Arquivos de Zoologia

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JOSÉ LUIZ MOREIRA LEME

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ABSTRACT

The family Strophocheilidae (sensu *Bequaert, 1948*) *is here divided into two — Strophocheilidae* s.s. *and Megalobulimidae, fam. n., on the basis of anatomical characters. New diagnoses are given for the genera of Strophocheilidae and a new systematic arrangement of the Neotropical Strophocheiloidea proposed.*

Representatives of 16 families of terrestrial, fresh-water and marine pulmonate gastropods were studied, besides some species of Prosobranchia and Opisthobranchia. Representatives of families of Pulmonata were selected to represent diverse evolutionary trends.

INTRODUCTION

This paper is part of a doctoral thesis presented December 1971 to the Instituto de Biociências da Universidade de São Paulo.

It was started with the intention of studying speciation patterns within the family Strophocheilidae (*sensu* Bequaert), but had as a final result the division of that family in two, Strophocheilidae *s.s.*, and Megalobulimidae, fam.n.

The discovery of efficient anatomical criteria for the separation of families led me to limit the present study to the generic level.

Bequaert's monograph (1948), strictly based on conchological characters, is my basis for the grouping of species, and bibliography. For this reason I do not give here complete synonymic lists or bibliographical references, citing Bequaert's paper as source for references.

For the generic diagnosis I have used as much as possible Bequaert's conchological descriptions, complemented with differential anatomical characters.

This being a work of synthesis, based on many years of observations and bibliographical research, all the concepts presented are based on the global knowledge acquired during the phases of the research. Some of the data are still unpublished, and are not presented, since they relate to specific details. These data will be published in the future, in the study of speciation.

Museu de Zoologia, Universidade de São Paulo. Bolsista do Conselho Nacional de Pesquisas.

MATERIALS

The main collection studied for this work was that of the Museu de Zoologia da Universidade de São Paulo, complemented by other collections, cited under the following abbreviations:

CCG	Collection Carlos Gofferjé, Blumenau, Santa Catarina.
CED	Collection Eliseo Duarte, Montevideo.
CJFV	Collection Jorge de Faria Vaz, São Paulo.
CLRT	Collection Luiz Roberto Tostes, Rio de Janeiro, Guanabara.
CWW	Collection Wolfgang Weyrauch, Tucumán.
FMNH	Field Museum of Natural History, Chicago.
INDPN	Instituto Nacional de Defesa do Patrimônio Natural, Curitiba.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MEG	Museu Paraense "Emilio Goeldi", Belém, Pará.
MHNM	Museo Nacional de Historia Natural, Montevideo.
MNRJ	Museu Nacional, Rio de Janeiro, Guanabara.
MRCN	Museu Rio-Grandense de Ciências Naturais, Porto Alegre, Rio Grande do Sul.
NRS	Naturhistoriska Riksmuseet, Stockholm.
SMUFJF	Setor de Malacologia da Universidade Federal de Juiz de Fora, Juiz de Fora, Minas Gerais.
USNM	United States National Museum, Washington, D.C.

METHODS

As the materials used include from specimens reared in the laboratory to specimens preserved in alcohol since 1896, data based on them cannot, of course, be homogeneous, but this, I think, does not alter the concepts presented here.

The following data were taken from living specimens: habitat, coloration, and color of mucus (also taken after the animal was killed). Specimens received in preserving fluid were extracted from the shell, either directly or after a rapid heating in water. Shells were always preserved.

Living specimens were killed in boiling water, in which they were maintained for some minutes, until the complete detachment of the columellar muscle. The exact time of immersion varies from specimen to specimen, and can only be determined with some practice. In some cases the animal can be easily slipped out of his shell; in others it has to be held by the foot and rotated contrary wise to the coiling.

Dissections were made under water, after a preliminary washing to partially eliminate the mucus; the isolated organs were drawn with the help of a camera lucida, and then preserved in Railliet-Henry's fluid.

Parts destined to histological studies were directly preserved in Bouin and stained with haematoxylin-eosin.

For the observation of radula and mandible, the pharyngeal bulbs were dissolved in hot 10% solution of KOH. Radulae were stained with hot Congo Red, and mounted on slides. Mandibles were washed, drawn and preserved in glycerinate alcohol.

The contents of the digestive tract were preserved, when possible, in 70° alcohol, for later observation. The same was done with spermatophores obtained during dissection of the genital apparatus. It was observed that spermatophores show good characters for specific identification.

Prior to the utilization of a character in any systematic taxon, the anatomical and conchological variations were studied.

ACKNOWLEDGMENTS

I am very much indebted to Prof. P. E. Vanzolini for orientation during the many years taken in the preparation of this paper.

To Dr. N. Macha and R.L. de Castro (Department of Histology, Sector of Odontology, University of São Paulo) my best thanks for the histological preparations and their interpretation; to Dr. W.S. Sasso, for his authorization to undertake the histological work in his laboratory.

To the curators of the above-mentioned collections, my deep gratitude for sending the materials.

I am also obliged to the colleagues of the Museu de Zoologia da Universidade de São Paulo, to Dr. Elfriede Kirschner of the Instituto de Ciências Biomédicas of the same University for reading and criticizing the manuscript, and especially to Dr. R.D. Turner, Museum of Comparative Zoology, Harvard University, for her valuable criticism.

I also gratefully acknowledge a grant (12572/69) received from the Conselho Nacional de Pesquisas and a grant for collecting (65/668) from the Fundação de Amparo à Pesquisa do Estado de São Paulo.

A DEFINITION OF THE FAMILY STROPHOCHEILIDAE

The meaning attached to the name "*Strophocheilus*" has changed considerably with time.

At the beginning of conchological studies, as happened with most terrestrial gastropods, "*Strophocheilus*" was placed in the family Helicidae, close to *Bulimulus* Leach and *Helix* Linnaeus.

In Pilsbry's (1896) first system *Strophocheilus* was included in the Acavinae, family Helicidae. A few years later the same author (1901: 564) raised the Acavinae to family level. In 1902 he erected the subfamily Strophocheilinae to incorporate *Strophocheilus* Spix and *Gonyostomus* Beck. In the same paper we already find a subdivision of *Strophocheilus* in two subgenera, *Strophocheilus* s.str. and *Borus* Alberts, 1850 (now *Megalobulimus* Miller, 1787).

Ihering (1912: 482-483) pointed out in an anatomical paper some very striking differences between species within the two subgenera, without, however, being able to distinguish the two groups generically, and not even finding characters to exclude the Strophocheilinae from the Acavidae. This same subfamily status was maintained by Connolly (1915), Germain (1924) and Boettger (1936) in papers on the zoogeography and origin of the Acavidae.

Thiele (1931) was the first author to consider the Strophocheilidae as a family, and for this reason most authors refer the family to him. It is, however, nomenclatorially more correct to consider the family Strophocheilidae as of Pilsbry (1902).

A monograph published by Bequaert (1948), although entirely based on conchological studies, is very important for its bibliographical and systematic review; the diagnoses and species groupings are generaly very sound. In this monograph *Strophocheilus* and *Megalobulimus* are still considered subgenera, together with *Microborus* Pilsbry (at present *Austroborus* Parodiz) and *Chiliborus* Pilsbry.

In a revision of the Brazilian species, based also only on the conchology, Morretes (1952) proposed some changes in the taxonomy, raising *Megalobulimus* to generic status, describing the new genus *Psiloicus,* as well as the subgenera *Mirinaba, Metara* and *Phaiopharus. Gonyostomus* and *Anthinus* were excluded from the Strophocheilidae because of their arboricolous habits.

Baker (1955) placed the families Strophocheilidae and Dorcasiidae in the suborder Mesurethra.

Zilch (1960) again placed the Strophocheilinae within the Acavidae. Taylor & Sohl (1962), however, placing the Acavidae in the suborder Sigmurethra, gave a better foundation for the superfamily Strophocheiloidea (Taylor & Sohl, 1962 and Franc, 1968).

With no anatomical basis Parodiz (1968) included the superfamily Strophocheilacea in the suborder Sigmurethra, believing that the conchological similarities between Strophocheilidae, Acavidae and Achatinidae were due to parallelism. For thim Strophocheilidae is an exclusively Neotropical family, its fossil and living species being considered as autochthonous.

The frailty of conchological characters for supraspecific taxonomy is well illustrated by the divergences found in the two most recent revisions (Bequaert, 1948, and Morretes, 1952) both based on the same character, the sculpture of the nepionic whorls. These disagreements are in fact, also found on other taxonomic levels.

It seems to me very difficult, if not impossible, to adopt conchological criteria to solve the proposed problems, and to provide data for a phylogenetic interpretation of the group.

Present knowledge of strophocheiloid anatomy is restricted to a few data on individual organs, frequently of incorrectly identified species. Exceptions are the papers by Scott (1939, 1965) and Baker (1926), which treat the general anatomy of individual species and offer an interpretation of the characters.

I have cheked the literature for anatomical data, and have found little more than what Bequaert lists. I list below all references found but, as they all refer to individual species, containing no comparative materials, I do not comment on them here.

The amount of conchological and anatomical data available being insufficient for a conclusions on the validity and relationships of the genera, as well as on the anatomical structure of the family, it became necessary to undertake comparative anatomical studies within the family, and to examine its relations within the Pulmonata.

INTERNAL ANATOMY

Descriptive anatomy

I have chosen *Strophocheilus debilis* Bequaert, 1948 for the illustration of this descriptive study, because this species was the only one of the genus *Strophocheilus* of which I still had complete specimens at the time of writing, and so would permit a demonstration of all phases of the dissection and of the localization of the organs used in the comparative study.

After death and extraction from the shell, the animal is contracted and in the resting position. In this position it is possible to recognize the following structures: the foot, the mantle's free edge and the visceral mass, which in the living animal is never exposed.

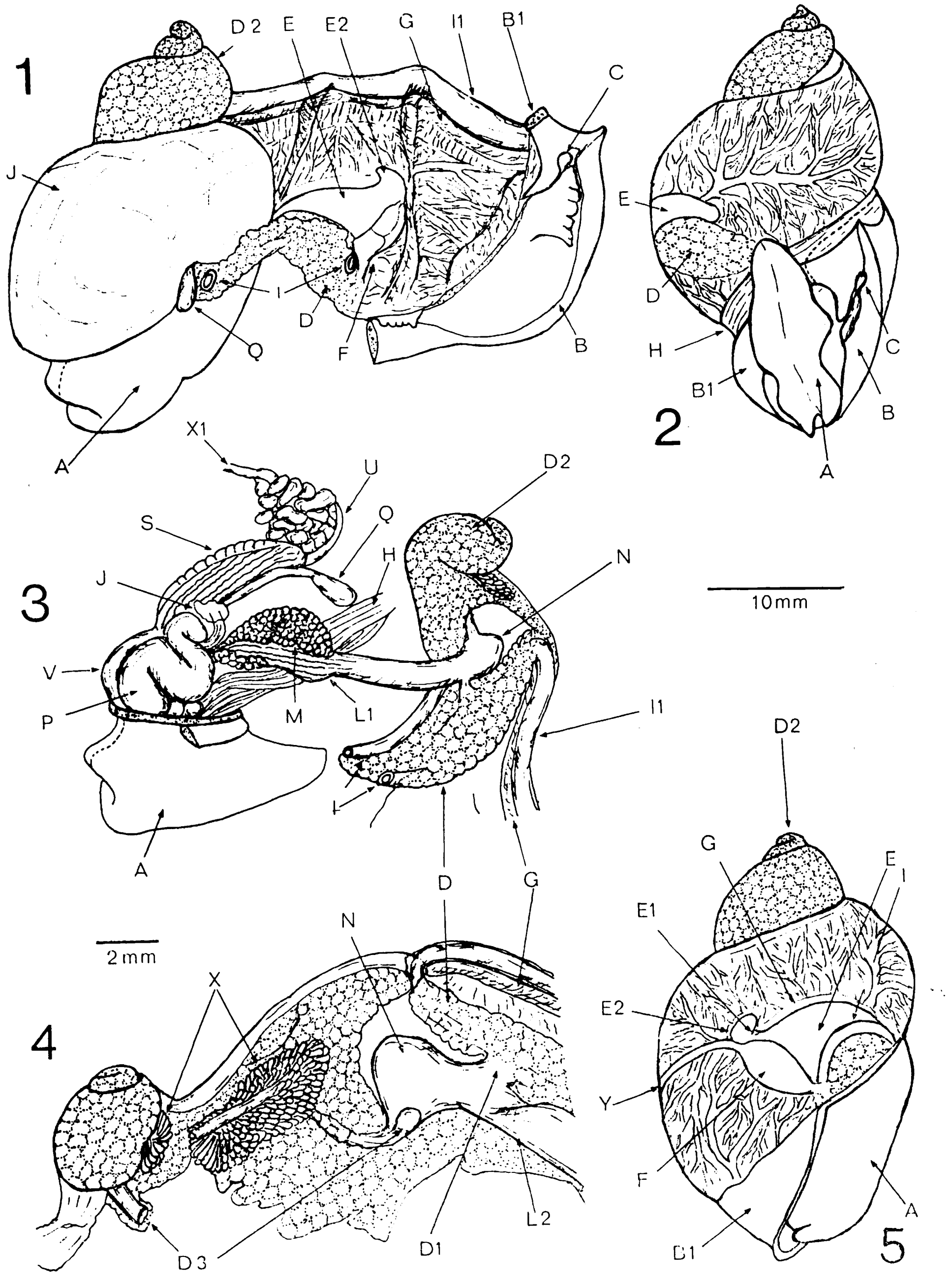
Figures 2 and 5 show a recently extracted animal, before it was cut. In figure 2 are shown, in frontal view, the foot (A), the border of the mantle, which forms a kind of collar around the pedal musculature, and the visceral mass. In the latter, two regions are clearly visible, the lower one formed by the portion of the mantle which composes the palial complex, and the upper one formed almost completely by the posterior lobe of the digestive gland (D2). The collar of the mantle can be divided into internal and external borders (B and B1), which correspond to the external and internal borders of the shell opening. On the ventral face of the external borders is the pneumostome (C), which is surrounded by two lips. Through the thin and transparent wall of the mantle it is possible to see the vascular system, formed by the lung, a caudal part of the kidney (E) and a small part of the anterior lobe of the digestive gland (D). In the same figures the columellar muscle (H) is visible beyond the stippled line which marks the first incision, between the collar of the mantle and the visceral mass.

