figure 1 and defined as follows:

Incisura angularis—the prominent angle formed by the dextral junction of the esophagus and stomach.
Corpus—that portion of the stomach to the left of the incisura angularis.
Antrum—that portion of the stomach to the right of the incisura angularis.
Fornix ventricularis—the section of the corpus that extends craniad beyond the gastro-esophageal junction.
Bordering fold—a pronounced ridge that marks the juncture of the two types of gastric mucosa (cornified squamous epithelium and glandular epithelium) lining the internal surface of the stomach.

Due to both the state of contraction and the amount of food contained at the time of preservation, the gross conformation of the stomach, especially the fornix ventricularis section, may vary substantially between individuals of the same species. To achieve some uniformity in comparisons, I selected for illustration stomachs that appeared to be maximally distended. Nevertheless, the basic anatomical features defined above are clearly discernible even in a fully contracted stomach. No sexual differences in gastric morphology were apparent at the gross level.

DESCRIPTIONS OF STOMACHS

The stomach morphology of most specimens examined accords with one or another of two anatomical designs, here termed unilocular-hemiglandular and bilocular-discoglandular.

The unilocular-hemiglandular stomach is single-chambered with a shallow incisura angularis that scarcely extends beyond the esophageal opening (Fig. 1A). The corpus is spacious, with a broad fornix ventricularis. Distribution of cornified and glandular linings coincides closely with the basic stomach divisions: cornified epithelium is found in the corpus while glandular epithelium is limited mainly to the antrum. The bordering fold crosses the lesser curvature at the apex of the incisura angularis and the greater curvature at a locus opposite the incisura angularis.

A bilocular-discoglandular stomach has a deep incisura angularis that projects well past the esophageal opening, thereby imparting a more strongly-defined bipartite condition (Fig. 1B). The fornix ventricularis

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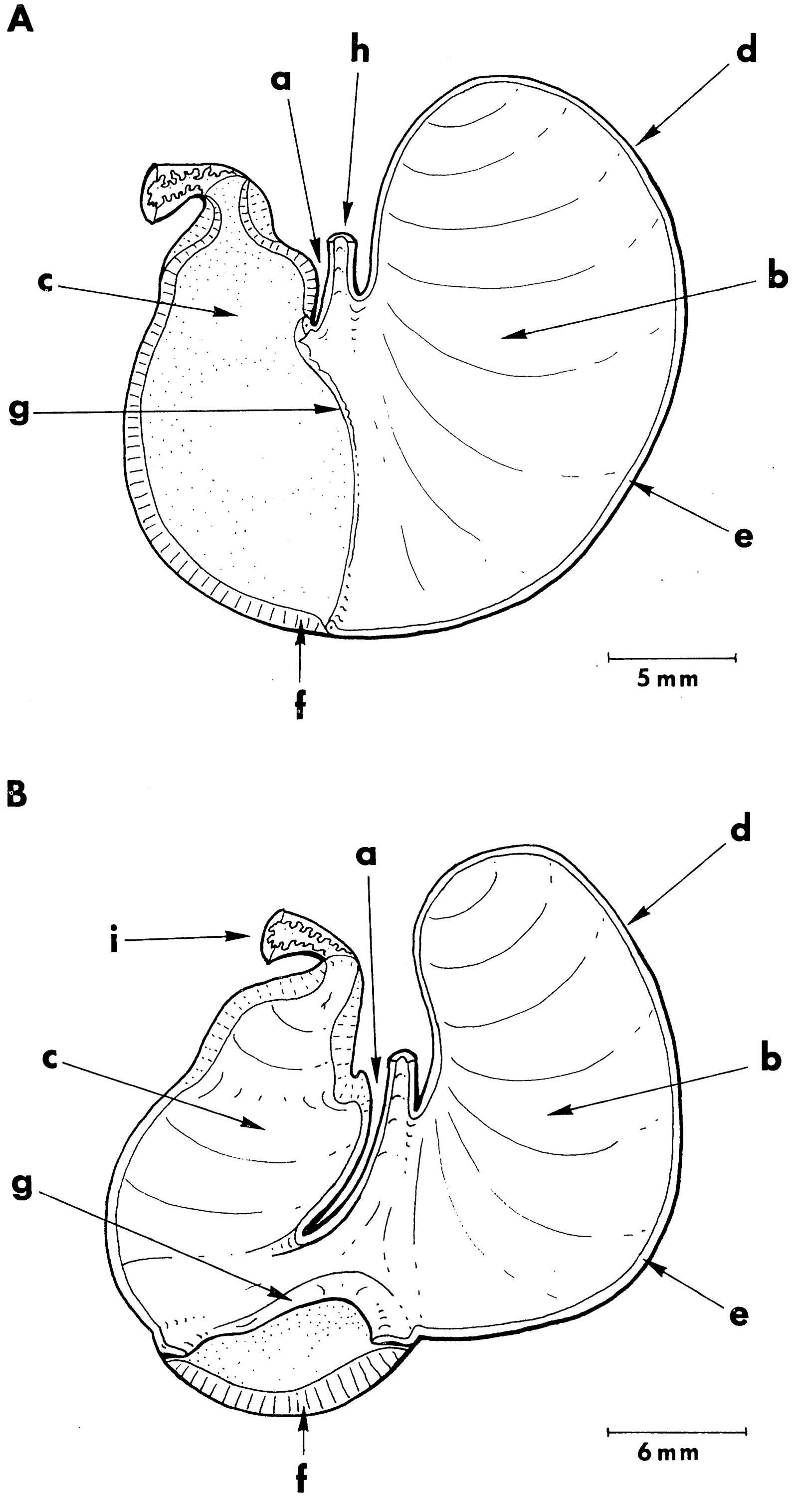
FIG. 1. Diagrams of A) the unilocular-hemiglandular stomach of a South American cricetine, *Oryzomys nigripes* (UMMZ No. 110444), and B) the bilocular-discoglandular stomach of a neotomine-peromyscine, *Neotomodon alstoni* (UMMZ No. 97664). Anatomical features indicated are: a, incisura angularis; b, corpus; c, antrum; d, fornix ventricularis; e, cornified squamous epithelium; f, glandular epithelium; g, bordering fold; h, posterior end of esophagus; i, anterior end of duodenum.


A
a
h
d
c
b
g
e
f
5 mm
B
d
a
i
c
b
g
e
f
6 mm

arches further beyond the esophageal orifice than in a unilocular stomach, and recurves slightly toward the esophagus. The size of the corpus, especially the fornix ventricularis section, varies greatly between individuals, the degree of distension corresponding to the amount of food contained. The walls of the antrum are conspicuously muscular, particularly near the pyloric orifice. The zone of glandular epithelium, surrounded by a distinct bordering fold, is restricted to a small disc-shaped area on the greater curvature. Cornified epithelium covers the remainder of the antrum and corpus.

SOUTH AMERICAN CRICETINES

Of the 27 genera investigated, 20 have a stomach conforming basically to a unilocular-hemiglandular pattern. Slight differences in the amount of gastric glandular epithelium are evident, however.

The unilocular-hemiglandular condition described above was observed in eleven genera: *Abrothrix, Akodon, Calomys* (Fig. 2A), *Eligmodontia,*

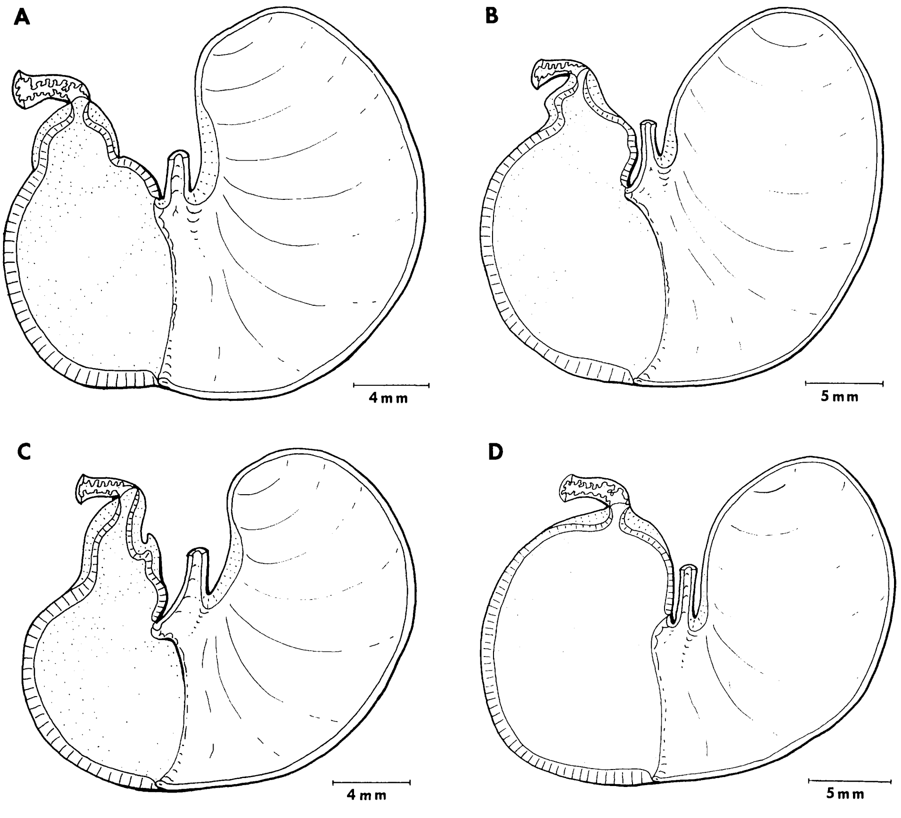


FIG. 2. Gastric morphology of four South American cricetines: A, *Calomys laucha* (UMMZ No. 115503); B, *Nyctomys sumichrasti* (UMMZ No. 113525); C, *Phyllotis griseoflavus* (UMMZ No. 109232); D, *Zygodontomys brevicauda* (UMMZ No. 111957).

Neacomys, Nyctomys (Fig. 2B), *Oryzomys* (Fig. 1A), *Otonyctomys, Phyllotis* (Fig. 2C), *Rhipidomys,* and *Zygodontomys* (Fig. 2D). In examples of these genera, the bordering fold approximately bisects the stomach on a line from the incisura angularis to a point opposite it on the greater curvature. Vorontsov (1962) figured stomachs of *Akodon arenicola* and *Oryzomys couesi* (=*palustris*). The 12 additional species of *Akodon* and 10 other species of *Oryzomys* examined agree with Vorontsov's figures and show no marked interspecific variation.

