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ANATOMY AND SYSTEMATICS OF THE WESTERN ATLANTIC ELLOBIIDAE (GASTROPODA: PULMONATA)

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ABSTRACT

Various conchological, radular and anatomical characters of the 18 Western Atlantic species of the pulmonate family Ellobiidae are evaluated and used in a systematic review of the family. The conchological features, especially protoconch, resorption of inner whorls, apertural dentition and radular morphology, are useful at the specific and generic levels. Features of the radula of the Melampinae change greatly with increasing age. The youngest individuals have strongly cusped crowns. Although the cusps usually disappear with age, some species retain various features of the juvenile radula. The reproductive and central nervous systems are most useful in defining subfamilial relationships. The monaulic, entirely glandular condition of the pallial gonoducts, and the greater width of the visceral nerve ring are hereby considered primitive. Morton's (1955c) subfamilial division of the halophilic Ellobiidae is corroborated. The Pythiinae have a monaulic, entirely glandular pallial gonoduct and a wide visceral nerve ring. The Ellobiinae have a diaulic reproductive system with entirely glandular pallial gonoducts, and a long visceral nerve ring. The Pedipedinae have a monaulic/incipient semidiaulic, partly glandular pallial gonoduct, and a concentrated visceral nerve ring. The Melampinae are characterized by an advanced semidiaulic reproductive system with nonglandular pallial gonoducts, and concentration of the ganglia of the visceral nerve ring.

The present work documents that *Microtralia* Dall, 1894, belongs in the Pedipedinae, not in the Melampinae; that *Laemodonta* Philippi, 1846, belongs in the Pythiinae, not in the Pedipedinae; that *Leuconia succinea* Pfeiffer, 1854, belongs in the Pedipedinae and in the new genus *Creedonia;* that *Apodosis* Pilsbry & McGinty, 1949, is synonymous with *Leuconopsis* Hutton, 1884; that *Myosotella* Monterosato, 1906, type species *Myosotella payraudeaui* "Shuttleworth" Pfeiffer, 1856 [= *Auricula myosotis* Draparnaud, 1801], is removed from *Ovatella* Bivona, 1832, and restored to generic rank; that *Detracia* Gray, 1840, as noted by Zilch (1959), is a subgenus of *Melampus* Montfort, 1810; that *Melampus monile* (Bruguière, 1789) belongs in the subgenus *Detracia* Gray, 1840; and that *Detracia clarki* Morrison, 1951, is a junior secondary homonym and is herein renamed *Melampus (Detracia) morrisoni. Leuconopsis manningi* new species, from Ascension Island, is described.

The phylogenetic relationships within the Ellobiidae are discussed, a tentative cladogram of the family is presented, some distributional patterns are considered and reference is made to the fossil record.

Key words: Archaeopulmonata, Ellobiidae, systematics, shell, radula, anatomy, genitalia, nervous system, Western Atlantic, mangroves, salt marshes.

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INTRODUCTION

The Ellobiidae are primitive pulmonate gastropods that characterize the malacofauna of the upper and supra-littoral zones of the mangroves of the tropical regions and salt marshes of temperate regions. The Ellobiidae were first assigned familial rank by Lamarck (1809) when he included his *Auricula* [= *Ellobium* Röding], along with three other unrelated genera, within the "auriculacées". Since then, several comprehensive works have been published. The group was illustrated in Reeve's *Conchologia Systematica* (1842) and *Conchologia Iconica* (1877). A pictorial presentation was given in Martini & Chemnitz' *Conchylien-Cabinet* by Küster (1844) and Kobelt (1897–1901). Pfeiffer (1854b) outlined a monograph of the Auriculacea [= Ellobiidae] in his *Synopsis* and fully developed the work in his *Monographia* in 1856, which he revised and completed twenty years later. Odhner (1925) rearranged the classification of the family on the basis of radular morphology; Morton (1955c) included morphology of the stomach and reproductive organs in his review of the group. Only a few genera have received comprehensive treatment. The genus *Plecotrema* [= *Laemodonta* Philippi] was first revised by H. & A. Adams (1853) and was studied by Sykes (1895) and, more recently, by Hubendick (1956). The genera *Ellobium* Röding and *Melampus* Montfort were studied by H. & A. Adams (1854). Cox (1882) worked on the nomenclature and distributuion of *Pythia* Röding, and Connolly (1915) did a similar study on the genus *Marinula* King. Noteworthy are the detailed anatomical and histological studies on *Melampus boholensis* H. & A. Adams (Koslowsky, 1933), *Myosotella myosotis* (Draparnaud) (Meyer, 1955; Morton, 1955b) and *Auriculinella (L.) bidentata* (Montagu) (Morton, 1955b). Marcus & Marcus (1965a, b) discussed the anatomy of *Melampus (M.) coffeus* (Linnaeus), *Melampus (D.) paranus* (Morrison), *Ellobium (A.) dominicense* (Férussac) and *Blauneria heteroclita* (Montagu). Giusti (1973) discussed the radula and anatomy of *Ovatella firminii* (Payraudeau), and the shell, radula and anatomy of *Myosotella myosotis* (Draparnaud) were dealt with by Giusti (1973, 1976) and Cesari (1973, 1976).

The Western Atlantic ellobiids were included in the very earliest conchological reports of American scientists. Say (1822), the first New World malacologist, described the common *Melampus (M.) bidentatus*. Gould (1841) illustrated Say's species and *Myosotella myosotis* (Draparnaud), which is thought to have been introduced to North America from Europe. Study of American ellobiids was particularly influenced by Binney (1859, 1865) and Dall (1885). Binney (1859) figured most of the common species; his later figures (1865) were copied by subsequent workers (Tryon, 1866; Dall, 1885, 1889; M. Smith, 1937; Abbott, 1974), sometimes without critical investigation. For example, Binney's inaccurate representation of *Melampus (D.) floridanus* Pfeiffer in fact represents a dwarf *Melampus (M.) bidentatus* Say.

Morrison (1946, 1951a, 1951b, 1954, 1958, 1959, 1964) addressed several aspects of American ellobiid systematics, life history and ecology, and Clench (1964) revised the Western Atlantic *Pedipes* and *Laemodonta*.

The only detailed comprehensive anatomical research on Western Atlantic ellobiids was that of Marcus & Marcus (1965a, b) on the four species mentioned above. Several aspects of the life history and anatomy of *Melampus (M.) bidentatus* Say have been investigated, almost exclusively in the New England area. Hausman (1932), Holle & Dineen (1957) and Grandy (1972) focused on various aspects of the ecology of this species, while Apley (1970) and Russell-Hunter et al. (1972) did extensive research on its early life history. Additional investigations have involved the morphology of the nervous system (Price, 1977; Kahan & Moffett, 1979), several aspects of physiology and behaviour (Price, 1979, 1980; Hilbish, 1981; Capaldo, 1983), locomotion (Moffett, 1979) and feeding (Thompson, 1984).

In the present work particular attention has been paid to shell morphology, the radula and internal anatomy, especially the reproductive and nervous systems. This holistic approach helps to clarify the systematic position and phylogenetic relationships of the Western Atlantic ellobiids.

MATERIALS AND METHODS

Materials

Thousands of specimens from many localities were studied to understand inter- and intrapopulational variation in shell morphology. To accomplish this I studied the collections at the Museum of Comparative Zoology, Harvard University, Cambridge, at the American Museum of Natural History, New York, at the Academy of Natural Sciences of Philadelphia and at the United States Museum of Natural History, Washington, D. C. Because museum collections were very poor in material with preserved soft tissue, the majority of the internal anatomical work was done on specimens from my collections.

Most of the Western Atlantic material was obtained during field trips along the Atlantic coast of the United States, to Bermuda, the Bahamas, Puerto Rico and Venezuela. Some specimens from R. C. Bullock's collection were also kindly made available to me. Field trips were very important in providing large series of most recorded species and in allowing examination of living animals in their habitats. Most of this material is now in my collection.

Material not from the Western Atlantic, besides that in the museum collections mentioned above, included Azorean ellobiids from my own collection, specimens from Malaysia sent by A. Sasekumar and another series of specimens from Hong Kong sent by B. S. Morton; all are now part of my collection. The British Museum (Natural History) has kindly allowed me to work on preserved specimens of *Marinula*.

Most of the Western Atlantic species of ellobiids were first studied and described by European scientists and much of the type material is thought to be in European museums. Only the type material studied in brief visits to the British Museum (Natural History) and to the Muséum National d'Histoire Naturelle de Paris, as well as that kindly supplied by the Muséum d'Histoire Naturelle de Genève, were incorporated in this work. Sherborn (1940) and Dance (1966) have been used to locate tentatively the collections that might contain required type material.

Throughout the text, the museums and collections in which the studied material is deposited are indicated by the following abbreviations:

AMNH	American Museum of Natural History, New York, NY, U.S.A.
ANSP	Academy of Natural Sciences of Philadelphia, PA, U.S.A.
BMNH	The Natural History Museum [formerly British Museum (Natural History)], London, U.K.
R.B.	Private collection of R. C. Bullock, University of Rhode Island, Kingston, RI, U.S.A.
FMNH	Field Museum of Natural History, Chicago, IL, U.S.A.
LSL	Linnaean Society of London, U.K.
A.M.	Private collection of A. M. F. Martins, University of the Azores, Ponta Delgada, São Miguel, Azores, PORTUGAL.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.
MHNG	Muséum d'Histoire Naturelle de Genève, SWITZERLAND
MNHNP	Muséum National d'Histoire Naturelle de Paris, FRANCE
NHMB	Natural History Museum of Basel, SWITZERLAND
RAMM	Royal Albert Memorial Museum, London, U.K.
USNM	National Museum of Natural History [formerly United States National Museum], Washington, DC, U.S.A.

Methods

Observation and Collection of Live Animals. Observations of external morphology were made in the field and in the laboratory. The animals were photographed with Kodachrome film. Notes on the habitat were taken during collecting.

Besides extensive search and collecting in a variety of habitats, six transects were made in January, 1981, in the mangroves of the Florida Keys. Duplicate transects were made in May, 1982, at two of the 1981 sites, one on the previously disturbed site, another adjacent to it. All ellobiids found in the transects were collected and preserved. Qualitative analysis of this data is included in notes on habitats of the different species.

Preservation. Most animals were immersed directly in 70% ethanol. Some were relaxed overnight in isotonic $MgCl_2$ (75.2 g $MgCl_2$/l of distilled water) and then preserved in 70% ethanol. Some of the contracted and relaxed animals were fixed in Bouin's solution after the shell was cracked to allow better penetration of the fixative; others were frozen in fresh water for later dissection. This latter method seemed quite useful, because the organs maintained their original colors and softness, allowing easier dissection many months later.

Measurements. Various numbers of specimens from different localities were selected (Table 1, Appendix). Shells and dissected reproductive systems were drawn using a Wild M8 microscope with drawing tube. All measurements were taken from these drawings using a GTCO digitizer and IBM microcomputer. Radular teeth were counted from SEM photographs.

Shell and Radula Preparations for Scanning Electron Microscope. Juveniles of most species and adults of the smaller species were mounted for SEM observation of the entire shell or the protoconch, or both. The shells were cleaned in 95% ethanol in an ultrasonic cleaner for two to ten seconds, depending on the fragility of the specimen, and then were mounted on a stub with double-sided tape.

The radulae were first cleaned in KOH (two pellets/10 ml distilled water), washed in distilled water and in 70% ethanol. Ultrasonic cleaning was reduced to two seconds for each step. The radula was mounted on a piece of cover slip, to which it adhered when dry, and the cover slip was affixed to the stub with double-sided tape. The use of 70% ethanol alone had the advantage of slower evaporation, which was preferable when small pieces had to be manipulated at the exact moment they dried, to ensure proper positioning and good adhesion. I found very helpful the use of human eyelashes attached to dissecting needles with "superglue." They are fine, flexible, but sufficiently rigid for clearing the membranes of the radula without tearing, and for facilitating positioning while mounting.

All specimens were first coated with a single layer of carbon and then two layers of gold-palladium (60:40) in a Denton DV-502 vacuum evaporator, and examined in an ISI MSM-3 SEM.

Histology. Serial sections were made of specimens of every species collected. Some specimens were relaxed overnight in isotonic $MgCl_2$ before fixation in Bouin's solution. For most of the specimens the shell was cracked and the pieces removed to allow better fixation.

Whole animals, dissected reproductive organs and stomach were embedded separately. Embedding was done with an Autotechnicon Duo, Model 2A. The specimens were dehydrated in S-29 and embedded in Paraplast. The blocks were refrigerated until sectioned. Sectioning was done with a Spencer 820 microtome. The thickness of the sections varied from 8 to 15 µm. Best results were achieved by keeping the block and the blade refrigerated during sectioning. The preparations were stained with Heidenhain's aniline blue, following Luna (1968).

ABBREVIATIONS USED IN FIGURES

aa	anterior aorta
acpn	anterior cutaneous pedal nerve
ad	anterior diverticulum
adgl	anterior lobe of digestive gland
agl	albumen gland
al	aperture length
aln	anterior labial nerve
alpn	anterolateral pedal nerve
amgl	anterior mucous gland
ampn	anteromedial pedal nerve
an	aortic nerve
angl	anal gland
ann	anal nerve
aoen	anterior esophageal nerve
au	auricle

avd	anterior vas deferens
aw	aperture width
bb	buccal bulb
bc	buccal commissure
bg	buccal ganglion
br	bursa
brd	bursa duct
bw	body whorl
bwl	body whorl length
C	central tooth
ca	gastric caecum
car	cardiac region of stomach
cbc	cerebrobuccal connective
cc	cerebral commissure
cg	cerebral ganglion
clpln	cutaneous-lateral pleural nerve
cm	columellar muscle
cmn	columellar muscle nerve
cpc	cerebropedal connective
cplc	cerebropleural connective
cr	crop
ct	columellar tooth
ctw	columellar tooth width
div	penial diverticulum
e	eye
epan	external pallial nerve
ev	elbow of vagina
f	foot
fgo	female genital opening
fp	fertilization pouch
gn	genital nerve
hd	hermaphroditic duct
hgl	hypobranchial gland
i	intestine
il	inner lip
ipan	internal pallial nerve
k	kidney
kp	kidney pore
L	lateral teeth
lpgl	lower pneumostomal gland
M	marginal teeth
m	mantle skirt
man	mantle skirt artery nerve
mb	muscular band
mgl	mucous gland
ml	mantle lappet
mln	medial lip nerve
mo	mantle organ
mpan	medial pallial nerve
ms	muscular strand of stomach
mv	mantle skirt vein
nn	nuchal nerve
oe	esophagus
og	osphradial ganglion
ol	outer lip
on	ocular nerve
osg	open spermatic groove
ot	ovotestis
p	propodium
pa	posterior artery
pc	pedal commissure
pcpn	posterior cutaneous pedal nerve
pcvn	posterior cutaneous visceral nerve
pd	posterior diverticulum
pdgl	posterior lobe of digestive gland
pe	penis
pec	pericardium
pen	penial nerve
per	penial retractor muscle
pg	pedal ganglion
pgl	pallial gland
phmn	pharyngeal retractor muscle nerve
phn	pharyngeal nerve
plg	pleural ganglion
pln	posterior lip nerve
plpc	pleuropedal connective
plpn	posterior lateral pedal nerve
plprc	pleuroparietal connective
pmgl	posterior mucous gland
pmpn	posteromedial pedal nerve
pn	pneumostome
pnn	pneumostomal nerve
poen	posterior esophageal nerve
ppn$_1$	first posterior pedal nerve
ppn$_2$	second posterior pedal nerve
pr	prostate gland
prcn	parietocutaneous nerve
prg	parietal ganglion
prg$_1$	anterior left parietal ganglion
prg$_2$	posterior left parietal ganglion
prvc	parietovisceral connective
pt$_1$	anterior parietal tooth
pt$_2$	posterior parietal tooth
ptn	peritentacular nerve
ptw	width of posterior parietal tooth
pv	pulmonary vein
pvd	posterior vas deferens
pyl	pyloric region of stomach
r	rectum
rb	riblets
rmc	roof of mantle cavity
s	stomach
sgl	salivary gland
sgln	salivary gland nerve
sh	shoulder of body whorl
sl	shell length
spc	subpedal commissure
spov	spermoviduct
sr	spire
srl	spire length
st	statocyst
stn	statocyst nerve
sv	seminal vesicle
sw	shell width

T	transitional teeth
t	tentacle
tcm	tentacular control muscle
tn	tentacular nerve
upe	unwrapped penis
upgl	upper pneumostomal gland
v	vagina
ve	ventricle
vg	visceral ganglion
wpe	wrapped penis

TAXONOMIC CHARACTERS

Mayr (1969: 121) stated, "A taxonomic character is any attribute of a member of a taxon by which it differs or may differ from a member of a different taxon." Application of this definition cannot be uniform and generalized. Although there is consensus that a holistic approach is essential to sound classification (Mayr, 1969; Solem, 1978), one must be aware of the difference between characters used at the species level or even for generic grouping and those used for higher taxa. Characters that stress differences are used to define lower taxa, whereas those characters sensitive to convergence and seemingly less affected by environmental factors are used to define phylogenetic relationships among higher taxa. For example, the pattern of the spiral grooves on the shell is useful in separating *Melampus (M.) coffeus* from *Melampus (M.) bidentatus,* whereas the arrangements of the nervous and reproductive systems are the most consistent characters in defining the subfamilies of the Ellobiidae. In the Ellobiidae the shell and radular morphology are useful mostly at the generic or specific level. Harry (1951) and Hubendick (1978) pointed out the value of anatomical studies for clarifying taxonomic relationships within the group. Morton (1955c), followed by Marcus (1965) and Marcus & Marcus (1965a, b), adopted this holistic approach by including analyses of the stomach and reproductive organs; this approach led to somewhat surprising results, such as inclusion of *Auriculinella* and *Blauneria* within the Ellobiinae.

In the present study conchological, radular and anatomical characters are used. Each of these different characters will now be considered in more detail.

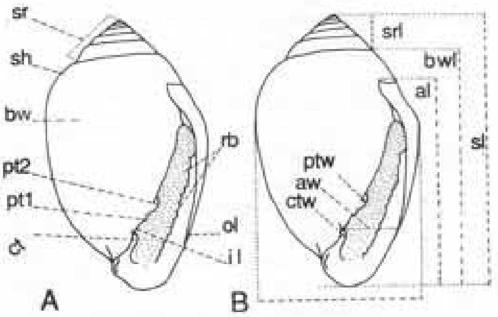


FIG. 1. Conchological characters. A, Shell terminology; B, Morphometry.

Conchological Characters (Fig. 1)

The shell, more than other molluscan structures, has the obvious advantages of permanence and ease of study. Traditionally it has been the important basis for distinction of most taxa (Zilch, 1959). Application of mathematical models and statistical analyses has provided tools for the interpretation of shell morphometry with accuracy and precision (Sokal & Sneath, 1963). Mathematical analysis of geometry of shell coiling has also been used (Raup, 1961, 1962, 1966, 1967; Raup & Michelson 1965; Rex & Boss, 1976; Warburton, 1979; Harasewych, 1981). This method aims at providing an opportunity for interpretation of evolutionary changes in shell morphology in functional terms and as an indication of strategies of adaptation to different habitats (Vermeij, 1971). Such interpretation has been challenged recently (Gould, 1984). In spite of modern refinements in analyses of conchological characters, it remains true that some, such as shell shape, have limited weight in assessing phylogenetic relationships because shell morphology is often strongly influenced by diverse environmental parameters (Hubendick, 1978; Solem, 1978).

Other shell characters, such as the protoconch, resorption of the inner whorls and apertural dentition, demonstrate more nearly constant patterns and are useful at the specific and even generic level.

The gastropod protoconch indicates the type of larval development that organisms in the different groups have undergone (Dall, 1924; Lutz et al., 1984). It might also have other very distinctive features that make it a useful taxonomic character (Walter, 1962; Bouchet & Warén, 1980; Turner & Lutz, 1984). Study of the protoconch has been aided greatly by the use of the scanning electron microscope, an increasingly important tool in malacology (Solem, 1970; Calloway & Turner, 1978). The SEM has been used to examine small and juvenile specimens, and to study the external morphology of the shell, radula and larvae. In this study the SEM was used to examine the protoconchs and radulae of most of the Western Atlantic ellobiids, and to provide photomicrographs of small and juvenile specimens.

Ellobiid protoconch morphology proved a very useful taxonomic character in most cases. The Melampinae, for example, have only one type of heterostrophic protoconch, which shows one-half of each nuclear whorl. This feature might reflect the fact that, as far as is known, all have free-swimming larvae. Indeed, a similar type of protoconch occurs in Pyramidellidae having larvae with a long pelagic phase (Haszprunar, 1985). The morphology of the protoconch in the other subfamilies of the Ellobiidae does not show an exclusive subfamilial pattern. For example, all the Pythiinae, Ellobiinae and the pedipedinian genera *Pedipes* and *Creedonia* have a bulbous protoconch with an umbilicus and a laterally facing aperture. The protoconch of the pedipedinian genera *Microtralia* and *Pseudomelampus* sits atop the teleoconch with the aperture facing the columellar axis, as in the Melampinae, rather than laterally as in all pythiinians and ellobiinians. Particular anatomical features indicate that these two genera belong to the Pedipedinae, however. The protoconch is very uniform within a species and, in the case of the West Indian *Pedipes,* it was the only consistent diagnostic conchological character that allowed clear separation of species.

Shell resorption, as seen in the Ellobiidae, also occurs in the Neritacea, Helicinidae and Conidae. It was first noted by Montagu (1803: 235) in his *Voluta denticulata* [= *Myosotella myosotis* (Draparnaud)] and was reported for most members of the Ellobiidae by Gray (1840: 220–221). Crosse & Fischer (1879, 1882), however, studied the phenomenon in more detail and are usually credited with its discovery. Resorption of the inner whorls provides a larger cavity in which the organs of the visceral mass can be rearranged with spatial economy. For example, in *Melampus* and *Microtralia,* which show a high degree of resorption, the conspicuous ovotestis has moved to an apical position and displaced the posterior lobe of the digestive gland; in *Pedipes* and *Creedonia,* which do not resorb the inner whorls, the ovotestis lies embedded in the apical, conspicuous posterior lobe of the digestive gland. This character varies within the different subfamilies of the Ellobiidae, but can be useful at lower taxonomic levels. In *Melampus s.s.*, for example, the partition of the inner whorls occupies only one-fourth of the body whorl (Figs. 225, 267), whereas in the subgenus *Detracia* it occupies at least three-fourths of the body whorl (Figs. 302, 316). The extreme case of variation within one subfamily occurs in the Pedipedinae, in which *Pedipes* and *Creedonia* completely retain the inner whorls (Figs. 106, 128, 153), whereas in *Microtralia* resorption reaches the most advanced stage in the Ellobiidae with less than a quarter of the interior partitions left (Fig. 178). In conjunction with other features, the lack of shell resorption justified the creation of the new genus *Creedonia.* The degree of resorption also supported the separation of *Detracia* as a subgenus of *Melampus s.l.* and was helpful in the interpretation of some anatomical differences observed between that subgenus and *Melampus s.s.*

Apertural dentition, an important character in gastropod classification, is a conspicuous feature of the Ellobiidae. One of the most commonly accepted functions of the apertural dentition is that of constituting a barrier against predators. From my observations on the disposition of the various branches of the columellar muscles along the conspicuous internal lamellae of *Melampus (D.) bullaoides* (Fig. 302), I think that this feature also helps in positioning the shell during locomotion. Although variable, there are some general patterns of apertural dentition. On this basis one can characterize broadly the different subfamilies as follows: Ellobiinae with biplicate inner lip, with columellar and parietal teeth very close together; Pythiinae with evenly spaced triplicate inner lip with first parietal tooth strongest; Pedipedinae with two columellar teeth and strong parietal tooth; Melampinae with inner lip dentition restricted to anterior half, columellar and posterior parietal teeth conspicuous, outer lip dentate. There are exceptions to these patterns, however, for the species in the melampinian genus *Tralia* have an inner lip structure very similar to that of the pythiinian genus *Myosotella.* The inner lip dentition of *Microtralia* deviates from

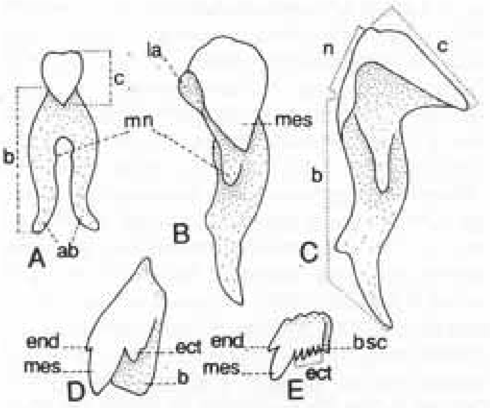


FIG. 2. Terminology for radular teeth of *Melampus (M.) coffeus*. A, Top view of central tooth; B, Top view of first lateral tooth; C, Lateral view of first lateral tooth; D, Top view of tenth marginal tooth; E, Top view of 20th marginal tooth.

the pattern of the Pedipedinae in having only one columellar tooth. The apertural structure of the pythiinian genera *Cylindrotis* and *Auriculastra* resembles that of the Ellobiinae and *Ellobium (E.) aurisjudae* has a conspicuous posterior parietal tooth.

Radular characters

The molluscan radula is a valuable character in the classification of higher taxa and is the basis of phylogenies proposed for the Gastropoda (Gray, 1853; Troschel, 1856–1893; Mörch, 1867). Some authors have studied ellobiid radulae in an attempt to divide the Ellobiidae into subfamilies. Classifications of the ellobiids by Odhner (1925) and Thiele (1931) were based mainly on radular morphology, but these authors differed in their subfamilial division. Odhner adopted six subfamilies whereas Thiele recognized only three. Observation of the radula with a light microscope provides only limited information on the intricate articulation of the different teeth with one another (Figs. 250, 395). The SEM opened new vistas in the study of radular morphology and function (Solem, 1972b, 1974).

The terminology used in this study follows that of Fretter & Graham (1962) and Oberholzer et al. (1970) (Fig. 2). The radula of the ellobiids characteristically has many teeth in each row; the central tooth usually has a small crown. In most species the transition from the lateral teeth, which have a strong mesocone, to the pectinate marginal teeth is gradual. Morphology of the radula in the Melampinae and Ellobiinae is rather uniform, but it varies in the Pedipedinae and Pythiinae. The radula of the Melampinae undergoes a series of morphological changes with age. The deeply indented crown of the lateral teeth of very young individuals becomes the unicuspid, triangular crown of adults. Some species, however, seem to have a radula with neotenic features, for example *Melampus (D.) floridanus* and *Melampus (D.) paranus*, which, as adults, have a conspicuous ectocone on the lateral teeth. This structure, present in the radula of the juveniles of some species of the Melampinae (Figs. 243–249, 370, 371), disappears with age. Marcus & Marcus (1963, fig. 8) observed the same morphological change in the radula of *Ellobium (A.) dominicense*. Their illustration of the radula of a very young specimen of that species shows a striking resemblance to the radula of an adult *Blauneria heteroclita*.

The Pedipedinae and Pythiinae display great radular diversity with as many as three radular types in each subfamily. Radulae of some Pedipedinae, such as *Microtralia*, resemble that of the Melampinae, whereas in the Pythiinae the strong mesocone on the radular teeth of *Cassidula* and *Pythia* resembles that in adult *Ellobium*.

The radula of the ellobiids is a much more useful character at the generic level than at the specific level. The minute differences in the radulae developed by analysis of closely related pairs such as *Melampus (M.) coffeus—Melampus (M.) bidentatus*, *Pedipes mirabilis—Pedipes ovalis* and *Leuconopsis novimundi—Leuconopsis manningi* failed to provide morphological evidence useful in the separation of these species pairs. On the other hand, the different genera, mainly within the subfamilies Pythiinae and Pedipedinae, are readily distinguished on the basis of their radular morphology.

Anatomical characters

A series of anatomical characters commonly used in devising classifications was listed by Solem (1978). Because all characters do not have the same taxonomic value weighting always must be applied. Those characters having greater influence on the cohesion of the group should be used in phylogenetic studies. Those same characters should be the least affected by nongenetic factors, such as environmental and competitive pressures, exemplified by habitat and food. Thus the reproductive and the nervous systems ought to be considered prime taxonomic characters for the interpretation of phylogenetic relationships among higher taxa.

Stomach: Graham's comprehensive studies (1939, 1949) of the functional morphology of the molluscan stomach showed an evolutionary trend toward the disappearance of the crystalline style and simplification of the sorting areas in conjunction with the adoption of a macrophagous carnivorous diet. He observed the forward migration of the cardiac opening, with consequent reduction of the stomach to a blind sac into which the digestive gland discharges, and the increase in the muscularity of the mid-section to form a gizzard.

It is generally recognized that the basommatophoran stomach originated from the prosobranch condition and it appears to me that it evolved along two different lines. The lower basommatophoran or archaeopulmonate stomach shows a tendency toward a forward migration of the cardiac opening. *Otina otis* (Turton), a primitive marine pulmonate, retains a vestigial style sac and has a rudimentary gizzard (Morton, 1955a). In the higher, limnic basommatophorans the stomach remains open-ended, with esophageal and intestinal openings at opposite ends, as shown in Carriker (1946) and Morton (1955c). In this group the simplest stomach occurs in *Acroloxus,* which lacks musculature, has a well-developed caecum similar to a style sac and a structure similar to a crystalline style (Hubendick, 1978). Morton (1952, 1953) also investigated the functional morphology of the gastropod stomach and, on the basis of the disposition of the internal ciliary patches and of the tendency toward stronger muscularity of the mid-section, used it as a character in the classification of the ellobiids (Morton, 1955c).

In this study only the external appearance of the stomach was noted. Without an understanding of the functional morphology of the internal parts, phylogenetic inferences and use in classification would be unwarranted and possibly misleading.

Reproductive System: Traditionally the molluscan reproductive system has been accorded special value in the understanding of the phylogenetic relationships among higher taxa (Duncan, 1960a, b; Visser, 1977, 1981; Gosliner, 1981; Haszprunar, 1985, 1988; Salvini-Plawén & Haszprunar, 1987). The importance of the reproductive system in gastropod evolutionary studies is corroborated by my studies.

A basic plan of the gastropod reproductive system consists of a posteriorly located gonad, a middle glandular section and an anterior duct associated with the pallial region, primitively glandular owing to its probable origin from the hypobranchial gland (Fretter, 1984). This simple tube becomes increasingly complex with the appearance of specialized evaginations and of the hermaphroditic condition (Ghiselin, 1966). In prosobranchs gonochorism is the rule, a condition currently considered primitive (Haszprunar, 1988). Cases of protandry and of simultaneous hermaphroditism exist in archaeogastropods and mesogastropods, however (Fretter, 1946). Simroth (1907) and Hubendick (1945) both thought that hermaphroditism was the original condition among the gastropods. Krull (1935, *fide* Fretter & Graham, 1962) also shared Simroth's view and, based on the fact that the pallial oviduct of the prosobranch hydrobiids is divided in a manner similar to that of the monaulic pulmonates (species with one bisexual duct), he suggested that the hydrobiids were the most primitive gastropods. This view has not been accepted by later authors. In the euthyneurans (opisthobranchs and pulmonates), once commonly thought to have evolved from the archaeogastropods (Pelseneer, 1894a; Hubendick, 1945; Morton, 1955c), but more probably from the mesogastropods (Fretter, 1946; Boettger, 1954; Duncan, 1960a; Gosliner, 1981) or Apogastropoda (Salvini-Plawén & Haszprunar, 1987; Haszprunar, 1988), hermaphroditism is the universal condition (Ghiselin, 1969). Opinions also differ as to which of the two hermaphroditic conditions appeared first, monaulic (one bisexual duct) or diaulic (two separate sexual ducts). Pelseneer's suggestion (1894b: 19) that hermaphroditism in mollusks arose by the secondary addition or grafting of a male system to the female individual has led to the view that monauly is the primitive condition (Ghiselin, 1966; Marcus & Marcus, 1965b; Visser, 1977, 1981; Hubendick, 1978). Solem (1972a, 1978) considered diauly the primitive condition, however, and stated that partial or total fusion of the male and female reproductive tracts has evolved independently in several groups. The choice of one or another hypothesis has obvious phylogenetic implications for the use of the reproductive system. Visser (1981) rejected Solem's opinion because there is no evidence of two separate gonads with two separate gonoducts in primitive gastropods. Visser, in contrast to Pelseneer, stated that hermaphroditism in the Basommatophora, unlike that of the Stylommatophora, was derived from a male prosobranch. As evidence he cited the consistency of the penial structure throughout the basommatophorans (see also Hubendick, 1978).

My work has led me to support the most commonly held view, namely that monauly and a glandular pallial gonoduct represent the primitive condition. The tendency toward reduction of the glandular elements of the reproductive system to the proximal, nonpallial portion is hereby taken as a derived trend. Supporting this view is the presence of glandular pallial gonoducts among littorinids and the primitive opisthobranchs (Gosliner, 1981). Existence of such glandular ducts in groups otherwise clearly primitive (Pythiinae, Ellobiinae) also is taken as supportive circumstancial evidence for the case.

The terminology used in this study follows that of Duncan (1975), Visser (1977), Berry (1977) and Tompa (1984). Histological studies were carried out to clarify some critical features of basic morphology, such as the extent of the mucous and prostate glands and to establish the aulic condition, the site of separation of male and female ducts. No distinction was made between the different components of the penial complex (penial sheath, preputium and penis) and this entire structure is herein called the penis. The degree of adhesion of the anterior vas deferens to the penis is also considered, the free condition being interpreted as derived.

Central Nervous System. Use of the pulmonate central nervous system as a primary taxonomic character has become increasingly accepted (Bargmann 1930; Van Mol, 1967; Bishop, 1978, Haszprunar, 1985, 1988; Salvini-Plawén & Haszprunar, 1987). Morton (1955c) and Regondeau et al. (1976) agreed that within the gastropods concentration of the ganglia is a derived character, but Morton shared Fretter & Graham's concern (1949) that sole reliance on characters of the nervous system to establish phylogenetic relationships can be misleading. Haszprunar (1985, 1988) emphasized the possibility that concentration of ganglia and consequent euthyneury could be associated with small size in some cases.

The degree of concentration of the ganglia of the central nervous system is considered important because the complexity of an entire system is generally unaffected by environmental pressures. Any major change in the arrangement of the ganglia probably would mean a greater rearrangement at most levels of anatomical organization. For this reason the morphology of the central nervous system is considered herein to be a taxonomic character useful at higher levels of classification.