Figure 5, lateral, left view, shows the foot (A), the internal border of the collar of the mantle (B1), the network of pulmonary vessels, the kidney (E), the pericardium (F), the anterior and posterior (D and D2) lobes of the digestive gland, and an intestinal loop (I).

The first incision starts at the internal border of the collar of the mantle, and extends between the columellar muscle and the rectum. The second cut follows the collar of the mantle, immediately below

ABBREVIATIONS

A = foot
B = external border of the mantle's collar
B1 = internal border of the mantle's collar
C = pneumostome
D = anterior lobe of digestive gland
D1 = duct of anterior lobe of digestive gland
D2 = posterior lobe of digestive gland
D3 = duct of posterior lobe of digestive gland
E = kidney
E1 = excretory pore
E2 = primary ureter delineation
F = pericardium
F1 = aorta
G = urinary gutter
H = columellar muscle
I = intestine
I1 = rectum
I2 = typhosole
I3 = pre-rectal valve
J = diaphragma
K = pharyngeal bulb
L = anterior chamber of oesophagus
L1 = intermedial chamber of oesophagus
L2 = posterior chamber of oesophagus
M = salivary gland
M1 = salivary gland duct
N = stomach
O = nerve ring
P = penis
P1 = epiphallus
P2 = penial retractor muscle
P3 = vas deferens
P4 = pseudo-epiphallus
P5 = basal penial papilla
Q = spermatheca
Q1 = duct of spermatheca
R = free oviduct
S = spermoviduct
S1 = uterus
S2 = prostate
S3 = seminal gutter
S4 = accessory genital gland
T = tentacle
T1 = eye
U = albumen gland
U1 = annex glandular sac
V = vagina
X = hermaphroditic gland = ovotestis
X1 = hermaphroditic duct
Y = pulmonary vein
Y1 = pulmonary septum



Strophocheilus debilis: Topographic anatomy. Scale of 2 mm belongs to figure 4 and the one of 10 mm to the others.

the line of contact with the musculature of the dorsal part of the foot. As a result the pulmonary cavity is opened and the field of dissection becomes freely accessible.

In this illustration can be seen, on the right, the roof of the pulmonary chamber, the position of the pneumostome being indicated by the external border of the collar, and, on the left, the remainder of the body and the foot. Visible on the densely folded surface of the lung are the kidney (E), the pericardium (F) and the anterior lobe of the digestive gland. Whithin the latter is seen an intestinal loop (I), which was ruptured during dissection and is therefore shown together with a part of the pericardium; another one is on the left, close to the spermatheca. The rectum (II), preceded by the urinary gutter (G), forms the upper limit of the pulmonary chamber.

The diaphragm (J), a thin muscular wall, forms the lower limit of the pulmonary chamber, and separates the organs of the lower chamber, some of which can be seen by transparence. After removal of the diaphragm (fig. 3), one sees on the left, the digestive tube above the muscular clusters of the columellar system and between two branches of the genital apparatus. To the right are the two lobes of the digestive gland, separated by the stomach.

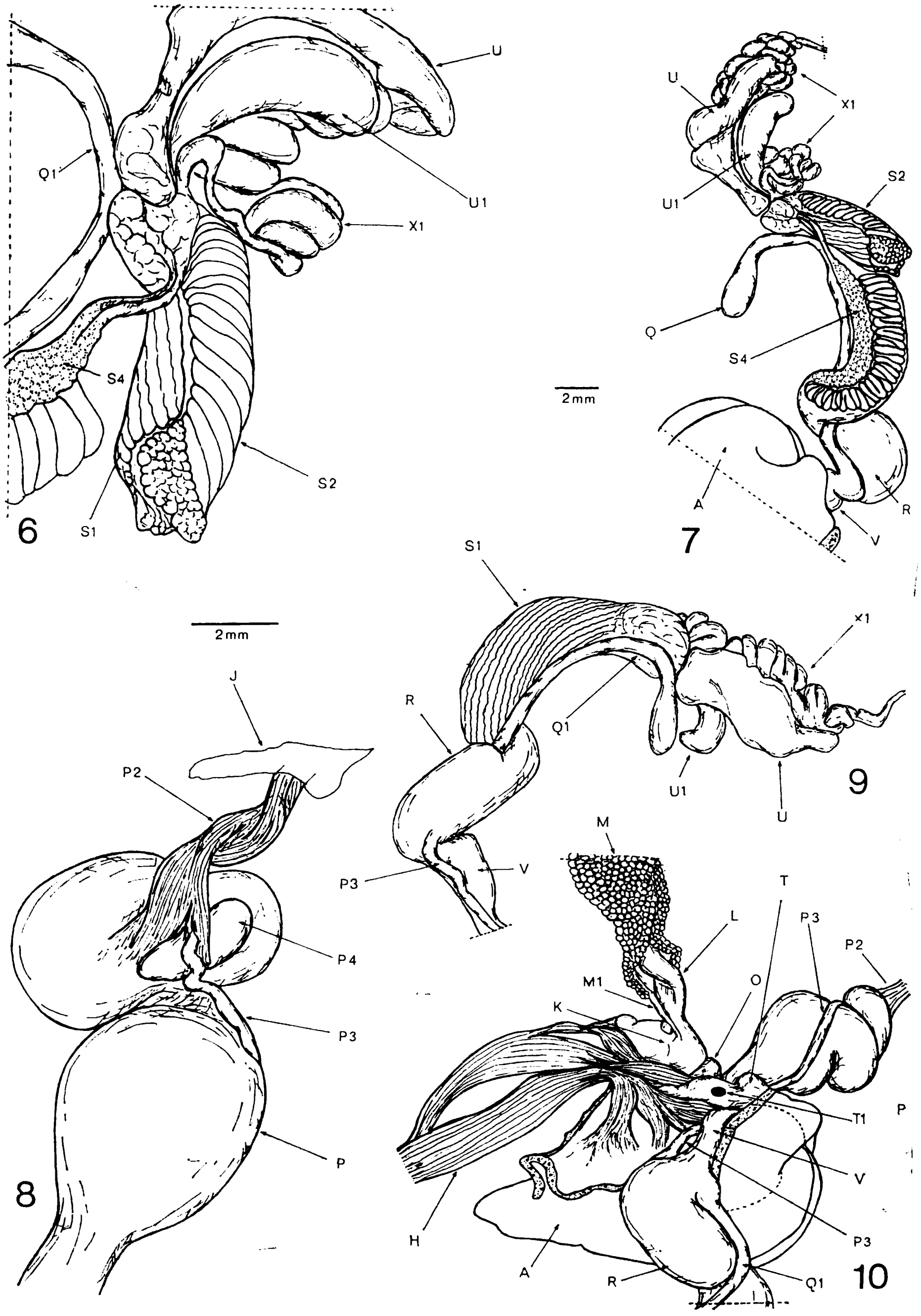
Fig. 4 shows the apical portion of the animal at higher magnification, showing the hermaphroditic gland buried in the posterior lobe of the digestive gland, and the duct of the two lobes (D1 and D3).

The third incision, along the line shown in fig. 3, exposes the cephalic organs, shown in fig. 10. Here the two branches of the genital apparatus, to the right the penis (P), to the left the vagina (V), the oviduct (R) and the duct of the spermatheca, are separated to show the right tentacle (I), the insertion of the muscular clusters (H), the pharyngeal bulb (K), the nerve ring (0), the anterior portion of the oesophagus and the duct of the right salivary gland (M).

The nervous and muscular systems will not be analyzed in the comparative study, and for this reason will not be mentioned in this descriptive part.

The digestive tube begins in the buccal opening, behind which is the mandible, which forms the external limit of the pharyngeal bulb, which contains the radula. The ducts of the salivary glands open in the pharyngeal bulb; the glands are in the second chamber of the oesophagus.

There is a divergence as to the nomenclature of the organs of the digestive tube; I call "oesophagus" the part between the pharyngeal bulb and the stomach. In *Strophocheilus debilis* Bequaert, as well as in most *Strophocheilidae*, this organ is divided into 3 chambers, which vary interspecifically in form and relative proportions. In *debilis* the intermediate chamber is dilated to form a crop (L1), while the terminal part is elongate. The latter receives the duct of the anterior lobe of the digestive gland, slightly anterior to contact with the stomach (N).



Strophocheilus debilis: Genital apparatus and organs of the cephalic region. Figures 7, 9 and 10 in the same scale; 6 and 8 in another.

The stomach has thick walls, and the internal surface is densely folded; it opens into the intestine, which is directed anteriorly in the proximal part, but soon passes below the terminal portion of the oesophagus and penetrates the mass of the anterior lobe of the digestive gland. Next to the pericardium it turns posteriorly and follows to the posterior limit of the stomach, where it leaves the digestive gland and enters the pulmonary chamber. Here it makes an elbow bend and forms the rectum, which continues to the pneumostome, where it ends in the anus.

The genital apparatus, of the simple type, begins with the hermaphroditic gland (= *ovotestis,* X), which is deeply buried in the mass of the posterior lobe of the digestive gland. The ovotestis opens into the hermaphroditic duct (X1), which is much convoluted, and ends in the proximal part of the "talon", which distally receives the duct of the annex glandular sac (U1), the latter placed on the ventral aspect of the albumen gland (U). Below this gland the tube is continued as a spermoviduct (S), formed by a tube with a large opening, densely folded internally, the uterus (SI), plus a cuneiform spermatic gutter, placed between the dorsal and the ventral laminae of the tube, and two isolated glands, the prostata (S2) and the accessory genital gland (S4).

Posteriorly the 2 ducts become separated, and the female duct forms the free oviduct (R), which opens into the vagina (V). The male duct changes from a simple internal gutter into an external and closed duct, the vas deferens (P3), which accompanies the vagina to its base, where it changes over to the left, running on the external wall of the penis, and opening at its apex, between the bundles of the retractor muscle of the penis (P2), after passing over the pseudepiphallus. The penis is cylindrical, widened superiorly, and has a well developed papilla.

The duct of the spermatheca opens between oviduct and vagina. This duct accompanies the spermoviduct to the proximity of the albumine gland, where it turns to the left, and ends in the spermatheca proper (Q), which is adjacent to the pericardium.

COMPARATIVE ANATOMY

Preliminary explanations

In this comparative study, the excretory system is taken as the most important character, due not only to its current use in the establishment of suborders in the Stylommatophora, but also and mainly to its adaptive value in the conquest of the aerial environment. Thus before using it in the systematics of the lower categories, a brief explanation of the evolution of the ureters in the Order Stylommatophora is needed.

According to kidney morphology and especially the development of the ureters, the Order Stylommatophora is divided in four suborders: Mesurethra, Orthurethra, Heterurethra and Sigmurethra.

The most primitive pattern is exhibited by the Mesurethra, where a simple excretory pore in the lateral wall of the kidney stands for an ureter. The most evolved condition is found in the Sigmurethra, which have primary and secondary ureters, both perfectly developed, displaying an elongate "S" shape, the last curve lodged at the bottom of the respiratory cavity.

Intermediate patterns are found in the Orthurethra and Heterurethra. In the former, the kidney is projected forward, tapering into an ureter which does not closely follow the distal segment of the rectum. The excretory pore opens near the pneumostome, but still within the respiratory chamber. In the Heterurethra, the kidney is wider than long, laying transverse to the pericardium up to the rectum; the primary ureter follows the anterior border of the kidney to its distal extremity, from which proceeds, forming a right angle, the secondary ureter, following the final segment of the intestine to the pneumostome, where it opens to the outside. The basic differences between Heterurethra and Sigmurethra lie in the morphology and the orientation of the kidney, and in the path followed by the ureters.

In the following analysis of the remaining characters the species of the family Strophocheilidae are compared to other species belonging to different families of Pulmonata. The setting up of a synoptic table was facilitated by the selection, after carrying out interspecific studies, of one single species representative of each pattern. I have studied the type-species of the genera grouped under Strophocheilidae with the purpose of gathering data for the solution of eventual problems of nomenclature that might arise in the course of the systematic and anatomical investigation. The species from other families of Pulmonata were chosen to represent different evolutionary trends.

The data obtained were analyzed for each of the species here included and, whenever possible, compared to those of a series of individuals of all of the species available within the genus. Thus, in Table 1, and in the following discussion each species mentioned stands for the set of characters common to a series of morphological variants grouped under one generic name.

The systematic structure adopted in Table 1 follows Van Moll (1967) for higher categories, and Taylor & Sohl (1962) from order downwards.

From the Order Archaeopulmonata Van Moll (1967), the species studied was *Melampus coffeus* (Linné, 1757), Ellobiidae. Among the aquatic Basommatophora, species presenting particular evolutionary tendencies were chosen as follows: flat spiral coiling, Planorbidae; sinistral coiling, Physidae; dextral coiling, Lymnaeidae.

Among the Stylommatophora, which comprise the large majority of terrestrial Gastropoda, species were chosen from families with the following tendencies: presence of raised spire, Subulinidae, Bulimulidae and Ortalicidae; flattened spire, Macrocyclidae, Camaenidae, Bradybaenidae, Helicinidae and Streptaxidae; shell reduced and internal, Amphibulimulidae and Lymacidae.

From the numerous family Bulimulidae genera were chosen displaying some degree of conchological resemblance to Strophocheilidae.

Finally, representing the Order Systelommatophora (= Soleolifera), I studied several species of the true slugs, lacking vestiges of shell, of the genus *Phyllocaullis*, Veronicellidae.