In the specimens representing nine other genera—namely *Chilomys* (Fig. 3A), *Euneomys* (Fig. 3B), *Holochilus* (Fig. 3C), *Irenomys, Nectomys* (Fig. 3D), *Neotomys, Notiomys, Reithrodon,* and *Sigmodon*—the glandular epithelium covers a slightly more extensive area of the stomach. The

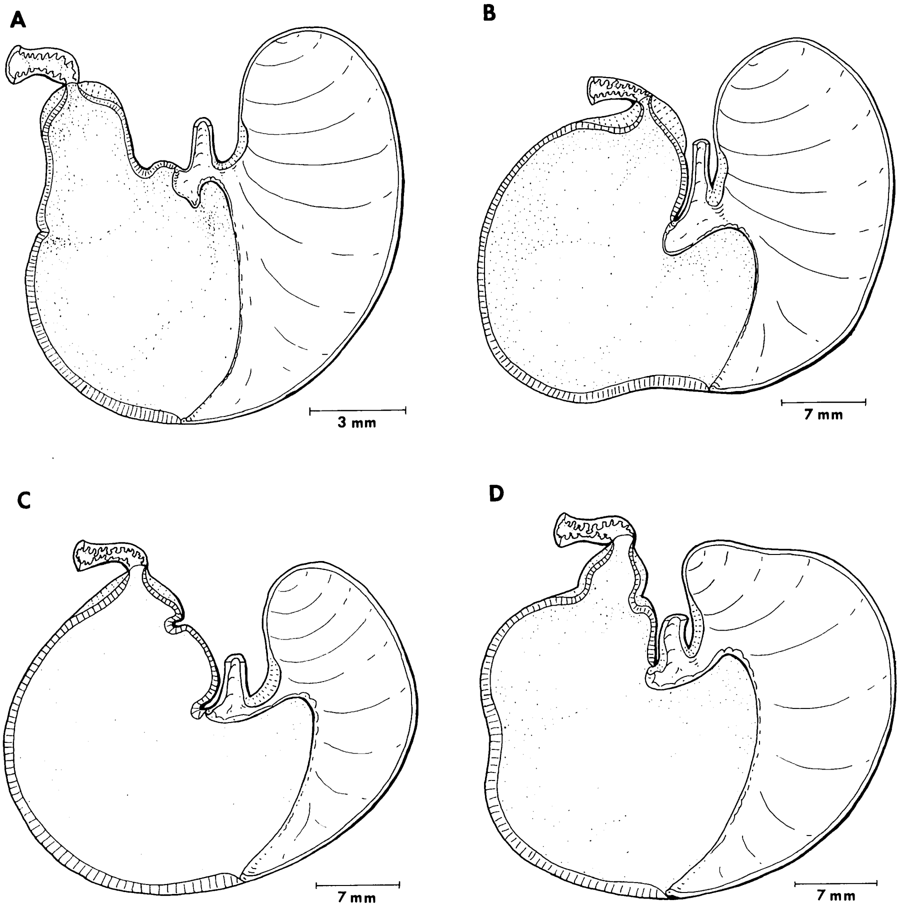


FIG. 3. The unilocular-hemiglandular pattern in four species of South American cricetines. In these forms, some glandular epithelium extends past the esophageal orifice into the corpus. A, *Chilomys instans* (AMNH No. 64640); B, *Euneomys chinchilloides* (MSU No. 7561); C, *Holochilus braziliensis* (MSU No. 18692); D, *Nectomys squamipes* (FMNH No. 46218).

bordering fold still crosses the lesser curvature at the apex of the incisura angularis, but then recurves sharply and passes to the left of the esophageal orifice. Thus the corpus contains some glandular epithelium. The stomach of *Sigmodon hispidus* has been figured and described by Tullberg (1899), Blank (1950), and Vorontsov (1957). *Sigmodon fulviventer, leucotis,* and *ochrognathus* resemble *hispidus* in gastric morphology. Vorontsov's (1957) figure of *Nectomys squamipes* shows the bordering fold bisecting the stomach, but in my example of that species the fold recurves strongly to the left (Fig. 3D).

Thomasomys is the only South American cricetine genus studied in which appreciable interspecific gastric differences were noted. The stomach in specimens of *T. baeops, hylophilus, ischyurus, paramorum,* and *rhoadsi* is basically unilocular-hemiglandular (Fig. 4A). In examples of *T. cinereus,*

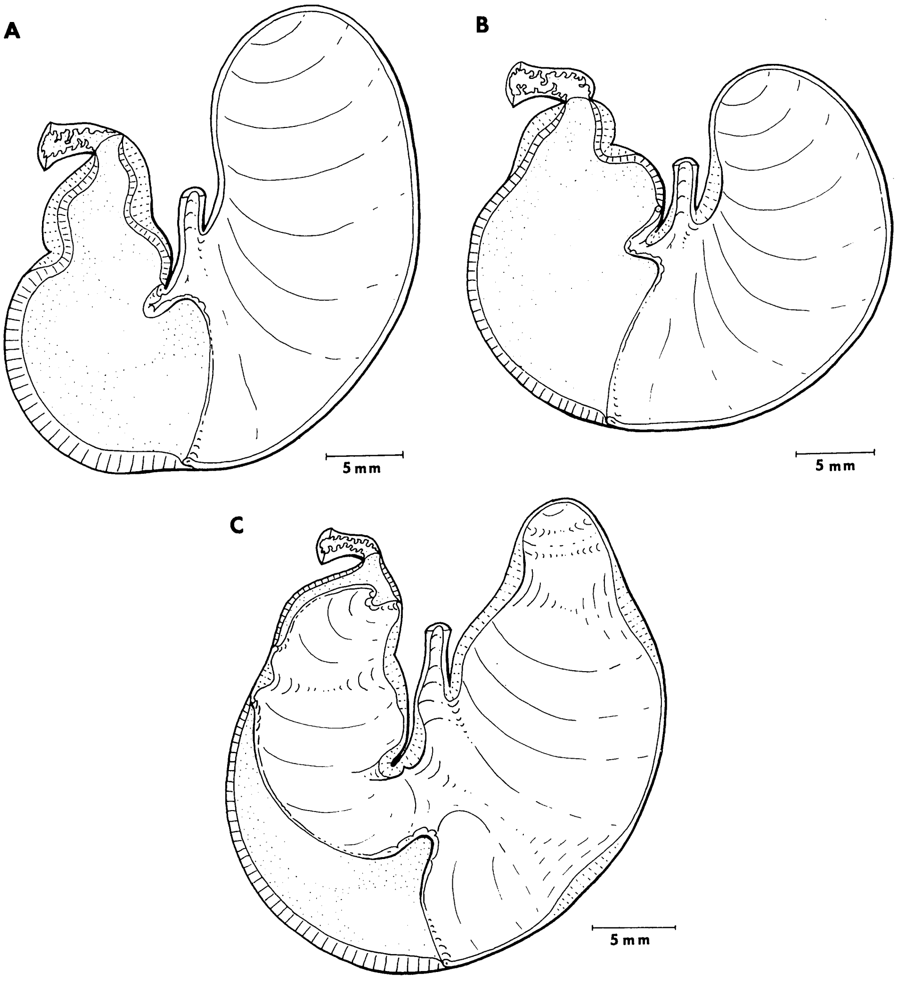


FIG. 4. Stomach morphology in three species of *Thomasomys:* A, *T. paramorum* (AMNH No. 63366); B. *T. cinereus* (FMNH No. 72400); C, *T. aureus* (FMNH No. 75588).

some cornified epithelium occurs in the antrum to the right of the incisura angularis (Fig. 4B). The bordering fold in this species crosses the lesser curvature slightly anterior to the incisura angularis rather than at its apex. *T. aureus* differs prominently from the previous six species in having a stomach with a markedly reduced area of glandular epithelium. Cornified epithelium extensively penetrates the antrum and separates the glandular epithelium into two zones: a small area adjacent to the pyloric orifice and a broad zone on the antral side of the greater curvature (Fig. 4C). The incisura angularis is considerably more pronounced than in other South American cricetines but the contracted condition of the fornix ventricularis in the one *T. aureus* specimen studied hinders close comparison with other species.

The stomach in examples of *Podoxomys roraimae* is unilocular but departs somewhat from a hemiglandular pattern. The bordering fold intersects the lesser curvature at a point midway between the incisura angularis and pylorus. Consequently, some cornified epithelium occupies the part of the antrum to the right of the esophageal opening (Fig. 5A).

A unilocular and discoglandular stomach was observed in examples of *Scapteromys tumidus* (Fig. 5B). The walls of the antrum are more thickly muscular than those in cricetines having a hemiglandular stomach. In addition to the discoglandular zone, a small area of glandular epithelium is situated adjacent to the pyloric orifice.

The glandular epithelium in the stomach of *Oxymycterus* is confined to a diverticulum located on the greater curvature (Fig. 5C). A minute aperture connects this glandular pouch with the main lumen of the stomach. The diameter of this opening measures .35 mm in the specimen of *O. platensis* and .35 and .50 mm in examples of *O. rutilans*. As in *Scapteromys,* the antral walls are conspicuously muscular. Tullberg (1899) pointed out the pouched stomach of *O. rufus* (= *rutilans*), and Vorontsov (1967) found a glandular pocket in the stomach of *O. nasutus*. The stomach morphology of species represented in this study agrees with their descriptions.

Specimens of the ichthyomyine genera *Daptomys, Neusticomys* and *Rheomys* possess a unilocular stomach yet differ noticeably from the hemiglandular condition (Figs. 6A, B, C). In all three, cornified epithelium projects along the greater curvature such that the bordering fold crosses on its ascending portion rather than at a point opposite the incisura angularis. The degree of cornification along the lesser curvature varies. In *Daptomys,* the bordering fold intercepts the lesser curvature at a point one-third of the way between the incisura angularis and pyloric opening (Fig. 6A). *Neusticomys* closely resembles *Daptomys* except that the bordering fold crosses the lesser curvature at a locus two-thirds of the distance between the incisura and pyloric opening (Fig. 6B). In *Rheomys,* cornified epithelium entirely lines the region of the antrum adjacent to the pylorus (Fig. 6C). The reduced area of glandular epithelium forms a broad band situated

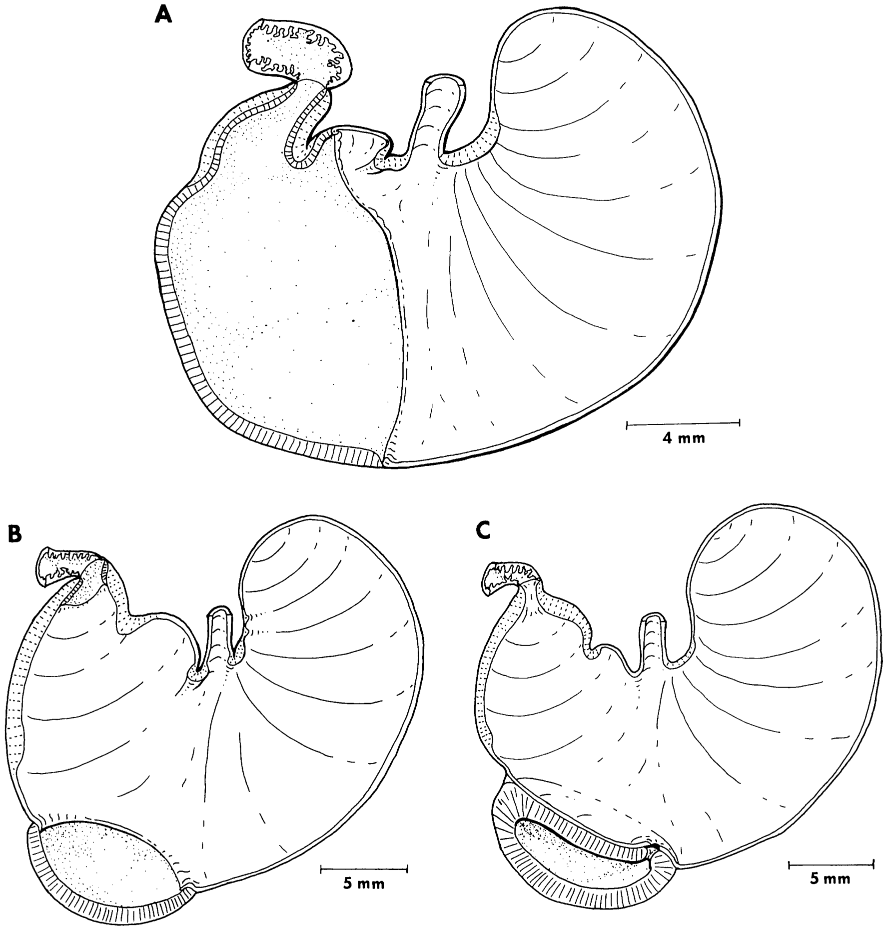


FIG. 5. Gastric structure in three species of South American cricetines having a reduced area of glandular epithelium. A, *Podoxomys roraimae* (AMNH No. 75584); B, *Scapteromys tumidus* (UMMZ No. 110441); C, *Oxymycterus rutilans* (UMMZ No. 115500).

largely in the antral part of the stomach. This condition holds in all examples of the three species of *Rheomys* examined.

NEOTOMINE-PEROMYSCINES

Of 11 genera investigated, a unilocular-hemiglandular stomach was observed in four: *Tylomys, Ototylomys* (Fig. 7A), *Scotinomys* (Fig. 7B), and *Baiomys* (Fig. 7C).