A detailed treatment of the ellobiid central nervous system is provided for *Ellobium (A.) dominicense* (Fig. 21) and *Melampus (M.) coffeus* (Fig. 255). The terminology adopted here is from several sources (Simroth 1912, 1925–1928; Bargmann, 1930; Carriker, 1946; Brisson, 1963; Price, 1977). For most species only the relative concentration of the ganglia seemed important, but the nerves were found to approximate the pattern in *Melampus (M.) coffeus.*

CLASSIFICATION OUTLINE, WESTERN ATLANTIC ELLOBIIDAE

- Family Ellobiidae H. & A. Adams *in* Pfeiffer, 1854
  - Subfamily Ellobiinae H. & A. Adams *in* Pfeiffer, 1854
    - Genus *Ellobium* Röding, 1798
      - Subgenus *Auriculodes* Strand, 1928
        - *Ellobium (A.) dominicense* (Férussac, 1821)
    - Genus *Blauneria* Shuttleworth, 1854
        - *Blauneria heteroclita* (Montagu, 1808)
  - Subfamily Pythiinae Odhner, 1925
    - Genus *Myosotella* Monterosato, 1906
        - *Myosotella myosotis* (Draparnaud, 1801)
    - Genus *Laemodonta* Philippi, 1846
        - *Laemodonta cubensis* (Pfeiffer, 1854)
  - Subfamily Pedipedinae Fischer & Crosse, 1880
    - Genus *Pedipes* Scopoli, 1777
        - *Pedipes mirabilis* (Mühlfeld, 1816)
        - *Pedipes ovalis* C. B. Adams, 1849
    - Genus *Creedonia* new genus
        - *Creedonia succinea* (Pfeiffer, 1854)
    - Genus *Microtralia* Dall, 1894
        - *Microtralia occidentalis* (Pfeiffer, 1854)
    - Genus *Leuconopsis* Hutton, 1884
        - *Leuconopsis novimundi* (Pilsbry & McGinty, 1949)
        - *Leuconopsis manningi* new species
        - *Leuconopsis* sp.
  - Subfamily Melampinae Stimpson, 1851

Genus *Melampus* Montfort, 1810
  Subgenus *Melampus s.s.*
    Melampus (M.) coffeus (Linnaeus, 1758)
    Melampus (M.) bidentatus Say, 1822
  Subgenus *Detracia* Gray *in* Turton, 1840
    Melampus (D.) bullaoides (Montagu, 1808)
    Melampus (D.) floridanus (Pfeiffer, 1856)
    Melampus (D.) paranus (Morrison, 1951)
    Melampus (D.) monile (Bruguière, 1789)
    Melampus (D.) morrisoni new name
Genus *Tralia* Gray *in* Turton, 1840
  Subgenus *Tralia s.s.*
    Tralia (T.) ovula (Bruguière, 1789)

SYSTEMATICS

Family Ellobiidae H. & A. Adams *in* Pfeiffer, 1854

Auriculidae Lamarck, 1809: 321 [corrected from "Les Auriculacées" by Gray, 1840].
Auriculae Lamarck. Férussac, 1821: 32.
Auriculadae Lamarck. Gray, 1824: 107.
Auriculacea Lamarck. Blainville, 1824: 245.
Auriculaceae Lamarck. Menke, 1828: 19.
Auriculoidea Lamarck. Cristofori & Jan, 1832: 6.
Auriculidea Lamarck. Beck, 1837: 101.
Auriculata Lamarck. Sismonda, 1842: 26.
Auriculiadae Lamarck. De Kay, 1843: 57.
Auriculina Lamarck. Agassiz, 1847: 41 [correction for Auriculacea]. *Non* Grateloup, 1838, *nec* Gray, 1847a.
Carychiadae (Leach MS) Gray, 1847b: 269.
Auriculae'inae Lamarck. Strobel, 1850: 32.
Conovulidae Clark, 1850: 444.
Melampidae Stimpson, 1851: 51.
Ellobiidae H. & A. Adams *in* Pfeiffer, 1854b: 146 [in synonymy with Auriculacea Lamarck].

Description: Shell spiral, dextral (except in *Blauneria*), oval-conic, sometimes umbilicate, smooth or with spiral sculpture, covered with brownish periostracum; aperture elongate, round at base, angulate posteriorly, with strong folds on inner lip, outer lip sharp or weakly reflected, often dentate. Inner whorls resorbed (except in *Pedipes* and *Creedonia*). Protoconch heterostrophic.

Animal completely retractable into shell. Head separated from foot by transverse groove, into which a large mucous gland opens. Operculum present in embryos, absent in adults. Mouth T-shaped; horny upper jaw sometimes with folded extremities lining lateral lips; one pair of subcylindric, contractile or subretractile tentacles; eyes sessile, medial to base of tentacles; foot long, anteriorly blunt, sometimes transversely divided, posteriorly tapered and entire or bifid; pneumostome on right side, medial to anal aperture.

Radula broad, elongate; teeth numerous; central tooth equilateral; lateral teeth inequilateral, becoming shorter toward outer edges of radula, abruptly or gradually changing into marginal teeth.

Digestive system moderately long; salivary glands usually elongate; esophagus long, thin walled, longitudinally grooved, opening posteriorly into wide crop; stomach generally tripartite with thin-walled cardiac region, muscular medial and pyloric regions and thin-walled, smaller posterior caecum; digestive gland usually bilobed, emptying anteriorly at crop, posteriorly at gastric caecum.

Reproductive system hermaphroditic; ovotestis acinose and embedded in digestive gland or leaf-like and covering part of stomach; hermaphroditic duct with generally convoluted seminal vesicle; glandular complex composed of whitish albumen gland, convoluted posterior mucous gland, straight anterior mucous gland and prostate gland covering pallial ducts (except in Melampinae); fertilization chamber follows posterior mucous gland and gives rise to oviduct and spermiduct, which might or might not be completely separate for their entire length; bursa duct and bursa arising from vagina at variable distances from aperture; female aperture medial to pneumostome, anterior to union of mantle with neck; male aperture on right corner of cephalic groove, under right tentacle; a fold of skin (sperm groove) runs from near female to male aperture, functional only in *Pythia;* in all others the vas deferens lies embedded in neck skin; it separates from skin inward near male aperture and enters penis at posterior end; penial complex (penis and penial sheath) lying over buccal bulb and cerebral ganglia.

The hypoathroid, pentaganglionate central nervous system is of the basommatophoran type (Bargmann, 1930; Haszprunar, 1985), composed of 11 discrete ganglia, joined by connectives of various lengths: paired cerebral, buccal, pleural, parietal and pedal ganglia, and an unpaired visceral ganglion.

Remarks: The Ellobiidae were first assigned familial rank by Lamarck (1809) under the vernacular Les Auriculacées. The group included Lamarck's *Auricula* and three other genera (*Melanopsis*, *Melania* and *Limnaea*) that were assigned subsequently by other authors to different families. Many incorrect Latinizations of Lamarck's vernacular name followed; Blainville's (1824) Auriculacea became well established and was used in major monographs on the family (Reeve, 1842; Küster, 1844; Pfeiffer, 1856a, 1876; Kobelt, 1898).

The correct Latin designation, Auriculidae, was first used by Gray (1840) and was widely accepted until the 1920s, when the names Ellobiidae H. & A. Adams *in* Pfeiffer, 1854, and Melampidae Stimpson, 1851, replaced Lamarck's name.

According to the International Code of Zoological Nomenclature Art. 11 (e) the name Auriculidae has priority because, when first published, it was based upon the name then valid for the contained genus *Auricula* Lamarck. Odhner (1925), however, preferred the name Ellobiidae H. & A. Adams because the type genus, *Auricula* Lamarck, 1799, is a synonym of *Ellobium* Röding, 1798. The name Ellobiidae has been in general use since that time. Works dealing exclusively with the family, such as those of Odhner (1925), Morton (1955b, c), Hubendick (1956), Clench (1964), Marcus (1965), Marcus & Marcus (1965a, b), Cesari (1973, 1976), or general ones, such as those of Thiele (1931), Zilch (1959), Hyman (1967), Franc (1968), Fretter (1975), Jones (1975), Runham (1975), Berry (1977), Hubendick (1978), Solem (1978, 1985), Boss (1982) and Haszprunar (1985, 1988), and even popular books, such as those of Morris (1973), Humphrey (1975), Emerson & Jacobson (1976) and Rehder (1981), are the most obvious examples of the acceptance of the name Ellobiidae.

Recently the name Melampidae Stimpson, 1851, has appeared in some influential malacological works, such as those of Keen (1971), Abbott (1974), Rios (1975) and Kay (1979). Morrison's reintroduction (1964) of the name Melampidae was unfortunate in several ways. It was an unnecessary disturbance of taxonomic stability, because the name Ellobiidae had already been universally accepted. It also required a change to a different type genus for the family. The appearance of the term Melampidae in influential malacological works obviously was leading to widespread use and consequent renewed taxonomic confusion.

Strict application of the law of priority to family-group names would upset general use of the name Ellobiidae. In accordance with Art. 23 (d) of the ICZN, a petition should be submitted to the International Commission on Zoological Nomenclature to place the name Ellobiidae on the Official List of Family-Group Names in Zoology, and to place the names Auriculidae and Melampidae on the Official List of Rejected Names.

Credit usually is given to H. & A. Adams (1855b) for the introduction of the name Ellobiidae. However, Pfeiffer (1854b), who had access to the Adams brothers' manuscript, referred to the to-be-proposed family name, but continued to use the name Auriculacea. For this reason the name Ellobiidae, which should be credited to H. & A. Adams, must take the date 1854, when it was first published by Pfeiffer as a synonym.

The family Ellobiidae varies greatly in morphology and anatomy, but it is nevertheless readily identifiable as a group at the familial level. Starobogatov (1976) exaggerated the differences in the reproductive system and raised the family name to ordinal status and considered existing subfamilies separate families. This view has not gained acceptance and I have concluded that the differences within the ellobiids are reconcilable within a single family.

Odhner (1925), using radular characters, and Zilch (1959), using shell morphology, recognized six subfamilies, Carychiinae, Melampinae, Pedipedinae, Pythiinae, Cassidulinae and Ellobiinae. Morton (1955c) and Hubendick (1978) merged the Cassidulinae with the Pythiinae on the basis of the similarities of their reproductive systems, and assigned the latter name to the group. My studies support Morton's conclusions and I have followed his scheme of classification for the division of the Ellobiidae into subfamilies.

Zilch (1959) recognized 20 genera of living halophilic ellobiids. Zilch's classification is accepted here with certain modifications and 21 genera are recognized in this paper. Zilch considered *Sarnia* H. & A. Adams a subgenus of *Tralia* Gray, but Marincovich (1973), on the basis of radular morphology, placed it in the Ellobiinae. *Sarnia* (Fig. 181) shows strong conchological similarity to *Pseudomelampus* and *Microtralia*, and for that reason I include it in the Pedipedinae. Further information on the reproductive and nervous systems is needed to confirm the systematic position of this genus, however. I have synonymized herein *Apodosis* Pilsbry & McGinty with *Leu-*

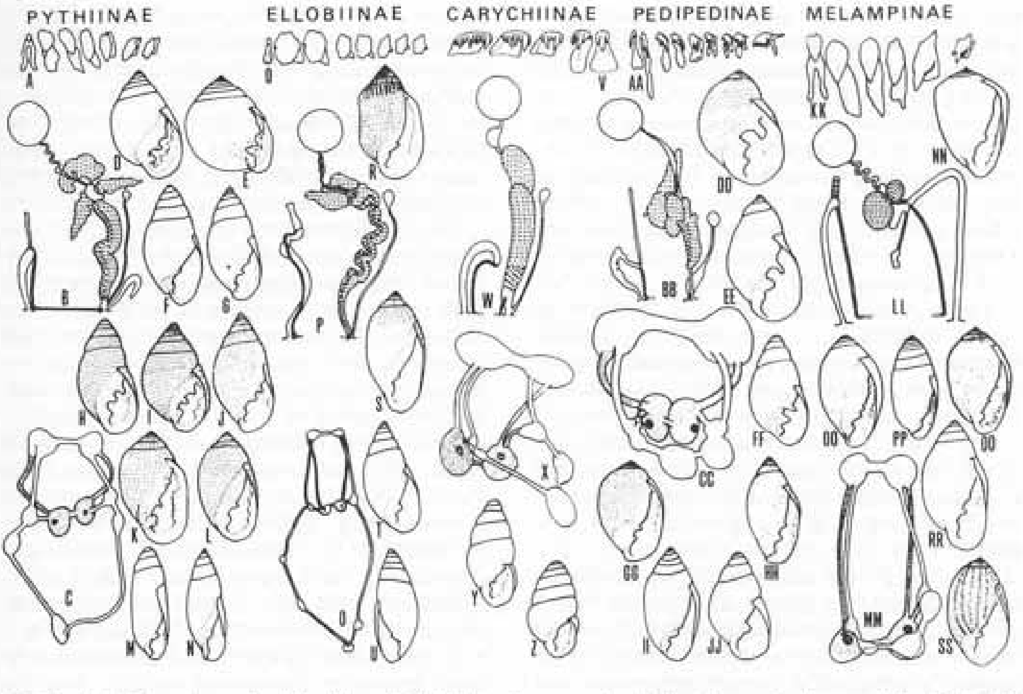


FIG. 3. Pictorial review of subfamilies of Ellobiidae, from most primitive to most advanced. A, *Pythia (P.) scarabaeus* (Linnaeus), radula; B, *Pythia (P.) scarabaeus,* reproductive system; C, *Pythia (P.) plicata* (Férussac), central nervous system; D, *Pythia (P.) scarabaeus;* E, *Pythia (Trigonopythia) trigona* (Troschel); F, *Ophicardelus australis* (Quoy & Gaimard); G, *Myosotella myosotis* (Draparnaud); H, *Ovatella firminii* Payraudeau; I, *Laemodonta octanfracta* (Jonas); J, *Allochroa bronni* (Philippi); K, *Cassidula (C.) aurisfelis* (Bruguière); L, *Cassidula (Cassidulta) doliolum* (Petit); M, *Cylindrotis quadrasi* Möllendorff; N, *Auriculastra subula* (Quoy & Gaimard); O, *Ellobium (E.) aurismidae* (Linnaeus), radula; P, *Ellobium (E.) aurismidae,* reproductive system; Q, *Ellobium (E.) aurismidae,* central nervous system; R, *Ellobium (E.) aurismidae;* S, *Ellobium (Auriculodes) gangeticum* (Pfeiffer); T, *Auriculinella (Leucophytia) bidentata* (Montagu); U, *Blauneria heteroclita* (Montagu); V, *Carychium tridentatum* (Risso), radula; W, *Carychium tridentatum,* reproductive system; X, *Carychium tridentatum,* central nervous system; Y, *Carychium minimum* Müller; Z, *Zospeum spelaeum* (Rossmässler); AA, *Pedipes mirabilis* (Mühlfeld), radula; BB, *Pedipes pedipes* (Bruguière), reproductive system; CC, *Pedipes pedipes,* central nervous system; DD, *Pedipes pedipes;* EE, *Marinula pepita* King; FF, *Creedonia succinea* (Pfeiffer); GG, *Pseudomelampus exiguus* (Lowe); HH, *Sarnia frumentum* (Petit); II, *Microtralia occidentalis* (Pfeiffer); JJ, *Leuconopsis obsoleta* (Hutton); KK, *Melampus (M.) coffeus* (Linnaeus), radula; LL, *Melampus (M.) coffeus,* reproductive system; MM, *Melampus (M.) coffeus,* central nervous system; NN, *Melampus (M.) coffeus;* 00, *Melampus (Micromelampus) nucleolus* Martens; PP, *Melampus (Detracia) bullaoides* (Montagu); QQ, *Melampus (Signia) granifer* (Mousson); RR, *Tralia (T.) ovula* (Bruguière); SS, *Tralia (Persa) costata* (Quoy & Gaimard).

conopsis Hutton, and have created the genus *Creedonia. Myosotella* Monterosato, treated by Zilch as a subgenus of *Ovatella* Bivona, is given herein generic status.

A pictorial review of the subfamilies is presented in Figure 3. The radula, nervous system and reproductive system of the type or of a representative species of each subfamily are shown, as well as the shells of all the type species of the genera and subgenera herein recognized. The reproductive and nervous systems provided the most consistent basis for the separation of the subfamilies.

Detailed descriptions of general anatomy and of the nervous system are provided under *Melampus (M.) coffeus;* these descriptions will be used as standards of comparison in discussions of other species.

Habitat: Ellobiids are mainly tropical. They commonly occur around the high-tide mark in mangrove areas, under rocks or pieces of decaying wood. In extratropical regions they live in eurhyaline environments of salt marshes or in upper littoral rocky areas.

Morton (1955c) divided the ellobiids into four groups according to habitat. The upper-tidal marine ellobiids, such as *Melampus, Myosotella, Ophicardelus, Cassidula* and *Ellobium*, prefer the high-tidal fringe of mangroves and marshes, never venturing far from the reach of the highest spring tides. The intertidal and crevice-dwelling species include the minute ellobiids of the genera *Auriculinella, Leuconopsis, Pedipes, Microtralia* and *Marinula*, to which *Creedonia, Laemodonta* and *Blauneria* might be added, which live buried at different depths in the sediment or under partly buried rocks, roots and fallen branches in the upper intertidal zone. *Pythia* is the only coastal terrestrial ellobiid; it always frequents moist places near the shore, although out of reach of the highest tides. The inland terrestrial ellobiids are *Carychium* and *Zospeum*, which live in very humid environments, frequently under forest leaf litter or in caves.

The ellobiids are commonly thought to have evolved from an estuarine ancestor. Conquest of the terrestrial habitat brought about modifications in the structure of the larval stages. Such modifications, however, are not exclusively related to distance from the sea and a single feature, such as suppression of a free-swimming veliger, can exist in intertidal and terrestrial species. A more or less modified veliger stage is present throughout the family. The Melampinae have a free-swimming veliger larva. Apley (1970) recorded two to six weeks of planktonic life for *Melampus (M.) bidentatus*, while Marcus & Marcus (1965a) suggested equally long periods for the veligers of *Melampus (M.) coffeus* and *Melampus (D.) paranus*. The veliger stage of the other subfamilies passes inside the egg and the embryo crawls immediately after hatching. Larvae of *Ellobium (A.) dominicense* have a ciliate velum and can swim for very short periods of time (Ewald, 1963). That same ciliated structure was found in *Blauneria heteroclita* by Marcus & Marcus (1963). Morton (1955c) observed that the velum of the larvae of *Myosotella myosotis* and of *Auriculinella (L.) bidentata* is reduced and lacks cilia.

Another feature of larval ellobiids is the widespread presence of an operculum, which is lost at an early age. *Blauneria heteroclita*, which normally reaches 7 mm in length, sheds the operculum at a shell length of about 0.7 mm (Marcus & Marcus, 1963). The reduced operculum of *Myosotella myosotis* and of *Auriculinella (L.) bidentata* helps to break the shell during hatching (Morton 1955b).

Range: The family Ellobiidae has worldwide distribution, but appears to have three main centers, a large Indo-Pacific center, characterized by *Ellobium, Cassidula* and *Pythia;* a smaller West Indian center, characterized by *Melampus;* and a much poorer Mediterranean region, characterized by *Myosotella* and *Ovatella*.

The fossil record of the Ellobiidae is relatively poor and is insufficient for the determination of evolutionary lineages. The presence of the Indo-Pacific genera *Ellobium* and *Cassidula* in Europe during the Eocene and Miocene (Zilch, 1959) suggests that the European shores were connected with the Indo-Pacific region. This is consistent with the existence of the Tethys Sea which, in various ways, extended longitudinally from Australia through Europe and northern Africa to the tropical West Indies and eastern Pacific. Existence of this seaway is indicated by the distribution of several groups of invertebrates, and has been more extensively studied for the Mediterranean region. Evidence of a Tethyan distribution in American faunas was found in Foraminifera (C.G. Adams, 1967), Ostracoda (McKenzie, 1967) and in bivalves and gastropods (Palmer, 1967). The ellobiid fossil record does not provide any new information about Tethyan relationships between Europe and America. The ellobiid fossils of North America are represented by the melampinine genera *Rhytophorus* and *Melampoides* from the Cretaceous of Wyoming (White, 1895; Henderson, 1935) and by the more recent *Melampus, Marinula, Tralia* and *Pedipes*, from the Eocene, Miocene and Pleistocene (Conrad, 1862; Dall, 1912; Woodring, 1928; Gibson-Smith & Gibson-Smith, 1979, 1982, 1985). The Mesozoic genera seem not to have European counterparts, but *Rhytophorus* was recorded from the Lower Cretaceous of China (Zhu, 1980). Present records are too sparse to allow elaboration of the meaning of such an occurrence. The Cenozoic genera represent only the Recent ellobiid fauna of the West Indian region.

Subfamily Ellobiinae H. & A. Adams *in* Pfeiffer, 1854

Auriculea Pfeiffer, 1853a: 9.

Ellobiinae "H. & A. Adams" Pfeiffer, 1854b: 146.

Auriculinae H. & A. Adams, 1855a: 30 [emendation of Auriculea Pfeiffer, 1853].

Description: Shell very small and thin (*Auriculinella, Blauneria*) to large and thick (*Ellobium*), dextral except in *Blauneria*. Spire low to high, with very faint to marked and granular spiral lines. Body whorl 60–80% of shell length, smooth or sculptured like spire. Aperture 70–80% of length of body whorl, oval-elongate; columellar tooth small, very oblique; anterior parietal tooth stronger, perpendicular to (*Auriculinella*) or weakly oblique to columellar axis; smaller posterior parietal teeth sometimes present; outer lip thin and sharp to thick and weakly reflected, smooth internally. Protoconch smooth, prominent, with umbilicus-like slit in apex.

Radula with central tooth small, triangular; lateral teeth bicuspid, with endocone smaller than mesocone; marginal teeth similar to lateral teeth but smaller.

Animal whitish; eyes often concealed by thick skin; tentacles short, subcylindric or with dilated tips; foot entire (*Ellobium*) or transversely divided. Mandible corneous, semilunate. Stomach tripartite; mid-section very muscular. Spermiduct separates from oviduct before the latter leaves posterior glandular complex; anterior mucous gland covers entire length of vagina; spermiduct surrounded by prostate gland and might communicate with base of bursa duct near vaginal opening. Penis large and complex to small and simple (*Blauneria*); associated vas deferens adheres to penis. Visceral nerve ring long, with evidence of streptoneury in *Ellobium;* right parietovisceral connective very short.

Remarks: There has been confusion in defining the limits of the subfamily Ellobiinae. Pfeiffer (1853a) was the first to try to group the genera of the Ellobiidae into higher taxa. On the basis of the absence or presence of a reflected outer lip he recognized the subfamilies Melampea and Auriculea. He assigned *Pythia, Auricula* [= *Ellobium*] and *Carychium* to the latter group. The two subfamilial names were emended to Melampinae and Auriculinae by H. & A. Adams (1855a). Pfeiffer (1854b), after seeing the unpublished manuscript of the *Genera of Recent Mollusca* by H. & A. Adams (1855), mentioned some of the Adams' conclusions, including the names Melampinae and Ellobiinae, and it is H. & A. Adams (*in* Pfeiffer) who should be credited with the introduction of the latter name (see the remarks under the Ellobiidae). Pfeiffer (1854b) continued to use his previous names and to the existing list of the Auriculea he added *Plecotrema* [= *Laemodonta*], *Cassidula, Alexia* [= *Myosotella*] and *Blauneria*. Two years later in his *Monografia* Pfeiffer (1856a) tentatively included the genus *Leuconia* [= *Auriculinella*] in this subfamily.

Odhner (1925) noted the peculiar radula of *Ellobium* and he admitted only this genus to the subfamily. He wrongly stated that *Ellobium (E.) aurismidae* lacks the central radular tooth (Fig. 17). Zilch (1959), who used conchological characters, also considered the Ellobiinae monotypic. Thiele (1931), on the basis of radular morphology, reached quite different conclusions and he included in the Ellobiinae the subfamilies Melampinae, Pythiinae and Cassidulinae.

Studies of the comparative anatomy of the group are essential to an understanding of the taxonomic relationships within the Ellobiinae and of the entire family as well. Morton (1955c) noticed the similarity of the reproductive tracts of *Auriculinella* and *Ellobium,* and placed those two genera in the subfamily Ellobiinae. Likewise on the basis of reproductive structures Marcus (1965) and Marcus & Marcus (1965b) added *Blauneria*. In spite of the sinistrality of *Blauneria* and the fact that *Blauneria* and *Auriculinella* are much smaller than *Ellobium,* the dentition of the inner lip shows a constant pattern in all three genera of the subfamily. This conchological similarity, corroborating the evidence shown by the reproductive system, makes these features useful phylogenetic characters. I therefore concur with the inclusion of *Auriculinella* and *Blauneria* in the subfamily Ellobiinae.

Habitat: The various genera of the Ellobiinae live in somewhat different habitats. *Ellobium* is common on the muddy surface of Indo-Pacific mangroves, just below the high-tide mark, around roots and decaying wood (Berry et al. 1967). *Blauneria* lives buried in the black sediment, and under rocks and rotting vegetable material at the high-tide mark (Marcus & Marcus 1965b; Martins, personal observation). *Auriculinella* lives closer to the low-tide mark than the other two genera; in the Azores it lives under rocks buried in gravel, sometimes into the intertidal zone (Martins, 1980).

Range: The Ellobiinae have a worldwide distribution, with only partial overlap of the different genera. *Ellobium,* which is characteristic of the Indo-West Pacific mangroves, has a single representative in the tropical Eastern

Pacific and another in the tropical Western Atlantic. *Blauneria* occurs only in the Western Indo-Pacific and in the Western Atlantic. *Auriculinella* is restricted to the Mediterranean, the eastern North Atlantic and Macaronesian Islands.

The subfamily seems to have had a Tethyan distribution, which is shown by the present distribution of *Ellobium* and by the presence of *Ellobium* and the *Blauneria*-like *Stolidoma* Deshayes in the Jurassic and Oligocene deposits of Europe (Degrange-Touzin, 1893; Zilch, 1959; Huckriede, 1967).

Genus *Ellobium* Röding, 1798

Ellobium Röding, 1798: 105. Type species by subsequent designation of Gray (1847a): *Ellobium midae* Röding, 1798 [= *Bulla aurismidae* Linnaeus, 1758].

Auricula Lamarck, 1799: 76. Type species by monotypy: *Auricula midae* (Röding, 1798) [= *Bulla aurismidae* Linnaeus, 1758].

Auriculus Montfort, 1810: 310. Type species by monotypy: *Auriculus judae* Montfort, 1810 [= *Bulla aurisjudae* Linnaeus, 1758].

Marsyas Oken, 1815: 305 [new name for *Ellobium* Röding].

Geovula Swainson, 1840: 344 [new name for *Ellobium* Röding].

Description: Shell moderately large and thin (25 mm) to large and thick (100 mm) and covered with pale brown periostracum. Spire low to moderately high, sculptured with granular spiral lines crossed by more or less conspicuous axial cords. Body whorl about 80% shell length, with same sculpture as spire, sometimes weakly depressed dorsoventrally. Aperture about 80% length of body whorl; small, very oblique, twisted columellar tooth; stronger anterior parietal tooth; posterior parietal tooth sometimes present; outer lip thin to thick, sharp to weakly reflected.

Radula with central tooth small, very narrow, without mesocone, with ectocones curved inwards; lateral teeth with very wide, bicuspid crown; marginal teeth similar to lateral teeth, but smaller.

Remarks: The name *Ellobium* Röding, 1798, was ignored for a long time in favor of its junior synonym *Auricula* Lamarck, 1799. Most probably the reason for maintaining the junior name was the acceptance of Lamarck's work and ignorance of the Bolten Catalogue published by Röding in 1798 (Fischer, 1857; Dall, 1915). The vernacular name Auricule was first published by Lamarck in the *Actes de la Société d'Histoire Naturelle de Paris* in 1795 or 1796 (*fide* Férussac, 1821: 95), but the Latinized name *Auricula* first appeared in Lamarck's (1799) *Prodrome*, published in the *Mémoires* of the same society.

Montfort (1810) pointed out that Lamarck (1799) had confused *Auricula midae* and *Auricula judae* by including in the references Argenville's (1757: 226, pl. 10 [13], fig. G) "oreille de Midas," which Montfort identified with *Auricula judae*. Montfort, then, renamed Lamarck's genus *Auriculus* and selected for its type species *Auriculus judae* [= *Ellobium (E.) aurisjudae* (Linnaeus)]. Pfeiffer (1876) preferred *Auriculus* Montfort to *Ellobium* Röding and *Auricula* Lamarck, both of which he dismissed as vague, owing to the heterogeneous assemblage of species that they included.

The genus *Ellobium* is conchologically well characterized by its auriform shape, by a finely reticulate sculpture and by the conspicuous straw-colored to dark brown periostracum (Figs. 4–9). The central tooth of the radula is greatly reduced but not lost in *Ellobium (E.) aurismidae*, as Odhner (1925) erroneously reported (Fig. 17). The mesocone of the central tooth has been lost and the ectocones curl inwards and resemble a pair of pincers (Figs. 13, 14).

Zilch (1959), on the basis of conchological characters, recognized the subgenera *Ellobium s.s.* and *Auriculodes* Strand. *Ellobium* was characterized as having a large, thick shell with a thick, reflected outer lip (Fig. 9), whereas *Auriculodes* had a smaller, thinner shell, with the outer lip sharp and weakly reflected (Figs. 4–8). Some scattered information on the reproductive system of species belonging to both subgenera (see remarks under *Auriculodes*) indicates that the penis and vagina are usually more complex in *Ellobium s.s.* More detailed research on a greater number of species of both subgenera is needed, however, to clarify the relative taxonomic positions of *Ellobium s.s.* and *Auriculodes*. Pending additional information, on the basis of shell thickness, I concur with Zilch (1959) in the recognition of these subgenera.

Subgenus *Auriculodes* Strand, 1928

Autonoe Guppy, 1868: 244. Type species by monotypy: *Autonoe riparia* Guppy, 1868 [= *Auricula dominicense* Férussac, 1821]. *Non* Leach, 1852.

Auriculina Kobelt, 1898: 77. Type species by original designation: *Auricula (Auriculina) gangetica* Pfeiffer, 1855. *Non* Grateloup, 1838, *nec* Agassiz, 1847.

Auricella Möllendorff, 1898: 160. Type species by original designation: *Auricula (Auricella) auricella* Férussac, 1821 [= *Bulimus auricula* Bruguière, 1789]. *Non* Jurine, 1817.

Auriculodes Strand, 1928: 64 [new name for *Auriculina* Kobelt, 1898].

Autonoella Wenz, 1947: 36 [new name for *Autonoe* Guppy, 1868].

Description: Shell to 25 mm long, thin to somewhat solid. Spire with fine spiral lines, sometimes granular and crossed by axial granular cords. Body whorl not flattened dorsoventrally, smooth and shiny or with granular appearance as in spire. Inner lip of aperture with very oblique, twisted columellar tooth and somewhat stronger, weakly oblique parietal tooth; outer lip sharp, sometimes slightly thick and somewhat sinuous at mid-length, slightly reflected in gerontic specimens.

Animal with portion of vagina anterior to confluence with bursa duct straight, very short; associated vas deferens adhering to anterior vagina; penis moderately long, straight; associated vas deferens adhering to penis.

Remarks: Guppy (1868), on the basis of a single beach specimen, introduced *Autonoe* [= *Autonoella* Wenz], which he considered allied to *Melampus* and *Laimodonta* [= *Laemodonta*]. Later, in the revised list of the species of Trinidad, Guppy (1872: 7) observed under Synonyms, etc., "Comp. *Auricula pellucens* [= *Ellobium (A.) dominicense* (Férussac)]." Thiele (1931) considered *Autonoe* a subgenus of *Melampus,* as did Zilch (1959) for *Autonoella* Wenz, a replacement name for the preoccupied *Autonoe* Guppy. From the original description of *Autonoella riparia* (Guppy), and from Guppy's illustration (1871: pl. 17, fig. 1), it seems that the specimen considered was a juvenile of *Ellobium (A.) dominicense* (Férussac). In view of this, I consider *Autonoella* Wenz a junior synonym of *Auriculodes* Strand.

Kobelt (1898) proposed *Auriculina* at the same time as Möllendorff (1898) introduced *Auricella* for the smaller and thinner-shelled forms of *Ellobium s.l.* Because both names were preoccupied, Strand (1928) introduced the substitute name *Auriculodes* for Kobelt's *Auriculina.*

Only two species of *Auriculodes* have been investigated anatomically, and they apparently differ greatly from each other in their pallial gonoducts. According to Marcus & Marcus (1965b) and Martins (this study) *Ellobium (A.) dominicense* has a very short, straight vaginal section anterior to the confluence with the bursa duct, and a moderately long, straight penis. Knipper & Meyer (1956) briefly described the reproductive system of *Ellobium (A.) gaziense* (Preston, 1913) and they mentioned the lack of separation between male and female ducts. This feature is not typical of the subfamily and could lead to removal of *Ellobium (A.) gaziense,* a species with typical *Auriculodes* shell (Fig. 8), from the Ellobiinae. Knipper & Meyer's representation of the nervous system is so similar to that of *Ellobium (A.) dominicense* (Martins, this paper), however, that the accuracy of their report on the reproductive system should be questioned instead. Apparently there are variations in the penial structure of *Ellobium s.s.* as well. The highly coiled penis of *Ellobium (E.) aurisjudae* (Linnaeus) is typical of the nominate subgenus (Morton, 1955b; Berry et al., 1967). Sumikawa & Miura (1978) observed a thick, straight penis in *Ellobium (E.) chinense* (Pfeiffer) although this species retains the characteristic long, coiled anterior vagina. Odhner (1925: pl. 1, fig. 10), on the other hand, represented a small, somewhat thickened, straight penis, and an equally straight vagina for *Ellobium (E.) subnodosum* (Metcalfe, 1851). All of these scattered anatomical observations on the genus hardly allow conclusions to be drawn concerning the correlation between conchological and anatomical characters of these two subgenera, but I find the conchological characters sufficient to justify the separation of *Auriculodes* from *Ellobium s.s.*

Habitat: Species of the subgenus *Auriculodes* prefer to live above the high-tide mark of mangrove swamps, gathering wherever there is rotten wood (Morrison, 1946; Marcus & Marcus, 1965b; Keen, 1971; Martins, personal observation).

Range: The subgenus *Auriculodes* is known from the eastern coast of Africa (Knipper & Meyer, 1956) and throughout the Indo-Pacific region. It is represented along the western coast of Central America by *Ellobium (A.) stagnale* (Orbigny, 1835) and in the West Indian region to Brazil by the closely related *Ellobium (A.) dominicense* (Férussac).

Ellobium (Auriculodes) dominicense
(Férussac, 1821)
Figs. 4–7, 10–16, 18–22

Auricula dominicensis Férussac, 1821: 103 [Santo Domingo Island (Hispaniola); lectotype herein selected MNHNP (Fig. 4)]; Beck, 1837: 103; Beau, 1858: 15.