Following a previous evaluation of the adequacy of anatomical characters for the separation of families, genera and species, the following structures were adopted for assessing family relationships: excretory system, stomach, buccal fringe, pulmonary septum, pre-rectal valve and genital accessory gland.

Table I summarizes the corresponding data; characters are codified as "stages" and each specific name stands for a group of homogeneous species, as pointed out above.

EXCRETORY SYSTEM

In mollusks, the excretory system is composed of a well developed kidney — an exception among invertebrates — and by urinary ducts (primary and secondary ureters), which may be lacking.

In the Subclass Pulmonata, the kidney is single and completely independent of the genital apparatus. It is lodged on the ceilling of the pulmonary chamber, being morphologically dextral, for it originates from the right half of the embryo. It communicates with the pericardium through the renopericardial opening and this relationship between kidney and pericardium apparently represents a character of importance in the systematics of suprageneric categories.

The degree of development of the ureters, as mentioned, provides characters for the separation of suborders. Nevertheless, some authors do not accept such a systematic arrangement, considering that groups so formed do not represent evolutionary trends.

Numerous bibliographic references and simplified descriptions of the main types of renal apparatus found in Pulmonata are presented by Franc (1968: 408-421). Ghose (1964) established a series of relationships between Prosobranchia and Pulmonata, which has facilitated our comparative study, and limited it to the Subclass Pulmonata.

In *Melampus coffeus* (Archaeopulmonata, Ellobiidae) I found a long kidney, anterior to the pericardium, with a simple and wide excretory opening in its anterior aspect; there is no primary ureter. These observations thoroughly agree with the findings of Marcus & Marcus (1965a, 1965b).

In the Basommatophora examined, the kidney is also long and anterior to the pericardium, but there is already some degree of development of the ureters.

The comparative study of the kidney of the Strophocheilidae led to assemble the species in two groups: (A) — species of the genera *Megalobulimus, Phaiopharus* and *Psiloicus,* with the excretory opening slightly above the middle of the lateral aspect of the kidney; (B) species of the genera *Strophocheilus, Mirinaba, Speironepion, Chiliborus, Austroborus, Gonyostomus* and *Anthinus,* with a sub-terminal excretory opening followed by a rounded, vesicle-like expansion, considered here as an incipient primary ureter. In both groups the urine is liberated into the pulmonary chamber, being drained by a gutter apposed to the rectum.

In the remaining members of the Order Stylommatophora I found a wide range of variation in the development of the secondary ureter.

Based on Ihering's (1884: 273) statements that: *Bulimulus aurisleporis* presents 1/3 of closed secondary ureter and 2/3 of open gutter; *B. papyraceus,* 2/3 of closed secondary ureter and 1/3 of open gutter; and *B. blainvilleanus* has the secondary ureter entirely closed and reaching the pneumostome, I carried out a series of dissections in specimens of the Suborder Sigmurethra, with the purpose of evaluating the degree of development attained by each of the species considered. Within the family Bulimulidae, *Thaumastus achiles* and *Plechocheilus flocosus* have a totally closed secondary ureter, while the following species still show open gutters, with the secondary ureter reaching different levels in relation to the pneumostome: *Drymaeus acervatus, D. papyraceus, D. coartatus, Bulimulus tenuissimus* and *Cochlorina aurisleporis.*

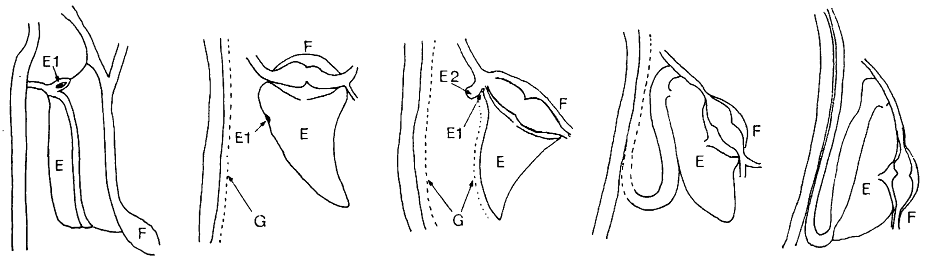
According to Randles (1900, Pl. IX, fig. 1), *Acavus phoenix* (Pfeiffer) presents only a rudimentary secondary ureter and according to Taylor & Sohl (1962), the genus *Acavus* belongs to the Suborder Sigmurethra, while the Strophocheilidae belong to the Suborder Mesurethra.

It is thus seen that between *Acavus* and *Thaumastus achiles* there is a series of intermediary forms, being admissible that *A. phoenix* might represent the lowest level of the sigmurethran pattern. On the other hand, it is also seen that Group B of Strophocheilidae fits in between *Acavus* and the typical Mesurethra. Transition between both types is not gradual; an intermediate pattern exists, sharply different, however, from the extreme patterns. Thus, this intermediate pattern might deserve a separate designation, but this I shall not do, as the adoption of one more renal pattern would bring about undesirable changes in the present concept of the Stylommatophoran suborders. I would rather consider it, for the time being, as the extreme pattern within the Mesurethra.

Admitting that, within the Pulmonata studied, the most primitive kidney belongs to *Melampus coffeus* and the most evolved is found in *Helix pomatia,* I have modified the scheme proposed by Scott (1939: 272) for the relationship between the strophocheilid groups A and B, and the remaining Pulmonata.

In the new system (figs. 11-15), it can be seen that, besides the development of the ureters, the Stylommatophora present another evolutionary tendency, namely, the gradual displacement of the pericardium towards the posterior section of the kidney. In Group A of the Strophocheilidae (fig. 12), the pericardium is obviously anterior to the kidney, while in the group B species, there is a sequence of positions of the pericardium on its way to becoming lateral relative to the kidney.

In the belief that the differences in renal patterns between the two groups of species of Strophocheilidae were a strong argument in favour of the nonhomogeneity of the family, as so far considered, I deepened the investigation of other organs, concluding finally that the following would be important:



11 12 13 14 15

Scheme of evolution of excretory apparatus of the Pulmonata, modified from Scott (1939): 11, Archaeopulmonata, *Melampus coffeus;* 12, Mesurethra, Group A of "Strophocheilidae"; 13, Group B of "Strophocheilidae"; 14, Sigmurethra, *Acavus phoenix,* after Randles (1900); Sigmurethra; *Helix pomatia.*

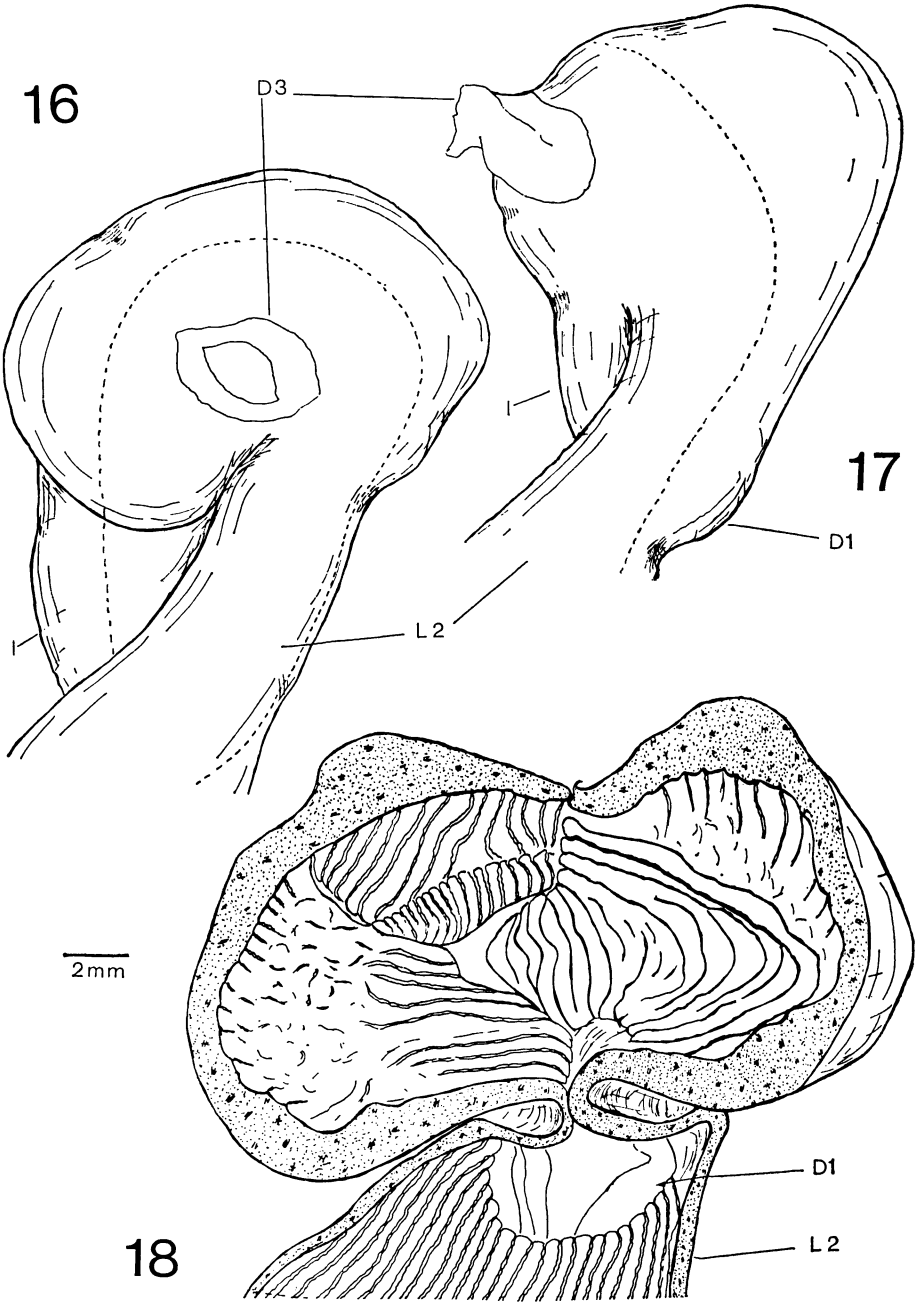
STOMACH

All organs of the digestive tract were studied: jaw, radula, pharyngeal bulb, oesophagus, stomach, salivary and digestive glands. The stomach turned out to be the only organ fit for the desired type of comparative study.

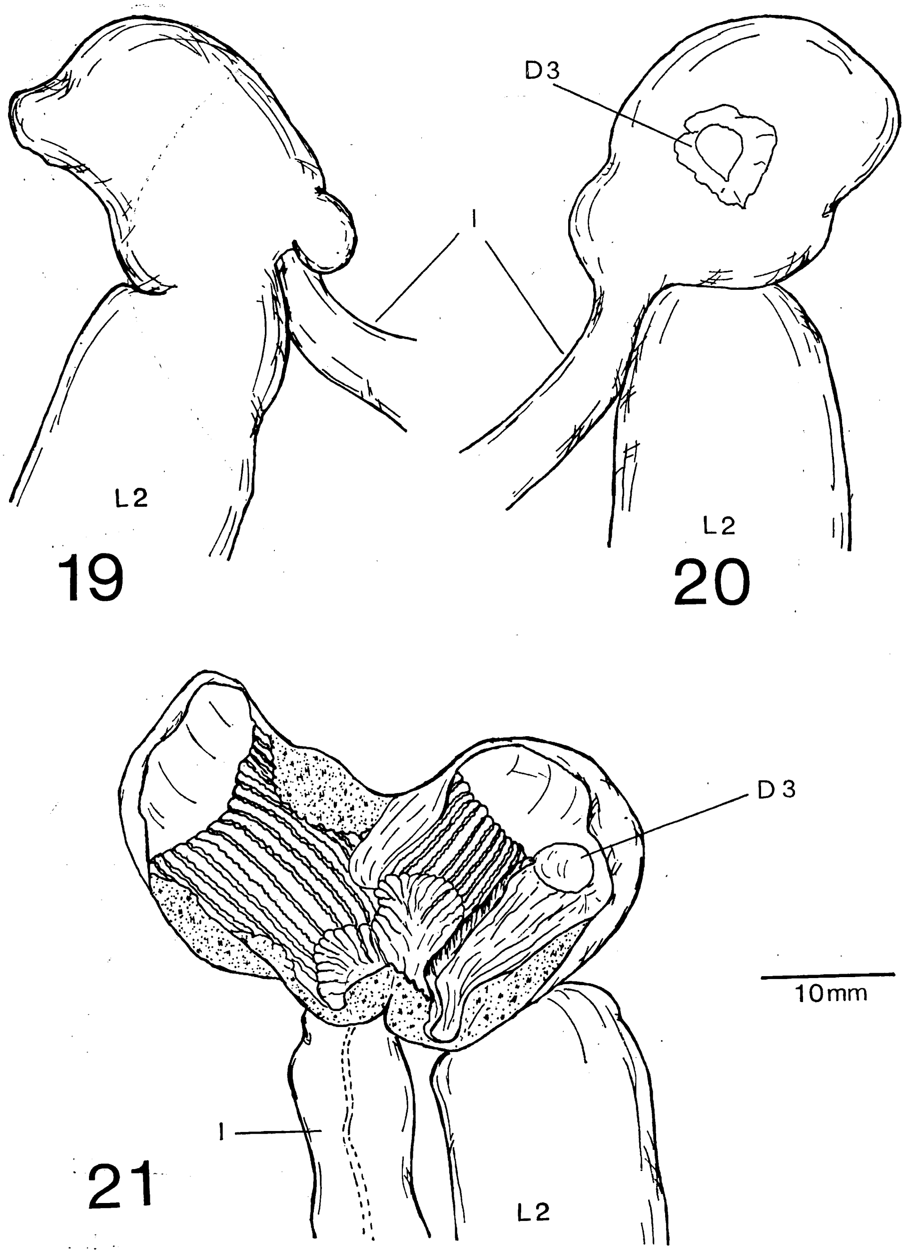
In the Pulmonata, the digestive tube undergoes an evolution towards structural simplification, toward the prevalence of chemical action over mechanical activity. So, in the most primitive groups muscles are well developed, the stomach being a dilated organ with a thick wall and sharp outline, which can act as a gizzard. In the more evolved groups, the whole digestive tube, with the exception of the pharyngeal bulb, has thin walls, at times, transparent and the stomach is but a simple straight-angle fold, with no definite outline and with no differentiation of the internal surface.