The stomach of *Ochrotomys nuttalli* differs from the latter four genera in the following aspects. The incisura angularis is appreciably deeper, and the bordering fold, after crossing the apex of the incisura angularis, angles into the antrum for a short distance (Fig. 7D). The glandular epithelium

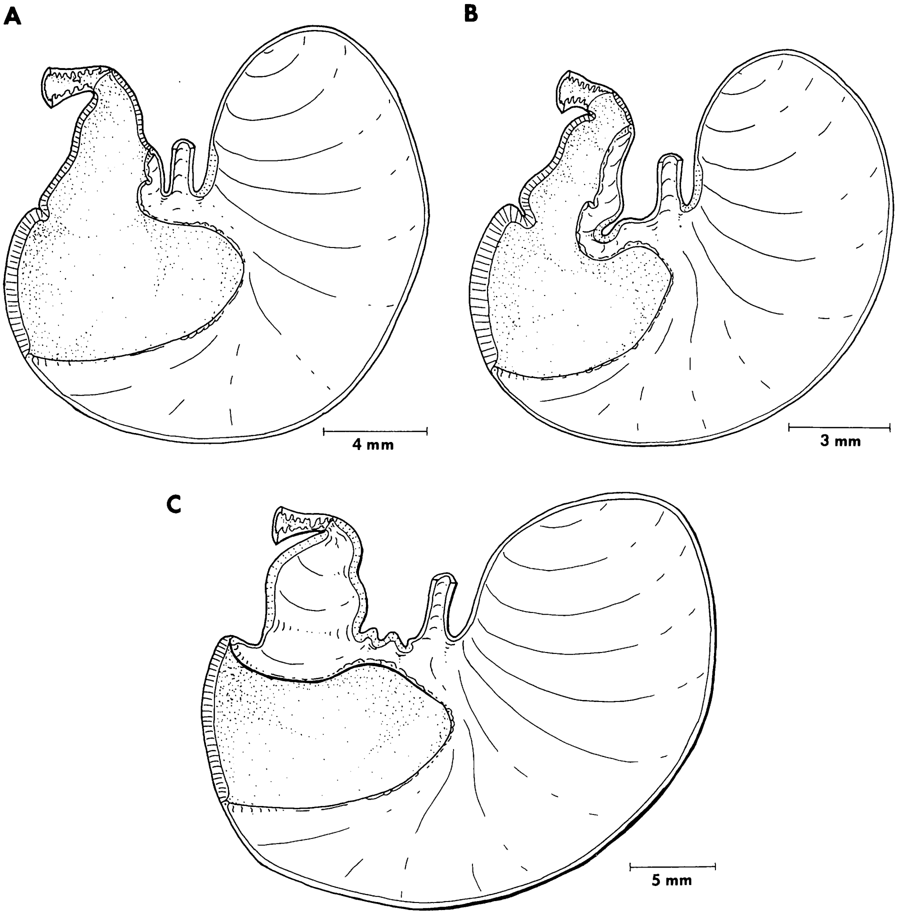


FIG. 6. Gastric morphology in three species of the ichthyomyine group. A, *Daptomys venezuelae* (AMNH No. 69908); B, *Neusticomys monticolus* (AMNH No. 64629); C, *Rheomys hartmanni* (UMMZ No. 111987).

therefore appears somewhat reduced compared to a strict hemiglandular condition.

The distribution of glandular and cornified epithelium varies substantially in specimens of *Reithrodontomys.* In *R. humulis* and *montanus,* the bordering fold crosses the lesser curvature at a point just to the antral side of the apex of the incisura angularis (Fig. 8A). As in *Ochrotomys,* the fold slants into the antrum; nevertheless, the incursion of cornified mucosa into the antrum of these two species surpasses that in *Ochrotomys.* The bordering fold of *R. fulvescens, megalotis, sumichrasti* and *gracilis* intersects the lesser curvature at a locus approximately midway between the incisura angularis and pyloric orifice (Figs. 8B, C). The indentation of cornified epithelium into the antrum of these species exceeds that of *R. humulis* and *montanus.* The bordering fold extends across the lesser curvature near the pyloric orifice in *R. microdon* (Fig. 8D). About half of the antrum contains

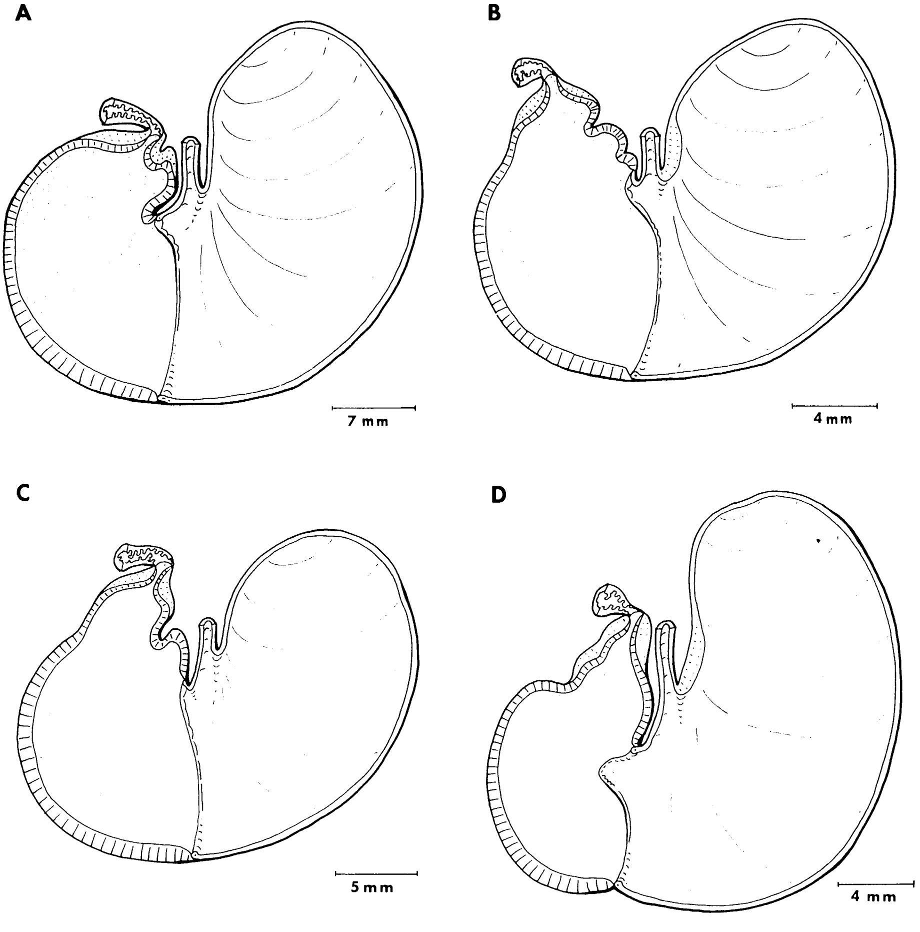


FIG. 7. Gastric morphology of four neotomine-peromyscines: A, *Ototylomys phyllotis* (UMMZ No. 63549); B, *Scotinomys xerampelinus* (UMMZ No. 111762); C, *Baiomys musculus* (UMMZ No. 108690); D, *Ochrotomys nuttalli* (UMMZ No. 110458).

cornified epithelium, while glandular epithelium lies along the greater curvature and narrows toward the pyloric opening. *R. brevirostris, mexicanus* and *creper* possess discoglandular stomachs (Figs. 8E, F). The small zone of glands occurs in the antral portion, situated somewhat on the ascending part of the greater curvature. Specimens of *R. creper* exhibit a relatively smaller glandular zone than those of *mexicanus* and *brevirostris.* In these three species, particularly *creper,* that section of the bordering fold on the left of the glandular perimeter is broad and covers some of the glandular lining. The incisura angularis is largely uniform in all species of *Reithrodontomys* and comparable in depth to *Ochrotomys.* The fornix ventricularis appears to arch somewhat farther craniad in members of the subgenus

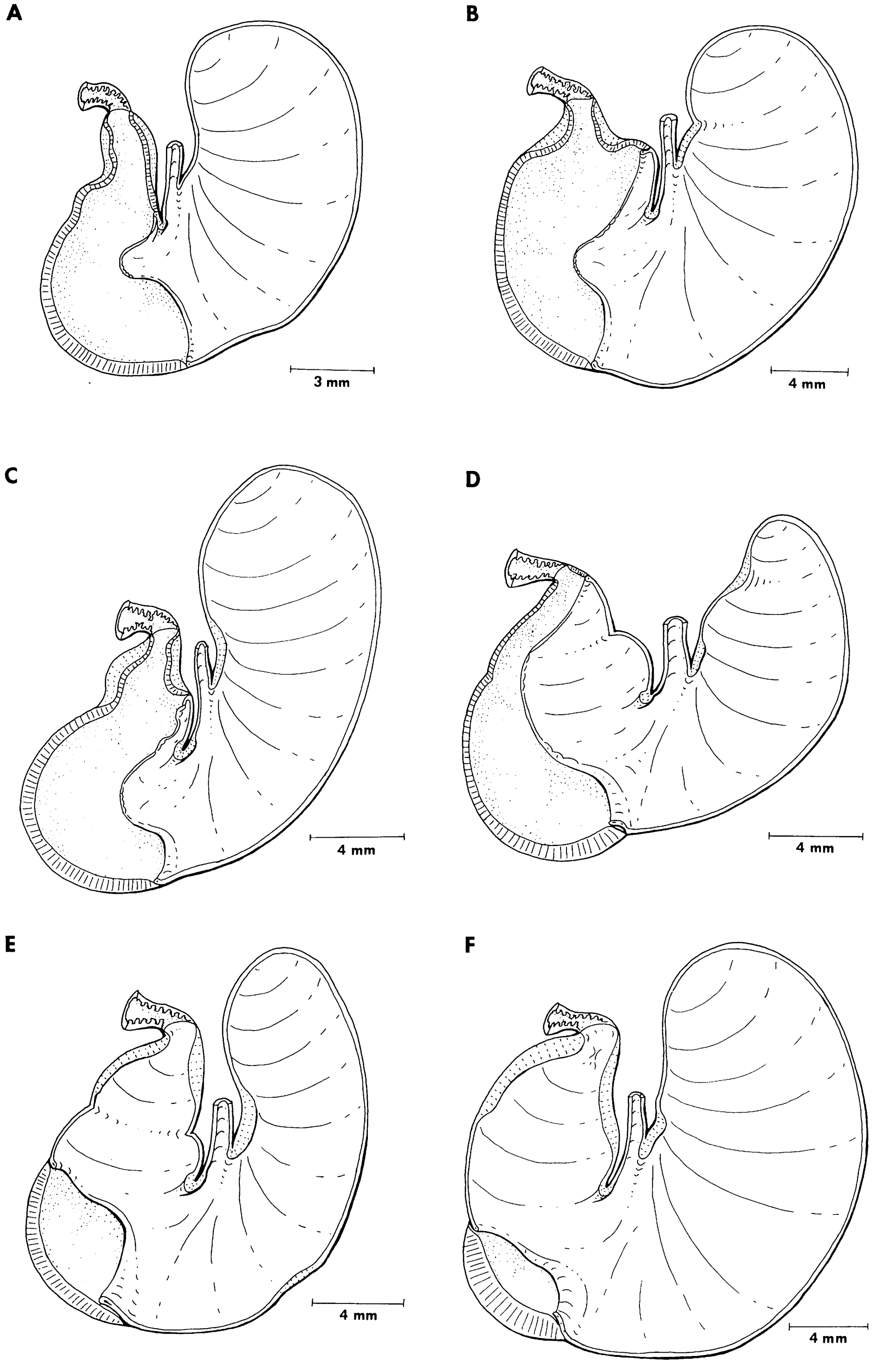


FIG. 8. Gastric morphology in six species of *Reithrodontomys:* A, *montanus* (UMMZ No. 56675); B, *sumichrasti* (UMMZ No. 109191); C, *gracilis* (uncat.); D, *microdon* (UMMZ No. 113723); E, *mexicanus* (UMMZ No. 115293); F, *creper* (UMMZ No. 111827).