Auricula pellucens Menke, 1828: 78 [Demerara (Guyana), South America; location of type unknown]; Menke, 1830: 36, 131; Küster, 1844: 17, pl. 2, figs. 16, 17; Pfeiffer, 1854b: 151; Pfeiffer, 1856a: 137; Binney & Bland, 1870: 87; Simpson, 1889: 68.

Conovulus pellucens (Menke). Voigt, 1834: 111.

Ellobium pellucens (Menke). H. & A. Adams, 1855b: 237; Morrison, 1951b: 10; Perry & Schwengel, 1955: 197, pl. 39, fig. 185; Morrison, 1958: 123; Marcus, 1965: 124–128 [taxonomy]; Marcus & Marcus, 1965b: 426–438, pl. 1, figs. 1–7, pl. 2, figs. 8–11, pl. 3, figs. 12–16 [anatomy, ecology, taxonomy]; Rios, 1970: 139; Abbott, 1974: 334, fig. 4106 [illustration from Dall (1885)]; Rios, 1975: 159, pl. 48, fig. 769; Altena, 1975: 88; Vokes & Vokes, 1983: 60, pl. 22, fig. 18.

Autonoe riparia Guppy, 1868: 244 [Mayaro Point, Trinidad; type presumed to be in Victoria Institute, Trinidad, destroyed by fire in 1920 (Sherborn, 1940); Guppy, 1871: 306, pl. 17, fig. 1 [type figured]; Guppy, 1872: 7.

Melampus riparius (Guppy). Pfeiffer, 1876: 317.

Auriculus pellucens (Menke). Pfeiffer, 1876: 359.

Auricula (Auriculastrum) pellucens Menke. Dall, 1885: 275, pl. 18, fig. 8; Dall, 1889: 90, pl. 47, fig. 8; Maury, 1922: 54.

Auriculastra pellucens (Menke). Kobelt, 1898: 101, pl. 15, figs. 5, 6; Haas, 1950: 197; Ewald, 1963: 11–14 [larval history].

Melampus (Autonoe) riparius (Guppy). Kobelt, 1898: 213, pl. 25, figs. 5, 6; Thiele, 1931: 467.

Auriculastrum pellucens (Menke). C.W. Johnson, 1934: 158; M. Smith, 1937, pl. 67, fig. 8 [plate from Dall (1885)]; Webb, 1942, pl. 11, fig. 21; M. Smith, 1951: 145, pl. 55, fig. 2, pl. 67, fig. 8; Coomans, 1958: 103.

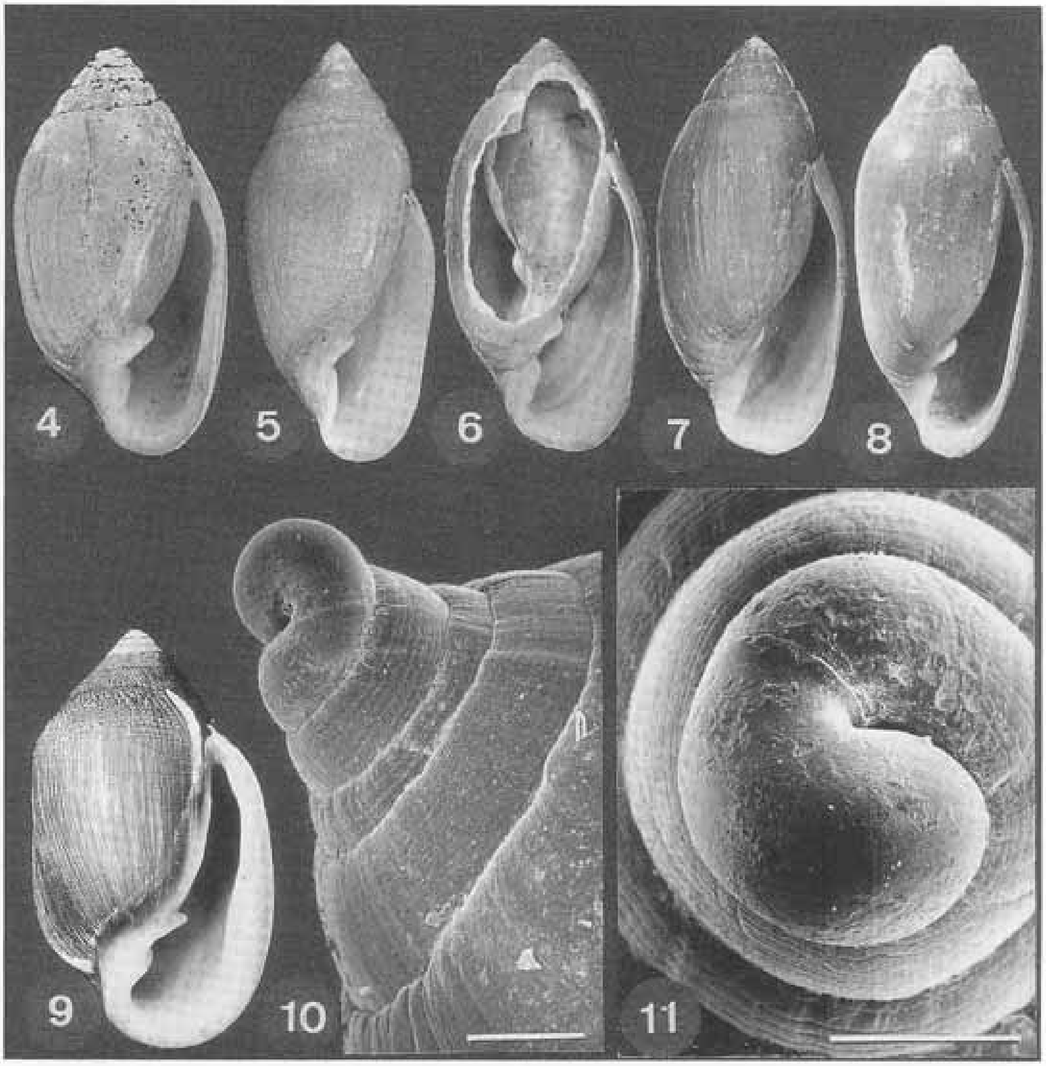
Melampus (Autonoella) riparius (Guppy). Zilch, 1959: 66, fig. 210.

Description: Shell (Figs. 4–7, 10, 11) to 27 mm long, oval-elongate, somewhat solid, whitish-yellowish, covered with brownish periostracum. Spire with as many as eight weakly convex whorls; sculpture as in subgenus. Body whorl about 85% of shell length, subcylindric, smooth or with same sculpture as spire. Aperture about 80% length of body whorl. Inner partition of whorls occupying one-third of body whorl (Fig. 6). Protoconch smooth, prominent, with about one whorl visible; lip weakly reflected at base, forming umbilicus-like perforation in apex (Figs. 10, 11).

Animal white; tentacles partly retractable, moderately long, subcylindrical, with swollen tip; eyes inside base of tentacles, deep in integumentum, barely visible; foot entire; mantle skirt white; anal opening continued by fold of mantle skirt forming longitudinally split tubular extension. Kidney long, narrow, whitish.

Radula (Figs. 13–16, 18) with formula (26+1+26)×70. Central tooth small; base roughly rhombic; posterior portion elongate, emarginate at anterior quarter, where crown of next tooth seems to articulate; crown very small; mesocone lacking; endocones thin, sometimes curled inwards. Lateral and marginal teeth not sharply distinct, here described always as lateral teeth; first seven to 12 with base short and wide, weakly projected lateroanteriorly, with median anterior notch with which posterior process of crown of next tooth articulates; crown wide, roughly triangular, bicuspid, with conspicuous posterior process; mesocone wide, somewhat rounded anteriorly; endocone sometimes barely defined, mainly in adult specimens; gradual narrowing of crown and somewhat sharper definition of endocone marks teeth 12 to 21; base shorter and narrower than that of first group of lateral teeth, with lateral projection resembling basal ectocone; crown somewhat narrow, elongate; endocone first very rudimentary, then absent; no clearly defined ectocone.

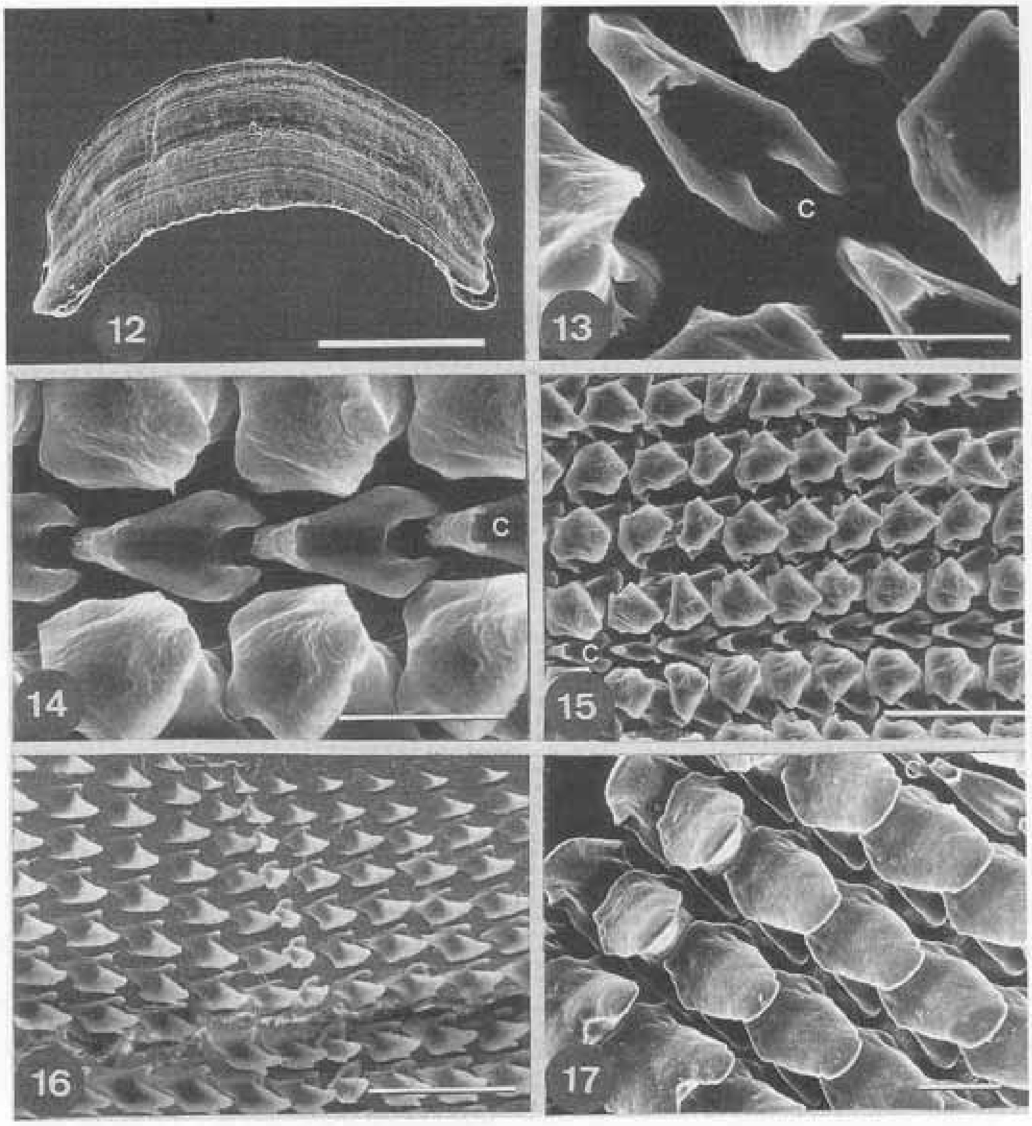
Digestive system with mandible solid, crescentic, with concave, sharp anterior edge and tapered ends (Fig. 12). Salivary glands fusiform, separated from each other, attaching to whitish esophagus by thin ligaments. Stomach tripartite (Fig. 19); anterior portion membranous, comprising cardiac and pyloric regions; mid-portion (gizzard) very muscular, subcylindric; gastric caecum thin, receiving posterior diverticulum anteri-



FIGS. 4–11. *Ellobium*. (4) *E. (A.) dominicense* (Férussac), lectotype (MNHNP), Santo Domingo [Hispaniola], sl 16.2 mm. (5) *E. (A.) dominicense*, Demerara, Guyana (ANSP 22251), sl 22.3 mm. (6) *E. (A.) dominicense*, Big Torch Key, Florida, sl 20.6 mm. (7) *E. (A.) dominicense*, Big Torch Key, Florida, sl 23.0 mm. (8) *E. (A.) gaziense* (Preston), syntype (BMNH 1969103), Gazi, British East Africa [Kenya], sl 18.2 mm. (9) *E. (E.) aurismidae* (Linnaeus), Malaysia, sl 90.4 mm. (10) *E. (A.) dominicense*, lateral view of spire and protoconch, Big Torch Key, Florida. (11) *E. (A.) dominicense*, top view of spire and protoconch, Big Torch Key, Florida. Scale 1 mm.

orly. Digestive gland bilobed, brownish; posterior lobe conic, partly covering ovotestis.

Reproductive system (Fig. 20) with ovotestis follicular, covering posterior portion of stomach, beneath posterior lobe of digestive gland; hermaphroditic duct thin, straight; separation of male and female ducts just anterior to fertilization chamber; secondary connection of posterior vas deferens with anterior end of bursa duct; bursa duct as long as pallial gonoducts, emptying into oviduct a short distance from female aperture; anterior mucous gland covers oviduct as far as confluence with bursa duct. Penis moderately



FIGS. 12–17. *Ellobium*, mandible and radular teeth. (12) *E. (A.) dominicense*, mandible, Big Torch Key, Florida; scale 1 mm. (13) *E. (A.) dominicense*, radula of young specimen, Big Torch Key, Florida, sl 5.4 mm; scale 100 µm. (14) *E. (A.) dominicense*, radula of young specimen, Big Torch Key, Florida, sl 5.4 mm; scale 100 µm. (15) *E. (A.) dominicense*, radula of young specimen, Big Torch Key, Florida, sl 5.4 mm; scale 200 µm. (16) *E. (A.) dominicense*, radula of young specimen, Big Torch Key, Florida, sl 5.4 mm; scale 200 µm. (17) *E. (E.) aurismidae*, radula, Malaysia, sl 90.4 mm; scale 200 µm.

long, somewhat thin, simple; ramifications of right tentacular retractor muscle attach to penis near male aperture; associated vas deferens adhering to penis; penial retractor short, attaching to nuchal region.

Nervous system (Fig. 21) with ganglia wrapped in thick connective tissue; cerebral commissure twice length of cerebral ganglion; pedal commissure very short; left cerebropedal and cerebropleural connectives somewhat longer than right ones, about as long as cerebral commissure; pleuroparietal

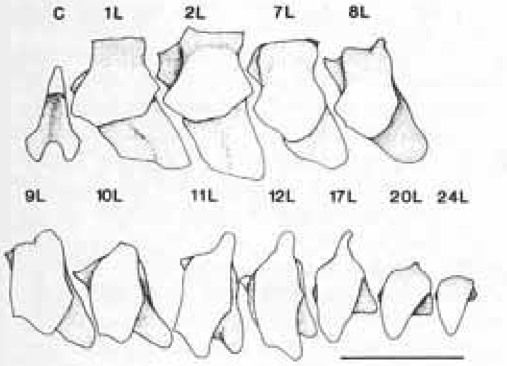


FIG. 18. *Ellobium (A.) dominicense*, radula, Big Torch Key, Florida. Scale 10 µm.

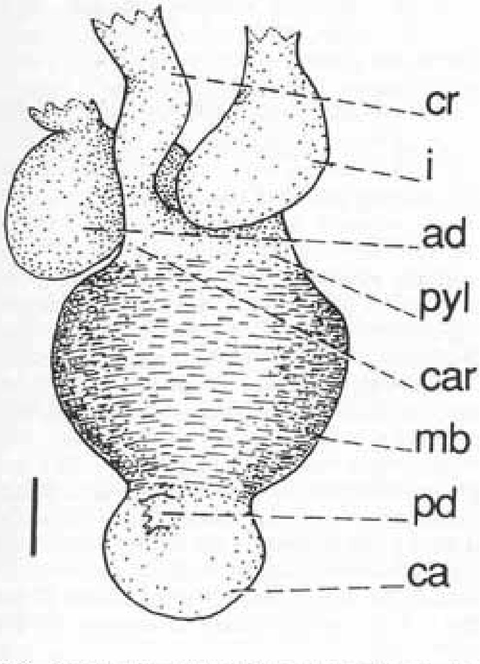


FIG. 19. *Ellobium (A.) dominicense*, stomach, Big Torch Key, Florida. Scale 1 mm.

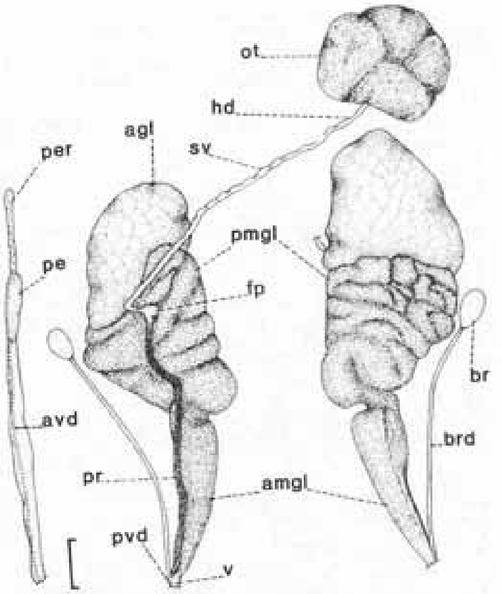


FIG. 20. *Ellobium (A.) dominicense*, reproductive system, Big Torch Key, Florida. Scale 1 mm.

connectives very long; left parietovisceral connective shorter than right one, beneath branch of columellar muscle coming from behind right tentacle; right parietovisceral connective crossing over left one before insertion in visceral ganglion (rudiment of chiastoneury); cerebral ganglia as large as pedal ganglia; left parietal ganglion double; anterior portion of left parietal ganglion giving off nerve to artery in mantle skirt, posterior portion giving off pallial internal and parietal cutaneous nerves; osphradial ganglion present on pneumostomal nerve; tentacular nerves split at their origin; penial nerve coming off median lip nerve.

Remarks: Ellobium (A.) dominicense (Férussac, 1821) has been considered a synonym of *Ellobium (A.) pellucens* (Menke, 1828) although Dall (1885: 276) stated that Férussac's species was described in such a way as to be unidentifiable. Férussac's reference (1821: 103) to the sculpture and size of the shell and comparison with *Auricula auricella*, which he had just introduced, constitute enough indication to recognize the species. Contention might arise owing to the fact that Férussac's *Auricula auricella* was not described (Pfeiffer, 1856a: 134, footnote), but the author referred to *Bulimus auricula* Bruguière, 1789, Lister (1770: pl. 577, fig. 326) [error for 32b] and Gualtieri (1742: pl. 55, fig. F). Férussac's description contains enough information to allow identification of the species and his name has priority over that of Menke (1828).

Emerson & Jacobson (1976) considered *Ellobium auricula* (Bruguière) to be the earliest name for the West Indian *Ellobium*. Bruguière (1789: 342) provided a description of a *Bulimus auricula* that indeed could apply to

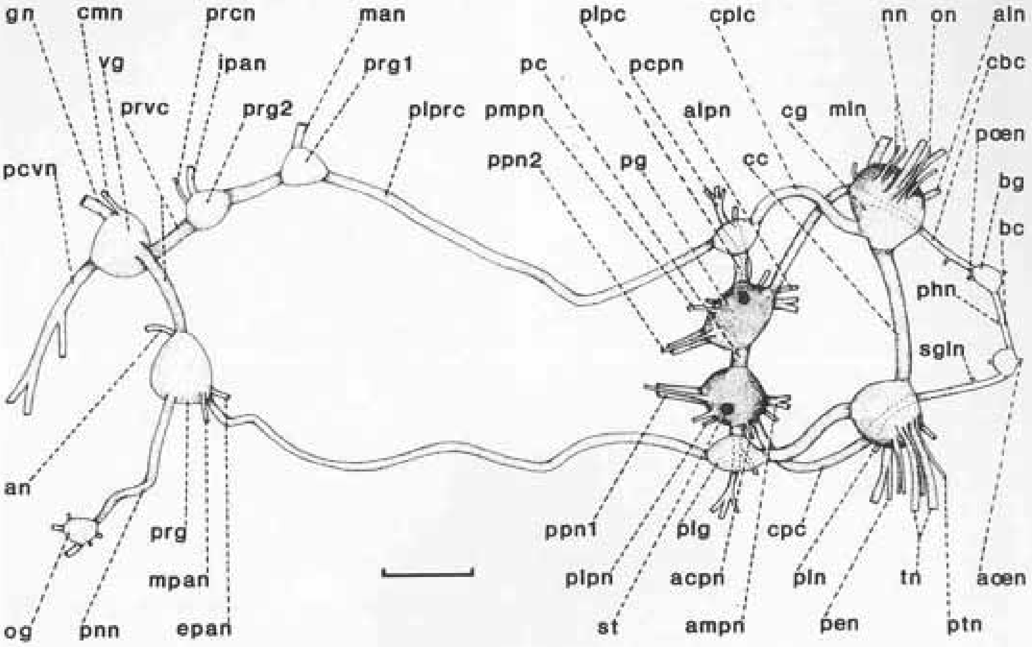


FIG. 21. *Ellobium (A.) dominicense,* central nervous system, Big Torch Key, Florida. Scale 1 mm.

the West Indian shells. No locality was given in the original description, and reference was made to the Gualtieri and Lister illustrations just cited. Férussac, as stated above, introduced without description *Auricula auricella* from Baie des Chiens Marins, New Caledonia. He mentioned in his synonymy of Bruguière's name the same synonymic references given by that author. The fact that some Indo-Pacific species are conchologically very similar to the West Indian species contributed to this confusion. *Ellobium (A.) dominicense* has been stated erroneously to live in Natal, East Africa (Krauss, 1848), probably the result of a misidentification of *Ellobium (A.) gaziense* (Preston, 1913), and Pfeiffer (1856a) considered the Indian *Ellobium ceylanicum* H. & A. Adams, 1854, a junior synonym of *Auricula pellucens* Menke, 1828 [= *Ellobium (A.) dominicense* (Férussac, 1821)]. All this circumstantial evidence indicates that Bruguière (1789) had described an Indo-Pacific shell, which was deposited at the Muséum d'Histoire Naturelle de Genève (Mermod & Binder, 1963). I therefore disagree with Emerson & Jacobson (1976), who misidentified Bruguière's name for the West Indian species.

Ellobium (A.) dominicense has been placed wrongly in *Auriculastra [Auriculastrum* is an unjustified emendation (Marcus & Marcus, 1965b)] by Dall (1885) and others. Martens (1880) created *Auriculastra* as a subgenus of *Marinula* for those species similar to *Ellobium s.s.*, but with visible eyes and knobbed tentacle tips. *Ellobium (A.) dominicense* has these characteristics, a fact which might explain Dall's decision. However, *Auriculastra elongata* (Parreyss, 1845), also originally listed by Martens and very similar to the type species, *Auriculastra subula* (Quoy & Gaimard, 1832), has a very different radula (Odhner, 1925) and appears to belong in the Pythiinae.

The nervous system and the radula of the specimens of *Ellobium (A.) dominicense* here examined, collected on Big Torch Key, Florida, differ from those of animals from Brazil studied by Marcus & Marcus (1965b). The central nervous system of the Floridian specimens is very similar to that of *Ellobium (A.) gaziense* (Preston), illustrated by Knipper & Meyer (1956: 106, fig. 6), differing only in that the left parietal ganglion is double in *Ellobium (A.) dominicense.* In the Brazilian specimens (Marcus & Marcus, 1965b: 431, pl. 3, fig. 13) there is only one left parietal ganglion. The latter authors did not refer to the osphradial ganglion and their figures indicate that the pleuroparietal connectives are shorter than the cerebropleural connectives. In the Floridian specimens the pleuroparietal connectives are three times longer than the cerebropleural connectives. The radula of the specimens from Florida is very similar to those of *Ellobium (E.) aurismidae* (Fig. 17) and *Ellobium (E.) aurisjudae*, both from Malaysia. Marcus & Marcus (1965b: 433, pl. 2, fig. 8) described and figured a tricuspid central tooth with a small, triangular mesocone and rudimentary ectocones. In the specimens from Florida the mesocone is lacking and the slender ectocones are sometimes curved inwards, resembling small fangs. Preserved material from northern South America was not available for comparative anatomical study; however, intrapopulational variability in shell shape and intensity of sculpture is seen throughout the range of the species, although the sculpture seems to be more marked in northern South American specimens (Fig. 5). I am unsure about the phylogenetic significance of the anatomical differences observed in the Brazilian specimens. Should further comparative anatomical research establish that the South American specimens are a separate taxon, Menke's name *pellucens* is available.

Deposited in the Muséum National d'Histoire Naturelle de Paris are two syntypes of *Auricula dominicensis* Férussac, from which a lectotype is herein selected and figured (Fig. 4).

Habitat: Ellobium (A.) dominicense lives in protected embayments in which mangrove growth is thin, buried in the soft black humic sediment or under rotting logs seldom covered by high tide. It seems to be an opportunistic species, usually found in colonies and apparently with very limited movement once established. Great numbers of shells clustered in a small area, indicative of former colonies, are often found without living animals in the immediate vicinity. It seems that the colonies are destroyed by lack of food or by some environmental change, even though apparently suitable habitats exist a few meters away (Ewald, 1963; Marcus & Marcus, 1965b; Martins, personal observation).

Range: Florida, from Miami to Cedar Key (Dall, 1885); Dominican Republic (Férussac, 1821); Haiti; Guadeloupe (Beau, 1858); Trinidad (Guppy, 1868); Yucatán, Mexico, to Cananeia, Brazil (Marcus & Marcus, 1965b). (Fig. 22).

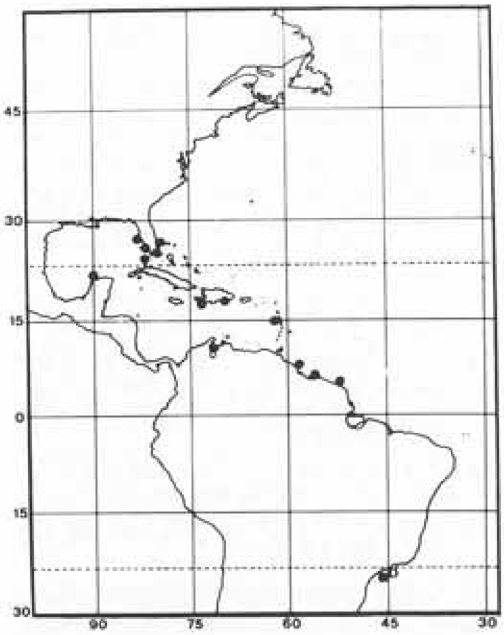


FIG. 22. *Ellobium (A.) dominicense*, geographic distribution. Open circle, locality from literature.

Specimens Examined: FLORIDA: Golden Beach (MCZ 157854); Miami (ANSP 77056; MCZ 104943); Virginia Key (USNM 338303); Key Biscayne (ANSP 345210; USNM 700836, 700911); Coconut Grove (MCZ 201646); Elliot Key (MCZ 110206); Key Largo (ANSP 192837; MCZ 243979; USNM 590644, 701421); Card Sound, Key Largo (A.M.); Rabbit Key (ANSP 88136); Big Pine Key (ANSP 106384); Big Torch Key (USNM 61046, 492482, 492484; A.M.); Middle Torch Key (USNM 663960); Oyster Bay (USNM 37596); Lossman Key (MCZ 291093); Cape Sable (MCZ 291085, 292564; USNM 525156); Rogers River (MCZ 3981); 2.5 km E of Chokoloskee Key (MCZ 58955); Harris Island, Ten Thousand Islands (USNM 381326); Blue Hill Island, near Goodland Point (ANSP 82742); S of Cape Romano (ANSP 62833); Marco (MCZ 292565); Bonita Springs (MCZ 291088); Carl E. Johnson Park, near Little Carlos Pass (A.M.); Fort Myers (ANSP 66963, 140799; USNM 87733, 492483); Punta Rassa (MCZ 291091, 291094, 292566; USNM 39804); Punta Gorda (USNM 592297); Sanibel Island (ANSP 170650; MCZ 13721, 291089, 291090, 292563); Bokeelia (MCZ 291087); Wulfert (ANSP 219866). HAITI: Île-à-Vache (USNM 403877, 404948). MEXICO: Silam, Yucatán (ANSP 62656). VENEZUELA: N of Sinamaica, Zulia (USNM 536129). GUYANA: Demerara (ANSP 2225, 22241; MCZ 146522; USNM 31572, 58857, 119552). FRENCH GUIANA: Cayenne (MCZ 102934; USNM 126413). SURINAME: Saramacca (USNM 635276).

Genus *Blauneria* Shuttleworth, 1854

Blauneria Shuttleworth, 1854a: 148. Type species by monotypy: *Blauneria cubensis* (Pfeiffer, 1841) [= *Voluta heteroclita* Montagu, 1808].

Blanneria Shuttleworth. Dall, 1885: 287 [in synonymy; error for *Blauneria*].

Blaumeria Shuttleworth. Verrill, 1901: 35 [error for *Blauneria*].

Description: Shell to 8 mm long, elongate, fragile, translucent, whitish, sinistral. Spire with as many as nine flattened whorls. Body whorl about 60% of shell length. Umbilicus absent. Aperture about 70% of length of body whorl, oval-elongate; inner lip with very small columellar tooth; outer lip sharp, smooth. Protoconch prominent, smooth, with about one and one-half whorls visible.

Radula having central tooth with wide, triangular, emarginate base; crown small, unicuspid. Lateral teeth gradually becoming smaller toward margin of radula, bicuspid, with strong mesocone and much smaller endocone; no morphological distinction between lateral teeth and marginal teeth.

Animal whitish, translucent, with short, cylindrical tentacles and very conspicuous black eyes. Foot transversely divided. Arrangement of organs sinistral. Separation of male and female ducts just anterior to fertilization chamber, before oviduct enters posterior glandular complex; posterior vas deferens secondarily communicates with anterior end of bursa duct. Penis small, simple; associated vas deferens adhering to penis. Connectives of visceral nerve ring long.

Remarks: The genus *Blauneria* is readily identifiable because it is the only sinistral ellobiid taxon. The history of this once enigmatic small group, before it was placed timidly in a separate genus by Shuttleworth (1854a), is connected with that of the type species *Blauneria heteroclita* (Montagu), and will be discussed in the remarks under that species.

Once it was discovered to be a member of the Ellobiidae, the genus *Blauneria* was placed in different subfamilies, depending upon which character assumed greater importance in the classification scheme of the particular malacologist. Fischer & Crosse (1880) included *Blauneria* and other "marine" ellobiids with an elongated spire in the Auriculinae [= Ellobiinae]. Odhner (1925), on the basis of radular characters, considered the genus to belong to the Cassidulinae. Thiele (1931), who based his classification largely upon Odhner's radular studies, did not recognize the subfamilies Pythiinae and Cassidulinae, and placed *Blauneria*, together with many other genera, in the heterogeneous subfamily Ellobiinae. Zilch (1959), probably on the basis of conchological similarities with the dextral *Cylindrotis* Möllendorff, 1895, removed *Blauneria* to the Pythiinae. Finally, Marcus (1965) and Marcus & Marcus (1965b), followed by Hubendick (1978), included *Blauneria* in the Ellobiinae owing to similarities of the reproductive system with those of *Ellobium* and *Auriculinella*. My anatomical studies confirm the taxonomic conclusions of these latter authors.

Habitat: Blauneria commonly lives in mangroves at the high-tide mark in the sediment under rocks and decaying branches. Pease (1869: 60) reported that his *Blauneria gracilis* from Hawaii lives in the same habitat as *Pedipes*, in the crevices of stones covered at high tide. He observed that *Blauneria* never crawls on the sides or tops of the rocks during low tide, but only around the base, which was always wet.

Range: The genus is known from the warm regions of the Indo-Pacific and from the tropical Western Atlantic. There is no known fossil record of this sinistral genus, but the conchologically closely related, dextral *Stolidoma* Deshayes, 1863, has been recorded from strata as old as the Paleocene of Europe (Degrange-Touzin, 1893; Zilch, 1959). Zhu (1980) described a *Blauneria* ? *elliptiformis* from the Cretaceous of northeastern China.

Blauneria heteroclita (Montagu, 1808)
Figs. 23–40

Voluta heteroclita Montagu, 1808: 169 [Dunbar, Scotland (error), herein corrected to Matanzas, Cuba; location of type unknown]; Laskey, 1811: 398, pl. 81, figs. 1, 2; Turton, 1819: 254.

Acteon heteoclita (Montagu). Fleming, 1828: 337.

Achatina (?) *pellucida* Pfeiffer, 1840: 252 [Cuba; location of type unknown].

Tornatellina cubensis Pfeiffer, 1841: 130 [Cuba; location of type unknown].

Auricula heteroclita (Montagu). Thorpe, 1844: 146.

Tornatella heteroclita (Montagu). Forbes & Hanley, 1852: 526.

Blauneria cubensis (Pfeiffer). Shuttleworth, 1854a: 148; Franc, 1968: 525.

Blauneria pellucida (Pfeiffer). Pfeiffer, 1854b: 152; Pfeiffer, 1856a: 153; H. & A. Adams, 1858: 643, pl. 138, fig. 8; Binney, 1859: 175, pl. 53, fig. 2; Binney, 1860: 4; Binney, 1865: 21, text fig. 22; Mörch, 1878: 5.

Oleacina (Stobilus) cubensis (Pfeiffer). H. & A. Adams, 1855a: 136.

Odostomia (Tornatellina) cubensis (Pfeiffer). Shuttleworth, 1858: 73.

? *Odostomia cubensis* (Pfeiffer). Poey, 1866: 394.