There is no general agreement concerning the nomenclature of the digestive organs; some authors consider the stomach to be the most dilated portion of the digestive tract between the first elbow-shaped curve and the small tube arising from the pharyngeal bulb, the tube being then considered as oesophagus. I follow Scott (1939), considering the stomach to be the very curvature where the duct of the posterior lobe of the digestive gland has its opening, whether it be strongly developed or a simple fold beyond which the intestine turns forward.

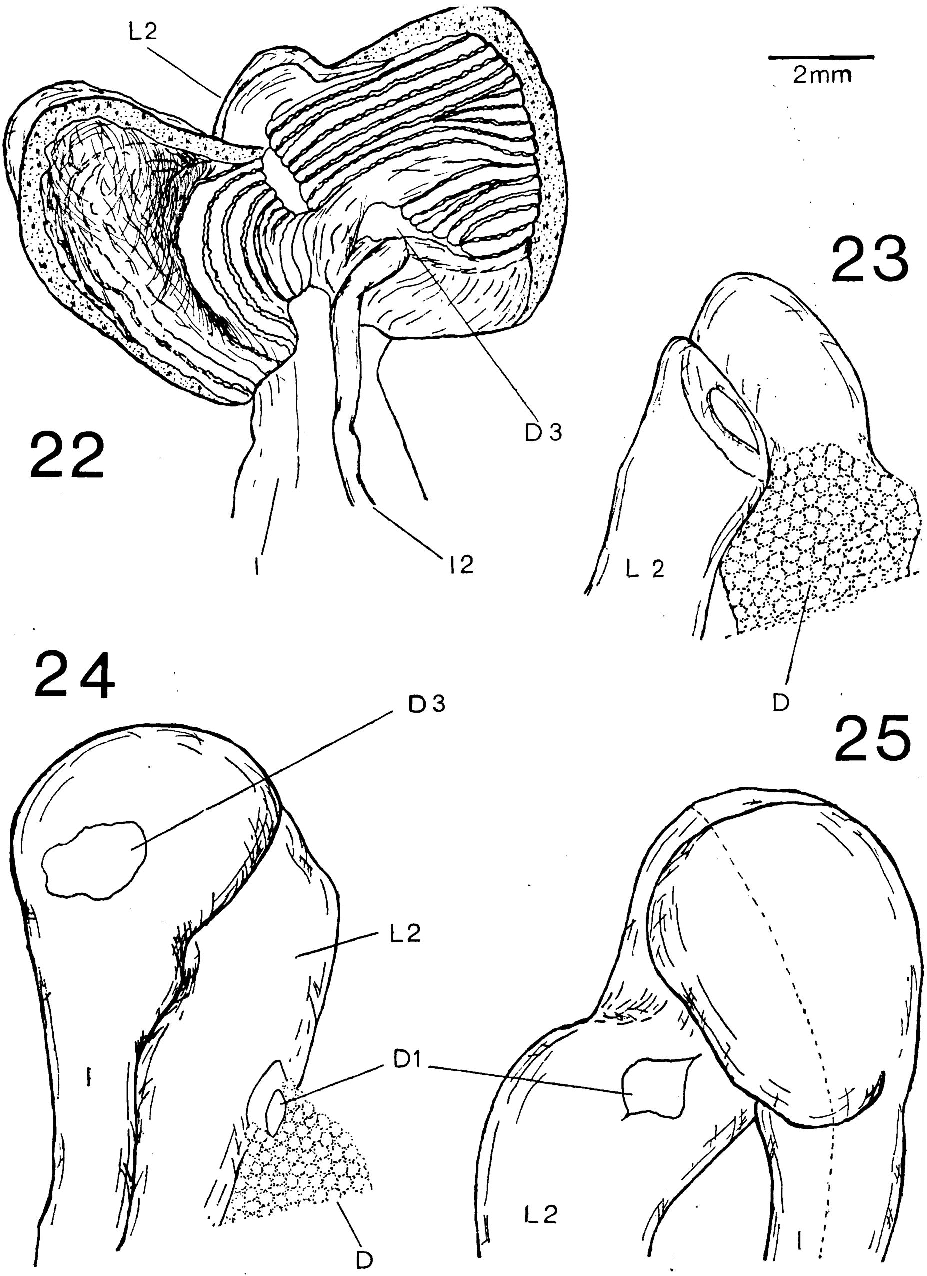
In group A species, the stomach is always muscular, its internal surface intensely folded and the external outline sharply defined, as shown in figs. 16-20. In some species, the musculature is considerably



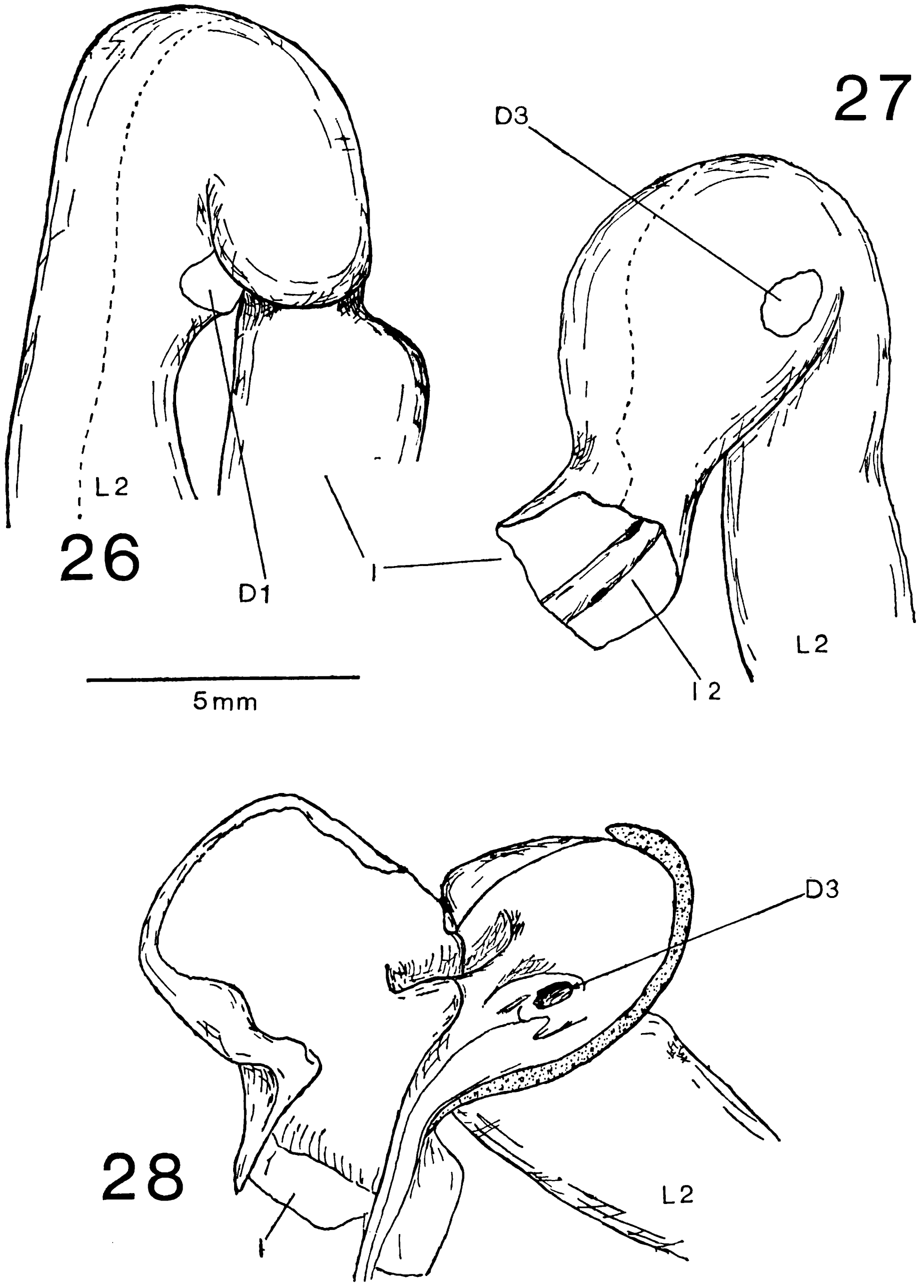
Stomach of *Megalobulimus granulosus*, Group A species: 16, ventral view; 17 lateral view; 18, longitudinally opened on the dotted line.



Stomach of *Megalobulimus popelairianus*, Group A species: 19, ventral view; 20 dorsal view; 21, longitudinally opened, showing a weakening of musculature in its upper region.



Stomach of *Strophocheilus pudicus,* Group B species: 22, muscular portion, longitudinally opened showing internal folds; 23, lateral view, showing adjacent portion of oesophagus, with thin and transparent wall; 24, dorsal view; 25 ventral view.



Stomach of *Chiliborus chilensis*, Group B species: 26, ventral view; 27, dorsal view; 28, longitudinally opened, showing the little thickness of musculature and absence of internal folds.

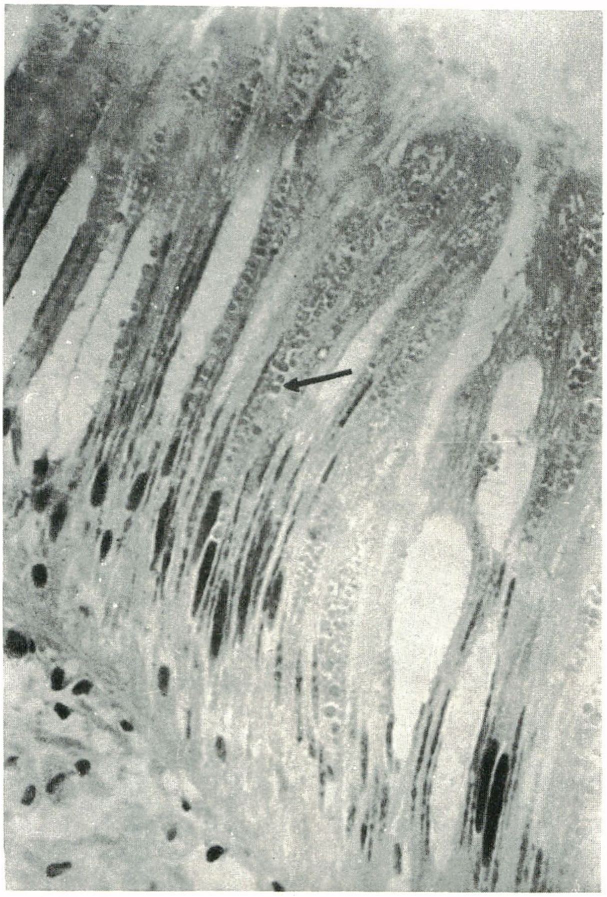


Fig. 29-A, *Megalobulimus abbreviatus:* Fotomicrography of transversal section of rectum. Arrow shows acidophilic secretion granules. (H. E., ± 1200 X).

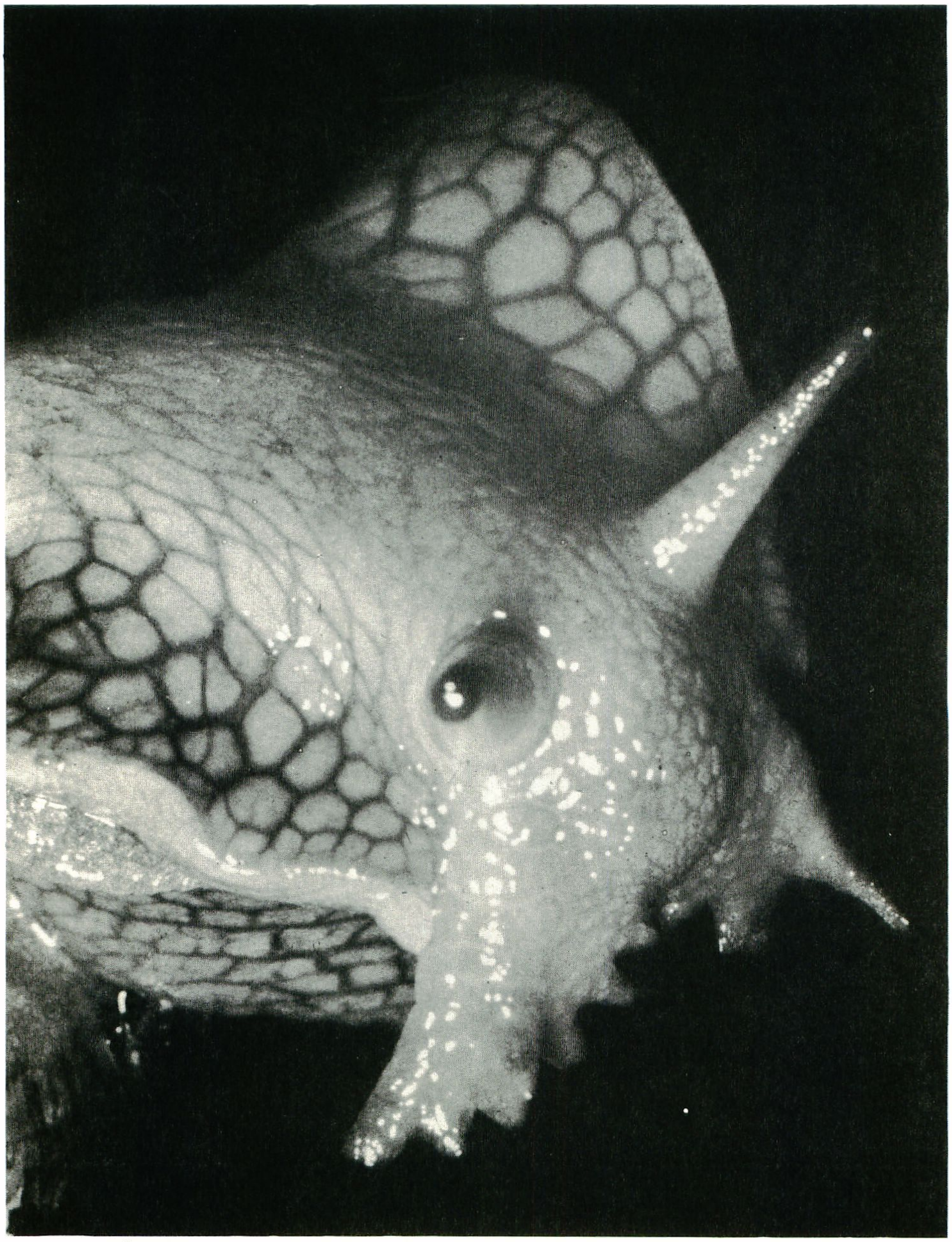


Fig. 29-B, *Megalobulimus yporanganus:* living specimen, showing the buccal fringe expanded.

thinner in the duct area of the posterior lobe of the digestive gland (fig. 21).