Aporodon but not strikingly. Vorontsov (1957) examined the stomach of *megalotis*.

The 39 species of *Peromyscus* sampled represent each of the seven subgenera recognized by Hooper and Musser (1964a). While 31 species have a bilocular-discoglandular stomach (Fig. 9A), modifications of the discoglandular zone are clearly evident in eight: *P. melanocarpus, pirrensis, grandis, guatemalensis, megalops, mexicanus, nudipes,* and *zarhynchus.* Still the stomachs in examples of these eight species are bilocular like those of their congeners. In the one example of *P. melanocarpus* and all specimens of *P. megalops melanurus,* the left edge of the glandular field folds slightly over on itself (Fig. 9B). In *P. pirrensis,* a glandular fold encompasses the entire circumference of the glandular zone to form a pocket with a relatively wide opening (Fig. 9C). This measures 3.5, 4.2, and 5.0 mm in diameter in the three specimens at hand. The glandular epithelium occupies an almost completely closed pouch located on the greater curvature in six species: *P. grandis, guatemalensis, megalops auritus* and *m. megalops, mexicanus, nudipes* and *zarhynchus.* The central lumen of the stomach is entirely lined with cornified epithelium (Fig. 9D). The opening to the glandular pouch is located at its middle and ranges from .45 to .75 mm in diameter for all specimens of the six species.

Species of *Peromyscus* that have received earlier attention include *P. leucopus* (Tullberg, 1899) and *maniculatus* and *californicus* (Vorontsov, 1957). Vorontsov stated that *P. californicus* has an incipient three-chambered stomach, the third chamber arising from a constriction of the antrum. My observations do not support this. In the five specimens of *californicus* dissected, as well as in examples of five other closely related species placed with *californicus* in the subgenus *Haplomylomys,* I found a typical bilocular arrangement. If Vorontsov examined only one specimen (he does not report the number of specimens inspected), the constriction of the antrum probably reflected a state of contraction at the time of preservation. Information on the motility of the human stomach indicates that intense peristaltic waves begin at the incisura angularis and may momentarily subdivide the antrum (see Glass, 1968: 49). Such a state of contraction may have led Vorontsov to interpret the stomach of *californicus* as three-chambered.

The stomachs of *Nelsonia neotomodon* and *Neotomodon alstoni* compare closely to the bilocular-discoglandular arrangement observed in species of *Peromyscus.* In *Nelsonia* and *Neotomodon,* however, the bordering fold appears broader along the left side of the glandular zone (Fig. 1B).

Of the 12 species of *Neotoma* studied, 11, representing the subgenera *Neotoma, Teonoma* and *Teanopus,* possess a bilocular-discoglandular stomach (Figs. 10A, B). The configuration of the incisura angularis and fornix ventricularis corresponds in development to specimens of *Peromyscus,* but the area of glandular epithelium is relatively greater. Tullberg (1899) depicted the stomach of *N. floridana,* and Howell (1926) illustrated the external gastric anatomy of *cinerea* and supplied comparative measure-

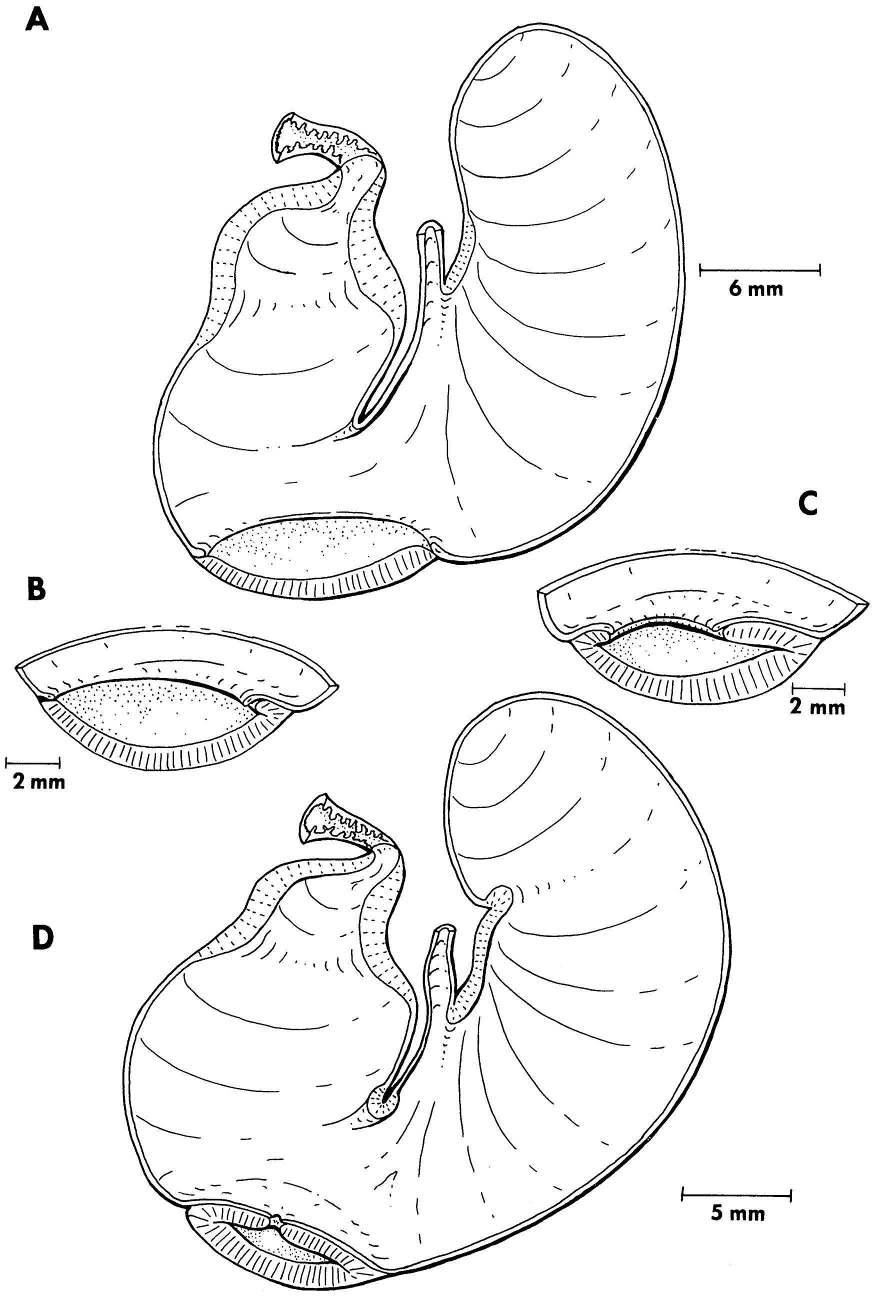


FIG. 9. A, The stomach of *Peromyscus thomasi* (UMMZ No. 113818), representing the bilocular-discoglandular pattern seen in most species of *Peromyscus;* B, Enlargement of the glandular zone in *P. megalops melanurus* (UMMZ No. 113782); C, Enlargement of the glandular zone in *P. pirrensis* (USNM No. 12727); D, Pouched stomach as seen in *P. mexicanus* (UMMZ No. 111886) and some other species of the *mexicanus* group.

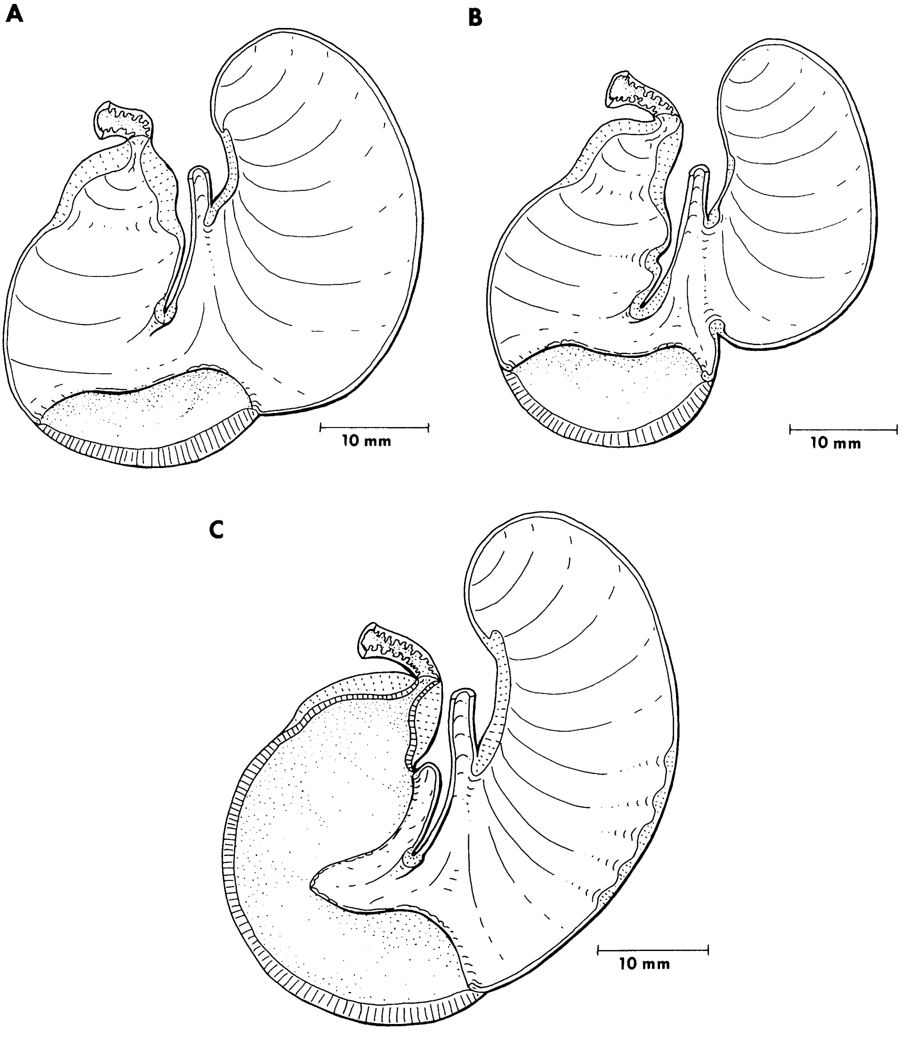


FIG. 10. Gastric anatomy of A, *Neotoma floridana* (UMMZ No. 110378); B, *Neotoma phenax* (ECB No. 1592); C, *Hodomys alleni* (UMMZ No. 113820).

ments of *cinerea, albigula,* and *fuscipes.* The deep incisura angularis and arched fornix ventricularis of *N. (Hodomys) alleni* resemble other species of *Neotoma,* but the area covered by glandular epithelium is more extensive (Fig. 10C). The bordering fold in this species crosses the lesser curvature at a point midway to the incisura angularis and pyloric orifice, and then angles deeply into the antrum. Recurving tightly, the fold returns to intersect the greater curvature opposite the opening of the esophagus.

Horner (1962) and Vorontsov (1962) reported on the pouched condition of the stomach of *Onychomys.* The opening to the glandular pocket is wider in *Onychomys* than in *Oxymycterus* or the six species of *Peromyscus*. Horner et al. (1964) report that the opening is 1–2 mm in diameter, while in my examples of *Oxymycterus* and *Peromyscus* (except *pirrensis*), this diameter measures less than one mm. The depth of the incisura angularis and size of the fornix ventricularis of *Onychomys* compare to that seen in specimens of *Ochrotomys* and *Reithrodontomys*.