Blauneria heteroclita (Montagu). Pfeiffer, 1876: 368; Arango y Molina, 1880: 60; Fischer & Crosse, 1880: 9, pl. 34, figs. 14, 14a, 14b [anatomy, radula, taxonomy]; Dall, 1885: 287, pl. 17, fig. 6; Dall, 1889: 92, pl. 47, fig. 14; Simpson, 1889: 60; Crosse, 1890: 259; Kobelt, 1900: 260, pl. 31, figs. 19, 20; Dall & Simpson, 1901: 369; Davis, 1904: 126; Peile, 1926: 88; Thiele, 1931: 466; Bequaert & Clench, 1933: 538; C.W. Johnson, 1934: 160; M. Smith, 1937: 147, pl. 67, fig. 14 [plate from Dall (1885)]; Morrison, 1951b: 10; Coomans, 1958: 104; Nowell-Usticke, 1959: 88; Zilch, 1959: 74, fig. 241; Warmke & Abbott, 1961: 152; Marcus, 1965: 124–128 [taxonomy]; Marcus & Marcus, 1965b: 438–446, pl. 4, figs. 25–29 [anatomy, taxonomy, habitat]; Rios, 1970: 139; Abbott, 1974: 334, fig. 4104 [illustration from Binney (1859)]; Altena, 1975: 87, fig. 42; Rios, 1975: 159, pl. 48, fig. 768; Hubendick, 1978; 20, fig. 164, 24, fig. 176 [nervous and reproductive systems redrawn from Marcus & Marcus (1965b)]; Vokes & Vokes, 1983: 60, pl. 31, fig. 19; Jensen & Clark, 1986: 458, pl. 153.

Blanneria pellucida (Pfeiffer). Dall, 1885: 287 [error for *Blauneria;* in synonymy].

Blaumeria heteroclita (Montagu). Verrill, 1901: 35 [error for *Blauneria*].

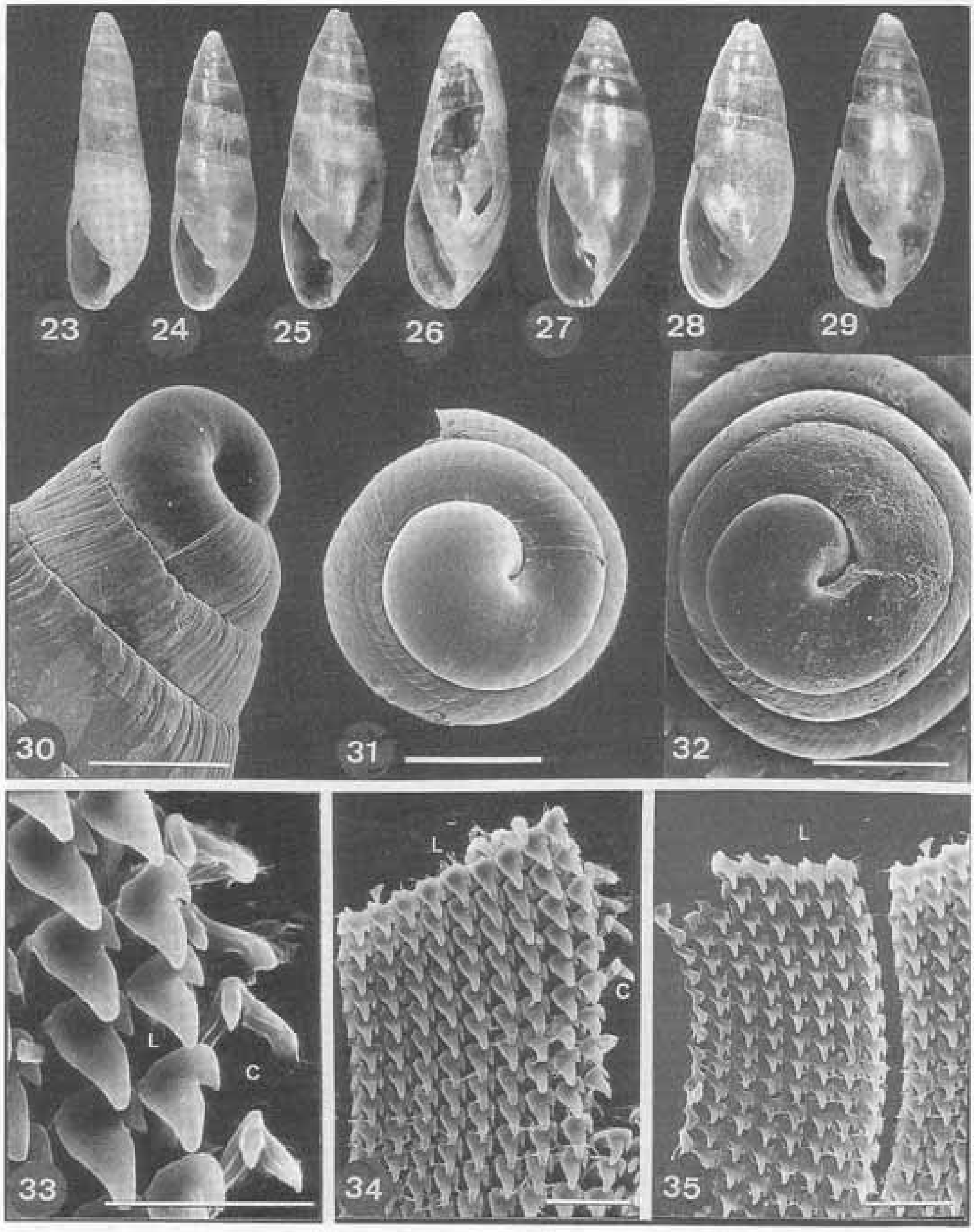
Description: Shell (Figs. 23–32) with length to 7 mm, elongate, fragile, transparent to translucent, shiny, whitish. Spire with as many as nine flat or weakly convex whorls; very faint spiral lines on teleoconch, crossed by irregular growth lines. Body whorl about 60% shell length in gerontic specimens, 70–75% in young individuals. Aperture about 70% body whorl length, oval-elongate; inner lip weakly canaliculate at base, with small, very oblique columellar tooth, stronger, oblique parietal tooth at mid-length of aperture; outer lip sharp, smooth inside. Partition of inner whorls occupying about three-quarters of the body whorl (Fig. 26). Protoconch smooth, well developed, with one and one-half whorls visible, leaving umbilicus-like perforation on apex (Figs. 30–32).

Radula (Figs. 33–36) having formula (17 + 1 + 17) × 70. Base of central tooth wide, triangular, deeply emarginate anteriorly; crown very small, narrow, unicuspid. Lateral teeth 15 to 18; base quadrangular, anteriorly oblique away from central tooth, with small notch on anterior edge; crown wider and longer than base, bicuspid; mesocone strong, long; endocone less than half the length of mesocone; from about sixth lateral tooth outward a process develops on posterolateral edge of crown, which articulates with notch in base of next tooth. Marginal teeth not morphologically distinct from lateral teeth except in gradual decrease in size.

Animal has external anatomy as in genus. Stomach (Fig. 37) with thin, somewhat dilated cardiac region, and smaller, slightly thicker pyloric region; gizzard very muscular, barrel-shaped; gastric caecum invaginable, without posterior diverticulum.

Reproductive system (Fig. 38) with ovotestis apical, granular, orange; hermaphroditic duct simple, with some pouch-like dilations (seminal vesicle) as it approaches albumen gland; male and female ducts separating just anterior to fertilization chamber; spermiduct thick, covered with prostatic tissue, communicating with bursa duct where the latter opens into vagina; anterior mucous gland covers oviduct until confluence with bursa duct. Penis small, simple; associated vas deferens adhering to penis; penial retractor very short, attaching to nuchal region.

Nervous system (Fig. 39) with cerebral ganglia largest; cerebral commissure as long as width of cerebral ganglion; pedal commissure very short; right cerebropedal and cerebropleural connectives longer than left coun-



FIGS. 23–35. *Blauneria heteroclita* (Montagu). (23) Hungry Bay, Bermuda, sl 6.7 mm. (24) Hungry Bay, Bermuda, sl 5.2 mm. (25) Hungry Bay, Bermuda, sl 4.3 mm. (26) Hungry Bay, Bermuda, sl 6.3 mm. (27) Plantation Key, Florida, sl 3.5 mm. (28) Matanzas, Cuba (MCZ 131769), sl 3.7 mm. (29) Isla Mujeres, Yucatán, Mexico (R.B.), sl 3.5 mm. (30) Lateral view of spire and protoconch, Big Pine Key, Florida. (31) Top view of spire and protoconch, Crawl Key, Florida. (32) Top view of spire and protoconch, West Summerland Key, Florida. (33) Lateral and central teeth of radula, Hungry Bay, Bermuda, sl 4.5 mm. (34) Lateral and central teeth of radula, Hungry Bay, Bermuda, sl 4.5 mm. (35) Lateral teeth of radula, Hungry Bay, Bermuda, sl 4.5 mm. Scale, Figs. 30–32, 1 mm; Figs. 33–35, 100 μm.

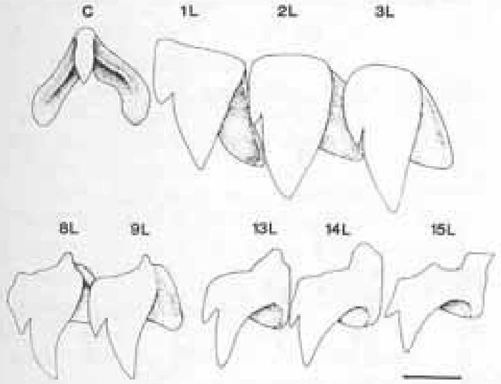


FIG. 36. *Blauneria heteroclita*, radula, Hungry Bay, Bermuda. Scale 10 μm.

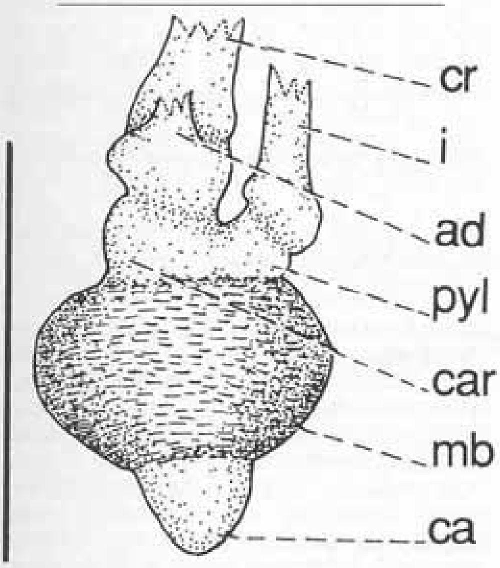


FIG. 37. *Blauneria heteroclita*, stomach, Hungry Bay, Bermuda. Scale 1 mm.

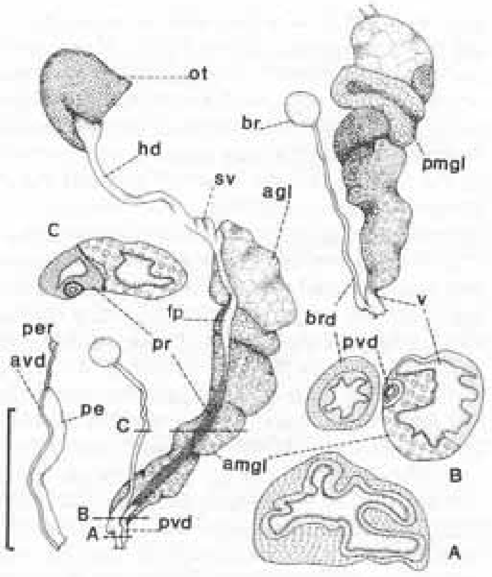


FIG. 38. *Blauneria heteroclita*, reproductive system, Hungry Bay, Bermuda. A-C, transverse sections and their locations. Scale 1 mm.

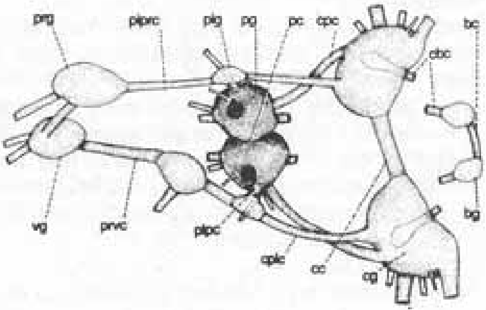


FIG. 39. *Blauneria heteroclita*, central nervous system, Hungry Bay, Bermuda. Scale 1 mm.

terparts; left pleuroparietal and right parietovisceral connectives very long, the latter somewhat shorter than the former; right pleuroparietal and left parietovisceral connectives about same size, about half length of cerebral commissure.

Remarks: Blauneria heteroclita (Montagu) was originally thought to belong to the English malacofauna. The appearance of this Western Atlantic shell on the shores of Dunbar, Scotland, can be attributed to the dumping of ballast of ships from the West Indies.

This little, fragile and elegant shell puzzled the European naturalists for some time. Pfeiffer, within 12 months, introduced the names *Achatina ? pellucida* (1840) and *Tornatellina cubensis* (1841) for specimens from Cuba. H. & A. Adams (1855b, 1858) treated those two names as referring to species in very different groups. They assigned *Tornatellina cubensis* to the terrestrial *Oleacina*, and they followed Pfeiffer (1854b) in allocating *Achatina ? pellucida* to *Blauneria*. The species in question was placed in seven different genera before Shuttleworth (1854a) hesitantly proposed that "*Odostomia cubensis*" probably should belong to a separate genus. Shuttleworth, in a presentation made at the Lyceum of New York a month before the appearance of that paper but published four years later, had considered the species to be marine on the word of the naturalist Blauner. Pfeiffer (1854b), upon receiving a communication from Gundlach that the animal in question had conspicuous eyes at the base of the tentacles (Pfeiffer 1856a: 153), immediately adopted Shuttleworth's name *Blauneria* and placed the genus within the Auriculidae [= Ellobiidae].

I have found some discrepancies between the specimens I studied and those from Brazil examined by Marcus & Marcus (1965b). The Marcuses stated (p. 443) that the endocone of the radular teeth is basal. The SEM photographs of my Bermudian specimens clearly show the endocone as part of the crown, not of the base (Figs. 33–35). Another discrepancy is found in the lengths of the pleuroparietal connectives of the visceral nerve ring (pl. 5, fig. 28). Based upon my observations in the current study I suspect that the Marcuses reversed the right and left connectives.

Blauneria differs from all other ellobiids in its sinistrality. Gerontic specimens have a very elongate and slender shell (Fig. 23). Most commonly, however, the body whorl of the shell is longer and wider than the spire (Figs. 27–29). This form has been the one commonly illustrated, represented by Binney (1865) and copied by Dall (1885), M. Smith (1937) and Abbott (1974).

Habitat: Blauneria heteroclita lives in mangroves above the high-tide mark, where it is usually deeply buried in the soft sediment under rocks, rotten wood or on the roots of the propagules, where it occurs with *Laemodonta, Creedonia* and *Microtralia.* Marcus & Marcus (1965b) stated that these animals are common in decaying banana trees washed ashore in Cananeia, Brazil.

Range: Bermuda; Florida to Texas and Yucatán, Mexico; West Indies; Panama (Olsson & McGinty, 1958); Suriname (Altena, 1975); Brazil (Fig. 40).

Binney (1859: 176) stated, "Dr. Foreman collected a few specimens in a garden of Washington city. He believes them to have been brought on plants from Charleston, S.C." Both places are distant from the range of the species and, because there has been no confirmation of either record, I do not include them in the range of the species.

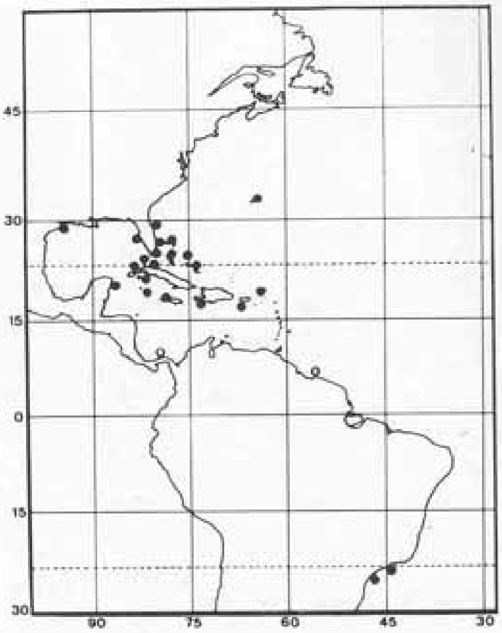


FIG. 40. *Blauneria heteroclita*, geographic distribution. Open circle, locality from literature.

Specimens Examined. BERMUDA: Fairyland (ANSP 99076); Old Road, Shelly Bay (A.M.); Cooper's Island (ANSP 131647); Hungry Bay, S of Ely's Harbour (both A.M.). FLORIDA (USNM 39843, 67953): St. Augustine (USNM 663064); Rose Bay, N of New Smyrna Beach (A.M.); Miami (MCZ uncatalogued); Barnes Sound (ANSP 196748; MCZ 291100); Key Largo (MCZ uncatalogued; USNM 597460); Tavernier Key (USNM 492513); S of Ocean Dr., Plantation Key (A.M.); Lignumvitae Key (ANSP 156648; MCZ 294648); Lower Matecumbe Key (USNM 492521); Long Key (A.M.); Grassy Key (ANSP 397277; MCZ 291102; A.M.); Crawl Key (A.M.); Big Pine Key (ANSP 104106); end of Long Beach Drive and W of Kohen Avenue, both Big Pine Key (both A.M.); Sugarloaf Key (ANSP 88804, 104107); Boca Chica Key (USNM 270352); Cape Sable (MCZ 291099, 291101); Marco (ANSP 22470; USNM 37615, 37616); Seminole Point (ANSP 105422); Starvation Key (ANSP 130061); Fort Myers (USNM 492512); E of St. James, Pine Island (ANSP 93432); Captiva Island (ANSP 149907); Sarasota Bay (USNM 30626); Mullet Key (USNM 652410, 653108; A.M.); Tampa Bay (USNM 37614); Boca Ciega Bay (ANSP 9570); Shell Key (USNM 466212); Clearwater Island (ANSP 9350). ALABAMA: Coden Beach (USNM 422371). TEXAS: Galveston (MCZ 227843); Port la Vaca (MCZ 223050); N end of Padre Island, 45 km S of Port Aransas (MCZ 228745). MEXICO: Isla Mujeres, Quintana Roo, Yucatán (R.B.). BAHAMA ISLANDS: GRAND BAHAMA ISLAND: North Hawksbill Creek (ANSP 370564); South Hawksbill Creek (ANSP 371810); GREAT ABACO ISLAND (ANSP 299496); ANDROS ISLAND: South Mastic Point (A.M.); Stafford Lake (ANSP 151931); Mangrove Key (USNM 180672, 269947, 270198); Smith's Place, South Bight (USNM 257569, 269649); Linder Key (USNM 270224); NEW PROVIDENCE ISLAND: Nassau (MCZ uncatalogued); SE shore of Lake Cunningham (ANSP 299720); Bonefish Pond (A.M.); ROYAL ISLAND (USNM 468124); AKLINS ISLAND: between Pleasant Point and Claret Cove (MCZ 225524). CUBA (ANSP 22471; MCZ uncatalogued; USNM 39842, 57726, 492511): Habana (ANSP 130745, 326340; MCZ 233993); Salt Works, Hicacos Peninsula (ANSP 157338); La Chorrera (MCZ 128256, 167956); Cajio (MCZ 167955); Matanzas (MCZ 131769; USNM 492510); Batabanó (ANSP 93730; MCZ 167957). JAMAICA (ANSP 16705, 22472; USNM 94765): Green Island Harbor (USNM 440791); Montego Bay (ANSP 329122); Port Morant (USNM 423688); Kingston (USNM 427130, 467555); Hunt's Bay (USNM 427117). HAITI: Île-à-Vache (USNM 403701, 403859, 403872, 404947); Landeprie Bay (USNM 383264); between Vieux Bourg and Baïe des Flamands (USNM 402467); Aquin (USNM 403149); Bizoton (USNM 403324). PUERTO RICO: Punta Arenas, N of Joyuda (A.M.); Puerto Real (A.M.). VIRGIN ISLANDS: ST. THOMAS (ANSP 22473). CARIBBEAN ISLANDS: GRAND CAYMAN ISLAND (ANSP 209768). BRAZIL: Cananeia (ANSP 305213; USNM 699448).

Subfamily Pythiinae Odhner, 1925

Scarabinae Fischer & Crosse, 1880: 5.
Pythiinae Odhner, 1925: 14.

Description: Shell variable in size. Aperture usually heavily dentate; one columellar tooth; one to three, commonly two parietal teeth, anterior one strongest; outer lip generally internally dentate.

Radula with mesocone of lateral teeth triangular, usually pointed; marginal teeth becoming smaller toward margin, with as many as three subequal cusps.

Animal with rudimentary anterior tentacles sometimes present; foot entire. Pallial gonoduct entirely hermaphroditic; anterior mucous gland and prostate gland covering spermoviduct along entire length; bursa duct emptying near vaginal opening; spermatic groove open in *Pythia;* penis simple; vas deferens adhering to penis externally or free in haemocoel. Ganglionic connectives of visceral nerve ring long, leaving pedal ganglia mid-way between cerebral ganglia and visceral ganglion; right parietovisceral connective longer than left one.

Remarks: Fischer & Crosse (1880) created the subfamily Scarabinae for *Scarabus* Montfort, 1810 [= *Pythia* Röding, 1798] on account of its oddly shaped, dorsoventrally flattened shell. Odhner (1925) used the name Pythiinae because by that time *Scarabus* Montfort was recognized as a junior synonym of *Pythia* Röding; he included *Alexia* [= *Myosotella*] and *Blauneria* on the basis of radular characters. *Cassidula* and *Ophicardelus* were added by Morton (1955c), who merged Odhner's Cassidulinae with the Pythiinae. Zilch (1959) reverted to Odhner's division and included in the Pythiinae the Recent genera *Pythia, Ovatella, Cylindrotis* and *Blauneria* and removed *Ophicardelus* and *Cassidula* to the Cassidulinae. Marcus (1965) and Marcus & Marcus (1965b) noted that in *Blauneria* the spermiduct and oviduct separate before the hermaphroditic duct enters the glandular complex, and so removed this genus to the Ellobiinae. In consideration of shell and anatomical features, I have concluded that *Laemodonta* must be included in the Pythiinae.

Dall (1885) included *Sayella* within the Ellobiidae and Zilch (1959) listed it, with a question mark, within the Pythiinae. Morrison (1939), however, showed that *Sayella* Dall is not an ellobiid, but a pyramidellid opisthobranch.

Separation of the Cassidulinae from the Pythiinae, as Odhner (1925) proposed and Zilch (1959) supported, is not justifiable. The two groups are similar in the basic pattern of the inner lip teeth of the shell aperture but their radular morphology shows too much diversity and overlap to constitute a useful taxonomic character at the subfamilial level. Both groups have a similar plan of the nervous system and, for this reason, Morton (1955c) regarded Odhner's Cassidulinae as superfluous. The nervous system of the Cassidulinae indeed shows the elongate right parietovisceral connective, characteristic of the Pythiinae. Morton erroneously stated that the pallial gonoduct of *Cassidula* is very similar to that of *Myosotella* in that it remains hermaphroditic until the vaginal aperture. According to Berry et al. (1967), Berry (1977) and Martins (personal observation) the vas deferens of *Cassidula aurisfelis* (Bruguière) separates from the oviduct some distance before the vaginal opening, and runs free until entering the neck skin to follow the spermatic groove. This feature can be considered secondary to the general pattern of the reproductive system, however, for the bursa duct opens at the same position relative to the separation of the vas deferens in *Cassidula* as it does in the other Pythiinae. The same arrangement occurs in the Ellobiinae. *Ellobium (E.) aurisjudae* also has a long, nonglandular vagina, which is in accordance with the highly specialized penial complex of the species. *Ellobium (E.) aurismidae,* on the other hand, has a less specialized penis and lacks the long, nonglandular vagina (Morton, 1955c; Berry et al., 1967; Martins, personal observation). In both species, however, the bursa duct opens at the anterior end of the glandular portion of the oviduct.

In view of the similarities of the reproductive and nervous systems of the two groups, as well as their similar patterns of apertural dentition, Morton's decision (1955c) to merge the Cassidulinae with the Pythiinae is hereby followed.

Habitat: The Pythiinae contain very primitive ellobiids such as *Pythia, Myosotella, Ophicardelus* and *Cassidula*. These groups have left the proximity of the sea and are less dependent upon that element than all other halophilic ellobiids. *Pythia* has acquired a semiterrestrial habitat, and *Myosotella, Ophicardelus* and *Cassidula* were placed by Morton (1955c) among the "supratidal and estuarine ellobiids." *Laemodonta* lives in rocky areas at the high-tide mark, with *Pedipes*, and in the mangroves at or just below the high-tide mark, under rocks and fallen branches.

Range: The Pythiinae have a worldwide distribution. *Pythia, Cassidula* and *Ophicardelus* are characteristic of the tropical Indo-Pacific; *Laemodonta,* also common in the Indo-Pacific, is represented in the West Indies by one species. *Ovatella* and *Myosotella* are represented in the Mediterranean, but the latter has been introduced to eastern North America (Binney, 1859; Verrill, 1880), California (Hanna, 1939), western South America, South Africa and Australia (Climo, 1982).

Genus *Mysotella* Monterosato, 1906

Phytia Röding, 1798. Gray, 1821: 231 [misspelling of *Pythia*].

Phitia Gray. Blainville, 1824: 246 [misspelling of Gray's misspelling of *Pythia*].

Phythya Gray. Deshayes, 1832: 762 [misspelling of Gray's misspelling of *Pythia*].

Jaminia Brown, 1827, pl. 51. Type species by subsequent designation of Gray (1847a): *Jaminia denticulata* (Montagu, 1803) [= *Auricula myosotis* Draparnaud, 1801]. *Non* Risso, 1826.

Alexia "Leach" Gray, 1847a: 179. Type species by monotypy: *Alexia denticulata* (Montagu, 1803) [= *Auricula myosotis* Draparnaud, 1801]. *Non* Stephens, 1835.

Kochia Pallary, 1900: 239. Type species by subsequent designation of Monterosato (1906): *Alexia (Kochia) oranica* Pallary, 1900 [= *Auricula myosotis* Draparnaud, 1801]. *Non* Frech, 1891.

Myosotella Monterosato, 1906: 126. Type species by original designation: *Myosotella payraudeaui* "Shuttleworth" Pfeiffer, 1856a [= *Auricula myosotis* Draparnaud, 1801].

Nealexia Wenz, 1920: 190 [new name for *Alexia* Gray, 1847, *non* Stephens, 1835].

Description: Shell to 10 mm long, fragile to somewhat solid, pale yellow to purplish red. Spire high, with as many as eight weakly convex, spirally striated whorls; only one spiral row of hairs in juveniles. Aperture oval-elongate; inner lip with small, very oblique columellar tooth, strong anterior parietal tooth and usually one, sometimes more, parietal teeth becoming smaller posteriorly; outer lip sharp, weakly reflected, commonly with one or more inner tubercles. Protoconch smooth, large, with one and one-half protruding whorls, leaving umbilicus-like slit in apex of shell (Figs. 76, 77).

Radula with base of central tooth wide, emarginate half of its length; crown of marginal teeth pointing medially, mesocone stronger than endocone.

Animal grayish-white; neck and tentacles sometimes darkly pigmented. Hermaphroditic duct convolute; pallial gonoduct hermaphroditic as far as the vaginal aperture; anterior mucous gland and prostate gland cover entire length of spermoviduct; bursa duct emptying near vaginal aperture; penis short, thick; vas deferens adhering to penis. Ganglia of visceral nerve ring widely spaced; osphradial ganglion present.

Remarks: The majority of modern literature has treated *Myosotella* Monterosato, 1906, as a subgenus of *Ovatella* Bivona, 1832. The anatomy of the type species of *Myosotella, Myosotella myosotis* (Draparnaud), has been studied extensively (Meyer, 1955; Morton, 1955b) and Giusti (1973) looked briefly into the anatomy of the type species of *Ovatella, Ovatella firminii* (Payraudeau, 1826). A study of the anatomy of *Ovatella aequalis* (Lowe, 1832) from the Azores (Martins, personal observation) revealed the presence of a pallial gland, not noted by Giusti (1973) for *Ovatella firminii,* similar to that in *Carychium tridentatum* (Müller) (Morton, 1955b), *Pythia scarabeus* (Gmelin, 1791) (Plate, 1897), *Cassidula labrella* (Deshayes, 1830) (Renault, 1966) and *Laemodonta cubensis* (Pfeiffer, 1854) (Martins, this study). In another work (Martins, 1980) *Ovatella aequalis* was shown to have a tripartite mandible with tapering ends, whereas that of *Myosotella myosotis* is entire and quadrangular. These two characteristics, corroborated by differences in the protoconch, justify the attribution of generic rank to *Myosotella.*

Some modern authors, following Kennard & Woodward (1919), treat *Myosotella* as a junior synonym of Gray's misspelling "*Phytia*" (Morrison, 1951a; M. Smith, 1951; McMillan, 1968; Keen, 1971; Climo, 1982). The word "*Phytia*" appeared in Gray (1821) and is obviously a misspelling of *Pythia* Röding, 1798, for two reasons. First, as Watson (1943) pointed out, the family Ellobiidae was, at the time of Gray's publication, divided into very few genera, and *Carychium* Müller, 1774, *Pythia* Röding, 1798, and *Auricula* Lamarck, 1799, all had been established many years earlier. *Pythia* had been introduced for *Pythia helicina* Röding [= *Helix scarabeus* Gmelin], a species which has a row of tubercles inside the outer lip. Group *b* of Gray's "Order 1. Adelopneumona" included the amphibious *Auricula, Carychium* and "*Phytia.*" Gray's only example of "*Phytia*" was *Voluta denticulata* Montagu, a form of *Myosotella myosotis* that also has two or more tubercles inside the outer lip. It can be assumed, therefore, that Gray was including *Voluta denticulata* Montagu within the already known genus *Pythia* Röding on the basis of the dentition of the outer lip. Second, Gray's publication is notorious for the number of misspellings it contains. For example, in the first nine lines of page 231, on which "*Phytia*" appears in the fifth line, one can read: *Clauselia* [= *Clausilia*], *Ancillus* [= *Ancilus*] and Phaneropneumana [= Phaneropneumona] and, near the bottom of the page, *Neritino* [= *Neritina*]. Furthermore, Gray (1847a) corrected "*Phytia*" to *Pythia.* In view of the above, "*Phytia*" of Gray must be treated as a misspelling of *Pythia* Röding, in accordance with Articles 19 and 32 ii of the ICZN, and as such it lacks taxonomic standing. Gray's misspelling was later misspelled by Blainville (1824) and Deshayes (1832).

Gray (1847a) also introduced *Alexia* for *Voluta denticulata* Montagu [= *Auricula myosotis* Draparnaud]. Stephens (1835) had used the same name for a genus of Coleoptera, however, rendering Gray's name preoccupied. This fact prompted Wenz (1920) to propose *Nealexia* as a new name for *Alexia* Gray, but *Myosotella* Monterosato, 1906, has precedence over Wenz' name.

In two more instances Gray made mistakes concerning *Ovatella* [= *sensu Myosotella*]. In 1840 he used *Ovatella* Bivona as a subgenus of *Conovulus* Lamarck for *Voluta denticulata* Montagu; later (1847a) he included "*Ovatella* Gray *non* Bivona" in the synonymy of his *Alexia.* Because *Voluta denticulata* was not included in Bivona's (1832) original species, "*Ovatella* 'Bivona' Gray" must be treated as a misuse of *Ovatella* Bivona. Gray (1847a) also included in the synonymy of his *Alexia* the name *Jaminia* Brown, 1827, but the latter name was preoccupied by *Jaminia* Risso (1826).

Pallary (1900) proposed *Kochia* as a subgenus of *Alexia* Gray and he included, among other species, *Alexia (K.) denticulata* (Montagu) and *Alexia (K.) oranica* Pallary [both junior synonyms of *Myosotella myosotis* (Draparnaud)]. The latter species was selected as type species by Monterosato (1906). Pallary (1921), unaware of Monterosato's selection, proposed *Alexia (K.) denticulata* as the type species of *Kochia,* noting at the same time that this name was preoccupied by *Kochia* Frech (1891).

Monterosato (1906) considered Montagu's *Voluta denticulata* and Draparnaud's *Auricula myosotis* not only as being different species, but as belonging to different genera. Leaving the former within Gray's *Alexia*, he included the latter within his genus *Myosotella*, which he created for a group of species under Pfeiffer's *Alexia* #2 (1856a: 147); he designated *Myosotella payraudeaui* ("Shuttleworth" Pfeiffer, 1856) as the type species. On the basis of Pfeiffer's description, I consider *Myosotella payraudeaui* conspecific with *Myosotella myosotis* (Draparnaud). Monterosato's name, then, is the earliest available name for the subgenus that includes *Myosotella myosotis* (Draparnaud).

Habitat: Myosotella lives mainly above the high-tide mark, sometimes even away from the influence of spring tides (Morton, 1955b).

Range: Although it has a worldwide distribution *Myosotella* is generally absent from the tropics.

Myosotella myosotis (Draparnaud, 1801)
Figs. 41–84

Auricula myosotis Draparnaud, 1801: 53 [Mediterranean coast; type probably in Vienna (Locard, 1895)]; Draparnaud, 1805: 56, pl. 3, figs. 16, 17; Férussac, 1821: 103; Lamarck, 1822, 6: 140; Blainville, 1824: 246; Blainville, 1825: 453, pl. 37 *bis*, fig. 6; Gould, 1833: 67; Griffith & Pidgeon, 1834: 36; Küster, 1844: 19, pl. 1, figs. 15–17; Moquin-Tandon, 1851: 348–351 [anatomy].

Voluta denticulata Montagu, 1803: 234, pl. 20, fig. 5 [Devon, England; lectotype herein selected RAMM 4100 (Fig. 41); paralectotypes RAMM 4100]; Dillwyn, 1817: 506; Wood, 1825: 90, pl. 19, fig. 18.

Voluta ringens Turton, 1819: 250 [England; lectotype herein selected USNM 859011 (Fig. 42); paralectotype USNM 55351].

Voluta reflexa Turton, 1819: 251 [Exmouth, England; holotype USNM 55370 (Fig. 44)].

Phytia denticulata (Montagu). Gray, 1821: 132; Gardiner, 1923: 64; Germain, 1931: 561, text fig. 597.

Auricula veneta Von Martens, 1824: 433 [Venice: location of type unknown (*fide* Cesari, 1976)].

Jaminia denticulata (Montagu). Brown, 1827, pl. 51, fig. 6.

Jaminia quinquedens Brown 1827, pl. 51, fig. 11 [Prestonpans, England; type probably at Manchester (Sherborn, 1940)].

Acteon denticulatus (Montagu). Fleming, 1828: 337.

Auricula tenella Menke, 1828: 36 [Type locality herein designated to be Norderney Island; location of type unknown]; Menke, 1830: 131; Küster, 1844: 57.

Carychium personatum Michaud, 1831: 73, pl. 15, figs. 42, 43 [Bretagne, France; lectotype herein selected MNHNP (Fig. 45)].

Melampus borealis Conrad, 1832: 345 [Newport, Rhode Island; type material presumed lost (Baker, 1964)]; Jay, 1839: 59; H. & A. Adams, 1854: 10.