In group B it is possible to follow a sequential reduction of the stomach muscles, from a perfectly outlined and muscular organ with intensely folded internal surface to a stomach of rather indefinite outline, with only a slight muscular thickening over a very restricted area and without any vestige of internal folds. Figures 22-28 illustrate extremes of this evolutionary line.

In *Strophocheilus pudicus* (figs. 22-25) it can be seen that the portion proximal of the stomach, next to the oesophagus, no longer has any muscular thickening or external sharp outline, while the distal portion, next to the intestine, is a muscular chamber with strong and raised internal folds (figs. 22-23).

In *Chiliborus chilensis* (figs. 26-28), there is only an external demarcation between stomach and intestine; the musculature becomes reduced to a thin layer, on the intestinal side, and internal folds are entirely absent.

Considering that reduction of the stomach muscles is gradual from species to species, and the difficulty of setting numerical values to this graduation, the species were simply assembled in two groups, one exhibiting muscular thickening and the other lacking it. In Table 1, the species belonging to the first group, that represent a more primitive stage, are coded by symbol I; those of the second, highly evolved species are given the symbol 0.

BUCCAL FRINGE

The integument of the upper region of the buccal slit forms two lateral expansions, a pair of retractile appendages of tactile function, densely lobulate on the ventral surface (fig. 29B)

Ihering (1912: 483) defines such an expansion as a lobulate process adjacent to the mouth, and states that it is to be found only in some species of the genus *Borus* (or *Megalobulimus* according to Bequaert's concept). Connolly (1915: 122), listing the primitive characteristics of his hypothetical precursor of the Acavidae, mentions this character under the designation of "labial lobes".

Scott (1939: 222) defines the buccal fringe as a paralabial expansion and states that it is one of the characters of the family Strophocheilidae. Scott considers this character common to all Strophocheilidae, while Ihering limits it to some species of *Borus*. I think this is an important character, as it is constant and exclusive of the species of Strophocheilidae which I have, based on kidney pattern, designated as Group A.

The buccal fringe would, then, represent the second character favouring the division of the family Strophocheilidae in two distinct groups of species, already proposed as Groups A and B.

PULMONARY SEPTUM

The pulmonary septum is a raised fold running obliquely from the pericardium up to the pneumostome. It forms a thick covering for the pulmonary vein, and appears as a complex lacunar network spread out over a large part of the kidney (figs. 30 and 31). The pulmonary septum is also exclusive of Group A Strophocheilidae and I think it is a primitive character, since I believe that its function is to prevent pollution of the respiratory area by the urine drained into the pulmonary chamber.

Under this hypothesis, I consider this septum as the first structure tending to isolate an excretory area within the respiratory chamber. In the more evolved Pulmonata the urinary excretion takes place through totally or partially closed tubes, the occurrence of any separatory wall therefore being superfluous.

In *Pila* sp. (Prosobranchia) Purchon (1968: 27-28, fig. 12) shows a mantle fold dividing the bottom of the palial chamber in two areas. Andrews (1965: 75, fig. 3) states that in *Pomacea canaliculata* (Prosobranchia, Pilidae) such a fold has the function of orienting the inhaling stream in the interior of the respiratory chamber.

In Planorbidae (Basommatophora), Rey (1956: 68) has shown the presence of two ridges on the roof of the respiratory chamber, the pulmonary and rectal (ridges) but did not discuss their function.

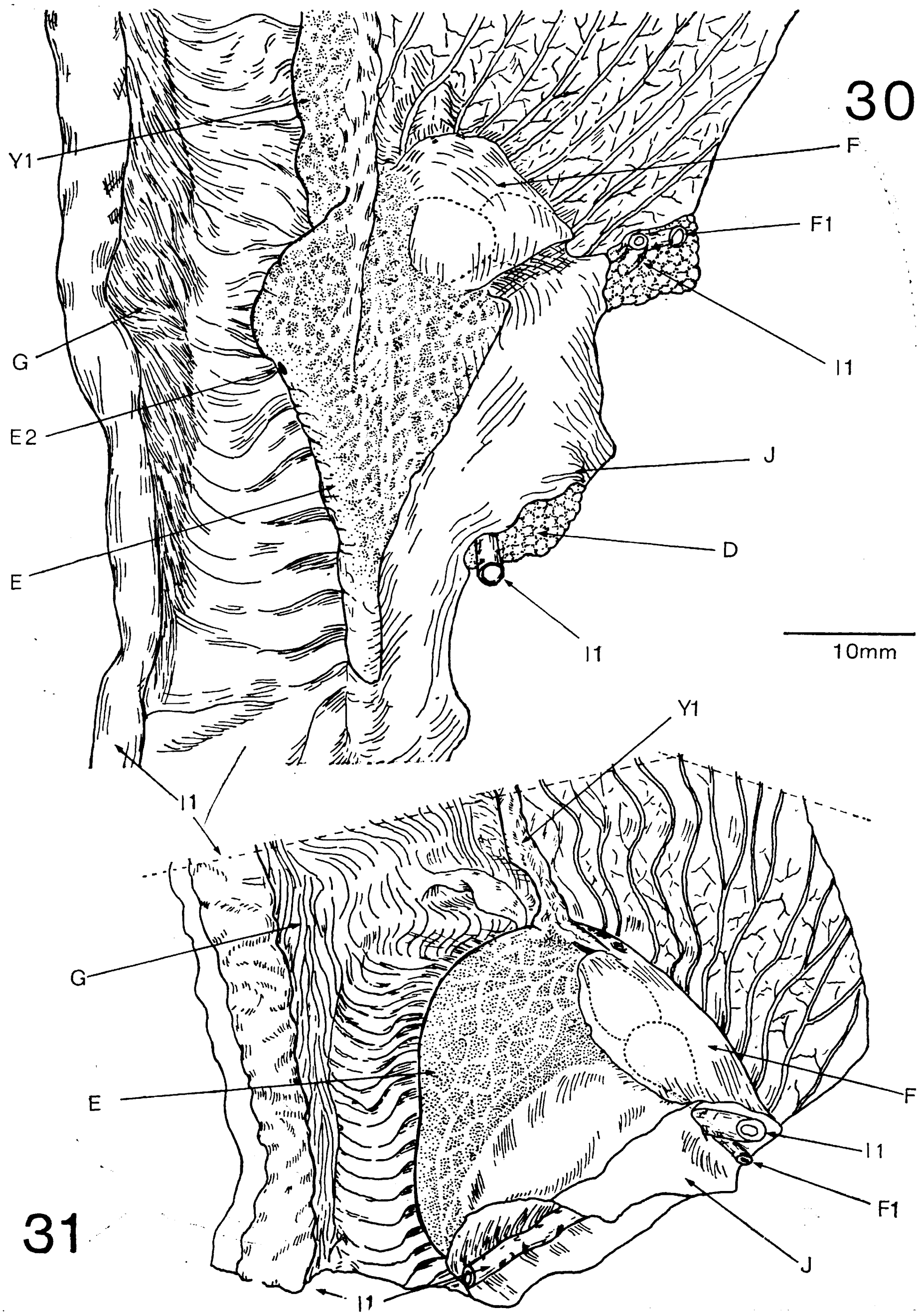
In the two examples above, the structure considered differs, both in shape and position, from the pulmonary septum of the Group A species. In neither one the folds are related to the pericardium or present the anastomotic lacunar network characteristic of a true pulmonary septum.

PRE-RECTAL VALVE

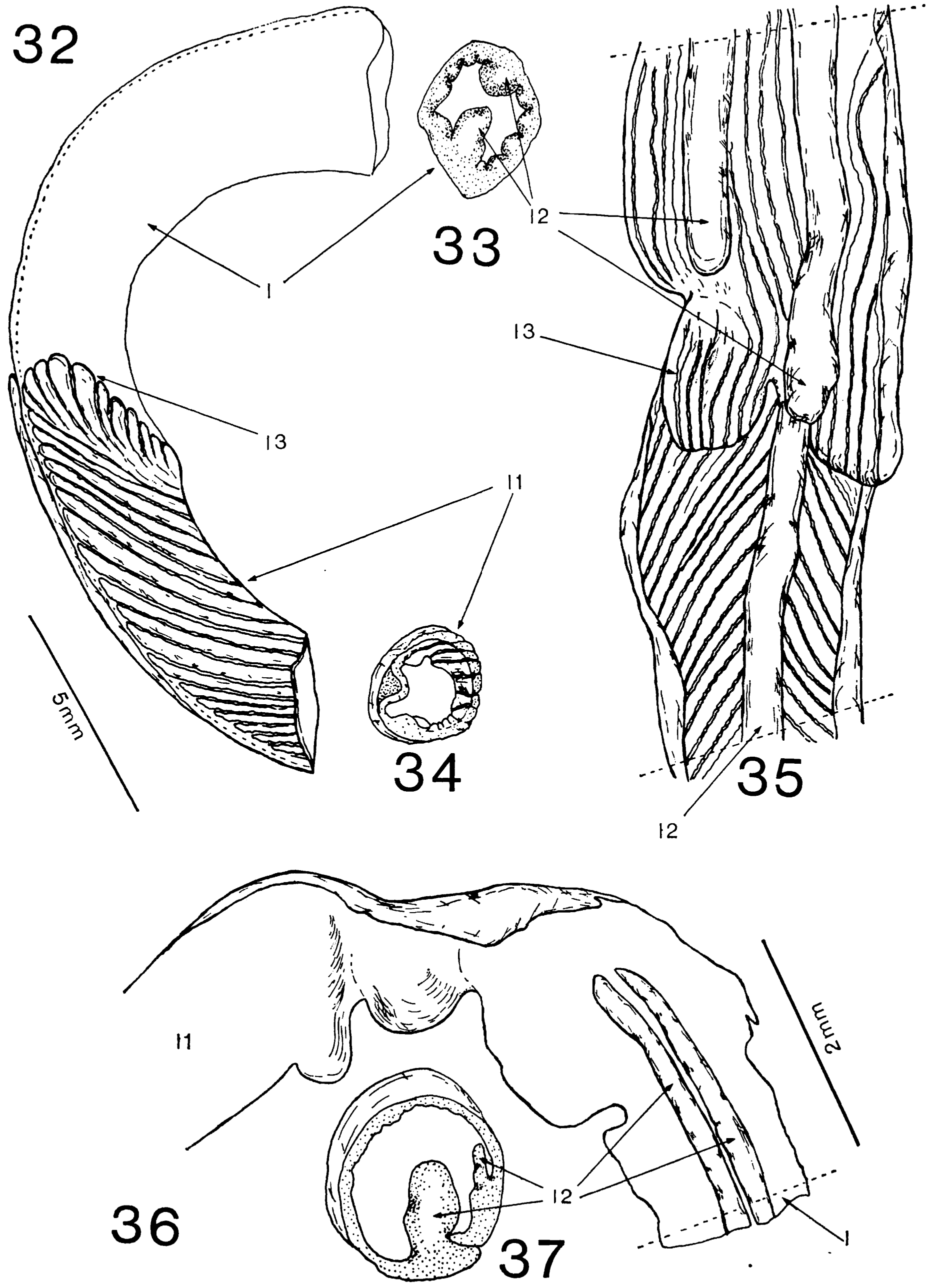
The pre-rectal valve is a bi-laminate valve located in the intestinal loop apposed to the pericardium and to the kidney, opening towards the posterior end of the animal. Its presence is connected to an abrupt morphological and histological transformation of the internal surface of the intestine. The intestinal folds, which run longitudinally from the stomach to the vicinity of the valve, become sharply oblique from then on.

In histological sections, prismatic cells were observed, with elongate nuclei exhibiting condensed chromatin and, at the apical portion, acidophilic secretion granules (fig. 29A). This pattern is not found in the segment of the digestive tract anterior to the valve.

The name pre-rectal, proposed here, is open to discussion due to the fact that the intestine forms two or more loops before turning into a rectum, and running forward. But, as along the entire portion preceding the valve, the internal structure remains uniform in spite of the loops, this name may be accepted provisionally. I found in the literature no mention of this structure.



Excretory apparatus of Group A species: 30, *Megalobulimus oblongus;* 31, *Megalobulimus bronni.*



Intestinal loop, pericardial region: 32-35, *Megalobulimus abbreviatus,* Group A species; 36-37, *Mirinaba unidentata,* Group B species.

The comparative study indicated that the pre-rectal valve is a character always present in the Group A species, although not exclusive. It occurs in the slugs Veronicellidae, as well, with a small difference in the position of the valve, brought about by the general plan of organization of the animal, which is somewhat different from the remaining Pulmonata. Along with the valve, in the Veronicellidae there is also a difference in the orientation of the intestinal folds, very similar to that of Group A.