OLD WORLD CRICETINES

Toepfer (1891) observed a two-chambered stomach in *Cricetus cricetus*. The bisaccular condition of the stomach of *C. cricetus* and other Old World cricetines except *Calomyscus bailwardi* (Vorontsov, 1967) differs from the bilocular arrangement recorded in many species of neotomine-peromyscines. The deep incisura angularis together with a pronounced sulcus on the greater curvature forms a narrow channel connecting the corpus and antrum (Fig. 11). Such a fixed infold on the greater curvature is lacking in the bilocular stomach found in neotomine-peromyscines, and consequently, they do not display the marked separation of corpus and antrum that typifies the stomach of most Old World cricetines. The epithelial linings of *C. cricetus* are distributed in a hemiglandular pattern, but variations in the extent of gastric glandular epithelium exist among other species of Old World cricetines. Vorontsov (1967) provides illustrations of these variations.

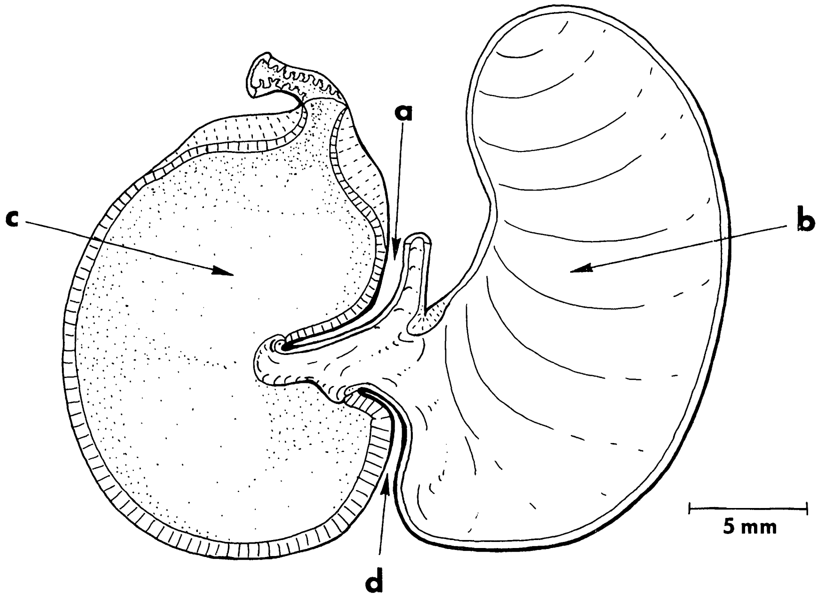


FIG. 11. The bilocular-hemiglandular stomach of an Old World cricetine, *Cricetus cricetus* (UMMZ No. 108461). Labels indicate the following anatomical features: a, incisura angularis; b, corpus; c, antrum; d, sulcus on the greater curvature.

DISCUSSION

STOMACH EVOLUTION IN NEW WORLD CRICETINES AND OTHER MUROIDS

A bilocular-discoglandular stomach probably evolved from the unilocular-hemiglandular condition. The strongest evidence supporting this viewpoint concerns the complement of glands present in the stomach. The stomach in most mammals contains three kinds of gastric glands: fundic, pyloric, and cardiac. Histological studies on cricetine species with a hemiglandular stomach have demonstrated the presence of these three glandular types (Blank, 1950; Maggese, 1969). Investigations on species having a discoglandular or pouched stomach, on the other hand, have revealed only two glandular types, cardiac and fundic (Golley, 1960; Dearden, 1969; Horner et al., 1964; Genest-Villard, 1968). The absence of pyloric glands associated with the discoglandular or pouched condition is clearly a secondary or derived situation in mammals and strongly suggests that the bilocular-discoglandular stomach evolved from a unilocular-hemiglandular state.

Toepfer (1891) originally inferred such an evolutionary transition in stomach morphology based on the few specimens he examined. Subsequent studies encompassing additional examples of muroid species (Tullberg, 1899; Bensley, 1902; Vorontsov, 1957, 1962, 1967) have corroborated Toepfer's initial perception and reinforced the opinion that the unilocular-hemiglandular plan represents the ancestral state for the Muroidea as a whole. Such a stomach type is ubiquitous among Gerbillinae examined and common in Nesomyinae, although the stomach of *Brachytarsomys albicauda* is something other than unilocular (Vorontsov, 1967). Furthermore, this stomach plan has been demonstrated in some species of Murinae and Microtinae (Tullberg, 1899; Vorontsov, 1962; Genest-Villard, 1968; Dearden, 1969). While the stomach of most Old World cricetines is bilocular and hemiglandular, that of *Calomyscus bailwardi* is unilocular-hemiglandular (Vorontsov, 1967). As documented in the present study, a unilocular-hemiglandular stomach occurs in numerous species of New World cricetines, particularly those of the South American cricetine fauna (Fig. 12).

Species with a reduced zone of gastric glandular epithelium are also found in various groups of muroids. A discoglandular stomach has been recorded for many species of Microtinae (Vorontsov, 1957; Dearden, 1969) and some of the limited number of Murinae studied (Tullberg, 1899; Vorontsov, 1967). In addition, the Old World cricetine *Phodopus roborovskii* has a discoglandular stomach. Among New World cricetines, a discoglandular pattern is common in neotomine-peromyscines but occurs in only one South American cricetine examined to date, *Scapteromys tumidus* (Fig. 12). A stomach with an enclosed diverticulum has been demonstrated in several species of *Peromyscus* (this study), both species of *Onychomys* (Horner, 1962; Vorontsov, 1962), examples of *Oxymycterus* (Tullberg, 1899; Vorontsov, 1967; this study), and an African murid, *Lophuromys sikapusi* (Genest-Villard, 1968). Whatever the functional significance of a reduced glandular zone, it seems to have evolved independently from the hemiglandular condition in several lines of muroids.

Increase in depth of the incisura angularis and in size of the fornix ventricularis is not necessarily concomitant with reduction of glandular epithelium. Among New World cricetines, several taxa provide exceptions. Species of *Reithrodontomys,* for instance, differ markedly in extent of glandular epithelium but conform in depth of the incisura angularis. *Scapteromys, Oxymycterus,* and species of the ichthyomyine group examined have stomachs with a reduced glandular area, yet in configuration of the incisura angularis and fornix ventricularis the stomachs in these species are unilocular.

TAXONOMIC CONSIDERATIONS

New World cricetines comprise an impressive assemblage of forms, numbering approximately 310 species of 52 genera. Several studies have contributed some insight to suprageneric affinities within this large group. Based on evidence of comparative myology, Rinker (1954) suggested two initial lines of descent in New World Cricetinae, one exemplified by a "*Sigmodon-Oryzomys*" complex and the other by a "*Neotoma-Peromyscus*" complex. Subsequent investigations have supported Rinker's discernment of a basic dichotomy in these cricetines. A series of papers by Hooper (1958, 1959, 1960, 1962) and Hooper and Musser (1964b) focused on the morphology of the glans penis and demonstrated a simple form among neotomine-peromyscines and a complex type in South American cricetines. Information derived from the male accessory reproductive glands (Arata, 1964), from ectoparasites and their host associations (Wenzel and Tipton, 1966), and from zoogeography (Hershkovitz, 1966a) have also reinforced the notion of an early divergence in the New World cricetine lineage, and Hershkovitz (1969) has formally used the tribal names Peromyscini and Sigmodontini to designate these two assemblages. Data on gastric morphology must be considered in light of this evidence.

The South American cricetine complex is less completely represented in the study material than is the neotomine-peromyscine one. The 73 nominal species from 27 genera of South American cricetines surveyed here constitute only a small sample of the 200 species of 40 genera which comprise this diverse group (Hershkovitz, 1966a, 1969). Nevertheless, some generalizations emerge from the data.

The majority of South American cricetines studied, 21 of 27 genera, have a unilocular-hemiglandular stomach (Fig. 12). These 21 genera are so fundamentally similar that gastric morphology, at least at the gross level, provides few clues to the intra- or interrelationships of previously defined generic groups (see Hershkovitz, 1955, 1962, 1966b; Hooper and Musser, 1964b). The more extensive distribution of gastric glandular epithelium in *Holochilus, Neotomys, Reithrodon* and *Sigmodon* agrees with their assignment together in the sigmodont group as defined by Hershkov-

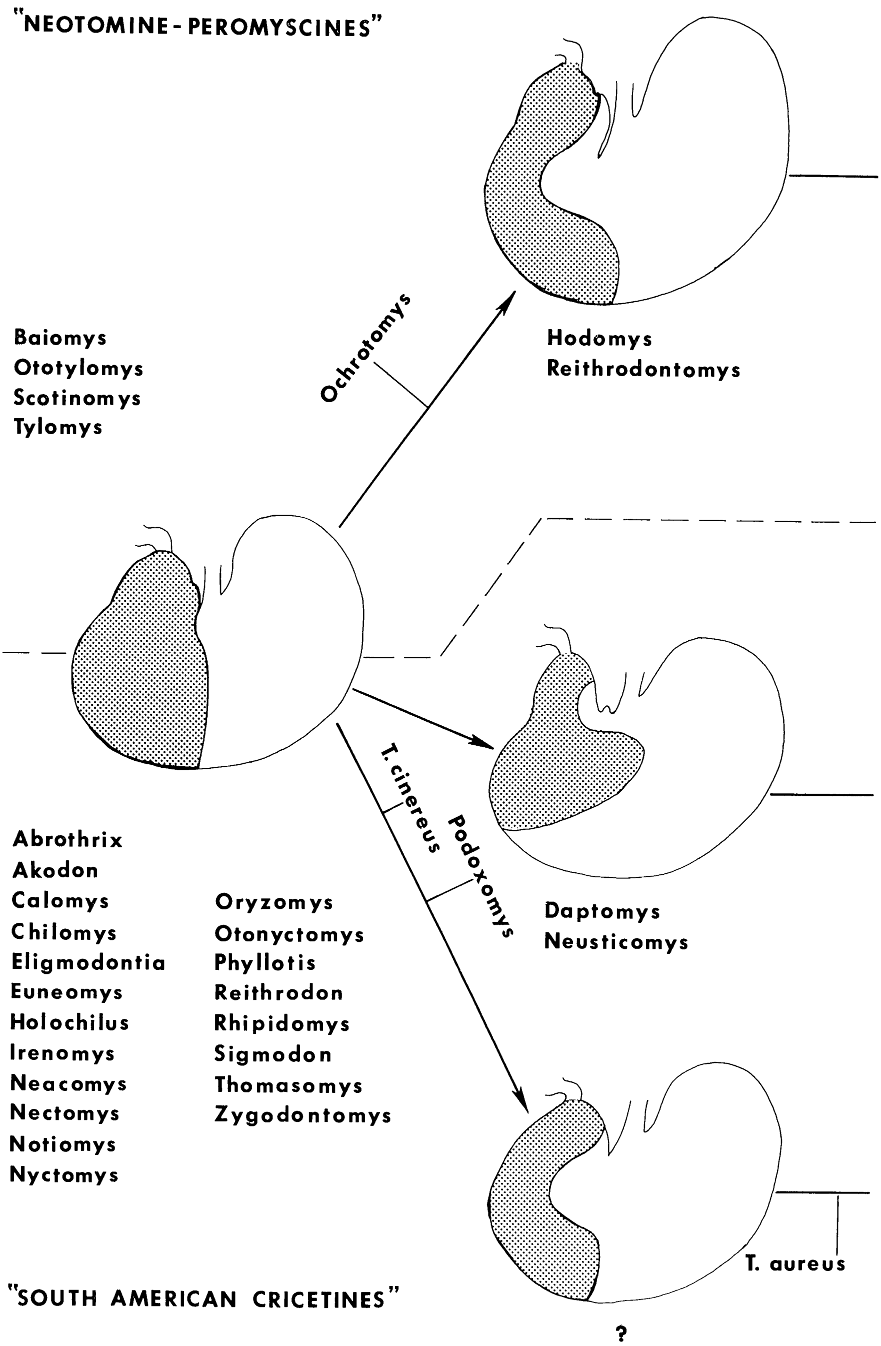
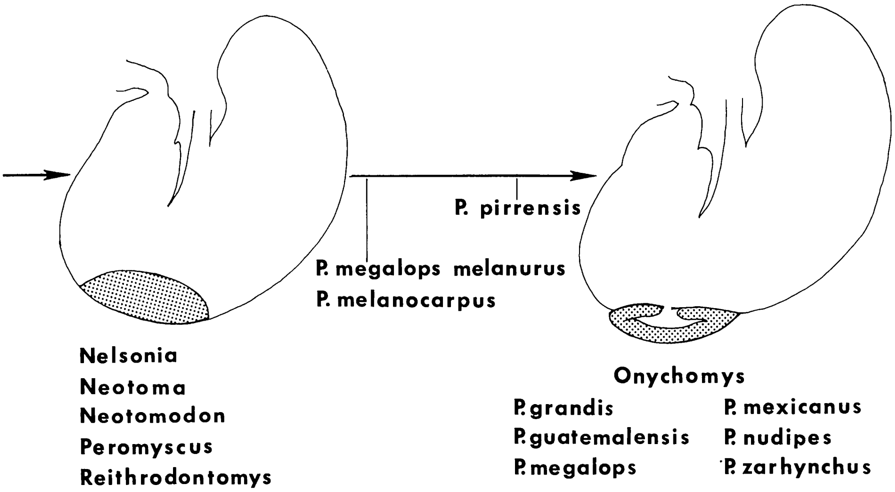
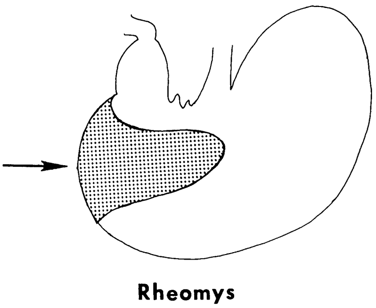
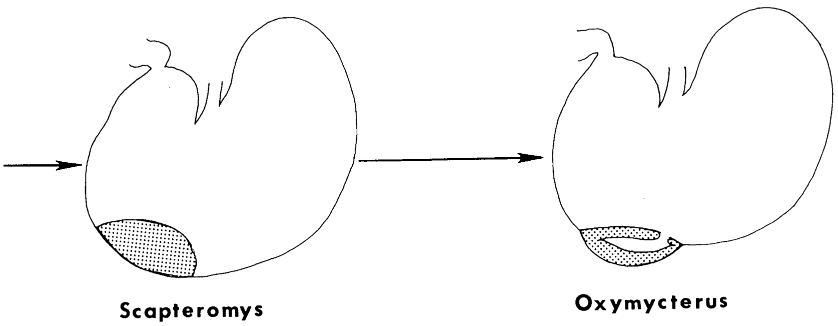