Melampus gracilis Lowe, 1832: 288 [Madeira; location of type unknown].

Auricula myosotis Lamarck. Orbigny, 1835: 23.

Pythia denticulata (Montagu) Gray. Beck, 1837: 103.

Pythia myosotis (Draparnaud). Beck, 1837: 104.

Auricula reflexilabris Orbigny, 1837: 326, pl. 42, figs. 1–3 [Lima, Peru; lectotype herein selected BMNH 1854.12.4.242 (Fig. 46)].

Auricula (Auricula) myosotis (Draparnaud). Anton, 1839: 48.

Auricula denticulata (Montagu). Gould, 1841: 199, fig. 129; De Kay, 1843: 58, pl. 5, fig. 93; Küster, 1844: 54, pl. 8, figs. 1–5; Reeve, 1877, pl. 7, fig. 61.

Auricula mysotis Draparnaud. Sowerby, 1842: 99 [misspelling of *myosotis*].

Auricula denticulata var. *borealis* (Conrad). De Kay, 1843: 58, pl. 5. fig. 91.

?*Auricula sayi* Küster, 1844: 42, pl. 6, figs. 14, 15 [United States of America; location of type unknown (*nomen dubium*)].

Auricula microstoma Küster, 1844: 52, pl. 1, figs. 18, 19 [Budua, Dalmatia; location of type unknown].

Auricula kutschigiana Küster, 1844: 54, pl. 8, figs. 11–14 [Servola near Trieste; Lissa Island; location of type unknown].

Auricula biasolettiana Küster, 1844: 56, pl. 8, figs. 18–20 [Niza; Trieste; coast of Dalmatia; location of type unknown].

Auricula myosotis var. *elongata* Küster, 1844: 69, pl. 8, figs. 21, 22 [Zara; location of type unknown].

Auricula myosotis var. *adriatica* Küster, 1844: 69, pl. 8, figs. 23, 24 [Trieste; Istria; Dalmatia; Zara; location of type unknown].

Auricula ciliata Morelet, 1845: 77, pl. 7, fig. 4 [Alcácer do Sal, Alentejo, Portugal; lectotype herein selected BMNH 1893.2.4.831 (Fig. 47)].

Auricula botteriana Philippi, 1846: 97 [Lesina Island, Dalmatia; location of type unknown].

Melampus denticulatus auct. Stimpson, 1851: 52.

Alexia denticulata (Montagu). Leach, 1852: 97; Locard, 1882: 182; Adam, 1947: 39; Sevo, 1974: 5, fig. 5.

Alexia obsoleta Pfeiffer, 1854a: 111 [Tergesti, Adriatic Sea; location of type unknown]; Kobelt, 1898: 131, pl. 19, figs. 5, 6.

Alexia myosotis (Draparnaud). Pfeiffer, 1854b: 151; Pfeiffer, 1856a: 148; Binney, 1859: 172, pl. 75, fig. 33, pl. 79, fig. 16; Binney, 1860: 4; Binney, 1865: 4, figs. 2–4; Tryon, 1866: 6, pl. 18, figs. 1, 2; Pfeiffer, 1876: 365; Nevill, 1879: 227; Verrill, 1880: 250; Locard, 1882: 183; Apgar, 1891: 130; Schneider, 1892: 116; Whiteaves, 1901: 208; C.W. Johnson, 1915: 178; Morse, 1921: 21, pl. 7, fig. 44; Nobre, 1930: 165, pl. 7, fig. 70; Nobre, 1940: 36; Adam, 1947: 38; La Rocque, 1953: 262; Porter, 1974: 300; Sevo, 1974: 6, fig. 6.

Conovulus denticulatus (Montagu). Clark, 1855: 297.

Alexia bermudensis H. & A. Adams, 1855a: 33 [Bermuda; lectotype herein selected BMNH 1969105 (Fig. 48)]: H. & A. Adams, 1855b: 241; Pfeiffer, 1856a: 152; Pfeiffer, 1876: 367; Kobelt, 1901: 282, pl. 33, fig. 3; Fénaux, 1939: 43, pl. 1, fig. 6.

Conovulus (Alexia) denticulata (Montagu). Woodward, 1856: 174.

Alexia payraudeaui "Shuttleworth" Pfeiffer, 1856a: 147 [Corsica; Nizza; Tergesti; location of type unkown]; Pfeiffer, 1876: 365; Kobelt, 1898; 130, pl. 17, figs. 21, 22.

Melampus turritus (Say MS) Binney, 1859: 174 [Rhode Island; type presumably deposited at ANSP, probably lost].

Auricula bicolor Morelet, 1860: 206, pl. 5, fig. 7 [Pico, Azores; lectotype herein selected BMNH 1893.2.4.822 (Fig. 49)].

Auricula vespertina Morelet, 1860: 210, pl. 5, fig. 9 [Pico, Azores; lectotype herein selected BMNH 1893.2.4.825 (Fig. 50)].

Alexia micheli Bourguignat, 1864: 140, pl. 8, figs. 34–36 [La Calle and Cherchell, Algeria; lectotype herein selected MHNG (Fig. 51)]. *Non* Mittré, 1841.

Alexia micheli var. *triplicata* Bourguignat, 1864; 141, pl. 8, figs. 37, 38 [La Calle, Algeria; lectotype herein selected MHNG (Fig. 52)].

Alexia algerica Bourguignat, 1864: 141, pl. 8, figs. 23–26 [Algeria; lectotype herein selected MHNG (Fig. 53)]; Kobelt, 1898: 128, pl. 17, figs. 18, 19.

Alexia algerica var. *quadriplicata* Bourguignat, 1864: 142, pl. 8, figs. 27–30 [Algeria; lectotype herein selected MHNG (Fig. 54)].

Alexia loweana Pfeiffer, 1866: 145 [Madeira Island; location of type unknown].

Melampus myosotis (Draparnaud). Jeffreys, 1869: 106, pl. 4, fig. 2 [*Voluta ringens* Turton illustrated (Fig. 43), probably type material].

Alexia setifer Cooper, 1872: 153, pl. 3, figs. A1–A3, A5–A6 [San Francisco Bay, California; holotype ANSP 22513a (Fig. 55)].

Alexia setifer var. *tenuis* Cooper, 1872: 154, pl. 3, fig. A4 [San Francisco Bay, California; holotype ANSP 22513b (Fig. 56)].

Alexia (Auricula) myosotis var. *hiriarti* Follin & Bérillon, 1874: 88 [Biarritz lighthouse; lectotype herein selected MNHNP (Fig. 57)].

Alexia setigera Cooper. Pfeiffer, 1876: 368; Fénaux, 1939: 43 [error for *setifer*].

Auricula (Alexia) meridionalis Brazier, 1877: 26 [Port Adelaide, South Australia; holotype ANSP 22506a (Fig. 58)].

Auricula watsoni Wollaston, 1878: 269 [Madeira; lectotype herein selected BMNH 1895.2.2.411 (Fig. 59)].

Auricula watsoni scrobiculata Wollaston, 1878: 269 [Salvages Islands (Madeira); lectotype herein selected BMNH 1895.2.2.417 (Fig. 60)].

Auricula bicolor var. *subarmata* Wollaston, 1878: 466 [Lanzarote (Canary Islands); location of type unknown].

Auricula (Alexia) denticulata (Montagu). Fischer, 1878: 309–312.

Alexia setifera Cooper. Nevill, 1879: 226 [unjustified emendation of *setifer*].

Alexia borealis Say Cooper. Nevill, 1879: 227.

Alexia hiriarti Follin & Bérillon. Locard, 1882: 183.

Alexia biasoletina (Küster). Locard, 1882: 183 [misspelling of *biasolettiana*].

Alexia ciliata (Morelet). Locard, 1882: 184; Kobelt, 1898: 129, pl. 17, fig. 20.

Tralia (Alexia) myosotis (Draparnaud). Dall, 1885: 277; Dall, 1889: 92, pl. 52, fig. 9.

Tralia (Alexia) myosotis var. *ringens* (Turton). Dall, 1885: 278.

Tralia (Alexia) myosotis forma *junior* Dall, 1885: 278 [new name for *Auricula ciliata* Morelet and *Alexia setifer* Cooper].

Alexia cossoni Letour neux & Bourguignat, 1887: 130 [Gabès and Cheiba, Cape Bon, Tunisia; lectotype herein selected MHNG (Fig. 61)].

Alexia terrestris Letourneux & Bourguignat, 1887: 130 [El-Hamma, S of Gabès, Tunisia; holotype MHNG (Fig. 62)].

Alexia globulus Bourguignat, *in* Letourneux & Bourguignat, 1887: 131 [Gabès, Tunisia; holotype MHNG (Fig. 63); on museum label as *Alexia ovum* Bourguignat].

Alexia letourneuxi Bourguignat, *in* Letourneux & Bourguignat, 1887: 131 [Mandara, near Alexandria, Egypt, and Djerba Island, Tunisia; lectotype herein selected MHNG (Fig. 64)].

Alexia pechaudi Bourguignat, *in* Letourneux & Bourguignat, 1887: 132 [Macta near Oran and Mdjerda, Tunisia; holotype MHNG (Fig. 65)].

Alexia acuminata Morelet, 1889: 15, pl. 1, fig. 11 [Port Elizabeth, Cape Colony, South Africa; specimen marked "type" broken, lectotype herein selected BMNH 1893.2.4.838 (Fig. 66)].

Alexia pulchella Morelet, 1889: 15, pl. 1, fig. 10 [Port Elizabeth, Cape Colony, South Africa; lectotype herein selected BMNH 1911.8.8.39 (Fig. 67)].

Alexia armoricana Locard, 1891: 132 [west coast of France; lectotype herein selected MNHNP (Fig. 68)].

Alexia exilis Locard, 1893: 62 [Le Croisic, Loire-Inférieure; Porquerolles (France); herein restricted to Porquerolles; lectotype herein selected MNHNP (Fig. 69)].

Alexia parva Locard, 1893: 62 [Le Croisic, Loire-Inférieure (France); lectotype herein selected MNHNP (Fig. 70)].

Alexia ringicula Locard, 1893: 62 [Arrdudon, Morbihan (France); lectotype herein selected MNHNP (Fig. 71)].

Auricula (Alexia) myosotis Draparnaud. Pelseneer, 1894a: 73, figs. 195–208 [anatomy].

Alexia bicolor (Morelet). Kobelt, 1898: 134, pl. 24, fig. 3.

Alexia vespertina (Morelet). Kobelt, 1898: 135, pl. 24, fig. 4.

Alexia (Kochia) oranica Pallary, 1900: 240, pl. 6, figs, 2, 2a [Oran, Tunisia; lectotype herein selected MNHNP (Fig. 72)].

Alexia myosotis marylandica Pilsbry, 1900a: 40 [Mouth of St. Leonards Creek, Patuxent River, Maryland; lectotype by Baker (1964) ANSP 22483a (Fig. 73)]; C.W. Johnson, 1934: 159.

Alexia myosotis bermudensis Pfeiffer. Pilsbry, 1900b: 504.

Alexia oranica Pallary. Kobelt, 1901: 280, pl. 31, figs. 8, 9.

Alexia bidentata Montagu forma *americana* Kobelt, 1901: 312, pl. 33, figs. 1, 2 [Bermuda; type Senckenberg Museum, Frankfurt-am-Main (not seen)].

Myosotella myosotis (Draparnaud). Monterosato, 1906: 126.

Phytia myosotis var. *bermudensis* (H. & A. Adams). Peile, 1926: 88.

Phytia myosotis (Draparnaud). Ellis, 1926: 96, pl. 2, fig. 3, pl. 5, fig. 49; Germain, 1931: 560, text figs. 295, 296, pl. 18, figs. 535, 536; McMillan, 1947: 264; McMillan, 1949: 67; M. Smith, 1951: 145, pl. 55, fig. 3, pl. 71, fig. 9; McMillan, 1968: 165; Climo, 1982: 43–48, fig. 1, A–L.

Alexia (Myosotella) myosotis (Draparnaud). Thiele, 1931: 466.

Phytia myosotis myosotis (Draparnaud). Winckworth, 1932: 238.

Phytia myosotis denticulata (Montagu). Winckworth, 1932: 238.

Alexia myosotis myosotis (Draparnaud). C.W. Johnson, 1934: 159.

Alexia myosotis var. *varicosa* Fénaux, 1939: 44, pl. 1, fig. 3 [Provence, France; type probably in Fénaux's collection, École des Mines, Paris].

Alexia subflava Fénaux, 1939: 45, pl. 1, fig. 9 [Bermuda; type in Fénaux's collection, École des Mines, Paris (not seen)].

Phytia bermudensis (H. & A. Adams). Morrison, 1951b: 10.

Phytia myosotis marylandica (Pilsbry). Morrison, 1951b: 10; Burch, 1960a: 182 [chromosomes].

Phytia myosotis borealis (Conrad). Morrison, 1951b: 10.

Ovatella myosotis (Draparnaud). Meyer, 1955: 1–43, pls. 1, 2 [anatomy, taxonomy, life history]; Morton, 1955b: 119–131, figs. [anatomy, life history]; Morton, 1955c: 127–168 [anatomy, taxonomy, evolutionary relationships]; Bousfield, 1960: 14, pl. 1, fig. 10; Coomans, 1962: 90; Kensler, 1967: 391–406 [ecology]; Jacobson & Emerson, 1971: 65, text fig.; Baranowski, 1971: 143; Abbott, 1974: 334, fig. 4103; Emerson & Jacobson, 1976: 192, pl. 26, fig. 28; Hubendick, 1978: 1–45 [taxonomic relationships]; Morrell, 1980: 208–209; Rehder, 1981: 650, fig. 232; Jensen & Clark, 1986: 458, figured.

Ovatella (Myosotella) myosotis (Draparnaud). Zilch, 1959: 73, fig. 236; Cesari, 1973: 181–210 [taxonomy, distribution, ecology]; Giusti, 1973: 124, figs. 4 A–N, pl. 2, figs. 1–4, pl. 3, figs. 1–3; Giusti, 1976; Cesari, 1976: 3–19, 5 pls. [taxonomy, anatomy, polymorphism]; Martins, 1978: 24, pl. 3, figs. 4, 4a, 4b, pl. 4, figs. 4, 4a, 4b, pl. 5, figs. 5, 6, D; Martins, 1980: 1–24, pl. 2, figs. f–o [habitat].

Ovatella (Alexia) myosotis (Draparnaud). Russell-Hunter & Brown, 1964: 134.

Ovatella myosotis bermudensis (H. & A. Adams). Abbott, 1974: 334 [fig. 4105, erroneously stated to be *Microtralia occidentalis*, appears to be *Myosotella myosotis* from Bermuda].

Description: Shell (Figs. 41–77) to 12 mm long, oval-elongate, fragile to somewhat solid, commonly pale yellow to purplish red, rarely whitish. Spire high, with as many as eight somewhat convex whorls; first three whorls of teleoconch with spiral rows of pits, becoming fewer as spire progresses (Figs. 76, 77); row of hairs, in juveniles, anterior to spiral rows of pits (Fig. 77). Body whorl about 70% of shell length, smooth except for faint, irregularly spaced growth lines. Aperture about 80% body whorl length, oval-elongate, anteriorly rounded; inner lip with small, very oblique and somewhat twisted, white columellar tooth; anterior parietal tooth strongest, white, of variable thickness and perpendicular to columellar axis; usually one, rarely none, sometimes as many as four posterior parietal teeth that gradually become smaller posteriorly; outer lip sharp, often weakly reflected in gerontic specimens, commonly with one, sometimes with as many as six whitish tubercles. Partition of inner whorls only in body whorl (Fig. 75). Protoconch as in genus.

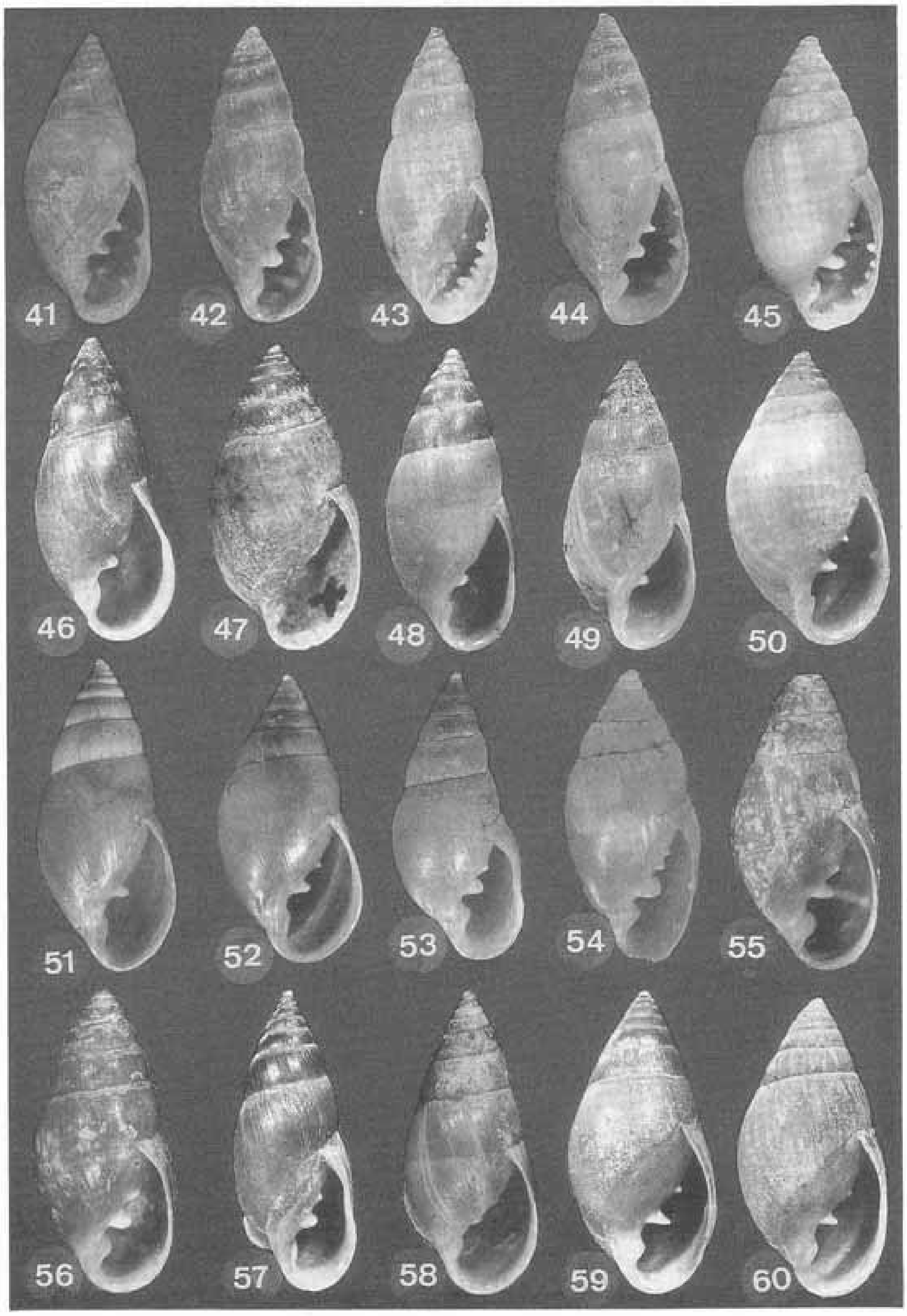
Animal grayish white to yellowish brown; neck usually darkly pigmented; tentacles subcylindric, darker than neck; rudimentary anterior tentacles present; foot not transversely divided, yellowish; mantle skirt grayish with dark spots.

Radula (Figs. 78–80) having formula (20 + 11 + 1 + 11 + 20) × 80. Width of central tooth base twice that of lateral teeth, with central emargination, anterior portion of arms somewhat sinuous; crown small, posteriorly depressed, unicuspid; mesocone triangular, somewhat rounded. Lateral teeth eight to 13; base quadrangular, elongate, oblique, with rounded lateral prominence over anterior third; crown cuneiform, about half length of base, posteriorly rounded. Marginal teeth 17 to 25; base becoming reduced anteriorly, projecting and square posteriorly; crown pointing medially, bicuspid; endocone somewhat smaller than mesocone.

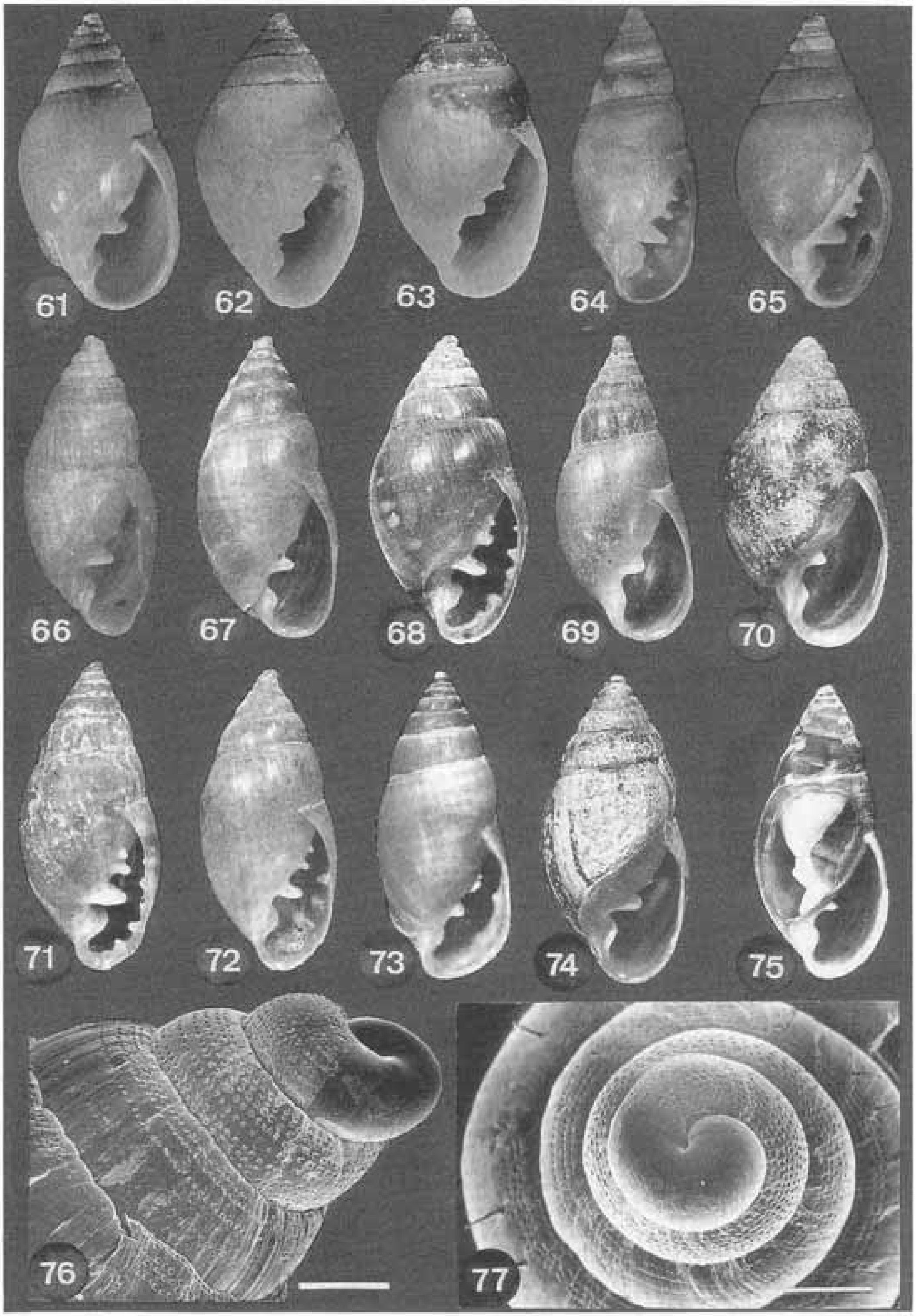
Stomach with anterior membranous chamber, median muscular gizzard and posterior membranous gastric caecum (Fig. 81).

Reproductive system (Fig. 82) with ovotes-

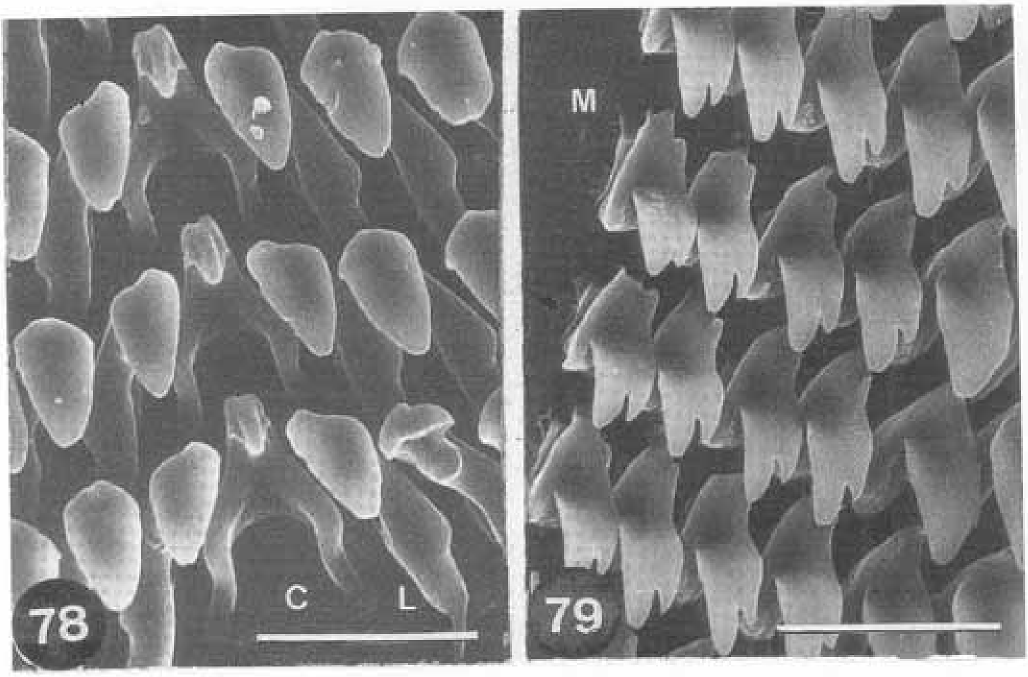
FIGS. 41–60. *Myosotella myosotis* (Draparnaud). (41) *Voluta denticulata* Montagu, lectotype (RAMM 4100), Devon, England, sl 8.5 mm. (42) *Voluta ringens* Turton, lectotype (USNM 859011), British Isles, sl 8.4 mm. (43) *Voluta ringens* Turton, figured in Jeffreys' *British Conchology*, pl. 98, fig. 29 (USNM 67947), sl 8.5 mm. (44) *Voluta reflexa* Turton, holotype (USNM 55370), British Isles, sl 9.2 mm. (45) *Carychium personatum* Michaud, lectotype (MNHNP), Boulogne, France, sl 6.5 mm. (46) *Auricula reflexilabris* Orbigny, lectotype (BMNH 1854.12.4.242), Lima, Peru, sl 9.0 mm. (47) *Auricula ciliata* Morelet, lectotype (BMNH 1893.2.4.831), Portugal, sl 7.8 mm. (48) *Alexia bermudensis* H. & A. Adams, lectotype (BMNH 1969105), locality not given [Bermuda], sl 7.6 mm. (49) *Auricula bicolor* Morelet, lectotype (BMNH 1893.2.4.822), Pico, Azores, sl 9.7 mm. (50) *Auricula vespertina* Morelet, lectotype (BMNH 1893.2.4.825), Area [Areia] Larga, Pico, Azores, sl 7.8 mm. (51) *Alexia micheli* Bourguignat, lectotype (MHNG), La Calle, Algeria, sl 9.2 mm. (52) *Alexia micheli* var. *triplicata* Bourguignat, lectotype (MHNG), La Calle, Algeria, sl 8.0 mm. (53) *Alexia algerica* Bourguignat, lectotype (MNHG), Mostaghanem, Algeria, sl 9.4 mm. (54) *Alexia algerica* var. *quadriplicata* Bourguignat, lectotype (MHNG), Cape Caxine near Alger, Algeria, sl 6.8 mm. (55) *Alexia setifer* Cooper, holotype (ANSP 22513a), San Francisco, California, sl 7.1 mm. (56) *Alexia setifer* var. *tenuis* Cooper, holotype (ANSP 22513b), San Francisco, California, sl 6.4 mm; Baker (1964) gave the length as 7.7 mm, which does not match the length of the shell marked as type. (57) *Alexia (Auricula) myosotis* var. *hiriarti* Follin & Bérillon, lectotype (MNHNP), Biarritz lighthouse, France, sl 10.1 mm. (58) *Auricula (Alexia) meridionalis* Brazier, holotype (ANSP 22506a), Port Adelaide, South Australia, sl 8.3 mm. (59) *Auricula watsoni* Wollaston, lectotype (BMNH 1895.2.2.411), Madeira, sl 8.1 mm. (60) *Auricula watsoni scrobiculata* Wollaston, lectotype (BMNH 1895.2.2.417), Salvages Islands [Madeira], sl 7.5 mm.



FIGS. 41–60.



FIGS. 61–77.



FIGS. 78, 79. *Myosotella myosotis*, radular teeth, Newport River, North Carolina, sl 5.1 mm. Scale 100 µm.

tis light colored, between lobes of digestive gland; hermaphroditic duct long, dilated, convoluted; pallial gonoduct hermaphroditic along its entire length; anterior mucous gland and prostate gland cover entire length of spermoviduct; bursa duct as long as spermoviduct, emptying near vaginal opening; spermatheca spherical. Penis short, thick; associated vas deferens adhering to penis.

Nervous system (Fig. 83) with cerebral commissure one and one-half times width of cerebral ganglion; left and right cerebropleural and cerebropedal connectives of same length; connectives of visceral nerve ring long; right pleuroparietal connective twice as long as left one; left parietovisceral connective longer than right one, sometimes with ganglionic swelling on anterior third, from which internal pallial nerve originates; rudimentary osphradial ganglion arising from pneumostomal nerve.

Remarks: Myosotella myosotis is an extremely variable species especially known from European coasts. Within one population the shape of the shell can vary from slim and

FIGS. 61–77. *Myosotella myosotis* (Draparnaud). (61) *Alexia cossoni* Letourneux & Bourguignat, lectotype (MHNG), Lagune de l'oued Cheiba, (Cap Bon), Tunisia, sl 7.3 mm. (62) *Alexia terrestris* Letourneux & Bourguignat, holotype (MHNG), El Hamma, S of Gabès, Tunisia, sl 5.4 mm. (63) *Alexia globulus* Bourguignat, holotype (MHNG), Gabès, Tunisia, sl 5.7 mm. (64) *Alexia letourneuxi* Bourguignat, lectotype (MHNG), Mandara, near Alexandria, Egypt, sl 5.7 mm. (65) *Alexia pechaudi* Bourguignat, holotype (MHNG), La Mactra, near Oran, Tunisia, sl 5.2 mm. (66) *Alexia acuminata* Morelet, lectotype (BMNH 1893.2.4.838), Natal, sl 5.0 mm. (67) *Alexia pulchella* Morelet, lectotype (BMNH 1911.8.8.39), Port Elizabeth, South Africa, sl 5.0 mm. (68) *Alexia armoricana* Locard, lectotype (MNHNP) Brest, Finisterre, France, sl 5.1 mm. (69) *Alexia exilis* Locard, lectotype (MNHNP), Porquerolles, France, sl 6.1 mm. (70) *Alexia parva* Locard, lectotype (MNHNP), Le Croisic, Loire-Inférieure, France, sl 5.0 mm. (71) *Alexia ringicula* Locard, lectotype (MNHNP), Arrdudon, Morbihan, France, sl 5.0 mm. (72) *Alexia (Kochia) oranica* Pallary, lectotype (MNHNP), Oran, Tunisia, sl 6.0 mm. (73) *Alexia myosotis marylandica* Pilsbry, lectotype (ANSP 22483a) Patuxent River, Maryland, sl 8.0 mm. (74) Jamestown, Rhode Island, sl 6.7 mm. (75) Old Road, Shelly Bay, Bermuda, sl 6.3 mm. (76) Lateral view of spire and protoconch, Jamestown, Rhode Island. (77) Top view of spire and protoconch, São Miguel, Azores. Scale 1 mm.

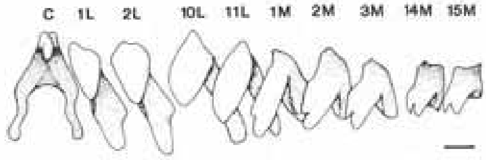


FIG. 80. *Myosotella myosotis*, radula, Beaufort, North Carolina. Scale 10 µm.

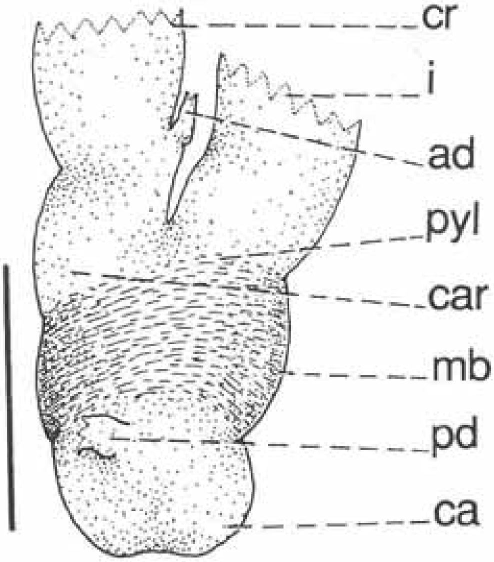


FIG. 81. *Myosotella myosotis*, stomach, Bermuda. Scale 1 mm.

high spired to globose, and the color ranges from pale yellow to purplish red (Martins, personal observations in Bermuda and Azores). Similar variability occurs in the apertural morphology, in which the number of parietal and outer lip teeth can vary considerably. It was the variability of these characters that evoked most of the many names given to this species. According to Locard (1895), Draparnaud (1801) was aware of this variability when he described *Auricula myosotis*, because the 113 syntypes included examples of the dentate form later described by Montagu (1803) as *Voluta denticulata*. Michaud (1831), who completed Draparnaud's work, described Montagu's form as *Carychium personatum* (Fig. 45).