Occurrence of this character in two groups so far apart in all characters of major importance especially the genital, excretory and respiratory systems, is explainable as a case of parallellism. Furthermore, it is interesting to note that there is also great similarity in the morphology and structure of the stomach, an organ of primitive pattern in both groups.

Taking into account the basic concept that the digestive system of the Pulmonata has envolved towards structural simplification, I consider the persistence of the pre-rectal valve as a character of primitivity. Therefore, it is symbolized as I in the table.

Figures 32 to 35 show the intestinal loop of a Group A species, evidencing the pre-rectal valve and the change of orientation of the internal folds. Figures 36 and 37 illustrate the absence of the valve and internal folds in a Group B species.

ACCESSORY GENITAL GLAND

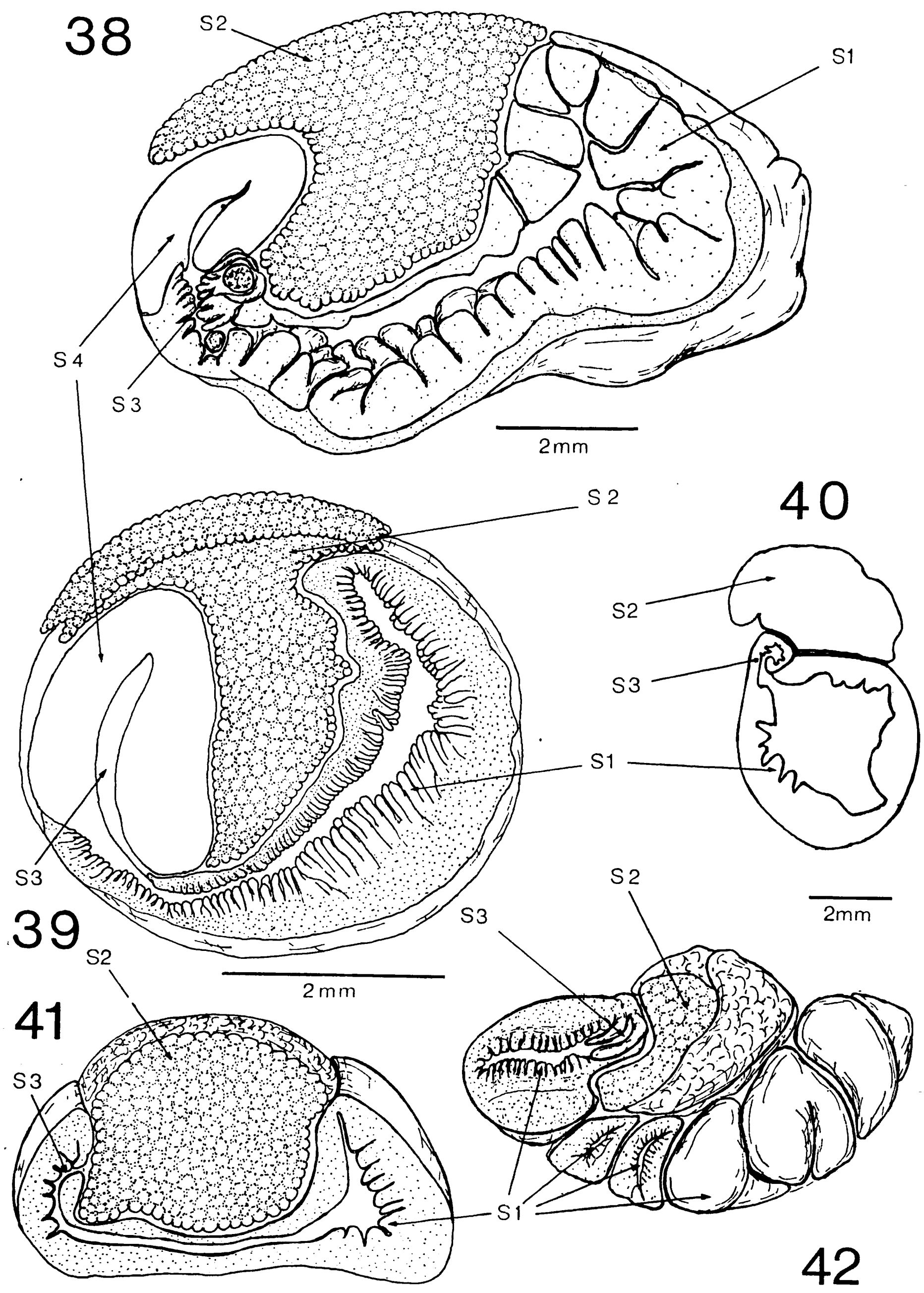
For the definition and interpretation of this character, a brief analysis of the separation of masculine and feminine ducts in the subclass Pulomata becomes necessary.

In some Archaeopulmonata and in the Basommatophora, separation of the masculine and feminine ducts takes place immediately at the boundaries of the albumen gland; spermatozoa are collected by the efferent duct, above which lays the prostate; eggs run down the uterus, which is a wide and richly folded tube (Duncan, 1960: 602; Leme, 1966: 274).

In the Stylommatophora, such splitting of the ducts takes place further below, the voluminous tubular portion considered as spermoviduct (Duncan, 1960: 602; Scott, 1929:260) stretching between the albumen gland and the vagina.

The spermoviduct is built up by the feminine duct, an ample chamber lined by a richly folded glandular epithelium, and by a longitudinal spermatic gutter laying between the dorsal and ventral laminae of the feminine duct which, on its turn, is partially surrounded by the prostatic gland. This description corresponds to the spermoviduct of *Helix* (figs. 40 and 42) and of most Stylommatophora.

In the course of this comparative study, it was seen that members of Group A present a second gland, almost as voluminous as the prostate, lodged along the spermatic gutter and perfectly distinct from the two plicae forming the feminine duct.



Transversal section of spermoviduct: 38, *Megalobulimus gummatus;* 39, *Megalobulimus popeilarianus,* Group A species; 40, classic scheme of the spermoviduct of *Helix pomatia* taken from Hyman (1967); 41, *Mirinaba planidens,* Group B species; 42, *Helix pomatia.*

Schirch & Wetzel (1922: 29-31), consider the uterus of *S. ovatus* as a gland made up by three different portions: papillary mucosa, acidophilous secretion area and basophilic secretion area. The first would represent the wall of a large tube, i.e., the feminine duct; the second would correspond to the prostate of the other Stylommatophora; the third would be exactly the same same structure found in all Group A species.

Although illustrating it very clearly, H.B. Baker (1926: 24, Pl. XV, A and C) did not describe such a gland, viewing it only as a wedge-shaped column set between the two laminae of the feminine duct. Scott (1939) does not mention the structure either, probably for not having sectioned the organ.

I have histological observations (figs. 38, 39) which entirely agree with those of Schirch & Wetzel regarding the structural aspect. Nevertheless, I disagree with their concept, as I consider that the spermoviduct is built up of three distinct glandular masses, besides the spermatic groove. The first mass is distributed over the internal surface of the feminine duct, constituting the glandular epithelium (S1), the second is the prostate (S2) and the third is the basophilic secretion gland (S4) characteristic of Group A Strophocheilidae.

This basophilic gland was found in all Group A species, as well as in *Strophocheilus pudicus* and *S. debilis* which, along with a few other species, make up the genus *Strophocheilus,* in the systematic scheme of the previous chapter. Being a gland of unknown function, restricted to a small group of Pulmonata, I propose that it be named accessory genital gland.

This gland is peculiar to Group A Strophocheilidae and to at least two species of Group B; more evolved Pulmonata do not show it. This may mean that the presence of the gland is: (i) a primitive character preserved by both groups; (ii) a character indicating that both groups are closely related; (iii) a result from convergence or parallelism. In view of the ensemble of anatomic observations reported in this paper, and not loosing sigth of the danger of circular reasonings, I prefer to believe that it is a primitive character preserved in both groups. This is why it is assigned I in the table.

The reduction and transformation of the accessory genital gland can be followed in figures 38 through 42. Figures 38 and 39 show cross sections of this gland in two species of Group A; figure 41 shows the corresponding section of the spermoviduct of a Group B species, already lacking the accessory genital gland, but with the feminine duct still unmodified. Figure 40 corresponds to the classic outline proposed by Meisenheimer for *Helix pomatia,* and figure 42, to a cross section through the spermoviduct of the same species.

CONCLUSIONS

The results presented in the previous section and summarized in Table I, have led to the following conclusions:

Table I. Summary of comparative anatomy

ORDERS	SUBORDERS	FAMILIES	SPECIES		CHARACTERS				
					A	B	C	D	E
ARCHAEOPULMONATA		Ellobiidae	*Melampus coffeus*		I	O	O	O	O
		Planorbidae	*Biomphalaria grablata*		I	O	O	O	O
BASOMMATOPHORA		Physidae	*Aplexa marmorata*		I	O	O	O	O
		Lymnaeidae	*Lymnaeia stagnalis*		I	O	O	O	O
STYLOMMATOPHORA	MESURETHRA	Strophocheilidae	* *popelairianus*	Group A	I	I	I	I	I
		"	* *granulosus*	" "	I	I	I	I	I
		"	* *oblongus*	" "	I	I	I	I	I
		"	* *pudicus*	Group B	I	O	O	O	I
		"	* *unidentatus*	" "	I	O	O	O	O
		"	* *erythrosoma*	" "	I	O	O	O	O
		"	*pilsbryi*	" "	I	O	O	O	O
		"	* *lutescens*	" "	I	O	O	O	O
		"	* *chilensis*	" "	I	O	O	O	O
		"	* *gonyostomus*	" "	I	O	O	O	O
		"	* *multicolor*	" "	I	O	O	O	O
	SIGMURETHRA	Subulinidae	*Stenogyra planispira*		I	O	O	O	O
		Bulimulidae	*Thaumastus achilis*		O	O	O	O	O
		"	*Plechocheilus flocosus*		O	O	O	O	O
		"	*Drymaeus acervatus*		O	O	O	O	O
		Ortalicidae	*Oxystila pulchela*		O	O	O	O	O
		Macrocyclidae	*Macrocyclis laxata*		I	O	O	O	O
		Camaenidae	*Solaropsis braziliana*		I	O	O	O	O
		Bradybaenidae	*Bradybaena similaris*		O	O	O	O	O
		Helicidae	*Helix pomacea*		O	O	O	O	O
		Streptaxidae	*Streptaxis* sp.		O	O	O	O	O
		Amphibulimulidae	*Peltella iheringi*		O	O	O	O	O
		Limacidae	*Limax flavus*		O	O	O	O	O
SYSTELOMMATOPHORA		Veronicellidae	*Phyllocaulis* sp.		I	O	O	O	O

LEGEND

A = stomach

B = buccal fringe

C = pulmonary septum

D = pre-rectal valve

E = annex genital gland

I = primitive

O = derivative

* = type-species

1. Group A of Strophocheilidae (established on basis of the renal pattern), comprising the species belonging to the "genera" *Megalobulimus, Phaiopharus,* and *Psiloicus,* stands out as a fairly homogeneous group, perfectly distinct both from Group B and from all the remaining families listed on the table. Its characteristic features are: (i) the excretory pore is single and situated laterally, lacking any vestige of ureter formation (typical Mesurethran pattern); (ii) the presence of a buccal fringe: (iii) of a pulmonary septum; and (iv) of a pre-rectal valve. This last character is the only non-exclusive one within the Subclass Pulmonata, as it is also found in the family Veronicellidae which, however, belongs into another order.

2. The renal pattern shown by Group A species (fig. 12) can be considered as the most primitive among the Stylommatophora, more so than that of the Basommatophora. Its stage of development is of the same level as that of the Archaeopulmonata (Van Mol, 1967).

The fact that *Melampus coffeus* exhibits a more primitive renal pattern if compared to the more advanced groups of Basommatophora, such as Planorbidae and Lymnaeidae, strongly suggests that the Ellobiidae should be placed in a separate order, Archaeopulmonata, as proposed by Van Mol (1967). This idea is also supported by Morton (1955) who, investigating the evolution of the Ellobiidae, demonstrated that the ancestor of the Stylommatophora might have belonged to this family. The position of the genus *Melampus* as one of the most advanced within the family Ellobiidae, illustrated by Morton (*l.c.*: 154, fig. 14), justifies its relation to Group A, perhaps the most primitive of the Stylommatophora. In *Melampus coffeus* the excretory pore is situated on the frontal face of the kidney, the urine being eliminated into the pulmonary chamber. The pericardium, many times smaller than the kidney, lays on the posterior left corner of the latter (fig. 11).

3. The Basommatophora are the first group to present a ureter; the pericardium has a small volume compared to that of the kidney (as is the case in the Archaeopulmonata), but is posterior to it. In the Lymnaeidae (Baker, 1911: 16 and personal observations), the ureter is short and broad, running straight to the anterior border of the respiratory cavity, before opening near the rectum. According to Baker, among the Basommatophora, a fold-free ureter signifies primitivity.

In the Planorbidae, as shown by Rey (1956: 85, figs. 27-30) a folded ureter appears for the first time, representing a more advanced stage over that reached by the groups of Strophocheilidae.

4. In Group B species (fig. 31) there is a suggestion of a primary ureter, represented by a dilation of the right anterior corner of the kidney, dilation which may or not bear the excretory pore. The pericardium, as in the species of Group A, has volume about half that of the kidney, and is on a definitely anterior position. It can be accepted

that, in the Stylommatophora, the pericardium anterior in relation to the kidney is a character of primitivity.

5. In *Acavus* (fig. 14) besides the full development of the primary ureter, the pericardium undergoes a volume reduction in relation to the kidney, as well as a translation to the left lateral face of the kidney. Finally, *Helix* (fig. 15) exhibits the climax of development reached by terrestrial Pulmonata, with well developed primary and secondary ureters, the kidney surpassing by far the volume of the pericardium, which has a posterior position.