FIG. 12. The genera of neotomine-peromyscines and South American cricetines studied arranged according to extent of glandular epithelium. Only four stomach grades are portrayed: hemiglandular, intermediate, discoglandular (and reduced glandular zone as seen in *Rheomys*), and the pouched condition. The stippled area equals glandular epithelium and the white area represents cornified squamous epithelium.


P. pirrensis
P. megalops melanurus
P. melanocarpus
Nelsonia
Neotoma
Neotomodon
Peromyscus
Reithrodontomys
Onychomys
P. grandis
P. guatemalensis
P. megalops
P. mexicanus
P. nudipes
P. zarhynchus


Rheomys


Scapteromys
Oxymycterus

itz (1955), but *Euneomys,* a phyllotine, and *Nectomys,* an oryzomyine, share this characteristic too. Although most South American cricetines cluster in regard to stomach morphology, a number of forms are set apart; these include *Thomasomys aureus* and species of the scapteromyine, oxymycterine, and ichthyomyine groups (Figs. 4, 5, 6).

The stomach of *Thomasomys aureus* differs markedly from those of other species of *Thomasomys* as well as additional representatives of the thomasomyine group examined (*Nyctomys, Otonyctomys, Rhipidomys*). The distribution of gastric glandular epithelium in *T. aureus* supplies a transitional stage between the hemiglandular plan common to most South American cricetines and the discoglandular stomach of *Scapteromys tumidus.* Hooper and Musser (1964b) noted that the structure of the glans penis of *T. aureus* contrasted with other thomasomyine species represented in their study and suggested the exclusion of *T. aureus* from that group. The extent of gastric variation in *Thomasomys* remains unknown since the present study treats only seven of a probable 30 species of this unrevised genus (Hershkovitz, 1966b). Since the stomach morphology observed in *T. cinereus* diverges slightly from the hemiglandular condition, one might expect gastric differences between other species of *Thomasomys* as well. If, however, further evidence on gastric morphology reveals a pervading hemiglandular pattern, then the distinctive features of the glans penis and stomach of *aureus* argue strongly for its separation from *Thomasomys.*

Certain representatives of the scapteromyine, oxymycterine, and ichthyomyine groups depart conspicuously from the hemiglandular condition. Nevertheless, characteristics of the incisura angularis and the fornix ventricularis in these genera conform to the unilocular configuration typical of other South American cricetines. The discoglandular stomach of *Scapteromys tumidus* warrants special attention. Vorontsov (1967: pl. 120, p. 54) postulated a form of stomach intermediate to a unilocular-hemiglandular stomach and the unilocular-pouched stomach seen in examples of *Oxymycterus.* The stomach of *Scapteromys tumidus* exactly fulfills this morphological grade. Hershkovitz (1966b) has suggested that *Scapteromys* and *Oxymycterus* may be intimately related and derived the scapteromyine and oxymycterine groups from an ancestral akodont stock.

The pouched stomach in *Oxymycterus* is distinct from that observed in other genera assigned to the oxymycterine group as constituted by Hershkovitz (1966b). Indeed, based on evidence of gastric morphology, the affinities of *Oxymycterus* appear nearer to *Scapteromys* than to the additional members of the oxymycterine group studied, namely *Abrothrix* and *Podoxomys.* The stomachs of *Abrothrix longipilis* and *mimus* are typically unilocular-hemiglandular while that of *Podoxomys roraimae* is only slightly modified from the hemiglandular condition.

The position of the reduced glandular zone of *Rheomys* is unique among New World cricetines studied to date. Neither the discoglandular stomach of many neotomine-peromyscines nor that of *Scapteromys* approaches the *Rheomys* condition. The only apparent resemblance to the stomach of *Rheomys* occurs in the hydromurine *Hydromys chrysogaster,* figured by Tullberg (1899). *Hydromys* may occupy an amphibious niche somewhat similar to that of *Rheomys* (McNally, 1960). Compared with *Rheomys,* the stomachs of *Daptomys* and *Neusticomys* are more generalized and constitute annectant grades between the hemiglandular state and reduced glandular zone evident in *Rheomys.* In other characters as well, *Daptomys* and *Neusticomys* qualify as the more generalized of the five ichthyomyine genera (Anthony, 1929).

Of the approximately 110 species of 12 genera of neotomine-peromyscines, I obtained examples of 72 species representing 11 genera. The prevalent stomach plan in the neotomine-peromyscines is discoglandular (47 spp.) while the least common is the unilocular-hemiglandular type (6 spp.) (Fig. 12). An intermediate grade to these two stomach plans is found in 9 species, and 11 forms have a stomach that is probably derived from the discoglandular state.

The stomachs of *Ototylomys, Tylomys, Scotinomys,* and *Baiomys* clearly conform to the unilocular-hemiglandular plan, a condition found in the majority of South American cricetines. Only the evaluation of other characteristics discloses their alignment with the neotomine-peromyscines (see Hooper and Musser, 1964b).

Three genera, *Ochrotomys, Neotoma,* and *Reithrodontomys* contain species that display a transitional stomach arrangement. With regard to the extension of cornified epithelium into the antrum, *Ochrotomys nuttalli* falls between *Baiomys* and species of *R. (Reithrodontomys).* The stomach of *Ochrotomys* contrasts sharply with the discoglandular stomach common in *Peromyscus,* which once included *O. nuttalli.* In view of the accumulation of evidence supporting the exclusion of *nuttalli* from *Peromyscus* (Blair, 1942; Hooper, 1958; Rinker, 1960; Arata, 1964; Patton and Hsu, 1967), the distinction in gastric morphology further emphasizes their separateness.

The stomach of *Neotoma alleni* does not match that of other species of *Neotoma* examined. The distribution of glandular epithelium in *N. alleni* recalls the situation observed in certain members of *Reithrodontomys,* although in morphology of the incisura angularis and fornix ventricularis *alleni* resembles other *Neotoma.* Although originally allocated to the monotypic genus *Hodomys* (Merriam, 1894), Burt and Barkalow (1942) relegated *alleni* to a monotypic subgenus of *Neotoma.* Other investigators have questioned the placement of *alleni* in *Neotoma* and instead have suggested its relationship to another woodrat form, *Xenomys nelsoni.* Sprague (1941) noted similarities of the hyoid apparatus of *alleni* and *X. nelsoni,* and Hooper (1960) commented on the likenesses of the glans penis of these two taxa. In a study of the habits of *X. nelsoni* and *alleni,* Schaldach (1960) urged retention of *Hodomys* at the generic level. In light of these studies and current information on gastric morphology, the reinstatement of *Hodomys* to its former generic status more appropriately reflects the characters distinguishing it from *Neotoma.* Accordingly, I have followed Schaldach's recommendation and subsequently refer to *alleni* under the genus *Hodomys.* No stomachs of *Xenomys nelsoni* were available for comparison.

The observed gradation in gastric morphology between species of *Reithrodontomys* is harmonious with Hooper's (1952) demonstration of gradation in other characters among species of that genus. Arrangement of the species examined according to their relative area of gastric glandular epithelium defines the following groupings (in order of greater to lesser area): A) *humulis* and *montanus*; B) *megalotis, fulvescens, sumichrasti,* and *gracilis*; C) *microdon*; D) *mexicanus* and *brevirostris*; E) *creper.* In general, this order based on morphological grade of the stomach agrees with Hooper's (1952:196) estimation of the degree of divergence of species in the genus from a common ancestor. Only *R. microdon* departs conspicuously from his ranking of specialization (assuming that the one specimen of *microdon* is representative); Hooper treated this species as more specialized than either *mexicanus* or *brevirostris.* Considering the gastric structure of the ten species examined, no dichotomy following the currently-accepted subgeneric divisions *R. (Reithrodontomys)* and *R. (Aporodon)* is apparent. Certain members of *R. (Reithrodontomys),* for example *fulvescens* and *sumichrasti,* resemble *gracilis,* a generalized form of *R. (Aporodon).* The data on gastric anatomy are therefore less in agreement with the arrangement of *Reithrodontomys* and *Aporodon* as separate genera (see Hershkovitz, 1962). Still other species warrant study of their gastric morphology, especially specialized members of *R. (Reithrodontomys)* such as *chrysopis* and *hirsutus.*

A bilocular-discoglandular stomach occurs in most members of *Peromyscus* (31 of 39 species examined). The other eight species also have a bilocular stomach, but one with modification of the glandular zone. These forms, seven from the *P. (Peromyscus) mexicanus* group and one from *P. (Isthmomys),* have a stomach with either a well-formed pouch or what appears to represent an incipient stage in pouch formation.

Gastric variation in the *mexicanus* group recommends reappraisal of the affinities of species included in it. I examined 12 of the 14 nominal species assigned to this group by Hooper (1968). One, *P. allophylus,* has been recently synonymized with *gymnotis* by Musser (1971). Examples of four of these species, namely *P. furvus, latirostris, ochraventer* and *yucatanicus,* possess a discoglandular stomach that is unremarkable in comparison to most of their congeners. Data on gastric morphology of *P. ochraventer* support Baker's (1951) recommendation of its relationship to *P. furvus* and *latirostris* but throw doubt on Hooper's (1968: 59) view that the affinities of *ochraventer* lie with the "*P. mexicanus* complex of forms." All six subspecies of *P. mexicanus* examined (*P. m. angelensis, gymnotis, mexicanus, saxatilis, teapensis,* and *totontepecus*) have a stomach of the pouched variety. Musser's (1969) reallocation of the subspecies *angelensis* to *P. mexicanus* also proves more compatible from the standpoint of gastric morphology than its classification by Osgood (1909) under *P. banderanus,* a species with a discoglandular stomach. In addition to *P. mexicanus,* a glandular diverticulum was observed in the stomachs of *P. grandis, guatemalensis, megalops* (except *m. melanurus*), *nudipes* and *zarhynchus*. The pouched stomach found in these six species suggests a close relationship between them. Gastric differences were noted between subspecies of *P. megalops*. While *P. megalops megalops* and *m. auritus* have a pouched stomach, *m. melanurus* exhibits one with a slight infolding of the glandular zone. This condition also occurs in *P. melanocarpus*. These observations challenge the alignment of *melanurus* as a subspecies of *P. megalops,* but the degree of kinship suggested by the gastric similarity between *melanurus* and *P. melanocarpus* awaits further clarification.