Even quite recently the question of the conspecificity of the European forms included in the genus *Myosotella* has been extensively debated. Germain (1931) accepted two European species, *Phytia myosotis* (Draparnaud), with only one posterior parietal tooth, and *Phytia denticulata* (Montagu), with a heavily dentate aperture. Winckworth (1932) treated both as subspecies of *Phytia*. Watson (1943) noted the differences between the two forms but added that there are intermediates. The slight differences he found in radular features could be explained by the different sizes of the specimens studied, and the differences in shell morphology could be attributed to the

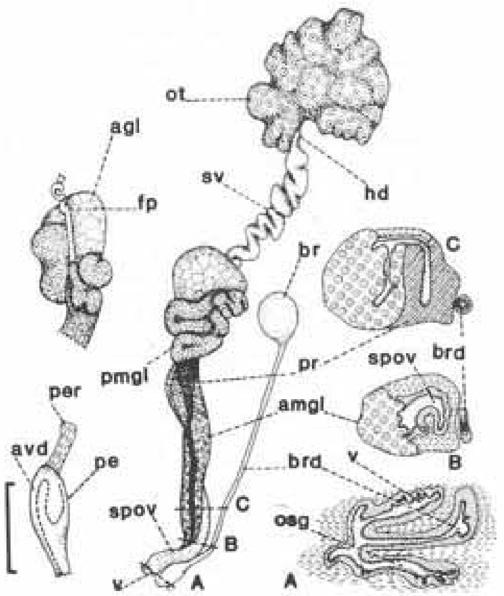


FIG. 82. *Myosotella myosotis*, reproductive system, Bermuda. A-C, transverse sections and their locations. Scale 1 mm.

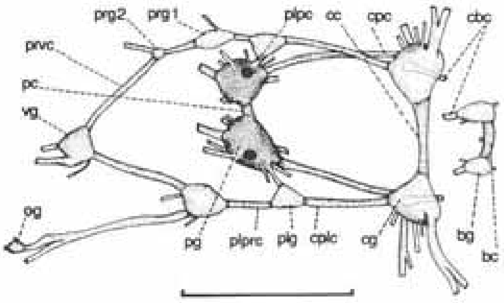


FIG. 83. *Myosotella myosotis*, central nervous system, Bermuda. Scale 1 mm.

more saline habitat of *Phytia denticulata*. Fénaux (1939), after examining hundreds of specimens from a stretch of coast between Toulon and Agde, southern France, found almost all the "species" described from Europe. Cesari (1973) was inclined to treat *Ovatella denticulata* as a synonym of *Ovatella myosotis* but later (1976), as did Watson (1943), he considered the case of *Ovatella denticulata* unclear pending a definite anatomical comparison. Considering the high degree of shell variability of *Myosotella myosotis (sensu lato)*, a wide range of anatomical variability is to be expected. The same condition is found in the Western Atlantic *Melampus (M.) bidentatus*, which exhibits high variability in shell morphology as well as in anatomical characters (see the remarks under that species). On the basis of the great range of variability in shell morphology, I think it justifiable to consider *Myosotella myosotis* as the only species living in Europe and North Africa. The names *Voluta ringens* Turton, *Voluta reflexa* Turton, *Auricula tenella* Menke, *Carychium personatum* Michaud, *Auricula botteriana* Philippi, *Alexia letourneuxi* Bourguignat, *Alexia armoricana* Locard, *Alexia ringicula* Locard and *Alexia oranica* Pallary all pertain to the dentate morph of *Myosotella myosotis*.

I have concluded previously (Martins, 1978, 1980) that *Auricula vespertina* Morelet and *Auricula bicolor* Morelet from the Azores are conspecific with *Myosotella myosotis*. Upon inspection of the type material of Wollaston's *Auricula watsoni* and *Auricula watsoni scrobiculata* from Madeira (Figs. 59, 60) I also include them in the synonymy of *Myosotella myosotis*.

Shell morphology can be affected by environmental factors. The Bermudian specimens (Figs. 48, 75) are larger and thicker than the specimens from New England (Fig. 74), but similar to those I found in North Carolina [*Alexia myosotis marylandica* Pilsbry (Fig. 73)] and in the Azores. The thickening and enhanced color of the shell seen nearer the warm regions is also observed in *Melampus (M.) bidentatus* (see the remarks under the species), and should be considered an environmentally determined character of little taxonomic value. The names *Alexia myosotis marylandica* Pilsbry and *Alexia bermudensis* H. & A. Adams, the latter considered a subspecies by Abbott (1974), are obviously only morphological variations of *Myosotella myosotis*. *Alexia subflava* Fénaux, also from Bermuda, was based upon a form with unusual apertural features, but it is clearly within the range of variation of *Myosotella myosotis*, and it too must be considered synonymous.

Myosotella myosotis (Draparnaud) and *Auriculinella (L.) bidentata* (Montagu, 1801) are often confused. The latter was erroneously reported from America and Bermuda. Dall's (1885) statement that *Melampus (Leuconia) bidentatus* (Montagu) [= *Auriculinella (Leucophytia) bidentata* (Montagu)] lived in America was based on Binney's remarks about *Myosotella myosotis*. Binney (1859: 174), after describing the animal, noted that it differed from H. & A. Adams' illustration of the animal of *Alexia denticulata* (1855b: pl. 82, fig. 5). He mentioned that, "from the exterior of the animal there appears no difference between it and *Melampus bidentatus*." Apparently Dall (1885) wrongly concluded that the species in question should also have the foot transversely divided, a characteristic shared by *Melampus (M.) bidentatus* and *Auriculinella (L.) bidentata*, but not by *Myosotella myosotis*. From Dall's description of *Melampus (Leuconia) bidentatus* (Montagu) it is clear that he was confused about differences between the shell of *Myosotella myosotis* and that of *Auriculinella (L.) bidentata*.

Kobelt (1901: 283) briefly described a supposedly biplicate variation of *Alexia bermudensis* H. & A. Adams, to which he later (p. 312, caption of pl. 33, figs. 1, 2) gave the name *Alexia bidentata* Montagu forma *americana*. The illustration hardly differs from that of *Alexia bermudensis* (pl. 33, fig. 3), which H. & A. Adams (1855a: 33) described as having "columella biplicata" (Figs. 48, 75). As noted above, *Myosotella myosotis* varies greatly in apertural morphology, especially in the conspicuousness of the posterior parietal teeth. *Alexia bidentata* Montagu forma *americana* Kobelt is just a phenotypic variant of *Myosotella myosotis*.

Three other names were applied to North American specimens. Küster (1844) described and figured an *Auricula sayi*. In the words of Binney (1859: 178), "Küster's figure represents no known American shell. There exists, however, a strong resemblance between it and his figure of *Alexia myosotis*." Pfeiffer (1856a) tentatively assigned Küster's name to *Marinula*, and compared it with *Auricula infrequens* C. B. Adams, 1852, from Panama. After examining C. B. Adam's type material I disagree with Pfeiffer's comparison. The dentition shown in Küster's illustration resembles that of *Creedonia succinea*, although the shell is too globose and acuminate to be referred with certainty to that species. In view of the conflicting diagnostic characters derived from the illustration and from the description given by Küster, I consider *Auricula sayi* Küster a *nomen dubium*.

The other two problematic names are *Melampus borealis* Conrad and *Melampus turritus* (Say MS) Binney, both from Rhode Island, and both undoubtedly conspecific with *Myosotella myosotis*. The former was misidentified by Pfeiffer (1856a) who, based upon misidentified specimens from Georgia in the Cuming collection, wrongly assigned them to *Melampus bidentatus* Say, var. γ *borealis* Conrad. Pfeiffer's description of this variety (1856a: 46) mentioned an "outer lip with a white callus, regularly with 6–10 plicae." *Melampus (D.) floridanus*, another Georgian species, has as many as ten riblets inside the outer lip, but it is doubtful that Pfeiffer, who had introduced the latter species 11 pages before, would have confused it with *Myosotella myosotis*. *Melampus (M.) bidentatus* normally exhibits the sort of denticulation on the outer lip mentioned by Pfeiffer, but this feature never has been found in *Myosotella myosotis*. One must conclude that Pfeiffer relied on misidentified specimens when he identified his variety with *Melampus borealis* Conrad. The description of *Melampus turritus*, found by Binney (1859) among Say's unpublished manuscripts, was published by that author only to provide additional information about *Myosotella myosotis*.

Myosotella myosotis can be differentiated conchologically from *Melampus (M.) bidentatus* and *Melampus (D.) floridanus*, with which it associates, by its less globose shape, by its shorter, anteriorly rounded and wider aperture, and by its lack of riblets within the outer lip. It differs from *Creedonia succinea* by its pointed spire and by the dentition of its inner lip, which in *Creedonia* has a very strong, posteriorly located parietal tooth. Some dwarf, thin-shelled forms of *Tralia (T.) ovula* can be confused with the solid, deeply colored forms of *Myosotella myosotis*. This fact probably accounts for Dall's (1885) report of the latter species from Jamaica. The nonmucronate apex, the sinuous outer lip and the white, equidistant teeth of the inner lip of *Tralia* constitute sufficient diagnostic characters, however. Gerontic individuals of *Myosotella myosotis* have a weakly reflected outer lip, a feature that led early authors to insist on including this species in the genus *Auricula*.

Detailed studies of life history and anatomy were published simultaneously by Morton (1955b) and Meyer (1955).

Habitat: Myosotella myosotis lives in salt marshes and adjacent areas, preferring piles of rocks and detritus above the high-tide mark. In Bermuda this species commonly lives under piles of rocks, farther onto land than any other halophilic ellobiid, a situation also observed in the Azores (Martins, 1980).

Range: Myosotella myosotis is well known as a Mediterranean and Eastern Atlantic species. "Species" very similar to *Myosotella myosotis* have been described from extra-European shores, such as Orbigny's (1837) *Auricula reflexilabris* (Fig. 46) from the Pacific coast of South America, Cooper's (1872) *Alexia setifer* (Figs. 55, 56) from California, Brazier's (1877) *Auricula (Alexia) meridionalis* (Fig. 58) from southern Australia and Morelet's (1889) *Alexia acuminata* (Fig. 66) and *Alexia pulchella* (Fig. 67) from South Africa. Hanna (1939) included Cooper's species among the "Exotic Mollusca in California" and I concur with Paulson (1957) in concluding that the Californian *Alexia setifer* Cooper does not differ from eastern American or European specimens. *Alexia setifer* Cooper, as well as *Auricula ciliata* Morelet, were named on the basis of the presence of hairs on the spire of juveniles. Clark (1855) first noted that this condition occurs in *Myosotella myosotis*. Taking into consideration the well-documented morphological plasticity shown by *Myosotella myosotis*, I concur with Climo (1982) in synonymizing Brazier's species, as well as the others just mentioned.

The wide range of *Myosotella myosotis* is attributed to its estuarine and supralittoral habits; most probably the animals were carried about in ballast or as egg masses laid on deck equipment and cargo that came in direct contact with marsh communities (Climo, 1982).

In the Western Atlantic this species occurs from Halifax, Nova Scotia (Bousfield, 1960), to Georgia, Bermuda and Cuba (Fig. 84). The Cuban specimen at the USNM (383711) should be classed as a spurious report until further confirmation because it is far from the range of the species in the Western Atlantic. Dall's report of this species from Jamaica is doubtful and it has not been confirmed by recent collections. Stimpson (1851), followed by Binney (1859, 1865), Verrill (1880) and Dall (1885), remarked that this species probably

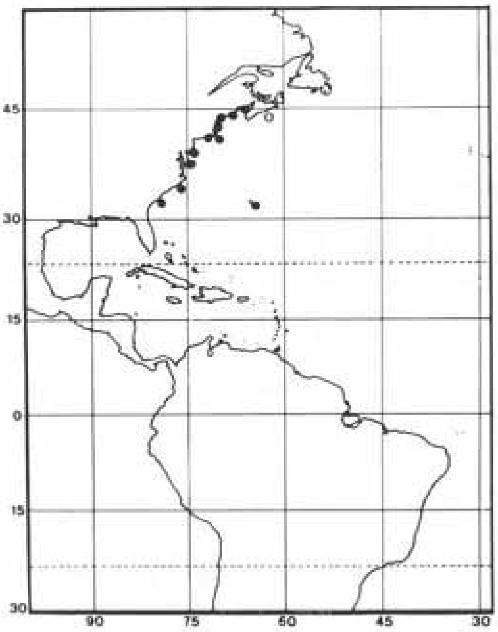


FIG. 84. *Myosotella myosotis*, geographic distribution, Western Atlantic. Open circle, locality from literature.

was introduced to the eastern coast of North America.

Specimens Examined: MAINE: Castine (MCZ 4180; USNM 492501); Portland (MCZ uncatalogued; USNM 24865, 73394); Newcastle (MCZ 34005). NEW HAMPSHIRE: Fabian Point, Great Bay, Newington (R.B.). MASSACHUSETTS (ANSP 22508; USNM 27740, 27913): Manchester (USNM 39800); Marblehead (MCZ 199478; USNM 492503); Boston (MCZ uncatalogued; USNM 41240); Woods Hole (ANSP 357609; MCZ 34004; USNM 158953, 525155); New Bedford (ANSP 22494; MCZ uncatalogued; USNM 139801). RHODE ISLAND (MCZ 34003; USNM 539238): Newport (MCZ 68946, 163167; USNM 39799, 67730); Warren (ANSP 60355); Maple Creek, Jamestown (A.M.); Wickford (MCZ 294645). CONNECTICUT: Branford (MCZ 34847; USNM 492502); New Haven (USNM 83471). NEW YORK: New York Harbor (USNM 492485); Cold Spring Harbor (MCZ 294167); Staten Island (MCZ 56738, 61847, 119477; USNM 59729, 407787, 492500). NEW JERSEY: Cape May (MCZ uncatalogued). MARYLAND: Patuxent River (ANSP 22483, 359154; USNM 492486); St. Leonards Creek, Patuxent River (ANSP 60971; USNM 465806); Crisfield (USNM 618924). VIRGINIA: Mollusk (USNM 791448); Watts Bay (USNM 701628); Chincoteague Island (MCZ uncatalogued); Fisherman's Island (USNM 422292); Norfolk (USNM 637142). NORTH CAROLINA: mouth of Newport River, S of Beaufort (A.M.). SOUTH CAROLINA: Charleston (MCZ uncatalogued); McClellanville (USNM 663059). GEORGIA: Isle of Hope (USNM 663053); Thunderbolt (USNM 663055). BERMUDA (ANSP 48594, 48595, 48596, 62743, 78217, 79937, 85588; MCZ 8972, 9971, 24407, 24408, 24409, 294163, 294166; USNM 6529a, 6537, 94436, 94437, 101401, 151271, 250298a, 492487, 492488, 482490): Hamilton (USNM 152134, 171941); Hamilton Beach (MCZ uncatalogued); Fairyland (ANSP 99074; USNM 208070); Gibbet Island (MCZ 294162); Flatts (ANSP 88572; MCZ 294164; USNM 1719340); Shelly Bay (MCZ 294165; USNM 492489); Old Road, Shelly Bay (A.M.); N of Shelly Bay Beach (A.M.); S of Coney Island (R.B.); Ferry Reach Park (R.B.); N of Long Bird Bridge (A.M.); Castle Harbour (ANSP 143320); Cooper's Island (ANSP 131644); Spitall Pond (A.M.); Hungry Bay (ANSP 88580; USNM 171947; A.M.); Paget (USNM 714209); W of Somerset Bridge (A.M.); S of Ely's Harbour (A.M.); Mangrove Bay (A.M.). CUBA: Los Canos, Guantánamo (USNM 383711).

Genus *Laemodonta* Philippi, 1846

Laemodonta Philippi, 1846: 98. Type species by monotypy: *Laemodonta [Auricula] striata* (Philippi, 1846) [= *Pedipes octanfracta* Jonas, 1845]. *Non* Martens, 1824, *nec* Anton, 1839.

Laimodonta Bronn, 1847: 4 [*nomen nudum*, *fide* Herrmannsen, 1852]. *Non* "Nuttall" H. & A. Adams, 1855a.

Plecotrema H. & A. Adams, 1853: 120. Type species by original designation: *Plecotrema typica* H. & A. Adams, 1853.

Bullapex Haas, 1950: 199. Type species by monotypy: *Laemodonta (Bullapex) cubensis* (Pfeiffer, 1854).

Description: Shell to 9 mm long, oval-conic, solid, sometimes hirsute. Umbilicus present. Spire moderately high, sculptured with more or less marked spiral cords. Body whorl 70–75% shell length, sometimes truncate at base, with same sculpture as spire. Aperture about 70% length of body whorl, oval-elongate, narrow; inner lip with three subequal teeth, one oblique columellar tooth and two parietal teeth; outer lip thickened, with one to three teeth about same size as parietal teeth. Protoconch smooth, globose, prominent.

Remarks: Philippi (1846: 98), following the description of his *Auricula striata,* noted, "*Laemodonta striata* Adams (ubi?). Bronn placed under this name this species from Sandwich Islands [Hawaii]." The name *Laemodonta* appeared as a *nomen nudum* in a sales catalogue of shells prepared by Bronn (1847, *fide* Sykes, 1894), who had sent the shells to Philippi. Although *Laemodonta* Philippi, 1846, was introduced in synonymy, this name must be accepted as valid according to the ICZN, Article 11, (*d*). Thiele (1931) and Zilch (1959) used *Laemodonta* and since 1961 the name has been universally accepted (Clench, 1964; Franc, 1968; Abbott, 1974; Hubendick, 1978; Kay, 1979).

The names *Laimodonta* and *Laemodonta* have been confused in many instances, the second being taken wrongly for a misspelling of the first. *Laimodonta* (Nuttall MS) H. & A. Adams, 1853, was introduced for a group of shells different from those assigned to *Laemodonta* Philippi. Often credit was given erroneously to Nuttall for the introduction of *Laimodonta.* It appears, however, that Nuttall never published the name (Sykes, 1894). Nevill (1879) considered "*Laimodonta* Nuttall" [= emendation of *Laemodonta* Philippi] and *Laimodonta* H. & A. Adams to be different taxa and Ancey (1887) introduced *Allochroa* to replace H. & A. Adams' supposedly preoccupied name. Sykes (1894), apparently unaware of Ancey's introduction, also stated that *Laimodonta* H. & A. Adams was preoccupied, not by Philippi's (1846) or by Bronn's (1847) names, which he considered undescribed, but by *Laimodon* Gray, 1841, a genus of birds. Sykes proposed the new name *Enterodonta. Laimodon* Gray, 1841, cannot be considered a homonym of *Laimodonta* or of *Laemodonta.* According to the ICZN, Art. 32 (*a*), in spite of the fact that Philippi (1846) misspelled Bronn's name, his spelling is to be considered the correct original spelling. *Laimodonta* (Nuttall MS) H. & A. Adams, although not a homonym of Philippi's name, has been abandoned in favor of *Allochroa* in important malacological works (Thiele, 1931; Zilch, 1959; Franc, 1968; Kay, 1979). A permanent solution to this problem would be the placement of *Laimodonta* "Nuttall" H. & A. Adams on the Official List of Rejected Names in Zoology.

Sykes (1894) and Hubendick (1956) in their monographs on *Laemodonta* preferred the name *Plecotrema* H. & A. Adams to Philippi's name. Sykes recorded in his synonymy *Lirator* Beck, which he felt had not been properly introduced. The name *Lirator,* indeed, was used by Beck (1837) for an undescribed *Melampus (Lirator) multisulcatus* from Opara Island. Pfeiffer (1856a, 1876) tentatively identified Beck's species with *Laemodonta striata* Philippi [= *Pedipes octanfracta* Jonas] and Hubendick (1956) accepted Pfeiffer's opinion without query. Because only circumstantial evidence connects Beck's names to a recognized species, however, one must conclude that both *Lirator* and *Melampus (Lirator) multisulcatus* are *nomina nuda.*

Hubendick (1956: 111) stated that Aguayo & Jaume (1947) had given "strong reasons for maintaining *Plecotrema* as the valid name of the genus." In fact, what Aguayo & Jaume (1947: No. 132) had stated was, "in the impossibility of deciding about the priority of *Laemodonta* [Philippi] 1847 [*sic*] over *Laimodonta* [Bronn] 1847, and about the validity of *Lirator* [Beck], we have decided to use the genus *Plecotrema* [H. & A. Adams] as many modern authors do." Later Hubendick (1978) used *Laemodonta* Philippi and relegated *Plecotrema* to synonymy. As stated above, *Laemodonta* Philippi is now universally accepted.

The genus *Laemodonta* has been assigned erroneously to the subfamily Pedipedinae on the basis of the shell. Although described as "fairly uniform" (Hubendick, 1956: 110) or as a "convenient group" (Sykes, 1894: 241), the name *Laemodonta* is used now for a mixture of genera. Examination of the radula of "*Laemodonta*" *punctigera* H. & A. Adams from Malaysia has a very wide, rounded mesocone, typical of the *Cassidula* group, and that species will be assigned to another genus pending more research. H. & A. Adams (1853: 120) had noted that *Plecotrema* [= *Laemodonta*] was "a genus of small shells allied to *Cassidula.*"

The present study of *Laemodonta cubensis* leads me to include this West Indian species within the Pythiinae on the basis of the radula and the reproductive and the nervous systems. Although preserved material of the type species was not available for anatomical comparisons, the remarkable resemblance of shell morphology, especially apertural dentition, of the West Indian species to *Laemodonta octanfracta* (Fig. 3I) has led me to conclude that they are congeneric. If further anatomical studies indicate the necessity of taxonomic separation, the name *Bullapex* Haas is available for *Laemodonta cubensis*.

I concur with Hubendick (1956) that the subgenus *Bullapex* Haas cannot be justified on the basis of shell characters alone. The true umbilicus of the West Indian species is often reduced to an umbilical depression, similar to the pseudoumbilicus mentioned by Haas (1950: 199) for *Laemodonta clausa* H. & A. Adams, 1853 [= *Laemodonta octanfracta* (Jonas)]. According to Hubendick (1956: 114) the inflated apex can be explained as an ecologically influenced character and as such is unreliable. The apex (protoconch) of *Laemodonta octanfracta*, although not so prominent as that of *Laemodonta cubensis*, appears to be somewhat inflated (Fig. 92).

According to Sykes (1894) and Hubendick (1956) the genus *Laemodonta* appeared in the Eocene. These earlier species, unlike those recorded from the Miocene, are smoother and more similar to the West Indian *Laemodonta cubensis*. The Miocene species have the heavy sculpture of the Indo-Pacific group. Hubendick concluded that the West Indian species and the Indo-Pacific group probably had common ancestors in the Tethys Sea.

Habitat: Because most of the data available to me pertain to *Laemodonta cubensis*, description of the soft parts and comments on the habitat are presented under that species.

Range: Hubendick (1956) noted the discontinuous distribution of *Laemodonta*. Most of the representatives are from the western Indo-Pacific, with one species in the West Indies and Bermuda. The genus is not represented in the Recent fauna of the Mediterranean or Eastern Atlantic.

Laemodonta cubensis (Pfeiffer, 1854)
Figs. 85–87, 89, 90, 93–101

Plecotrema cubensis Pfeiffer, 1854b: 153 [Cárdenas, Cuba; location of type unknown]; Pfeiffer, 1856a: 107; Pfeiffer, 1876: 348; Arango y Molina, 1880: 60; Crosse, 1890: 259; Kobelt, 1900: 236; Peile, 1926: 88; Aguayo & Jaume, 1947: 132; Hubendick, 1956: 111, text. fig. 1A, pl. 23, fig. 7 [distribution].

Plecotrema cubense Pfeiffer. Sykes, 1895: 245; Pilsbry, 1900b: 504, pl. 62, fig. 11.

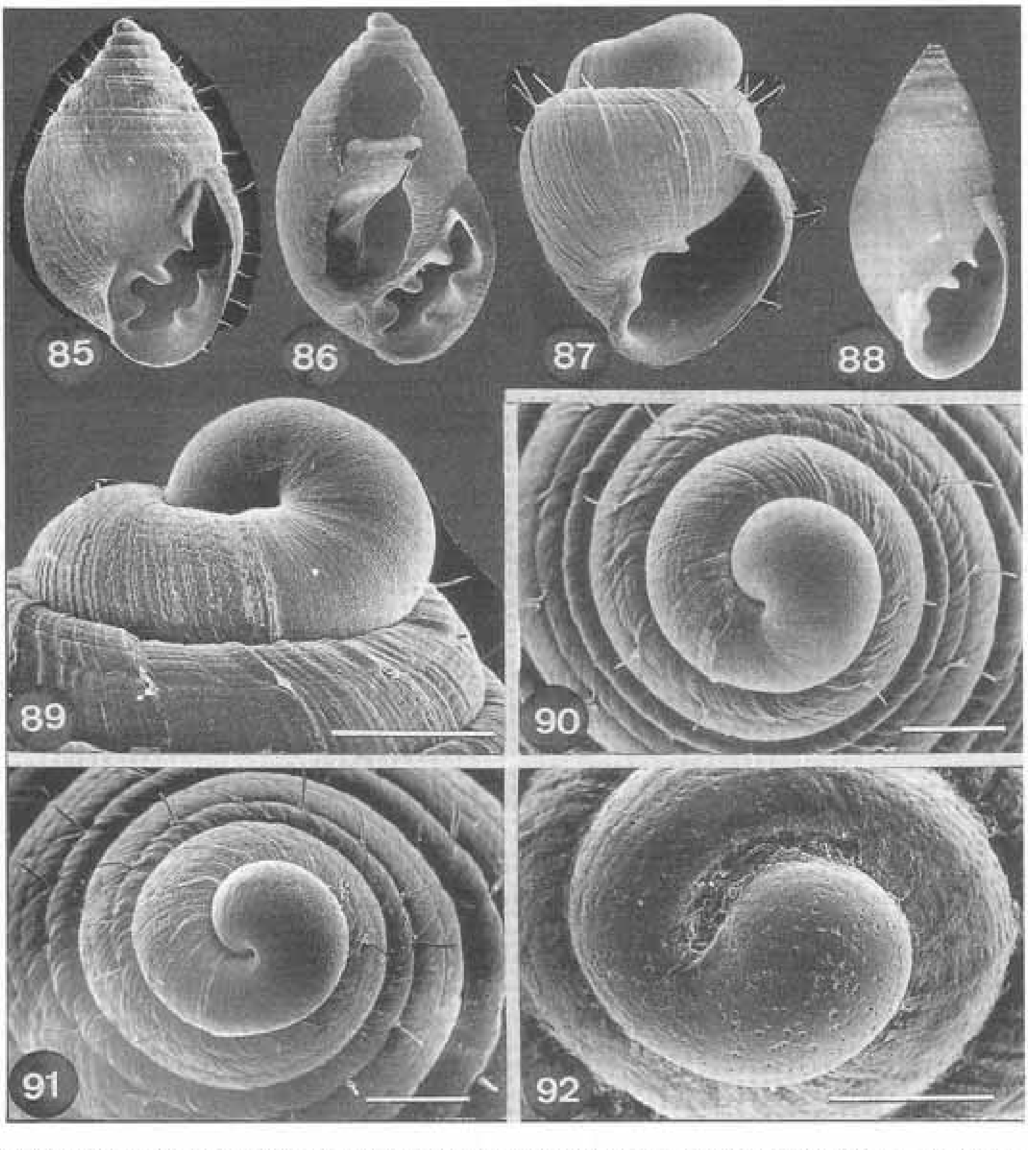
Laemodonta cubensis (Pfeiffer). Thiele, 1931: 464; Morrison, 1951b: 9; Morrison, 1958: 118–124 [habitat]; Abbott, 1974: 333, fig. 4101; Emerson & Jacobson, 1976: 190, pl. 26, fig. 20; Rehder, 1981: 650, fig. 222; Jensen & Clark, 1986: 458, figured.

Laemodonta (Bullapex) cubensis (Pfeiffer). Haas, 1950: 199, pl. 22, figs. 6–8; Zilch, 1959: 69, fig. 225; Clench, 1964: 123, pl. 79 [taxonomy, distribution]; Vokes & Vokes, 1983: 60, pl. 31, fig. 18.

Description: Shell (Figs. 85–87, 89, 90) to 3.5 mm long, oval, somewhat solid, pale yellow to light brown, hirsute. Narrow umbilicus or umbilical depression present. Spire moderately high, whorls as many as six and one-fourth, weakly convex, with two incised spiral lines near suture; first whorls of teleoconch with fine, compact spiral striae, crossed by very fine, somewhat irregular growth lines. Body whorl about 70% shell length, with incised spiral lines. Aperture oval; inner lip with three evenly spaced teeth; columellar tooth oblique toward base, moderately strong; anterior parietal tooth smallest, oblique posteriorly; outer lip sharp, with two conspicuous teeth, sometimes with one or two much smaller tubercles posteriorly. Partition of inner whorls occupying about three-quarters of body whorl (Fig. 86). Protoconch whitish, smooth, inflated, oblique or perpendicular to columellar axis of teleoconch (Figs. 89, 90).

Animal whitish, translucent; tentacles long, thin, subcylindric, translucent; foot entire, rounded posteriorly. Pallial cavity long; kidney long and thin; mantle gland curved, tubular, empties near vaginal opening.

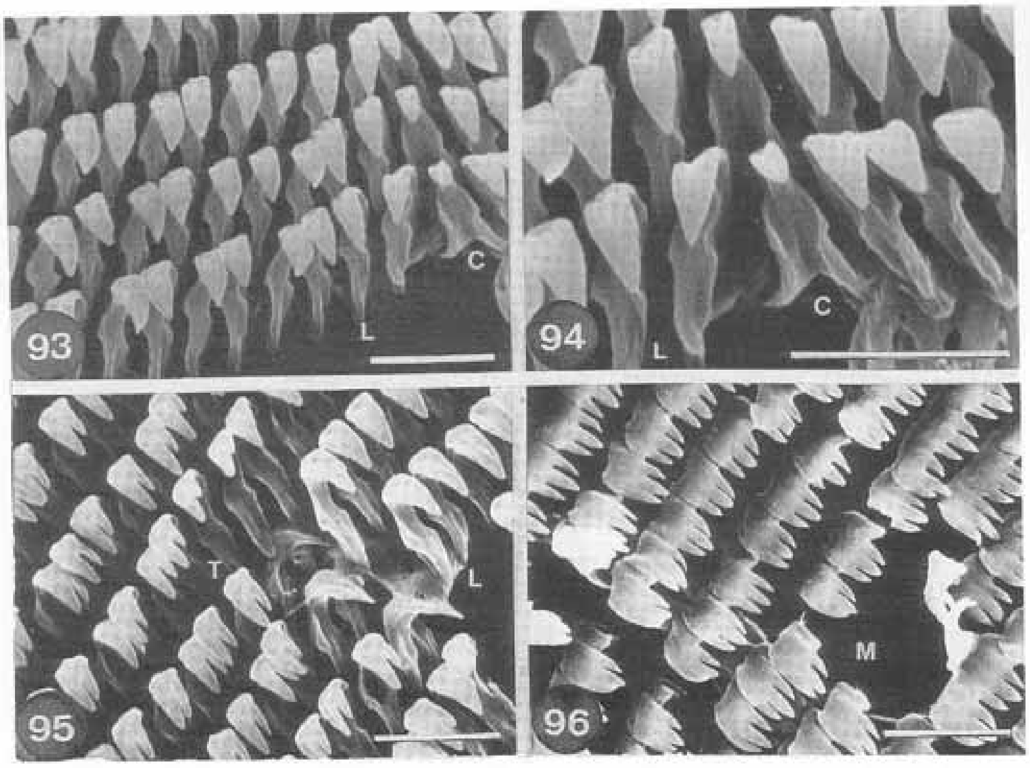
Radula (Figs. 93–97) having formula $[24 + (7 + 7) + 1 + (7 + 7) + 24] \times 100$. Central tooth at about same plane as lateral teeth; base triangular, weakly emarginate anteriorly, with lateral prominences at mid-length; length of crown about half that of crown of lateral teeth, unicuspid; mesocone somewhat sharp. Lateral teeth seven to ten; base weakly bent medially at posterior third, with lateral and medial prominences, the latter anteriormost; crown about half the length of the base, unicuspid, cuneiform. Transitional teeth five to nine; base similar to that of lateral teeth; crown bicuspid; endocone somewhat shorter and weaker than mesocone. Marginal teeth 21 to 24; base becoming



FIGS. 85–92. *Laemodonta, Ovatella*. (85) *L. cubensis* (Pfeiffer), West Summerland Key, Florida, sl 2.9 mm. (86) *L. cubensis*, Grassy Key, Florida, sl 3.2 mm. (87) *L. cubensis*, Crawl Key, Florida, sl 0.84 mm. (88) *O. aequalis* (Lowe), São Miguel, Azores, sl 9.3 mm. (89) *L. cubensis*, lateral view of spire and protoconch, Grassy Key, Florida. (90) *L. cubensis*, top view of spire and protoconch, Grassy Key, Florida. (91) *O. aequalis*, top view of spire and protoconch, São Miguel, Azores. (92) *L. octanfracta* (Jonas), top view of spire and protoconch, Hawaii. Scale 1 mm.

shorter and wider than that of lateral teeth, developing lateral basal cusp covered by next tooth; crown tricuspid; endocone, mesocone and ectocone sharp, becoming subequal, with mesocone somewhat longer and stronger.

Digestive system with salivary glands small, attaching posteriorly to esophagus through large area. Stomach (Fig. 98) tripartite; anterior portion corresponding to cardiac region, thin, dilated; mid-portion very muscular, with muscle also covering pyloric region; gastric caecum somewhat thin, not muscular, receiving dilated, pouch-like posterior diverticulum



FIGS. 93–96. *Laemodonta cubensis*, radular teeth, Grassy Key, Florida, sl 3.5 mm. Scale 50 µm.

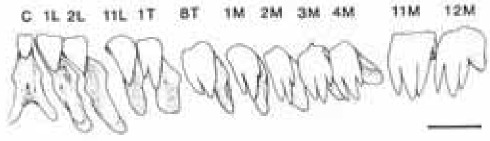


FIG. 97. *Laemodonta cubensis*, radula, Grassy Key, Florida. Scale 10 µm.

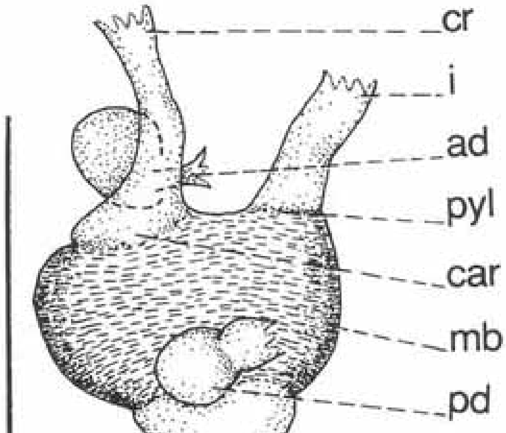


FIG. 98. *Laemodonta cubensis*, stomach, Bermuda. Scale 1 mm.

anteriorly, at boundary with mid-region. Digestive gland with two subequal lobes.

Reproductive system (Fig. 99) with ovotestis between lobes of digestive gland; seminal vesicle of hermaphroditic duct convoluted at mid-length; pallial gonoduct hermaphroditic to the vaginal aperture; anterior mucous gland and prostate gland cover entire length of spermoviduct; bursa duct about same length as spermoviduct and empties just posterior to vaginal opening; bursa spherical. Penis short, thin; vas deferens adhering to penis; penial retractor about as long as penis, inserting on floor of pallial cavity.