6. Morton (1955: 135-136, fig. 3) shows that the type of stomach of the more evolved Basommatophora, such as *Lymnaea* for instance, did not derive from that of the Ellobiidae, and that in this latter family the primitive stomach, occurring in the genus *Ophicardelus*, has given origin to two more advanced types, found in the genera *Melampus* and *Rangitotoa*.

The stomach of Group A Strophocheilidae fits perfectly into the primitive pattern of *Ophicardelus;* however, the evolution observed in the Stylommatophora follows a different path from that of the Ellobiidae.

7. In view of the above it can be accepted that in renal pattern, Group A is at the same level with the genus *Melampus,* whereas, with regard to the stomach, it is comparable to the most primitive genera of family Ellobiidae.

8. If in the stomach thick musculature and heavily folded mucosa are taken as characters of primitivity, and almost complete disappearance of musculature as the climax reached by the Stylommatophora, the Group A species will be placed on a more primitive level than the Group B species. In the former, the stomach outline is always sharply defined, as are the internal plicae, whereas Group B species vary from a heavily muscular stomach, with folded mucosa, to a delicate stomach of imprecise external outline and internally smooth (without reaching, however, the stage attained by the more evolved genera of Pulmonata, such as *Peltella* and *Helix*).

9. Examination of the contents of the digestive tract shows that there is a relationship between muscular thickening and type of food. Group A species take in large amounts of food, in coarse particles, which are found, almost intact at times, at the terminal portion of the intestine. As there is no selection of the food ingested, a mechanical separation becomes necessary. This is accomplished by the folds of the mucosa, which has ciliate cells, and by the stomach wall musculature.

In Group B species, there is a better selection of the ingested food regarding quality, quantity and particle size. This specialization in alimentary habits is accompanied by structural simplification.

I consider the presence of the pre-rectal valve a character of primitivity in the Stylommatophora. The coincident occurrence of this character in Group A Strophocheilidae and in the species of Veronicellidae is taken, here as a case of parallelism.

10. Based on the localization of the pre-rectal valve near the pericardium, I raise the hypothesis that this valve, besides preventing the reflux of ingested food, actuates in the establishment of pressure gradients which allow the inflow of liquid from the intestine into the pericardium.

11. The pulmonary septum is an exclusive character of Group A; among the Pulmonata, it must be considered as a primitive character. In the respiratory chamber of other groups we can find septa, folds or ridges separating the pallial organs, but these structures do not correspond to that found in these Strophocheilidae.

It is possible that the pulmonary septum is linked to the development of the urinary tract, so very necessary for the conquest of the aerial environment.

In aquatic mollusks, urine can be discharged directly into the respiratory chamber and drained to the environment by the circulating water. In the terrestrial ones, a whole sequence of adaptation is found, up to the constitution of a completely closed urinary tract, represented by the primary and secondary ureters. In this sequence of transformations, it can be admitted that the first step is found in the Strophocheilidae Group B species, in which a vesicle-like expansion can already be found, as a precursor of the ureter.

The pulmonary septum is absent in Group B, although the urine is still eliminated through an open gutter. A hypothesis might then be raised here, that the mutations responsible for the changes in the excretory system might have influenced, from an early beginning, the elimination of the pulmonary septum.

An opposite hypothesis would be that of Group B originating from an ancestor lacking the pulmonary septum.

12. The buccal fringe is a tactile organ exclusive of Group A Strophocheilidae. In spite of the fact that it has been pointed as a primitive character of the hypothetical precursor of the Acavidae, it is not found in any species of the Basommatophora or Prosobranchia, from which the primitive stock should have arisen.

In the Archaeopulmonata and Basommatophora, the tegument surrounding the borders of the mouth opening does not exhibit any noticeable differentiation, and is designated *velum.*

According to Andrews (1965: 21), *Pomacea canaliculata* (Prosobranchia), of amphibious habits, has the latero-dorsal area of the mouth transformed into a pair of sensorial tentacle-like palps, fairly well developed. This character has also been observed in several species of the genus *Pomacea* (*Ampullaria,* auct.).

Tentacle-like labial palps are also found in the Subclass Opistobranchia; of these, I have examined one species, *Marionia cucullata* Gould, which has fringed labia very much similar to those found in Group A species. This may be held a case of parallelism, but I think it better to mention it.

In most of the Stylommatophora, the perioral tegument does not exhibit any noticeable differentiation, an exception being the family Oleacinidae, carnivorous, its species being provided with a pair of tentacle-like labial palps.

Considering that (a) — in the conquest of ecological niches the arboreal habit has evolved from the terrestrial; (b) — the species bearing the buccal fringe are exclusively terrestrial; (c) — the large majority of Stylommatophora are arboreal and do not have a buccal fringe, it may be accepted that the arboreal environment requires less tacticle exploration than the soil.

13. The accessory genital gland is found in all Group A species and, among those of Group B, in *Strophocheilus pudicus* and related species. This coincidence further supports the hypothesis raised about the disappearance of the pulmonary septum, namely, that both groups of Strophocheilidae do have a common ancestor.

The persistence of this gland is one more character evidencing the primitivity of Group A Strophocheilidae and of the genus *Strophocheilus* amongst Group B genera.

14. Of the five characters analyzed in the comparative study, it can be said: two are exclusive of Group A (buccal fringe and pulmonary septum) ; two are shared with other groups (genital gland, genus *Strophocheilus;* pre-rectal valve, family Veronicellidae) ; the remaining character, the stomach, exhibits a morphological gradation towards a progressive reduction of the musculature.

15. Group B species do not present any exclusive character, showing closer relationships with the remaining Stylommatophora, their closest affinity being with the family Dorcasiidae, which is restricted to Southwest Africa. I could not obtain a sample of dorcasids with the soft parts preserved for examination; therefore, I can claim no personal conclusion concerning the relationships between Group B and genera *Dorcasia* and *Trigonephrus.* However, based on Connolly's (1915) descriptions of these two genera, it may be accepted that such a relationship is fairly close. The arrangement proposed by Taylor & Sohl (1962), considering both groups as separate families, Dorcasiidae in Africa and Strophocheilidae in South America, but assembled, along with Group A species, in a superfamily Strophocheiloidea, seems acceptable.

16. As *Strophocheilus pudicus* (Müller) is the type-species of the genus *Strophocheilus* Spix, member of Group B, the latter should con-

tinue to bear the name Strophocheilidae; and the definition of the family should be revised.

17. It has been shown that Group A is homogenous and very distinct not only from Group B, but from all the families analyzed; therefore, it must be considered as an independent family. Taking into account that I accept inside it one single genus, *Megalobulimus* Miller, obviously the corresponding family name should be Megalobulimidae. This family, on account of its primitive characters can be considered as the most primitive among the Stylommatophora. Its relationships to *Melampus* indicate that a primitive stock of Archaeopulmonata might have originated the Strophocheilidae, a branch entirely separated from that of the Basommatophora.

A NEW SYSTEMATIC ARRANGEMENT OF THE NEOTROPICAL STROPHOCHEILOIDEA

The superfamily Strophocheiloidea is composed of the African Dorcasidae and the South American Strophocheilidae and Megalobulimidae, new.

As I have no preserved African materials available for anatomical comparison, and as the data in the literature are insufficient, it is at present impossible to further differentiate Dorcasiidae from Strophocheilidae.

According to Connolly (1915), it seems that Dorcasiidae and Strophocheilidae are very closely related with regard to palial complex, genital apparatus, radula and the absence of buccal fringe.

So, I prefer to exclude the family Dorcasiidae from the systematic analysis and study only the American families.

KEY TO FAMILIES

Shell small to medium-sized (19 to 70 mm), animal without buccal fringe, kidney with a primary ureter delineation near its anterior edge, roof of respiratory chamber without pulmonary septum, intestine without pre-rectal valve	Strophocheilidae
Shell medium sized to large (50 to 160 mm) ; animal with buccal fringe, kidney without any vestige of primary ureter; excretory pore near the middle of the lateral free face of the kidney; roof of pulmonary chamber with longitudinal septum, intestine with pre-rectal valve	Megalobulimidae

Strophocheilidae

Diagnosis

Mesurethra. Kidney elongate or nearly triangular, with incipient primary ureter. Excretory pore near to anterior end of kidney. Roof of pulmonary chamber with low or high vessels, but no longitudinal septum separating an excretory from a respiratory region. Genitalia simple; vas deferens inserted directly on penis or enlarged into an epiphallus, without flagellum. No dart sac, no mucous glands or vaginal appendix.

Buccal fissure without lateral fringed expansion, jaw solid, smooth, vertically striate or with slightly thickened riblets; all teeth unicuspid; walls of gut thin and sometimes transparent, stomach with or without internal folds, pre-rectal valve absent. Shell small to medium sized (19 to 70 mm), periostracum often persistent.

ANATOMICAL KEY TO THE GENERA

1. Annex glandular sac straight (fig. 45) 2
Annex glandular sac an inverted "U" (fig. 46) 4

3. Spermoviduct with accessory genital gland ...... *Strophocheilus*
Stomach with internal folds; penis with basal papilla (figs. 53, 54) 3

3. Spermoviduct with accessory genital gland .... *Strophocheilus*
Spermoviduct without accessory genital gland .... *Mirinaba*

4. Penis with epiphallus (fig. 52) .... *Anthinus*
Penis with pseudo-epiphallus (figs. 49,53) 5

5. Pseudo-epiphallus in the same axis as penis or parallel to it, but not detachable from external penial wall ...... *Gonyostomus*
Pseudo-epiphallus parallel to penial axis and easily detachable from its external wall (fig. 50) 6

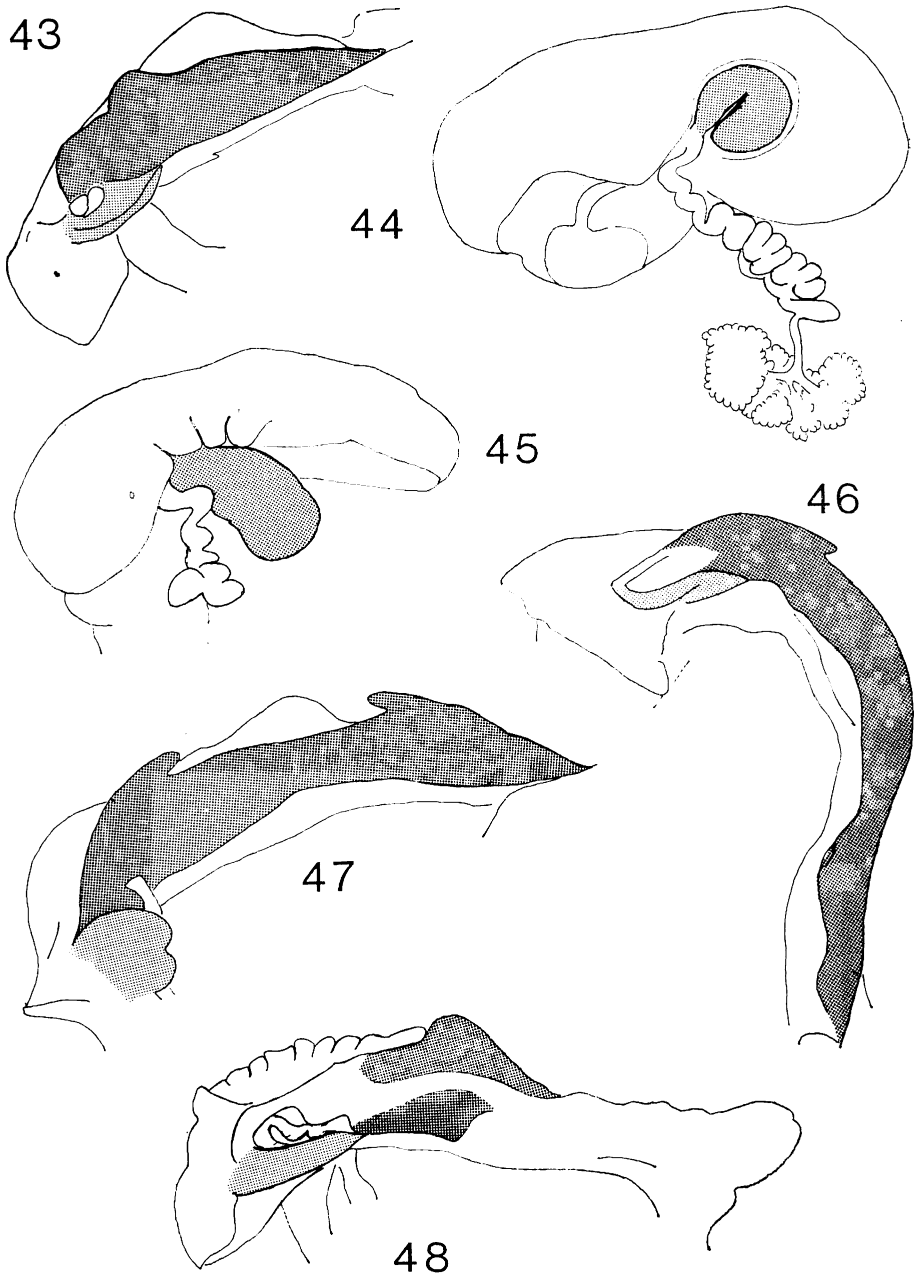
6. Ventral aspect of mantle's free edge with two developed folds, separated by a saddle-shaped depression (fig. 47) . *Chiliborus*
Ventral aspect of mantle's free edge with two parallel folds near the pneumostome (fig. 48) .... *Austroborus*