The intermediate condition of the stomach of *P. pirrensis* cautions against a premature judgment of close affinity for the six species in the *mexicanus* group with a pouched stomach. The possibility of the independent evolution of a gastric diverticulum must also be recognized. Despite the similarity in gastric structure, *P. pirrensis* is probably not closely related to species included in the *mexicanus* group, as consideration of other characters of *pirrensis* has led to its allocation to a different subgenus, *Isthmomys* (Hooper and Musser, 1964a; Linzey and Layne, 1969). If the infolded nature of the glandular zone does embody an early stage in the evolution of a pouched stomach, then the independent acquisition of a pouch may have occurred in the above-mentioned six species of the *mexicanus* group and may now be occurring in *P. pirrensis* and possibly in *P. melanocarpus* and *P. megalops melanurus*. Moreover, the incidence of a pouched stomach in other muroids—*Onychomys,* a neotomine-peromyscine; *Oxymycterus,* a South American cricetine; and *Lophuromys sikapusi,* an African murid (Genest-Villard, 1968)—convincingly attests to the possibility of parallel evolution of this character.

In summary, data from gastric anatomy support the notion of a fundamental dichotomy in New World cricetines. This dichotomy is expressed not as a constant difference in stomach morphology between members of the two assemblages but rather in terms of the frequency of occurrence of the two basic stomach plans: the majority of South American cricetines examined exhibit the ancestral unilocular-hemiglandular condition, while most neotomine-peromyscines have the derived bilocular-discoglandular form. Compared to the South American cricetines examined, the neotomine-peromyscines contain more species displaying intermediate grades to the unilocular-hemiglandular and bilocular-discoglandular patterns. Furthermore, the few examples of South American cricetines having a reduced area of glandular epithelium still retain a unilocular arrangement, while in neotomine-peromyscines a stomach with a reduced glandular area is usually bilocular. One can demonstrate, however, a morphological continuum between the unilocular-hemiglandular stomach general in South American cricetines and the bilocular-discoglandular stomach prevalent in neotomine-peromyscines. Additional knowledge of gastric structure is clearly required for South American cricetines. One might encounter deviations from the unilocular-hemiglandular plan in other members of the oxymycterine group, in the scapteromyine *Kunsia,* or in the remaining genera of the ichthyomine group, *Anotomys* and *Ichthyomys.*

FUNCTIONAL IMPLICATIONS

Previous Hypotheses

Two major hypotheses have been advanced to explain the trend of increased cornification and concomitant glandular reduction. One, advocated by Bensley (1902:49), emphasizes that ". . . the changes have been primarily due to the mechanical action of the food on the mucous membrane . . ." His theory stresses the effect wrought by abrasive foodstuffs, for example, coarse grasses and the chitinous exoskeleton of insects. In like manner, Horner et al. (1964:534) interpret the enclosure of gastric glands into a pouch in *Onychomys* as an adaptation for ". . . safeguarding the soft tissue of the gastric glands from abrasion by the rough chitinous material ingested by the rodent." Acceptance of this thesis proves difficult in view of the number of mammals, including whole orders, that consume foods that may be equally characterized as coarse and abrasive and yet do not possess cornified stomachs. For instance, the stomach of *Castor canadensis* is completely glandular although the beaver typically consumes quantities of willow and poplar bark, food items that should properly qualify as coarse and abrasive (Nasset, 1953). Lagomorphs, which also have a completely glandular stomach (Bensley, 1902), ingest many abrasive foods—leaves, grasses, sedges, twigs and bark (Todd, 1927; Dalke, 1942). One might also expect the stomachs of Insectivora and insectivorous Chiroptera to be cornified, but recent studies fail to affirm this (Myrcha, 1967; Rouk and Glass, 1970). If the physical consistency of the ingested food constitutes a sufficient selective pressure favoring cornification of the stomach lining, then it is not apparent why similar trends of cornification do not appear in these and other groups of mammals.

The other hypothesis suggests that changes recorded in muroid stomachs reflect accommodation to a herbivorous diet. Originally proposed by Toepfer (1891), this idea has been more thoroughly elaborated by Vorontsov (1957, 1962, 1967). Vorontsov's diagnosis of alimentary tract specializations indicates an orthodirectional shift from a protein-lipid diet to a predominantly cellulose one. He argues that this transition demanded reduction of the highly acidic glandular zone and increased sacculation in order to permit the existence of symbiotic organisms capable of digesting cellulose. His supposition draws strongly on analogy to gastric adaptations noted for ruminants. Unquestionably, the function of the rumen as a fermenting vat for cellulose has been substantiated in the artiodactyl suborders Ruminantia and Tylopoda (Cuthbertson, 1959; Vallenas, 1965; Williams, 1963). Furthermore, ruminant-like digestion has been documented in the sacculated stomachs of bradypodid edentates (Jeuniaux, 1962), colobine primates (Kuhn, 1964) and macropodid marsupials (Moir et al., 1956).

In view of the multitude of myomorph rodents, it seems remarkable that there are few comparable studies on cellulolytic gastric symbionts. In one such study (Camain et al., 1960), the authors isolated a sample of *Bacillus* from the corpus of *Cricetomys gambianus.* Enzymatic activities listed for this *Bacillus* include the fermentation of glucose, production of acetylmethyl carbinol, hydrolysis of starch and the proteins casein and gelatin, and nitrate reduction, but not the fermentation of cellulose. It should be noted that the corpus of *Cricetomys* contains a dense mat of cornified papillae that markedly increases its surface area, whereas in most muroids the cornified squamous lining of the corpus is smooth. Like *Cricetomys, Mystromys albicaudatus* and *Myospalax* display these fingerlike projections of the corpus (Vorontsov, 1967). In light of the demonstrated bacterial flora and the papillated corpus, some absorption of fermentation products may take place, although they did not demonstrate this. Still, the presence of cellulolytic gastric symbionts, crucial to Vorontsov's hypothesis, has yet to be firmly documented for these rodents.

A number of subsidiary considerations question the appropriateness of drawing analogy to ruminant gastric adaptations in order to explain the stomach modifications observed in muroid rodents. First, the degree of sacculation in the muroid stomach does not approach the extreme compartmentalization found in true ruminants. No anatomical division separates the glandular and cornified areas in muroids with a unilocular stomach, and in those with a bilocular one this separation is less pronounced than in a ruminant stomach. Only the bilocular stomachs of some Old World cricetines show a marked constriction between the corpus and antrum. As mentioned above, the three-chambered stomach noted by Vorontsov (1957) for *Peromyscus californicus* is suspect. Present knowledge of gastric morphology in muroids indicates only one, *Lophiomys imhausi,* that possesses a stomach with divisions appearing, at least superficially, analogous to the compartments of a ruminant stomach (Vorontsov, 1967). Studies of gastric digestion in this rodent would be particularly interesting. The comparatively weak subdivisions of the muroid stomach do not exclude the possibility of cellulolytic gastric symbionts, but they do raise questions about the notion that muroids have attained the level of cellulose digestion achieved by artiodactyl ruminants. Second, as recognized by Vorontsov (1967), the section of cornified epithelium in the distal area of the antrum of a bilocular-discoglandular stomach does not have a counterpart in the ruminant stomach. Third, as discussed below, a loss of pyloric glands accompanies reduction of epithelium to a discoglandular state, whereas pyloric glands occur in the abomasum of the ruminant stomach (Bensley, 1902). Fourth, it is difficult to perceive why two fermenting vats for cellulose should evolve in these rodents when in other mammals those with caecal fermentation display a comparatively simple stomach, while those with gastric fermentation exhibit a complex stomach and unremarkable caecum (Moir, 1968). As documented by Vorontsov (1967), many muroids, even those with a discoglandular stomach, possess a well-developed, capacious caecum. Lastly, where the diet of a given species has been fully elucidated, the food habits do not necessarily substantiate Vorontsov's estimation of the adaptive significance of its gastric structure. In fact, striking contradictions are sometimes found. The bilocular-discoglandular stomach present in members of *Peromyscus,* for example, should indicate a predominantly herbivorous diet according to Vorontsov's hypothesis. Yet the species *P. boylei, leucopus* and *maniculatus,* for which considerable data on feeding habits are available, eat mainly seeds and insects and to a lesser extent fungi, berries, other arthropods and cellulose items (Hamilton, 1941; Jameson, 1952; Williams, 1959; Brown, 1964; Whitaker, 1963, 1966).

In view of the weaknesses in the above hypotheses, the functional consequences of the divergent gastric types deserve further consideration. Accordingly, the following discussion incorporates a survey of relevant literature with attention to other functional possibilities. The purpose of this discussion concerns fruitful areas for subsequent research, not the formulation of a third hypothesis.

Gastric Histology and Function

Knowledge of the specific gastric glands present commands foremost consideration in understanding the functions of the various stomach types. Information on gastric histology for New World cricetines includes *Sigmodon hispidus* (Blank, 1950), *Akodon azarae* and *Calomys laucha* (Maggese, 1969), and *Onychomys torridus* (Horner et al., 1964). The hemiglandular region of the first three species contains cardiac, pyloric and fundic glands, which occur in most mammalian stomachs (see Bensley, 1902). Moreover, these glands are distributed similarly in all three species. The cardiac glands occupy a saddle-shaped area on the lesser curvature near the esophageal orifice; the pyloric glands cover the area of the antrum toward the pyloric orifice; and the fundic glands constitute the remainder of the glandular zone and extend over the largest area. This distribution of glands compares basically to that observed in *Mus musculus* and *Rattus norvegicus,* which also possess a hemiglandular pattern (Toepfer, 1891; Kammeraad, 1942), and perhaps this scheme prevails in most rodents with a hemiglandular stomach. The concentration of glands located in the pouch of *Onychomys torridus* consists of just two types: (1) a small zone of cardiac glands surrounding the pouch aperture and (2) a close mass of fundic glands (Horner et al., 1964). Pyloric glands, common in most mammalian stomachs, do not occur. Similarly, the glandular diverticulum of *Lophuromys sikapusi* lacks pyloric glands but contains fundic glands; cardiac glands were not mentioned (Genest-Villard, 1968).

The loss of the pyloric glands probably occurs prior to the evolution of a pouched stomach. Histological studies on microtines with a discoglandular stomach—*Ondatra zibethicus* (Bensley, 1902); *Microtus pennsylvanicus* (Golley, 1960; Dearden, 1969); *Dicrostonyx groenlandicus* and *Lagurus curtatus* (Dearden, 1969); and *Clethrionomys rutilus* (Orlov, 1968)—reveal that the circular zone contains only fundic glands and a narrow perimeter of cardiac glands (the latter two authors do not mention the cardiac glands but both Bensley and Golley comment on them). This variation in glandular composition prescribes additional histological examinations, especially on New World cricetines. Species that exhibit an intermediate stage to the hemiglandular and discoglandular stomachs deserve particular attention with regard to what glands persist and in what proportions.