Nervous system (Fig. 100) with cerebral commissure short, about half width of cerebral ganglion; right cerebropedal and cerebropleural connectives two-thirds length of left ones; left and right connectives of vis-

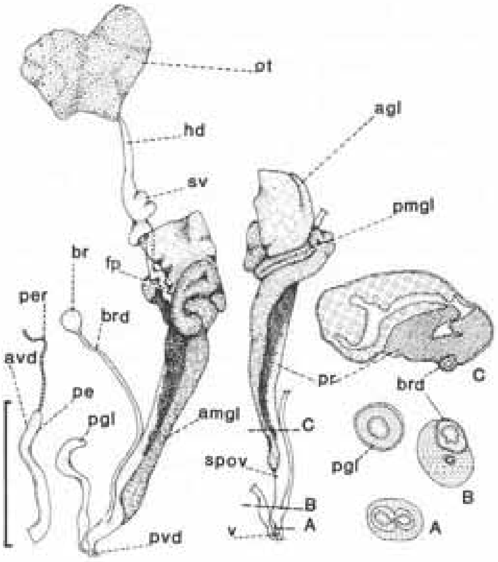


FIG. 99. *Laemodonta cubensis*, reproductive system, Hungry Bay, Bermuda. A-C, transverse sections and their locations. Scale 1 mm.

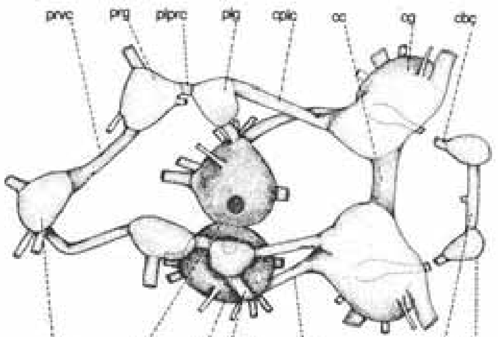


FIG. 100. *Laemodonta cubensis*, central nervous system, Hungry Bay, Bermuda. Scale 1 mm.

ceral nerve ring equal; pleuroparietal connectives very short; parietovisceral connectives very long, the right one longer; visceral ganglion beneath tentacle retractor muscle.

Remarks: Laemodonta cubensis is the only representative of the genus in the Atlantic. All other species live in the Indo-Pacific region. The West Indian species is somewhat isolated conchologically, owing to its thinner, much less sculptured shell. Kobelt (1900) and Thiele (1931) were not sure whether this species should even belong to this genus. As stated in the remarks under the genus, this species is included in *Laemodonta* because of the great similarity of its apertural morphology to that of the type species, *Laemodonta striata* (Philippi, 1846) [= *Laemodonta octanfracta* (Jonas, 1845)]. The description of the radula of *Plecotrema clausa* H. & A. Adams, 1853, a junior synonym of the type species, given by Odhner (1925) is very similar to that of *Laemodonta cubensis* except for the lesser number of teeth in a row in the latter.

In the original description of *Laemodonta cubensis*, Pfeiffer (1854b: 153) characterized the shell as "hispidula" [slightly hairy], a feature also noticed by Haas (1950). A pilose shell appears also in some Pacific species; Garrett (1872) noted that his *Plecotrema hirsuta* [= *Laemodonta molinifera* (H. & A. Adams)] had short, curved hairs.

The presence of a pallial gland was somewhat unexpected in *Laemodonta*. This organ of unknown function was first noticed by Plate (1897) in *Phytia scarabeus* (Linnaeus) and observed later in *Carychium tridentatum* (Risso) (Morton, 1955b), in *Cassidula labrella* (Deshayes) (Renault, 1966) and in *Ovatella aequalis* (Lowe) (Martins, personal observation). *Carychium* lives inland, frequently in the mountains and, although preferring humid environments such as forest leaf litter, it is obviously a terrestrial species. *Pythia* is also considered a terrestrial ellobiid because it lives in the upper fringe of mangroves. *Ovatella aequalis* lives just above the high-tide limit and *Laemodonta* at or just below the high-tide mark. Information is not available concerning the precise habitat of *Cassidula labrella*. Morton (1955b, c) advanced the hypothesis that this was probably a case of parallel evolution in response to some environmental parameter associated with terrestrial life. According to that same author, the possible functions of the pallial gland range from help in forming egg cases to aid in keeping the body moist or secretion of bacteria-killing substances as a protective device while the animal is crawling. The presence of the pallial gland in two supposedly marine ellobiids demands a review of the hypotheses about the evolution and function of this organ.

Laemodonta cubensis is very distinct from all other West Indian mollusks because of its hirsute, oval shell and its apertural dentition. Its protoconch and juveniles are very similar to the protoconch and hirsute juveniles of the Macaronesian and western European *Ova-*

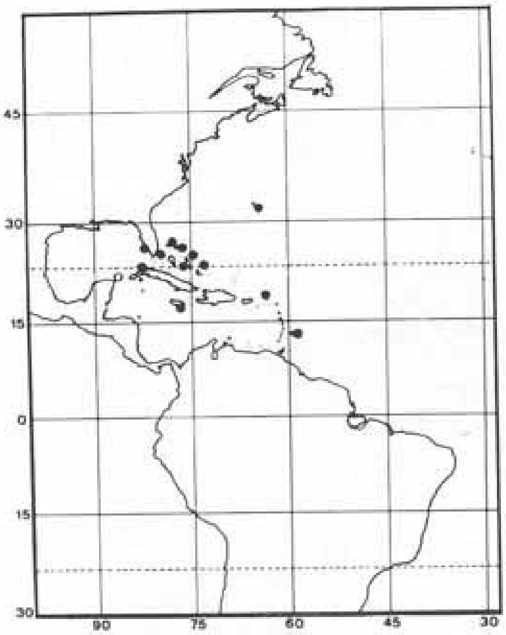


FIG. 101. *Laemodonta cubensis*, geographic distribution. Open circle, locality from literature.

tella aequalis (Lowe) (Figs. 89, 90). The strength of the palatal tooth of the aperture (Figs. 85, 88), the similarity of the radular teeth and the presence of the pallial gland (personal observations) also suggest a generic relationship between *Laemodonta cubensis* (Pfeiffer) and *Ovatella aequalis* (Lowe).

Habitat: *Laemodonta cubensis* lives at or just below the high-tide mark, aggregating under half-buried porous rocks, rotting wood and leaves, and among the roots of propagules, together with *Pedipes, Blauneria, Microtralia* and *Creedonia*. It is common, along with *Pedipes*, in rocky areas, either under loose stones near the sediment, or in crevices in rock beds at about the high-tide mark. They prefer the part of loose stones that touches the sediment.

Range: Bermuda; Captiva Island, on the western coast of Florida, south to the Florida Keys; Bahamas and Cuba, Jamaica south to Barbados; Mexico (Vokes & Vokes, 1983) (Fig. 101).

Specimens Examined: FLORIDA: Third Ragged Key above Sand Key (USNM 462737, 614608); Key Largo (MCZ 235475); N of Tavernier Key, Key Largo (A.M.); S of Ocean Drive, Plantation Key (A.M.); Indian Key Fill, N of Indian Key Channel (A.M.); Indian Key (USNM 462893, 492557); Long Key (A.M.); Grassy Key (A.M.); Crawl Key (MCZ 235469; A.M. Bonefish Key (ANSP 174978, 219861; MCZ 110178; USNM 599365); Knight Key (A.M.); Bahia Honda Key (ANSP 104109; MCZ 235472; USNM 492464); West Summerland Key (A.M.); Big Pine Key (ANSP 104110); Long Beach Drive and W end of Kohen Avenue, both Big Pine Key (A.M.); Little Torch Key (MCZ 235470); Big Torch Key (A.M.); Ramrod Key (MCZ 235471); Sugarloaf Key (ANSP 89559); Boca Chica Key (ANSP 104111; USNM 270348); Garden Key, Dry Tortugas (USNM 492509, 492522); Seminole Point (ANSP 105438); Captiva Island (ANSP 149410). BERMUDA (ANSP 62842, 293543; MCZ 24229; USNM 250298): Fairyland (ANSP 99078); N of Shelly Bay Beach (A.M.); North of Long Bird Bridge (A.M.); near St. Georges (ANSP 100821); Castle Harbour (ANSP 143321); Hungry Bay (A.M.); W of Somerset Bridge (A.M.); Ely's Harbour (A.M.); Mangrove Bay (A.M.). BAHAMAS ISLANDS: GRAND BAHAMA ISLAND: Hepburn Town, Eight Mile Rock (ANSP 375427, 375455); Bell Channel, Lucaya (ANSP 370709); Dead Mans Reef [Sandy Bevan's Cay] (ANSP 371224); Bahama Beach Canal (ANSP 371802); Silver Cone Canal (ANSP 372886); North Riding Point (ANSP 375563); West End (ANSP 368764); GREAT ABACO ISLAND: Mores Island (MCZ 116720); Sand Bank, Crossing Bay (MCZ 235474); S of Witch Point (MCZ 235478); Wilson City (MCZ 235479); North Hawksbill Creek (ANSP 370566); ANDROS ISLAND (ANSP 151873): Morgan's Bluff (A.M.); South Mastic Point (A.M.); Mangrove Cay (USNM 590609, 614605); Solomon Pond, Mangrove Cay (USNM 614606); First island off Mintie Bar, SE of South Bight (USNM 590610, 614607); NEW PROVIDENCE ISLAND: Bar Point (A.M.); W of Rock Point (A.M.); W of Clifton Point (A.M.); E of Clifton Pier (A.M.); shore of Millars Road (A.M.); Malcolm Creek (A.M.); ELEUTHERA ISLAND: S of Rock Sound (MCZ 235473); EXUMA CAYS: NE coast, Hog Cay (MCZ 235476), Western End, Hog Cay (MCZ 235477). CUBA (ANSP 22544): near Habana (ANSP 130743); El Vedado, Habana (MCZ uncatalogued). JAMAICA: Falmouth (ANSP 397272); Robin's Bay (USNM 442000). PUERTO RICO: San Juan (R.B.). VIRGIN ISLANDS: ST. THOMAS (USNM 6427). LESSER ANTILLES: BARBADOS: off Lazareto (USNM 502107).

Subfamily Pedipedinae
Fischer & Crosse, 1880

Pedipedinae Fischer & Crosse, 1880: 5.

Description: Shell to 11 mm long, globose to elongate. Spire low to high, with as many as six and one-half whorls. Body whorl 80–90% of shell length. Aperture broad to narrow; columellar teeth one or two; parietal teeth one or two; outer lip smooth, with one strong tooth or with internal axial, ribbed callosity (*Pseudomelampus*). Inner whorls resorbed except in *Pedipes* and *Creedonia*.

Animal whitish; foot transversely divided (except in *Microtralia*), posteriorly tapered, tip rounded. Mantle skirt broad, fused posteriorly. Pallial cavity not occupying entire body whorl; kidney white, long to broadly triangular; pneumostomal glands white and anterior to kidney; anal gill well developed; mantle organ lacking.

Radula having very variable formula. Central tooth slightly posterior to lateral teeth, unicuspid or tricuspid. Lateral teeth bicuspid. Transition to marginal teeth gradual. Marginal teeth with as many as five cusps.

Digestive system with mandible broadly rectangular, composed of numerous longitudinal fibers. Salivary glands white, small, fusiform. Digestive gland of two roughly equal lobes; anterior lobe empties into crop through wide anterior diverticulum, just before crop enters stomach; posterior lobe empties into gastric caecum through posterior diverticulum. Stomach tripartite, middle section very muscular and with a caecum.

Reproductive system with hermaphroditic duct not convoluted (except in *Marinula s.s.*), posteriorly dilated; anterior mucous gland and prostate gland extending over proximal half of spermoviduct; bursa duct emptying just posterior to female opening, at which vas deferens separates from vagina (except in *Pseudomelampus* and *Leuconopsis*). Penis thick, usually with more or less developed diverticulum, simple in *Microtralia;* vas deferens free, enters penis apically; penial retractor short, attached to columellar muscle or to floor of pallial cavity.

Nervous system with cerebral ganglia well developed; cerebropedal connectives about as long as cerebropleural connectives; pleuroparietal connectives and parietovisceral connectives very short, somewhat longer in *Leuconopsis.*

Remarks: Fischer & Crosse (1880) created the subfamily Pedipedinae for *Pedipes,* the only ellobiid genus then known to retain its inner whorls. On the basis of radular characters Odhner (1925) added to the subfamily the genera *Marinula* and *Plecotrema* [= *Laemodonta*], Thiele (1931) included *Pseudomelampus* and *Leuconopsis* and Morton (1955c) added *Rangitotoa* [= *Microtralia*]. In 1959 Zilch transferred *Rangitotoa* to the Melampinae and added *Apodosis,* which I consider a junior synonym of *Leuconopsis.* Abbott (1974) listed *Microtralia* within the Cassidulinae and erroneously considered *Ovatella* [*sensu Myosotella*] to belong to the Pedipedinae. My analysis of nervous and reproductive systems leads to the inclusion of *Microtralia* in the Pedipedinae and to the removal of *Laemodonta, Ovatella* and *Myosotella* to the Pythiinae. A new genus, *Creedonia,* is here created upon the basis of the conchological and radular characters of *Creedonia succinea* (Pfeiffer, 1854), formerly placed in the genus *Marinula. Creedonia* does not resorb the inner whorls, its central and lateral radular teeth are broad with only a few in a row and the marginal teeth have several endocones but lack ectocones. The radulae in those species of *Marinula* studied have numerous, very long, narrow lateral teeth and marginal teeth with one endocone and several ectocones (Figs. 163–168).

The subfamily is best characterized anatomically. The nervous and reproductive systems have very consistent patterns, whereas the shell and radula vary somewhat. The short connectives of the visceral ring cause the concentration of those ganglia. This feature also exists in the Melampinae and sets these two groups apart from the remaining subfamilies, which have long visceral ring connectives. The cerebral ganglia in the Pedipedinae are proportionally much larger than the other ganglia. The reproductive system differs from that of the Melampinae by its acinose ovotestis, its unconvoluted seminal vesicle of the hermaphroditic duct, its longer spermoviduct, its junction of the bursa duct near the female opening, and its elaborate penial complex, sometimes with a long diverticulum. From the other three subfamilies it differs by its elaborate penial complex with free anterior vas deferens, and by its prostate and anterior mucous glands that cover only the posterior half of the spermoviduct.

The genus *Leuconopsis* deviates in some anatomical features from the typical Pedipedinae pattern in that its visceral nerve ring is longer and its reproductive system is semidiaulic, the vas deferens and vagina separating from the common spermoviduct halfway along the pallial gonoduct. The visceral nerve ring is not so long as that of any of the species belonging to the Pythiinae and Ellobiinae here studied and does not justify *per se* the exclusion of *Leuconopsis* from the Pedipedinae. The organization of the pallial gonoducts of *Leuconopsis* resembles that of *Pseudomelampus* (Martins, personal observation) in that the vas deferens separates from the spermoviduct some distance before reaching the female opening, giving rise to a long, nonglandular vagina. The arrangement of the reproductive organs in *Leuconopsis* is, then, within the range of variation seen within the Pedipedinae. Shell and radular characters also justify the inclusion of *Leuconopsis* within the Pedipedinae.

The Pedipedinae are represented in the West Indies by *Pedipes, Creedonia, Leuconopsis* and *Microtralia,* all of which are readily distinguishable on conchological characters. *Pedipes* is globose, generally heavily sculptured, with two strong columellar teeth, a large oblique, posteriorly placed parietal tooth and a readily visible callous tooth on the outer lip, opposite the parietal tooth. *Creedonia* has an apertural configuration similar to that of *Pedipes,* but lacks the tooth on the outer lip and has an elongate, smooth and very thin shell. The minute *Leuconopsis* has an elongate, thick shell that lacks the parietal and teeth on the outer lip. The shell of *Microtralia* is very thin and transparent and has a long, narrow aperture with the outer lip smooth inside, one columellar tooth and two anteriorly placed parietal teeth, of which the anterior is the strongest.

Habitat: The Pedipedinae are a group of small species that live at or below the high-tide zone (Morton, 1955c; Martins, 1980), sometimes reaching the low intertidal area (Spencer, 1979). They live mainly in crevices and under half-buried rocks. Some (*Creedonia, Microtralia*) live in the soft, black sediment of the high-tide region of mangroves, or in the spaces around the underground root system of propagules and adult plants.

Range: Worldwide, warm and temperate areas. In the Western Atlantic the Pedipedinae occur in Bermuda and from south Florida to the West Indies, Central America south to Brazil, Ascension Island and Tristan da Cunha (Connolly, 1915).

Genus *Pedipes* Scopoli, 1777

Pedipes Scopoli, 1777: 392. Type species by subsequent designation of Gray (1847a): *Pedipes afra* (Gmelin, 1791) [= *Pedipes pedipes* (Bruguière, 1789)].

Carassa Gistel, 1847 [1850]: 555 [substitute name for *Pedipes* Scopoli].

Description: Shell to 6 mm long, globose, solid to fragile, white to dark brown. Spire low, with as many as five rapidly expanding convex whorls, with incised spiral grooves. Body whorl averaging 87% of shell length. Aperture about 70% length of body whorl, ovate, widely rounded at base; exposed portion of columella flat and depressed, with two strong columellar teeth, posterior one stronger; parietal tooth strongest, oblique; outer lip sharp, smooth or with thick, elevated tooth opposite parietal tooth. Inner whorls not resorbed. Protoconch with apex involute in first teleoconch whorls, smooth, translucent, yellowish to brown.

Animal grayish; tentacles long, pointed, with transparent base, blackish toward tip.

Radula with 150 to 450 teeth in a row; first 30 to 40 rows without marginal teeth. Central tooth at same level as lateral teeth; base long, slightly indentate anteriorly, wide and angular in first quarter, longitudinally depressed in the middle, becoming narrower posteriorly; crown as wide as base, falciform, with long mesocone. Lateral teeth as narrow as but longer than central tooth, laterally compressed; base irregularly thickened longitudinally; crown falciform, laterally compressed; mesocone long; endocone half length of mesocone, pointed. Transitional teeth four to eight, with base becoming shorter, crown becoming wider; two or three endocones. Marginal teeth cteniform, with very thin, short base; wide rounded crown, connected to base by long neck bent upwards; as many as six short endocones; mesocone somewhat stronger than endocones.

Visceral mass coiled. Digestive gland yellowish; posterior diverticulum becoming pouch-like before entering anterior portion of gastric caecum. Stomach tripartite; anterior thin-walled, pouch-like section that receives crop on left and empties into intestine on right; middle thick-walled, very muscular gizzard; posterior membranous, extensible caecum that receives posterior diverticulum at junction with gizzard. Ovotestis acinose, embedded in posterior lobe of digestive gland; hermaphroditic duct dilated along most of its length; bursa spherical. Penis unevenly thickened, convoluted in middle. Cerebral commissure long; connectives of visceral ring very short; penial nerve originating from right middle labial nerve.

Remarks: The name *Pedipes* was first used by Adanson (1757), who gave a very detailed and accurate description of a species from Senegal later described as *Pedipes pedipes* and accepted as the type species of the genus. Adanson, a contemporary of Linnaeus, derived the generic group name from the French word, pietin, meaning pedestrian, which refers to the way in which the animal progresses, first advancing the anterior half of the transversely divided foot, then moving the posterior half, seemingly advancing by steps. Adanson's work (1757) antedates the starting point of zoological nomenclature and therefore he is not credited with introducing *Pedipes*. The first post-Linnaean use of *Pedipes* was that of Scopoli (1777), who briefly characterized *Pedipes* "Adanson" as having the shell aperture diversely dentate. The only known species, not mentioned by Scopoli, was Adanson's African "pietin," introduced by Bruguière (1789) as *Bulimus pedipes*. *Helix afra* Gmelin, 1791 [= *Pedipes pedipes* (Bruguière, 1789)] was designated type species of *Pedipes* by Gray (1847a).

Férussac (1821) used *Pedipes* in a restricted sense but Blainville (1824), using the sharp outer lip as the major diagnostic character, included a heterogeneous assemblage, i.e., *Conovulus* [= *Melampus*] and the opisthobranch genus *Tornatella*. Lowe (1832), following Lamarck (1822) and Menke (1828), treated *Pedipes* as a genus of the family "Plicacea" and tried to prove that the animal was a pectinibranch. After Crosse & Fischer (1879) noticed that *Pedipes* was the only known ellobiid that did not resorb the inner whorls of the shell, the genus could be separated easily from otherwise conchologically similar groups, e.g., *Marinula*. In this study the genus *Creedonia* too was found not to resorb the inner whorls. The radula of *Pedipes* too is unique because the posteriormost 30 to 40 rows lack marginal teeth (Fig. 140).

The genus *Pedipes* is represented in the Western Atlantic by two species. The larger (6 mm) *Pedipes mirabilis* has a thick, globose, generally heavily sculptured shell; the visible part of the protoconch consists of hardly more than one whorl and has a sinuous, elongate apertural lip. The smaller (3.5 mm), more elongate *Pedipes ovalis* has a thicker-shelled, rock-dwelling form and a thinner-shelled, mangrove-inhabiting form. The protoconchs of both forms are identical, with more than one and one-third whorls visible and with round, not sinuous, apertural lips.

Habitat: The genus *Pedipes* lives in mangroves near the sea, in which animals are abundant under fallen leaves and branches below the high-tide mark. They also live along open rocky shores in crevices and under stones frequently covered by waves at high tide.

Range: Worldwide, warm temperate to tropical regions. In the Western Atlantic they occur in Bermuda, southern Florida to Texas, the West Indies and Central America south to Brazil and Ascension Island.

Pedipes mirabilis (Mühlfeld, 1816)
Figs. 102–106, 108–110, 112–120

Turbo mirabilis Mühlfeld, 1816: 8, pl. 2, figs. 13a, b [Locality unknown, herein designated Cabo Rojo lighthouse, Puerto Rico; type specimens presumed lost, *fide* Clench (1964); neotype herein designated MCZ 188476a (Fig. 102)].

Pedipes mirabilis (Mühlfeld). Beck, 1837: 105; Pfeiffer, 1856a: 70; Pfeiffer 1876: 333; Mörch, 1878: 5; Nevill, 1879: 221; Pilsbry, 1900b: 503; Dall & Simpson, 1901: 369, pl. 53, fig. 8; Aguayo & Jaume, 1947: 218; Morrison, 1951b: 9; Morrison, 1958: 121 [ecology]; Nowell-Usticke, 1959: 88; Warmke & Abbott, 1961: 152, pl. 28, fig. j; Rios, 1970: 138; Morris, 1973: 274, pl. 74, fig. 12; Rios, 1975: 159, pl. 48, fig. 767; Rosewater, 1975: 23; Emerson & Jacobson, 1976: 189, pl. 21, fig. 20; Rehder, 1981: 648, fig. 234; Vokes & Vokes, 1983: 60, pl. 31, fig. 16 [juvenile; not positively this species]; Mahieu, 1984: 314 pp; Jensen & Clark, 1986: 458, figured.

Pedipes quadridens Pfeiffer, 1840: 251 [Cuba; location of type unknown]; C. B. Adams, 1849: 41, 42; C. B. Adams, 1851: 186; Pfeiffer, 1854b: 148; Shuttleworth, 1854b: 102; H. & A. Adams, 1855b: 149; Shuttleworth, 1858: 73; Poey, 1866: 394.

Pedipes globulosus C. B. Adams, 1845: 12 [Jamaica; lectotype by Clench & Turner (1950), MCZ 177347 (Fig. 103)]; Clench & Turner, 1950: 288, pl. 49, fig. 9.

Pedipes globulsus "Petit" Pfeiffer, 1856a: 70 [Haiti; type from Cuming's collection, not seen at BMNH]; Pfeiffer, 1876: 333. *Non* "Férussac" H. & A. Adams, 1854 (*nomen nudum*).

Pedipes mirabilis (Mühlfeld) [in part] Arango y Molina, 1880: 60; Dall, 1889: 92, pl. 47, fig. 17; Crosse, 1890: 259; Kobelt, 1900: 255, pl. 24, figs. 19, 20; Maury, 1922: 54; C. W. Johnson, 1934: 159; M. Smith, 1937: 145, pl. 55, fig. 8 [probably *Pedipes ovalis;* pl. 67, fig. 17 is *Pedipes ovalis*]; M. Smith, 1951: [same illustrations as in first edition, 1937]; Clench, 1964: 119, pl. 76, figs. 1, 3, pl. 77 [fig. 2 is lectotype of *Pedipes ovalis* C. B. Adams; systematics, distribution]; Andrews, 1971: 144, text fig. [figure probably is of *Pedipes ovalis*]; Abbott, 1974: 333, fig. 4096 [in part]; Andrews, 1977: 181, text fig. [figure probably is of *Pedipes ovalis*].

Pedipes mirabilis Megerle. Peile, 1926: 88.

Description: Shell (Figs. 102–106, 108–110) to 6 mm long, globose, very solid, white to brown. Spire low, as many as five convex whorls, sculptured with incised spiral grooves and fine axial striae. Body whorl averaging 88% of shell length, with average of 22 deeply incised spiral grooves. Sculpture as on spire; spiral grooves sometimes subdivided by fine spiral cords. Aperture about 70% of length of body whorl, widely ovate, round to angular at base, sometimes with weak angle at shoulder; columella flat and weakly concave, with two strong, rounded, subequal teeth perpendicular to columellar axis; parietal tooth strongest, oblique and slightly curved anteriorly; outer lip wide and smooth in juveniles, thick and crenulated in adults owing to grooves of body whorl; opposite parietal tooth one large tooth very weakly extends inside aperture. Protoconch with barely more than one whorl visible, apertural lip sinuous (Figs. 108–110).

Radula (Figs. 112–116) as in genus; formula $[120 + (6 + 70) + 1 + (70 + 6) + 120] \times 120$.

Stomach (Fig. 117) as in genus.

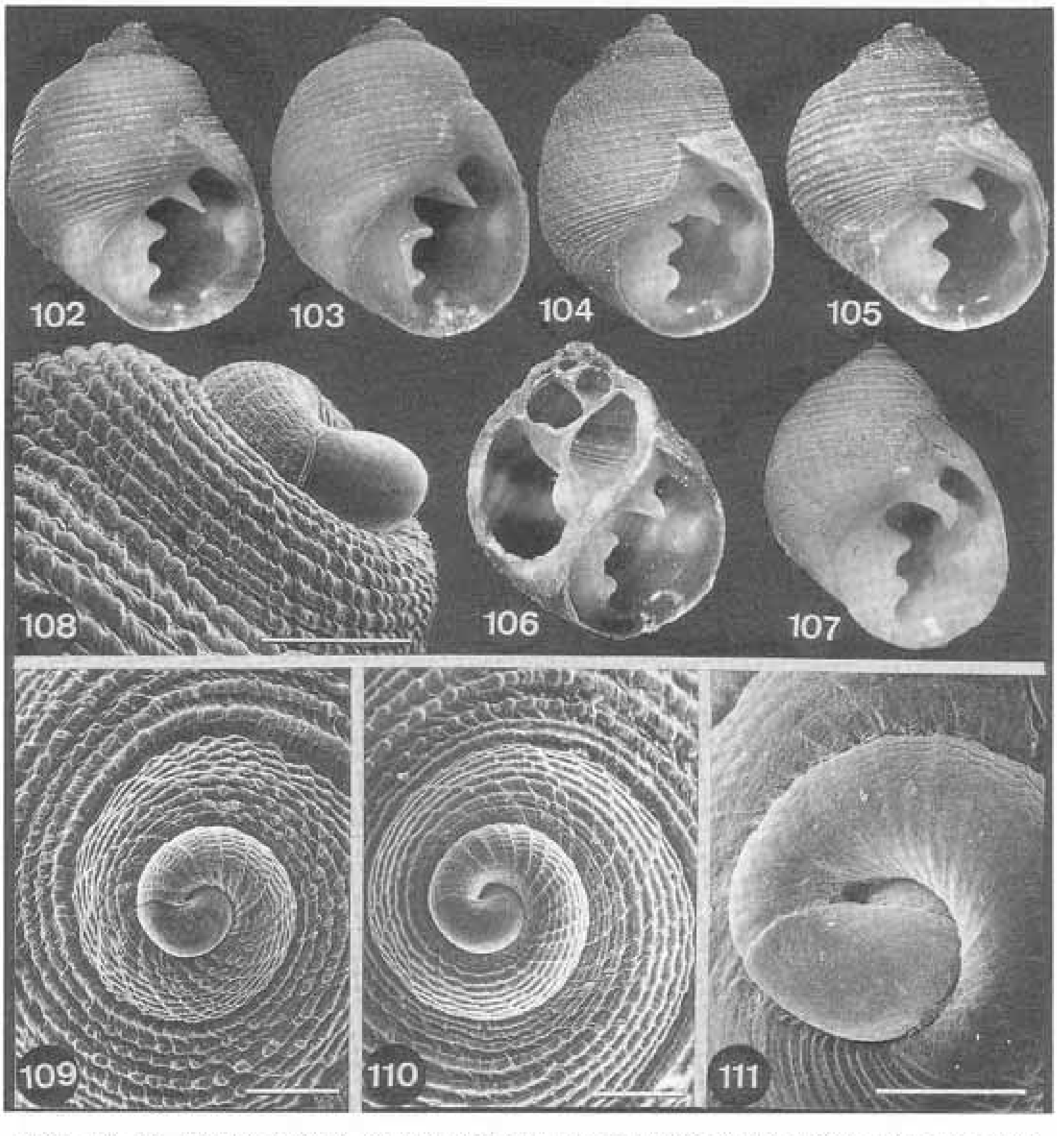
Reproductive system (Fig. 118) with hermaphroditic duct with longitudinally dilated seminal vesicle; bursa duct longer than spermoviduct and albumen gland conbined. Posterior half of penis thicker than anterior portion.

Nervous system (Fig. 119): left cerebropedal and cerebropleural connectives longer than right ones; left parietovisceral connective twice length of right one; visceral ganglion largest of five in visceral ring; left pleural and left parietal ganglia smaller than right counterparts.

Remarks: In spite of the great variability shown by West Indian *Pedipes,* recent authors consider all of the named forms conspecific. According to Clench (1964) variability in *Pedipes* is a result of colonization strategy. Most colonies might have begun from one individual or from one cluster of eggs. Clench based this observation upon the meager representation of *Pedipes* in museum collections, because he clearly stated (p. 118), "there is nothing in the literature . . . concerning their life history." The colonies are not so rare as Clench implied. *Pedipes* species are among the most common West Indian ellobiids just below the high-tide mark, at least in mangroves (Martins, personal observation).

Pedipes mirabilis prefers piles of loose rocks around the high-tide mark. The shell is always thick, deeply grooved, with the aperture constricted in adults by a thick outer lip tooth. The body whorl of gerontic animals shows asymmetric growth. The name "*quadridens*" of Pfeiffer (1840) reflects the change in apertural aspect with age, and the names "*globulosus*" of C. B. Adams (1845) and "*globulus*" of Pfeiffer (1856a) refer to the allometric growth of this species.

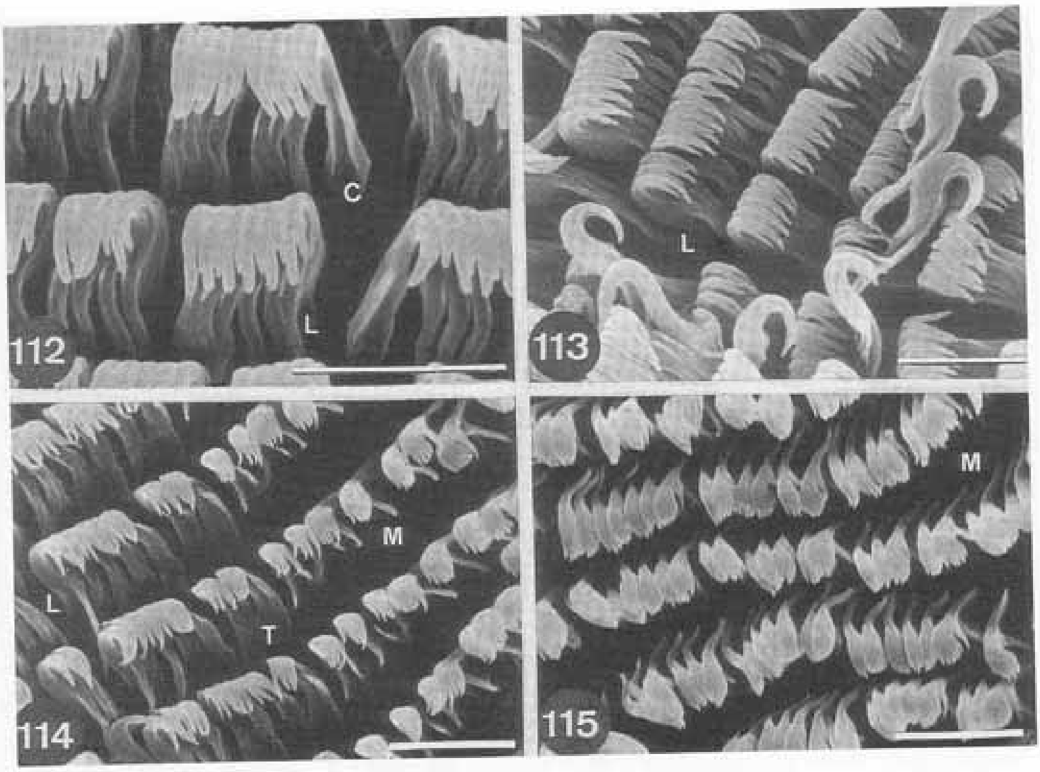
In 1849 C. B. Adams cautiously introduced *Pedipes ovalis,* calling attention to its strong affinity with Pfeiffer's *Pedipes quadridens.* Although the latter species is here considered a junior synonym of *Pedipes mirabilis, Pedipes ovalis* is recognized here as a separate species on the basis of size, sculpture and protoconch. The thick-shelled, heavily toothed *Pedipes ovalis* that C. B. Adams described from Jamaica rarely occurs in mangroves (Martins, personal observation), where the much thinner-shelled, smoother *Pedipes tridens* Pfeiffer [= *Pedipes ovalis* C. B. Adams] abounds. Their similar protoconchs and the sizes suggest, however, that both rock-dwelling and mangrove-dwelling forms are expressions of the same species. The simi-



FIGS. 102–111. *Pedipes*. (102) *P. mirabilis* (Mühlfeld), neotype (MCZ 188476a), Cabo Rojo lighthouse, Puerto Rico, sl 4.7 mm. (103) *P. globulosus* C. B. Adams, lectotype (MCZ 177347), Jamaica, sl 4.6 mm. (104) *P. mirabilis*, Puerto Cabello, Venezuela, sl 6.0 mm. (105) *P. mirabilis*, Rio Grande do Norte, Brazil (ANSP 300179), sl 3.8 mm. (106) *P. mirabilis*, Morgan's Bluff, Andros Island, Bahamas, sl 5.0 mm. (107) *P. pedipes* (Bruguière), Senegal (AMNH 22590), sl 7.7 mm. (108) *P. mirabilis*, lateral view of spire and protoconch, Maravén, Venezuela. (110) *P. mirabilis*, top view of spire and protoconch, Shelly Bay, Hamilton, Bermuda. (111) *P. pedipes*, top view of spire and protoconch, São Miguel, Azores. Scale 1 mm.

larities of *Pedipes ovalis* with *Pedipes mirabilis* should, then, be interpreted as adaptations for life in rocky environments. A more detailed comparison between these two species is presented under the remarks on *Pedipes ovalis*.