Genus **Strophocheilus** Spix

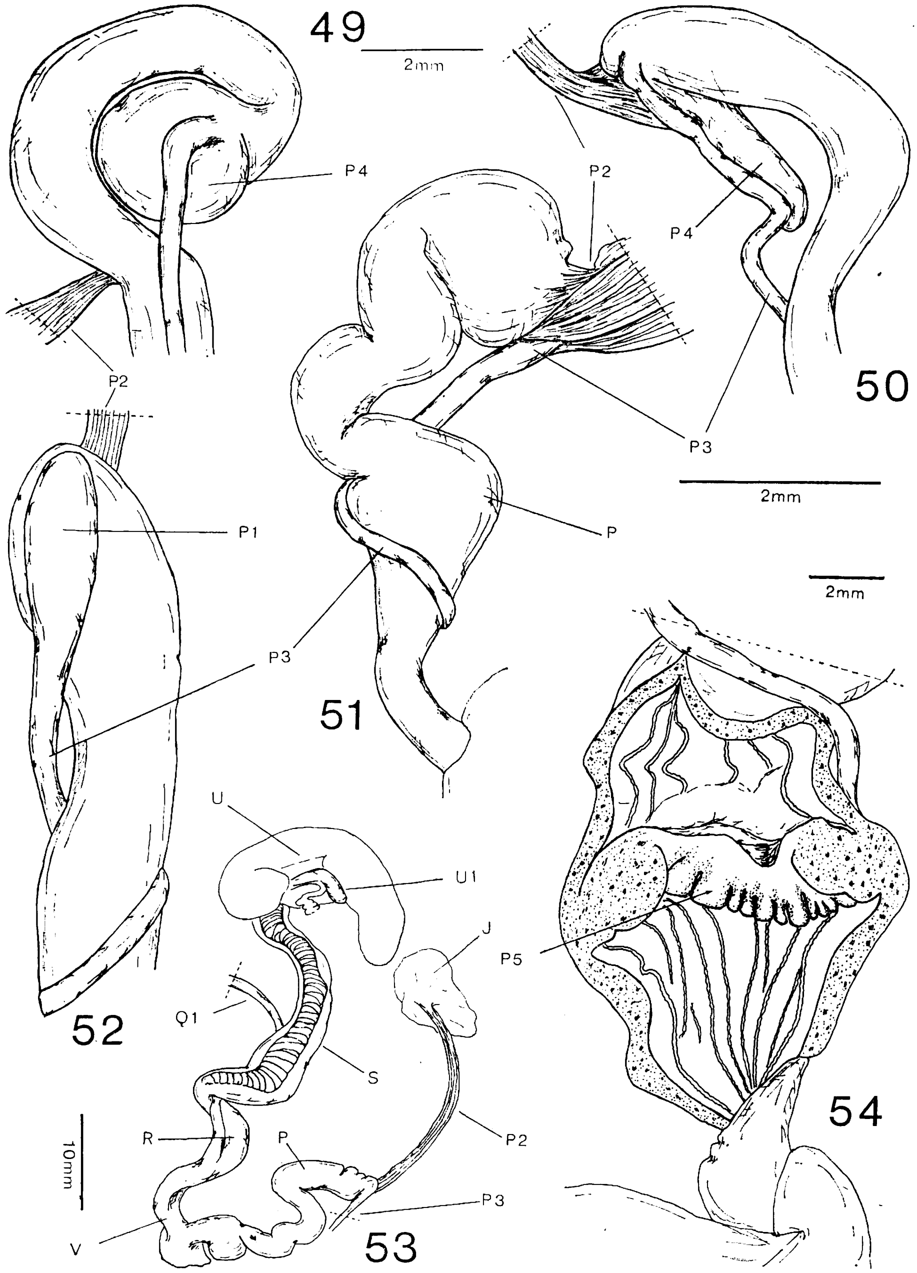
Strophocheilus Spix, 1872: 12. Type-species, *Strophocheilus almeida* Spix, 1872 (= *Helix pudica* O.F. Müller, 1774, by designation of G. Nevill, 1879, *Hand. List. Moll. Indian Mus.* 1 (1878): 122; apud Bequaert, 1948: 27).

Diagnosis

Shell medium sized (40 to 70 mm), ovate-oblong or spindle-shaped, dorsoventrally flattened; base of boby-whorl not swollen nor saccate



Characters of anatomical key to genera: 43-44, *Gonyostomus;* 45-46, *Mirinaba;* 47, *Chiliborus;* 48, *Austroborus.*



Characters of anatomical key to genera, genital apparatus: 49, *Chiloborus;* 50, *Austroborus;* 51, 52 and 54, *Mirinaba;* 53, *Mirinaba planidens.* Figures 50 and 52, 51 and 54, in the same scale, respectively.

to the left of the columella; sutures deep, therefore indenting the whorl's contour and rendering the spire more evident; coloration uniform; nepionic whorls mostly with a vertical sculpture of regular riblets and not granulated; later whorls with wrinkled or malleated surface, without minute spirae; columella with a more or less developed fold, parietal wall straight and oblique, outer lip with reflexed rim.

Animal with uniform coloration; stomach part muscular, with internal folds; annex glandular sac straight; penis with basal papilla, pseudo-epiphallus short; spermoviduct with a little-developed accessory genital gland.

List of species

calus Pilsbry, 1901
contortuplicatus (Reeve, 1850)
debilis (Bequaert, 1948)
miersi (Da Costa, 1904)
pudicus (Müller, 1774)
roseolabris Bequaert, 1948

Genus **Mirinaba** Morretes, status n.

Mirinaba Morretes, 1952: 111 (as subgenus of *Strophocheilus*. Type-species, *Strophocheilus erithrosoma* Pilsbry 1895, orig. des.).

Metara Morretes, 1952: 111 (as subgenus of *Strophocheilus*. Type-species, *Partula unidentata* Sowerby, 1825, orig. des.). Syn. n.

Diagnosis

Shell medium-sized (40 to 70 mm), ovate-oblong or spindle-shaped, flattened dorsoventrally, apex acute but first whorl not prominent, base of body-whorl not swollen to the left of columella, spire reasonably tapering, nepionic whorls with very fine raised riblets, sometimes undulate or interrupted, surface malleated, post-nepionic whorls with or without very fine spiral lines; peristome expanded and reflected, with or without developed tooth on the outer lip, columella without fold or with a hardly defined fold.

Animal with uniform coloration, stomach with strong musculature and with well developed internal folds; annex glandular sac straight; spermoviduct without accessory genital gland; penis with basal papilla, epiphallus or pseudo-epiphallus varying in shape or absent (fig. 51).

List of species

antoninensis (Morretes, 1952), comb. n.
cadeadensis (Morretes, 1952), comb. n.
curytibana (Morretes, 1952), comb. n.
cuspidens (Morretes, 1952), comb. n.

erythrosoma (Pilsbry, 1895), comb. n.
fusoides (Bequaert, 1948), comb. n.
jaussaudi (Morretes, 1937), comb. n.
planidens (Michilin, 1831), comb. n.
unidentata (Sowerby, 1825), comb. n.

Genus **Speironepion** Bequaert, status n.

Speironepion Bequaert, 1948: 26 (as subgenus of *Strophocheilus*). Type-species, *Bulinus* (*sic*) *milleri* Sowerby, 1838, orig. des.

Diagnosis

Shell medium-sized (45 to 71 mm) ovate-oblong, markedly flattened dorsoventrally; nepionic whorls mostly with fine, crowded spiral striae; later whorls with finely beaded spiral rows of granules. Columella without fold; outer lip flaring, with reflexed rim.

Animal unicolorous; lower aspect of the free edge of the mantle with two developed folds, with a saddle-shaped depression between them; stomach with weak musculature, without internal folds; annex glandular sac straight; spermoviduct without accessory genital gland, vas deferens ending in an epiphallus parallel to penis; penis without basal papilla.

List of species

iguapensis (Pilsbry, 1901), comb. n.
kronei (Ihering, 1901), comb. n.
milleri (Sowerby, 1838), comb. n.
pilsbryi (Ihering, 1900), comb. n.

Genus **Austroborus** Parodiz

Microborus Pilsbry, 1926: 6 (as sect. of subgenus *Borus, Strophocheilus*). (Type-species, *Bulinus* (*sic*) *lutescens* King & Broderip, 1832, orig. des.).

Austroborus Parodiz, 1949: 189 (as subgenus of *Strophocheilus*). (Nom. nov. for *Microborus* Pilsbry, 1926); Klappenbach & Olazarri, 1970: 181 (as genus).

Diagnosis

Shell relatively small (23 to 36 mm), elongate elliptical to broadly elliptical, scarcely dorsoventrally flattened, with broadly rounded and decussated by spiral engraved lines into granules, later whorls with minute granulation, columella without fold, outer lip thick, little or not reflexed, sometimes accrescent in old age.

Animal with uniform color; ventral aspect of the free edge of the mantle with only two parallel folds near the pneumostome, stomach with thin musculature and without internal folds; annex glandular sac curved, inverted U-shaped; spermoviduct without accessory genital gland, penis without basal papilla, pseudo-epiphallus long, parallel to the penial axis and easily detachable from the outer penial wall.

List of species

cordillerai (Döring, 1876)
d'orbignyi (Döring, 1876)
lutescens (King & Broderip, 1832)

Genus **Chiliborus** Pilsbry

Chiliborus Pilsbry, 1926: 6 (as subgenus of *Strophocheilus*). (Type-species, *Bulinus* (*sic*) *chilensis* Sowerby, 1833). Klappenbach & Olazarri, 1970: 181 (as genus).

Diagnosis

Shell small to medium-sized (19 to 67 mm), not dorsoventrally flattened, subglobose-ovate to elongate-ovate; nepionic whorls completely covered with very fine raised spiral lines; later whorls with strong or weak growth wrinkles and distinct or obsolete granulation; columella without fold, outer lip thick, reflexed, often accrescent in old age; a thick and solid epighragm closes the aperture during dormancy.

Animal unicolorous, lower aspect of the free edge of the mantle with two developed folds separated by a saddle shaped depression, stomach with weak musculature, without internal folds; annex glandular sac curved, inverted U-shaped; spermoviduct without accessory genital gland; pseudo-epiphallus enlarged, penis without basal papilla.

List of species

bridgesii (Pfeiffer, 1872)
chilensis (Sowerby, 1833)
pachychilus (Pfeiffer, 1842)
rosaceus (King & Broderip, 1832)
seneri (Jousseaume, 1884)

Genus **Gonyostomus** Beck

Gonyostomus Beck, 1837: 53. Type-species, *Helix* (*Cochlogena*) *gonistoma* Férussac, 1821 (by designation of Gray, 1847: 174).

Diagnosis

Shell medium-sized (40 to 62 mm), slender, elongate-fusiform, surface completely covered by fine granulose spiral lines. Aperture smaller than half length of shell, contracted and with base strongly angulate, building a channel distinguished externally by an obtuse keel; periostracum thin, but often well preserved, unicolorous chestnutbrown or purplish-brown with whitish-yellow oblique flames, and blotches.

Animal with two or more longitudinal colored bands on the antero-dorsal region; stomach with weak musculature and without internal folds; annex glandular sac inverted U-shaped; spermoviduct without accessory genital gland; penis without basal papilla, pseudo-epiphallus in the axis of penis or parallel to it, but not detachable from its external wall.

List of species

egregius (Pfeiffer, 1845)
goniostoma (Férussac, 1821)

Genus **Anthinus** Albers, status n.

Anthinus Albers, 1850: 148 (as a subgenus of *Bulimus*). Type-species, *Helix multicolor* Rang, 1831, by designation of v. Martens, 1860: 189).

Diagnosis

Shell medium-sized (40-55 mm, elongate-conic, ovate-conic or fusiform, surface completely covered by fine granulose spiral lines. Aperture over half the total length, broadly and evenly curved below, the base of the body-whorl not channelled nor carinate. Periostracum thin, but often well preserved, colored in mosaic or forming an irregular checkered pattern.

Animal with two or more longitudinal colored bands on the antero-dorsal region; stomach with weak musculature and without internal folds; annex glandular sac curved, inverted U-shaped; spermoviduct without accessory genital gland; penis without basal papilla, epiphallus short, parallel to penis and perfectly detachable from its external wall.

List of species

albolabiatus (Jaeckel, 1927), comb. n.
henselii (Martens, 1858), comb. n.
miersii (Sowerby, 1838), comb. n.
multicolor (Rang, 1831), comb. n.
turnix (Gould, 1846) comb. n.

Megalobulimidae, fam. n.

Diagnosis

Mesurethra; kidney long or short, globose or cordiform, without any vestige of primary ureter; excretory pore near middle of lateral free aspect of kidney. Roof of pulmonary chamber with surface divided by a longitudinal septum in two zones, respiratory and excretory. Genitalia simple, without dart sac, without mucous gland, with or without vaginal appendix, epiphallus always present, sometimes with two flagella. Buccal fissure with a pair of laterally expandible fringed lips, jaw strong, always with thickened and raised ribs, radula with all teeth unicuspid, digestive tube often with thickened walls, stomach muscular and perfectly delimited, with strong internal folds; intestine always with pre-rectal valve. Shell medium-sized to large (50 to 160 mm), periostracum persistent or caducous.

THE PROBLEM OF THE GENERA OF MEGALOBULIMIDAE

As seen above, there is wide divergence as to the concept of genera in the *Megalobulimus* species groups. While Bequaert places *Megalobulimus* as subgenus of *Strophocheilus,* Morretes considers it valid, with two subgenera (*Megalobulimus* and *Phaiopharus*), in addition to *Psiloicus,* erected for a relatively homogeneous group of species.

As said at the beginning, Morretes' categories were considered genera for the purposes of immediate discussion. However, anatomical studies show the insufficiency of the analyzed characters for establishment of well-defined genera. I consider at present a single genus, *Megalobulimus,* comprising all the species of the family.

This is the most primitive family of Stylommatophora; its characters, however, are so constant and homogeneous that no generic differentiation can be found. In the material examined no conchiological or anatomical character could be employed for the purpose.

The existence of closely related groups of species, with overlapping characters is possible to be admitted. The study of these groups, together with their distribution and ecology, is the subject of another research which is being undertaken. For that reason, those data are not presented here.

One may accept the existence of species-groups, with an overlap of characters. I hope to make this the subject of another investigations.

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