The functional outcome of the loss of pyloric glands merits exploration. Investigations on the human stomach reveal three primary roles for the pyloric glands (see Glass, 1968): 1) secretion of mucus; 2) secretion of electrolytes that confer an acid buffering property to surface mucus and thereby prevent chemical injury to the stomach mucosa; 3) secretion of the hormone gastrin which stimulates elaboration of hydrochloric acid and pepsin by the fundic glands. Since the Muroidea contains species exhibiting intermediate stages in the loss of pyloric glands, comparative studies of selected species could discover what the apparent lack of these functions connotes for the digestive process of these rodents.

One possible consequence of pyloric gland loss relates to the effectiveness of mechanical degradation of the food bolus in the antrum. The replacement of glandular epithelium by cornified squamous epithelium offers a more resistant triturating surface as peristaltic waves knead and mix the food. While peristaltic waves pass over the entire stomach, most of the effective mixing of the food occurs in the antral area since the strongest muscular contractions originate at the incisura angularis and progress toward the pyloric orifice (Davenport, 1966). The pronounced incisura angularis in rodents with a bilocular stomach could increase the area for intensive mixing and reworking of the food bolus. Moreover, as noted in the description, the prominent muscularity of the antral walls of most bilocular stomachs may be significant in this regard. Such an arrangement for physically reducing coarse foodstuffs is not implausible. Various anteaters, e.g. *Orycteropus* and *Manis,* display hypertrophy of the pyloric musculature which forms a gizzard-like mechanism, sometimes equipped with keratinous teeth, at the gastroduodenal junction (see Griffiths, 1968, Appendix One).

The loss of pyloric glands from a hemiglandular stomach would clearly leave a more extensive area of fundic glands than exists in a discoglandular stomach. Therefore, in addition to pyloric gland loss, reduction in area of glandular mucosa indicates a diminution of the fundic gland complement. Dearden (1969) observed a relationship between the ratio of zymogen to parietal cells and the area of glandular mucosa in several species of microtine rodents. In *Microtus pennsylvanicus,* which has a relatively greater area of glandular epithelium, the number of parietal cells exceeds that of zymogen cells; however, in *Dicrostonyx groenlandicus,* a species, with a smaller glandular zone, zymogen cells predominate. Dearden (1969:67) speculates that the latter condition ". . . would seem to imply that a large quantity of pepsin is mandatory and is perhaps more critical than the hydrochloric acid titre." Further, since the maximal output of HCl correlates with the parietal cell mass in the gastric mucosa (Card and Marks, 1960), marked differences in acidity may be expected in the various stomach types and the optimal pH range of pepsin activity may be altered.

While Vorontsov's hypothesis focuses on gastric digestion of the polysaccharide cellulose, it is important to remember that other carbohydrates of high molecular weight, namely glycogen and starch, provide nutrition for mammals. Although cellulases occur in some invertebrate animals, mammals are not known to possess such enzymes. Accordingly, they obtain nutrition from cellulose only through the fermenting action of symbiotic organisms inhabiting the gut. Mammals do possess a battery of enzymes capable of degrading glycogen and starch. The enzyme alpha-amylase is involved in the initial hydrolysis of these polysaccharides and is secreted by both salivary glands and the pancreas. Even in the human stomach, with its large area of pepsin and HCl-producing fundic glands, some digestion of starch takes place (see Davenport, 1966, Chapt. 13). The action of salivary amylase continues in the stomach as long as a comparatively high pH exists (human salivary amylase remains active over a pH range of 4 to 11 with optimal activity at 6.9—Davenport, op. cit.). Eventually the low pH of the stomach inactivates this digestion. Evidence on passage of food through the rat stomach indicates that some amylase activity may concontinue. Glass (1968:47) states:

> "Food which enters the stomach is lodged in the innermost core of the gastric content. Thus, it is least exposed to gastric digestive juices acting on the outside of the gastric content. . . . This arrangement makes it possible for the food entering the stomach to maintain its relatively high pH and allows continual action of salivary ptyalin inside the bolus."

Due to the extensive area of nonsecretory cornified squamous epithelium in the rat stomach (hemiglandular type), salivary amylase (=ptyalin) could remain active much longer than in a human stomach.

A pouched stomach might also function to sustain salivary amylase digestion. Conceivably, the enclosure of glands in a diverticulum permits the maintenance of a high pH in the main lumen of the stomach. Since the diet of *Onychomys* and *Lophuromys* consists largely of insects (Bailey and Sperry, 1929; Horner et al., 1964; Genest-Villard, 1968), glycogen may be the important carbohydrate upon which the amylase acts. The mass of fundic glands in the diverticulum suggests that at some appropriate phase of gastric digestion the orifice of the pouch may open wider to allow unimpeded flow of gastric juice to act on the protein component of ingested food.

The studies of Griffiths (1965, 1968) on *Tachyglossus aculeatus* support the plausibility of reduction and loss of glands in order to sustain salivary amylase activity. The echidna's stomach completely lacks glands of any sort and maintains a relatively high pH. Yet the stomach lining of cornified squamous epithelium has not resulted from mechanical abrasion by the ants and termites in the echidna's diet but relates to more effective digestion of carbohydrate. Griffiths states (1968:41): "The stomach lining has no intrinsic digestive enzyme activity, but the saliva contains an alpha amylase at neutral pH so that doubtless the enzyme is active in the stomach degrading glycogen in the homogenized insects to carbohydrates of low molecular weight." Griffiths also notes that the rate of food passage through the echidna's alimentary tract is slow, another possible mechanism to ensure complete assimilation of carbohydrates. In this regard, Kostelecka-Myrcha and Myrcha (1964) have compared the rate of passage of green plant parts and seeds for several species of microtines and show that seed passage takes from 2.5 to 3 times longer; their study did not, however, isolate the region(s) of the digestive tract where retardation of seed passage occurs.

If reduction of glandular epithelium allows prolongation of amylase activity, one might expect changes in the salivary glands that correspond to the type of stomach characteristic of a species. While an extensive survey is lacking, the investigation of Siuda and Szymanska (1961) intimates some such relationship. Their comparative histological study of *Rattus norvegicus, Mus musculus, Clethrionomys glareolus,* and *Microtus agrestis* demonstrates that the first three species contrast with the last with regard to cell types present in the parotid and submandibular glands and to the morphology of their secretory ducts. These differences obviously transcend the phylogenetic alignment of the species studied, but do accord with the type of stomach they possess. *Rattus norvegicus, Mus musculus,* and *Clethrionomys glareolus* have essentially hemiglandular stomachs (Kammeraad, 1942; Toepfer, 1891; Orlov, 1968), while *Microtus agrestis* has a discoglandular one (Tullberg, 1899). Although the significance of the observed salivary gland differences remains unknown, the possibility of a functional association with stomach morphology deserves investigation.

Food Habits

Ultimately one hopes to relate the gastric morphology of these rodents to food habits. Yet the relationship may be more complex than a straightforward correlation with a certain food category such as grasses, seeds or insects. Some insight as to the functional significance of the various gastric plans might be gained through a comparison of food habits of species with contrasting stomachs. In order to attribute any observed differences in preferred foods to dissimilar stomachs, however, one should demonstrate exact correspondence of the remainder of the digestive tracts of the compared species. Such a close conformity is unlikely, and Vorontsov (1967) recounts significant variations in other sections of the digestive tract as well. A thorough accounting of a species' food preferences, and more importantly the nutritional value derived from those foods, would entail study of the complete alimentary canal and associated glands from mouth to anus (and back again in instances of coprophagy).

The paucity of detailed quantitative food studies presents a more practical obstacle to such comparisons. The dietary regimen of most New World cricetines is either unknown or consists of cursory and anecdotal accounts. Still, one commonly discovers references to a given rodent characterized as a herbivore, granivore, or insectivore, often with insufficient or no documentation justifying such categorization. The prevalent yet largely unfounded notion that rodents are fundamentally herbivorous exemplifies such typological thinking, and Landry's (1970) extensive survey of rodent species that consume various sorts of animal matter forcefully disputes this idea. Unfounded allocation of a rodent to a certain trophic category may grossly misrepresent the situation occurring in the wild. It may be more realistic to emphasize the diversity in the diet, and how this diversity corresponds to the availability of foods in the rodent's habitat.

The studies of Jameson (1952) on *Peromyscus boylei* and *maniculatus,* Whitaker (1966) on *P. leucopus, P. maniculatus* and *Mus musculus,* and Batzli and Pitelka (1971) on *Microtus californicus* impress one not only by the variety of foods consumed but also by the temporal spacing of a given food item's importance in the diet. For example, in *P. maniculatus* inhabiting a coniferous forest, consumption of seeds and arthropods equaled 81% and 16% (by volume) respectively during January, but in July, seeds accounted for only 27% of the diet and arthropods 58% (Jameson, 1952). In a population of *Microtus californicus,* grass leaves and stems composed 80% of the diet in the wet season, but during the dry season, grass seeds assumed greater importance, totaling about 80% of the diet. As these papers lucidly attest, short-term food studies may yield an incomplete and biased picture of a rodent's total diet. Information from more critical, year-round food studies is required, especially on forms displaying a unilocular-hemiglandular stomach. Do populations of other muroid species encounter the dramatic and regular fluctuations in food sources as demonstrated for the above-mentioned species?

In an environment where seeds constitute a large part of the diet, at least during some critical part of the year, selection may have favored those individuals that could more completely utilize the starch content of the seeds. A decrease in the fundic gland complement could serve to protract the action of salivary amylase and, thus, more effectively digest the starch. Depending on the prevailing trophic regimen in the environment of the population, the extent of glandular reduction may reflect the relative intensities of selection favoring hydrolysis of the protein (by fundic glands) versus the carbohydrate (by salivary amylase) fraction of available foods. Equally probable, such a reduction could permit extended salivary amylase action upon the glycogen content of arthropods in the diet. I have suggested the sustained digestion of starch as a critical factor, since in food studies on species of *Peromyscus* and *Microtus californicus,* seeds comprise the major food type common to both. *M. californicus* also has a bilocular-discoglandular stomach (unpubl. data).

In regard to Genest-Villard's report on the diminutive gastric glandular area of *Lophuromys,* Landry (1970:361) remarks that "This is exactly the opposite of what we would expect of animals adapted to a high protein diet." That *Lophuromys* and other muroids with a glandular pouch are adapted to a high protein diet requires substantiation. Given the heterogeneous biochemical composition of an insect, the fact that a rodent eats mainly insects is not, by itself, adequate proof of adaptation to a high protein diet. Although the echidna feeds mainly on termites and ants, Griffiths' (1965; 1968) analysis of digestion and excretion indicates mechanisms designed for maximal assimilation of the carbohydrate fraction of those foods. In effect, the concentration of gastric glands in an enclosed diverticulum achieves a stomach entirely lined with cornified squamous epithelium as found in the echidna. With the large mass of fundic glands of the pouch, these rodents may accomplish some digestion of both the carbohydrate (pouch closed) and protein (pouch opened?) fractions of their diet before the food bolus passes into posterior segments of the gut. The complex and varied composition of seeds provoke similar questions concerning digestion in the stomach. Perhaps gastric morphology in muroid rodents reflects differing degrees in the initial digestion of protein, carbohydrate, or fat, rather than digestion of a certain food class as grasses, seeds or insects.

The function(s) of the various gastric patterns evident in muroid rodents is still much in question. Clearly more basic information on gastric histology and histochemistry, rate of food passage, nature of gastric symbionts, and food habits is needed to more precisely interpret the adaptive significance of the divergent kinds of stomachs. The two major hypotheses to date invoke common causal factors for the different groups of mammals that show somewhat similar gastric modifications. Bensley (1902) ultimately favored the physical effect of various kinds of coarse food items on the stomach mucosa, while Vorontsov (1967) interpreted this similarity as an adaptation for processing a single class of food, plant cellulose. Nevertheless, the occurrence of similar gastric modifications in various mammals, i.e. some degree of compartmentalization, a variable extent of cornification, and reduction or loss of glands, does not necessarily signify the operation of the same selective forces. Certainly, in ruminants and the echidna, the demonstrable cornification of the stomach epithelium relates to contrasting nutritional strategies. Further investigation of gastric function in muroid rodents may elucidate still other nutritional adaptations.

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