Pedipes mirabilis is similar to the Eastern Atlantic *Pedipes pedipes* (Bruguière), mostly in the shape of the protoconch (Fig. 111). The Eastern Atlantic species, however, has a double outer lip tooth and a bifid, downward-curved parietal tooth (Fig. 107).



FIGS. 112–115. *Pedipes mirabilis*, radular teeth. (112) Shelly Bay, Bermuda, sl 2.3 mm. (113–115) El Palito, Venezuela, sl 3.2 mm. Scale 50 µm.

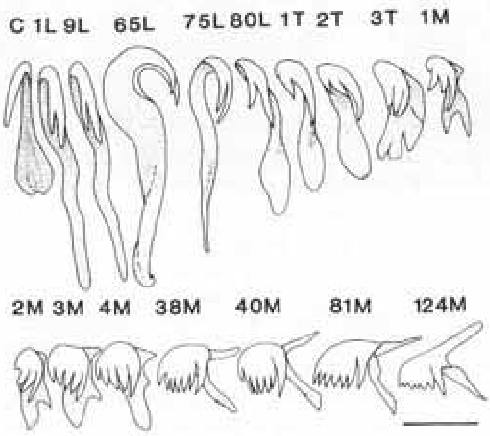


FIG. 116. *Pedipes mirabilis*, radula, El Palito, Venezuela. Scale 10 µm.

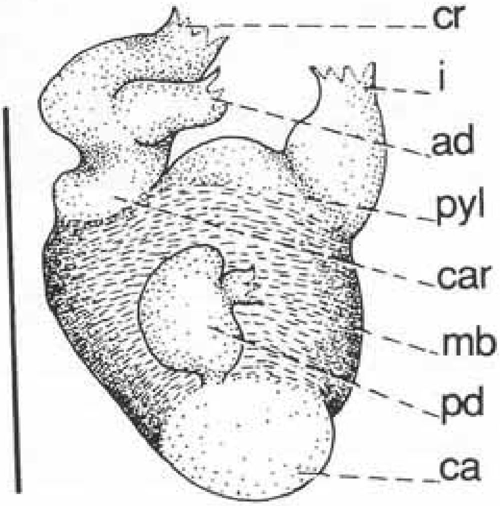


FIG. 117. *Pedipes mirabilis*, stomach, Bahamas. Scale 1 mm.

H. & A. Adams (1854) listed a *Pedipes globulus* Férussac, which might be confused with the homonym introduced by Pfeiffer

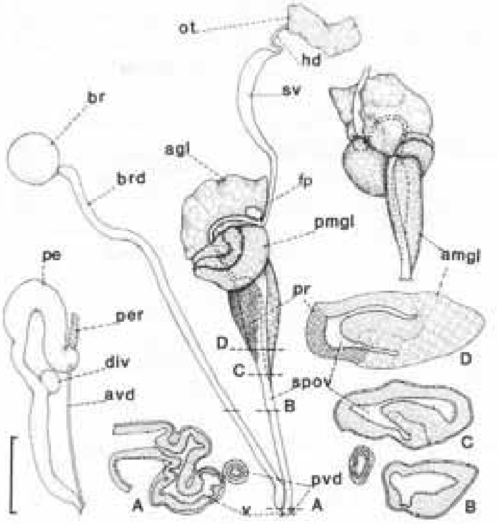


FIG. 118. *Pedipes mirabilis,* reproductive system, Clifton Pt., New Providence, Bahamas. A-C, transverse sections and their locations. Scale 1 mm.

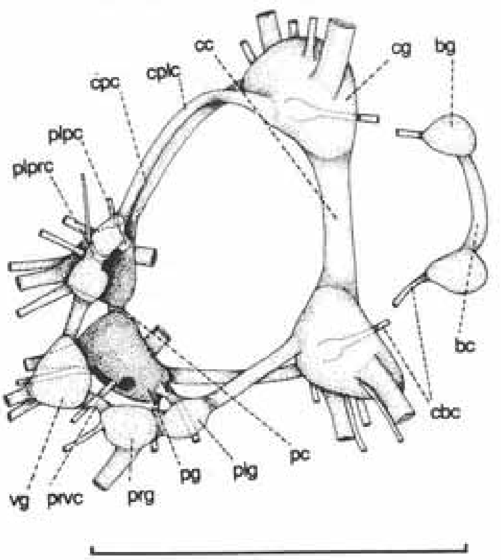


FIG. 119. *Pedipes mirabilis,* central nervous system, Clifton Pt., New Providence, Bahamas. Scale 1 mm.

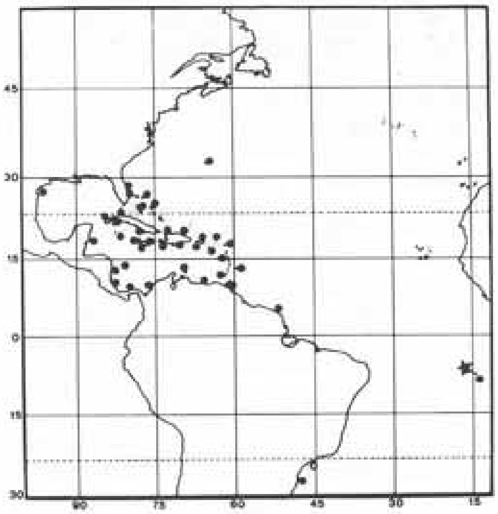


FIG. 120. Geographic distributions, *Pedipes mirabilis* (circles) and *Leuconopsis manningi* (star). Open circle, locality from literature.

(1856a) for a West Indian specimen. Such a name does not appear in Férussac (1821). The Adams brothers might have intended to refer to *Pedipes ovulus,* which Férussac (1821: 109) described as "longer than *afra* [= *Pedipes pedipes*], smooth and shiny, without tooth on the outer lip." Perhaps Férussac was dealing with a specimen of *Marinula,* which Connolly (1915) with doubt referred to *Marinula xanthostoma* H. & A. Adams. *Pedipes globulus* was described by Pfeiffer (1856a) using Petit's manuscript name in the Cuming collection, and it is considered synonymous with *Pedipes mirabilis.* The name *Pedipes globulus* "Férussac" H. & A. Adams should be considered a *nomen nudum.*

A *Pedipes,* tentatively assigned to *Pedipes mirabilis,* was found in the Early Miocene Cantaure Formation in Venezuela (Gibson-Smith & Gibson-Smith, 1979). Recently (1985) the Gibson-Smiths described those fossils as *Pedipes mirandus,* which I consider a junior synonym of *Pedipes ovalis* (see the remarks for this species).

Habitat: Pedipes mirabilis usually lives on rocky shores, often where wave action is strong. The animals aggregate in fairly large numbers under rocks at or just below the high-tide mark.

Range: Bermuda; Florida, Texas; West Indies, Central America, northern South America to São Paulo, Brazil (Rios, 1975); Ascension Island (Fig. 120).

Specimens Examined: FLORIDA: Daytona (USNM 162346, 253173); Indian River (USNM 758222); Lake Worth (MCZ 205366;

USNM 599349); Palm Beach Inlet (MCZ 110215; USNM 543392); Boca Raton (ANSP 219865); S Bayshore Dr., Miami (USNM 701950); Biscayne Bay (MCZ 291105); Haulover Beach Park, Biscayne Bay (USNM 809777). TEXAS: Port Aransas (MCZ 225522, 229626); Mustang Island, Port Aransas (MCZ 235614); South Padre Island (ANSP 319092; USNM 758649); Port O'Connor (USNM 711183). BERMUDA (ANSP 48599, 62741; MCZ 9952, 24251, 167937): Flatts (USNM 171948); Shelly Bay (MCZ 25523; A.M.); N of Long Bird Bridge (A.M.); W of Somerset Bridge (A.M.); Ireland Island (USNM 712378). BAHAMA ISLANDS: GRAND BAHAMA ISLAND: W of Eight Mile Rock (R.B.); Hepburn Town, Eight Mile Rock (ANSP 370410); Caravel Beach, Freeport (ANSP 370228); Tamarind Shipway, Lucaya (ANSP 370708); GREAT ABACO ISLAND: Wilson City (ANSP 299513; USNM uncatalogued); Sweeting's Village (MCZ 24142); Sand Bank, Crossing Bay (MCZ 116721); Mores Island (MCZ 116719); ANDROS ISLAND: Morgan's Bluff (A.M.); South Mastic Point (A.M.); Mangrove Cay (USNM 180462a); PARADISE ISLAND (A.M.); NEW PROVIDENCE ISLAND: Bar Point (A.M.); Delaport Point (A.M.); Rock Point (A.M.); Clifton Point (A.M.); E of Clifton Pier (A.M.); ROYAL ISLAND (MCZ 78360). CUBA: El Vedado (MCZ 167983); Matanzas Bay (ANSP 167481; MCZ 83308, 109334, 167984); Peñas Altas (MCZ 127866); Playa de Bellamar (ANSP 222590, 345332); Versalles (MCZ 92075); Muelle de la Aduana, Matanzas (MCZ 188903); Chivera, Bahia de Santiago (MCZ 167985); Cayo Francés (MCZ 167982); Guantánamo Bay (ANSP 313059). JAMAICA (ANSP 22565, 22570, 22572; MCZ 117347, 117348, 185170; USNM 90459, 94747): Montego Bay (USNM 441609); Robin's Bay (MCZ 167896; USNM 441978); Jack's Bay (MCZ 167895; USNM 441836); Manchioneal (USNM 492493); Port Morant (USNM 423674); Rock Fort (MCZ 167894; USNM 423792); Kingston (USNM 442594); Kingston Harbor (MCZ 314005); Palisadoes (USNM 442540); Mouth of Rio Cobre, Port Royal (USNM 426870); Hunt's Bay (USNM 441675); Little River (USNM 492506). HAITI: St. Louis (MCZ 167899; USNM 439397); Port Salut (MCZ 167891; USNM 440000); Les Cayes (USNM 439780); Aquin (USNM 367339, 440107); Baïe Anglaise, near Aquin (USNM 439605); Saltrou (MCZ 167897, 167898, 223892; USNM 439341); W of Metesignix (USNM 404730); Bizoton (USNM 439843). DOMINICAN REPUBLIC: Santo Domingo (ANSP 60920; USNM 492507); Santa Bárbara de Samaná (ANSP 173412; MCZ 57783); Cayo Chico, 4 km E of Santa Bárbara de Samaná (MCZ 57784). PUERTO RICO: Piñones, W of Boca de Cangrejos (A.M.); Puerta de Tierra, San Juan (A.M.); Punta Arenas, N of Joyuda (A.M.); Cabo Rojo lighthouse (MCZ 188476, 188476a); Humacao (MCZ 166297); Ensenada Honda, Culebra Island (USNM 159675). VIRGIN ISLANDS: ST. CROIX (USNM 621393, 706774): Christiansted (MCZ 188477); ST. THOMAS (ANSP 22569; USNM 119543); GUANA ISLAND: North Beach (MCZ 89245); ST. JOHN (ANSP 22568). LESSER ANTILLES: ST. THOMAS (MCZ 294220); ST. KITTS (MCZ 167935); BARBUDA: Spanish Point (ANSP 353819); GUADELOUPE (ANSP 22566; MCZ 181419); MARTINIQUE (MCZ 167936, 294221; USNM 612694); Pointe Pie, 2.5 km S of Ste. Anne (MCZ 248315); GRENADINES: Union, Admiralty Bay, Bequia Island (MCZ 216484); BARBADOS (MCZ 167900, 167939; USNM 502106); TOBAGO: Buccoo Bay (ANSP 188276); TRINIDAD (MCZ 90508): Toco (MCZ 62326). CARIBBEAN ISLANDS: CAYMAN ISLANDS: Cayman Brac (MCZ 294222); ARUBA (USNM 663655). CURAÇAO: Port Marie & Daaibooi Baai (R.B.). COSTA RICA: Portete (USNM 702836, 706405). PANAMA: Toro Point, Fort Sherman (USNM 734066); Limon Bay, inside Toro Point (USNM 732870; R.B.); Fort Randolph (USNM 759237). COLOMBIA: Sabanilla (MCZ 167890; USNM 103468, 193615). VENEZUELA: Cayo Punta Brava (A.M.), Parque Nacional de Morrocoy, Tucacas (A.M.); El Palito (A.M.); Puerto Cabello (A.M.); Maravén, Borborata (A.M.). BRAZIL: Praia do Forte, Natal, Rio Grande do Norte (ANSP 300179). ATLANTIC ISLANDS: ASCENSION ISLAND (USNM 735717).

Pedipes ovalis C. B. Adams, 1849
Figs. 121–148

Pedipes ovalis C. B. Adams, 1849: 41 [Jamaica; lectotype by Clench & Turner (1950) MCZ 177349 (Fig. 121)]; C. B. Adams, 1851: 186; Pfeiffer, 1854b: 148; H. & A. Adams 1855b: 249; Pfeiffer, 1856a: 70; Pfeiffer, 1876: 333; Clench & Turner, 1950: 321, pl. 141, fig. 14 [lectotype figured]; Morrison, 1951b: 9; Morrison, 1958: 121 [ecology]; Morton, 1955c: 127–168 [evolution].

Pedipes tridens Pfeiffer, 1854b: 148 [*nomen nudum*].

Pedipes tridens Pfeiffer, 1855: 122 [Bermuda and Cárdenas, Cuba, herein restricted to Bermuda; lectotype herein selected BMNH 1967590 (Fig. 122)]; H. & A. Adams, 1855b: 249; Pfeiffer, 1856a: 72; Pfeiffer, 1876: 333; Pilsbry, 1900b: 503, pl. 62, fig. 10; Peile, 1926: 88; Haas, 1950: 198, pl. 22, fig. 4.

Pedipes naticoides Stearns, 1869: 108, text fig. [Rocky Pt., Tampa Bay, Florida; holotype USNM 37598 (Fig. 123)]; Pfeiffer, 1876: 334; Dall, 1883: 323; Dall, 1885: 279, pl. 18, fig. 17; Simpson, 1889: 69.

Pedipes mirabilis (Mühlfeld) [in part]. Arango y Molina, 1880: 60; Dall, 1889: 92, pl. 47, fig. 17; Crosse, 1890: 259; Kobelt, 1900: 255, pl. 24, figs. 19, 20; Maury, 1922: 54; C.W. Johnson, 1934: 159; M. Smith, 1937: 145, pl. 55, fig. 8 [probably *Pedipes ovalis;* pl. 67, fig. 17 is *Pedipes ovalis*]; M. Smith, 1951: [same illustrations as in first edition, 1937]; Clench, 1964: 119, pl. 76, figs. 1, 3, pl. 77 [fig. 2 is lectotype of *Pedipes ovalis* C. B. Adams; systematics, distribution]; Andrews, 1971: 144, text fig. [figure probably is of *Pedipes ovalis*]; Abbott, 1974: 333, fig. 4096 [in part]; Andrews, 1977: 181, text fig. [figure probably is of *Pedipes ovalis*]. *Non* Mühlfeld, 1816.

Pedipes insularis Haas, 1950: 197, pl. 22, fig. 3 [Lover's Lake, St. George's, Bermuda; holotype FMNH 30171 (not seen); paratype ANSP 212176 (Fig. 124)].

Pedipes mirabilis, forma *ovalis* C. B. Adams. Robertson, 1960: 22.

Pedipes mirandus Gibson-Smith & Gibson-Smith, 1985: 88, fig. 1 [Early Miocene Cantaure Formation, Paraguaná Peninsula, Venezuela; holotype NHMB No. H 17113 (not seen)].

Description: Shell (Figs. 121–139) to 3.5 mm long, oval, solid to thin, yellow to dark brown; spire low, whorls four and one-half, convex, sculptured with incised spiral grooves; microsculpture of grooves composed of very fine, irregular, compressed axial lamellae, sometimes crossed by spiral lines; ribs smoothish, sometimes with incised spiral lines; slightly matte appearance caused by fine growth lines crossing spiral ribs. Body whorl averaging 85% of shell length, with 15 to 34 deeply incised spiral grooves. Aperture about 70% of length of body whorl, widely ovate to squarish, round to somewhat angulate at base; columella flat and weakly concave, with two rounded teeth, the posterior one stronger, anterior one sometimes very weak; parietal tooth oblique, longest; outer lip somewhat angular posteriorly, frequently smooth in thin-shelled forms (Figs. 122–124, 126–128); thick-shelled forms usually with strong, ridge-like tooth opposite parietal tooth, extending inside aperture (Figs. 121, 125, 129, 132). Protoconch with more than one and one-third whorls visible, apertural lip round, not sinuous (Figs. 133–139).

Radula (Figs. 140–144) as in genus; formula $[75 + (5 + 50) + 1 + (50 + 5) + 75] \times 120$.

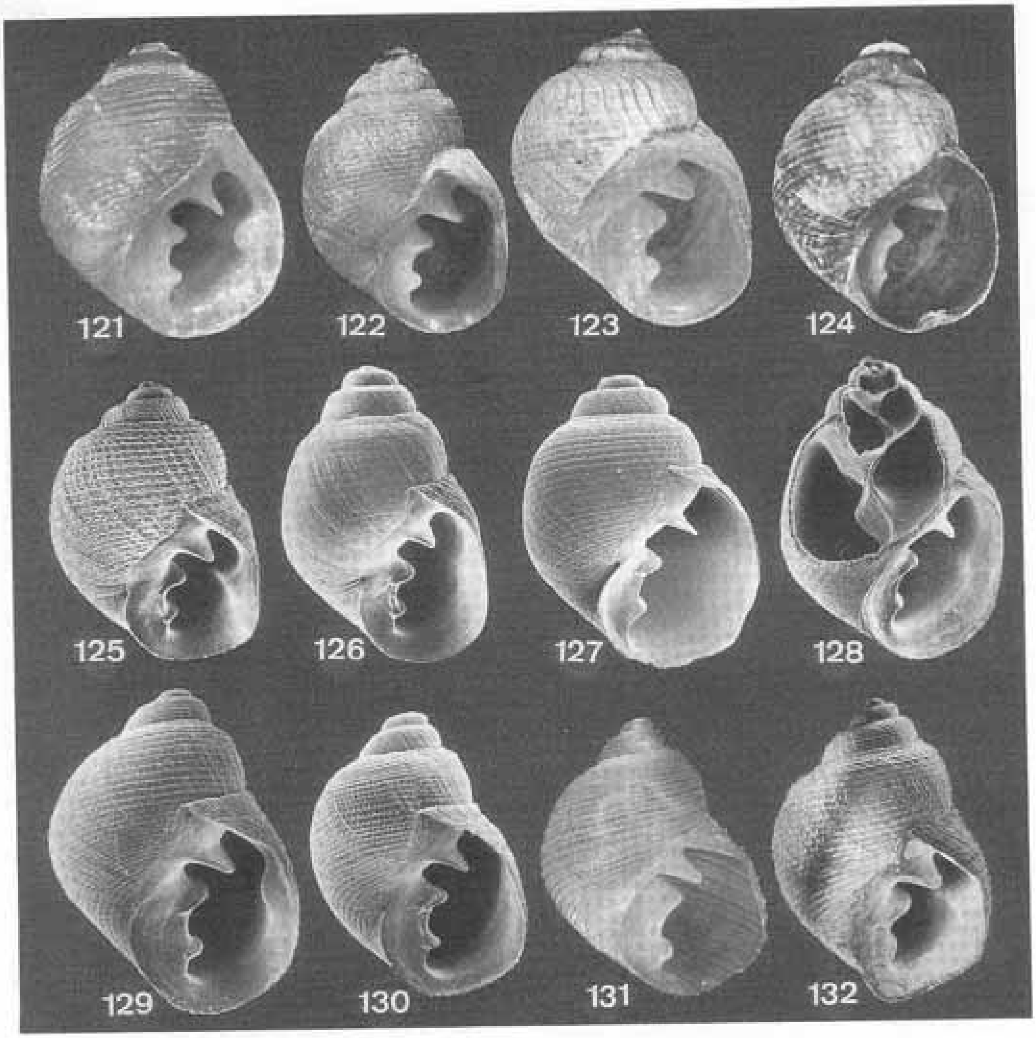
Stomach (Fig. 145) as in genus.

Reproductive system (Fig. 146) with hermaphroditic duct anteriorly dilated to form seminal vesicle; bursa duct shorter than spermoviduct and albumen gland combined. Anterior half of penis thicker than posterior half.

Nervous system (Fig. 147) with left cerebropedal and cerebropleural connectives about twice length of right ones; left parietovisceral connective about as long as right one; visceral ganglion largest of five in visceral nerve ring; left pleural ganglion and left parietal ganglion three times larger than right counterparts.

Remarks: Pedipes ovalis is very variable (Figs. 121–132). A stout, highly sculptured form could be confused with *Pedipes mirabilis.* In fact, C. B. Adams (1849: 41) introduced his description of *Pedipes ovalis* with the words, "*Pedipes ovalis* may be a variety of *Pedipes quadridens* Pfeiffer [= *Pedipes mirabilis* (Mühlfeld)]." As C. B. Adams pointed out, it differs from *Pedipes mirabilis* by the smoothness of its body whorl and the less conspicuous tooth on the outer lip. The outer lip tooth in *Pedipes ovalis* is often ridge-shaped and it gradually diminishes into the aperture, whereas in *Pedipes mirabilis* this tooth is more tubercle-shaped. In *Pedipes ovalis* the anterior columellar tooth usually is weaker than the posterior one. The most consistent character differentiating these species, however, is the protoconch, which in *Pedipes ovalis* is larger and has a rounded, not sinuous, lip.

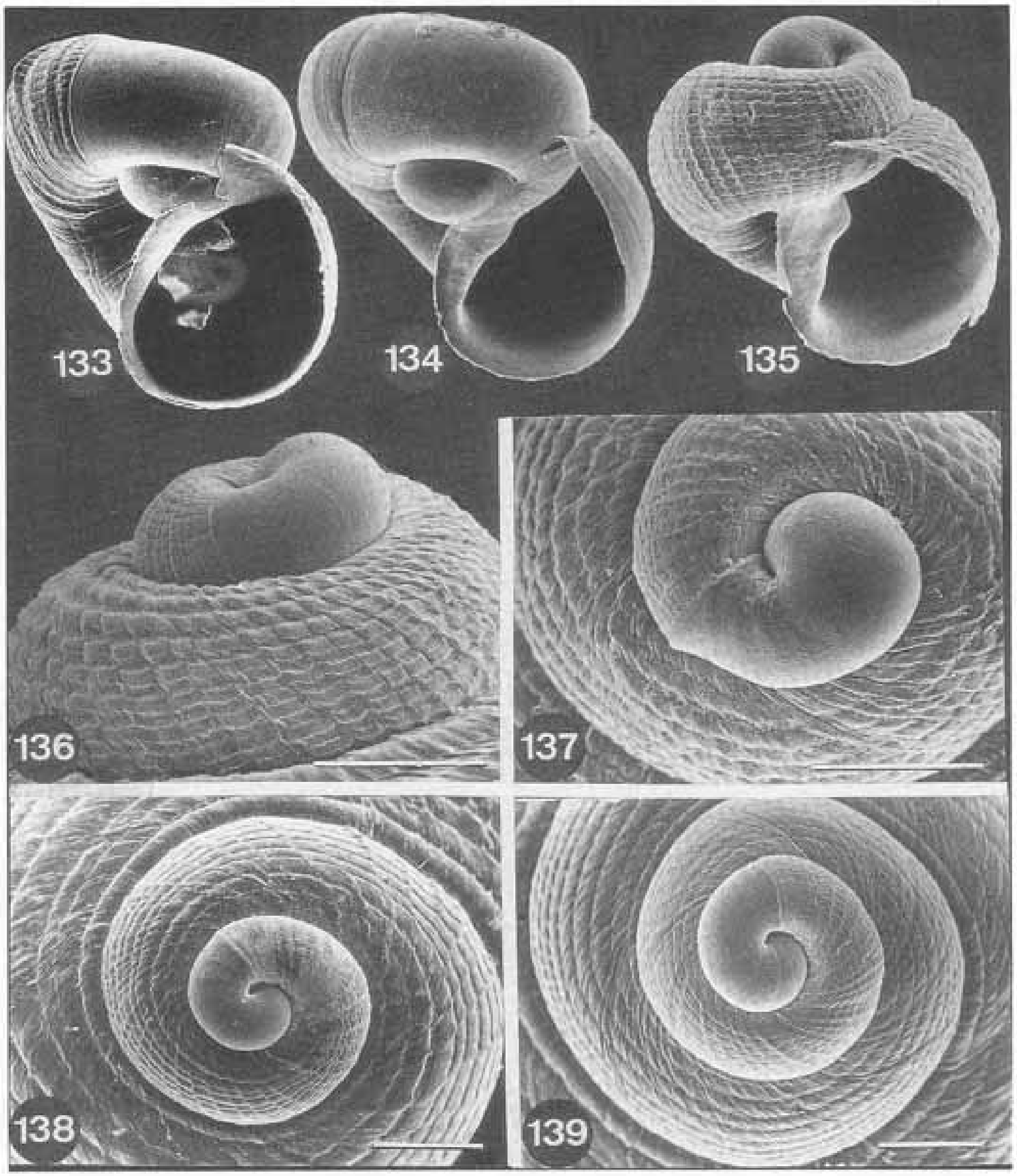
Smoother, thin-shelled examples were named *Pedipes tridens* by Pfeiffer (1855), *Pedipes naticoides* by Stearns (1869) and *Pedipes insularis* by Haas (1950) (Figs. 122–124). This form differs from the typical thick-shelled form in the greater number of grooves on the body whorl and in the wider, somewhat quadrangular aperture that some-



FIGS. 121–132. *Pedipes ovalis* C. B. Adams. (121) Lectotype (MCZ 177349), Jamaica, sl 3.1 mm. (122) *P. tridens* Pfeiffer, lectotype (BMNH 1967590), Bermuda, sl 3.4 mm. (123) *P. naticoides* Stearns, holotype (USNM 37598), Tampa Bay, Florida, sl 2.4 mm. (124) *P. insularis* Haas, paratype (ANSP 212176), Lover's Lake, Bermuda, sl 2.4 mm. (125) Clifton Pt., New Providence, Bahamas, sl 2.3 mm. (126) Shore of Millars Road, New Providence, Bahamas, sl 2.3 mm. (127) Crawl Key, Florida, sl 2.3 mm. (128) Plantation Key, Florida, sl 3.5 mm. (129) Punta Arenas, Puerto Rico, sl 2.8 mm. (130) Isla Mujeres, Yucatán, Mexico (R.B.), sl 2.6 mm. (131) Fort Sherman, Panama (USNM 620532), sl 3.3 mm. (132) Puerto Cabello, Venezuela, sl 3.0 mm.

times has a weak tooth inside the outer lip. The smoothness of the body whorl is very evident in the thin-shelled form although there is much variability and overlap with the thick-shelled form. Owing to unifying features, such as the identical protoconch, and the continuation and gradual disappearance of the outer lip tooth into the aperture, however, the thin-shelled form should be considered conspecific with *Pedipes ovalis*.

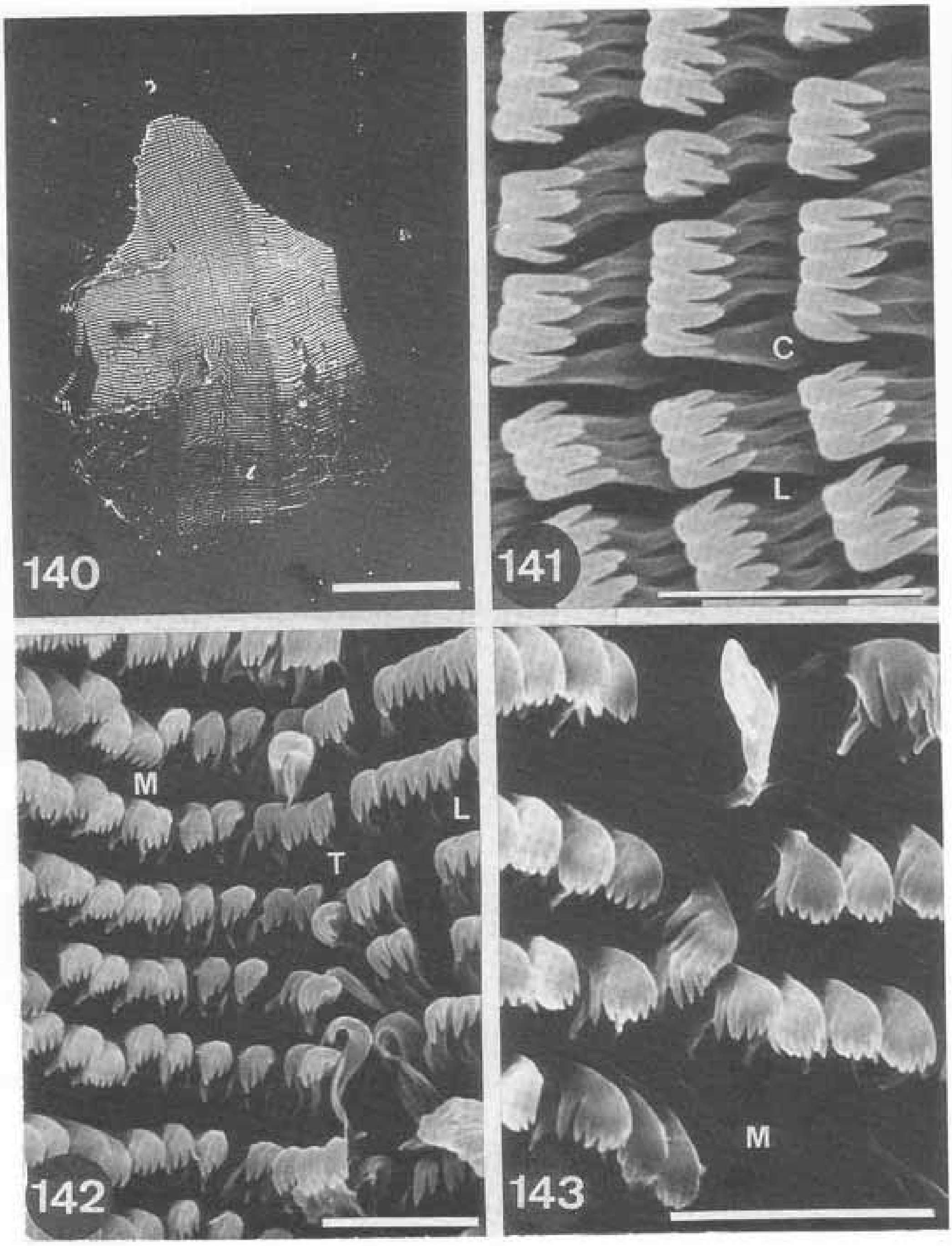
The thick-shelled forms of *Pedipes ovalis* live mostly in rocky habitats, whereas the thin-shelled forms are predominantly mangrove-dwellers. In Punta Arenas, Puerto Rico, both species of *Pedipes* live in an area in which mangrove trees cover the rocky shore. At this site *Pedipes ovalis* showed a wide range of thickness and corresponding variability in the conspicuousness of the tooth on the outer lip (Fig. 129). In the Florida



FIGS. 133–139. *Pedipes ovalis*. (133) Juvenile, Crawl Key, Florida, sl 0.45 mm. (134) Juvenile, Crawl Key, Florida, sl 0.55 mm. (135) Juvenile, Crawl Key, Florida, sl 0.55 mm. (136) Lateral view of spire and protoconch, Clifton Pt., New Providence, Bahamas. (137) Top view of spire and protoconch, Clifton Pt., New Providence, Bahamas. (138) Top view of spire and protoconch, Punta Arenas, N of Joyuda, Puerto Rico. (139) Top view of spire and protoconch, Isla Mujeres, Yucatán, Mexico. Scale 1 mm.

Keys, in which I failed to collect *Pedipes mirabilis* and from which I could not confirm any museum records referring to that species, *Pedipes ovalis* in most mangroves appears as Pfeiffer's *Pedipes tridens* or Stearns' *Pedipes naticoides*. In rocky areas, however, the sculpture and shape approach those of *Pedipes mirabilis*.

Anatomical research yielded some small differences in the reproductive and nervous



FIGS. 140–143. *Pedipes ovalis,* radular teeth. (140) Whole radula, Ely's Harbour, Bermuda, sl 3.1 mm. (141) Morgan's Bluff, Andros Island, Bahamas, sl 2.7 mm. (142, 143) Ely's Harbour, Bermuda, sl 2.7 mm. Scale, Fig. 140, 1 mm; all others, 50 µm.

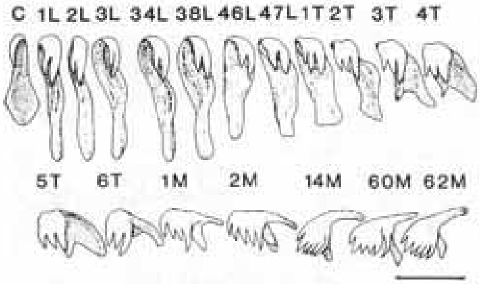


FIG. 144. *Pedipes ovalis,* radula, Ely's Harbour, Bermuda. Scale 10 μm.

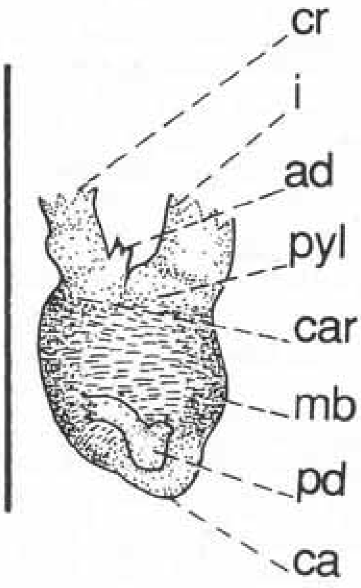


FIG. 145. *Pedipes ovalis,* stomach, Florida. Scale 1 mm.

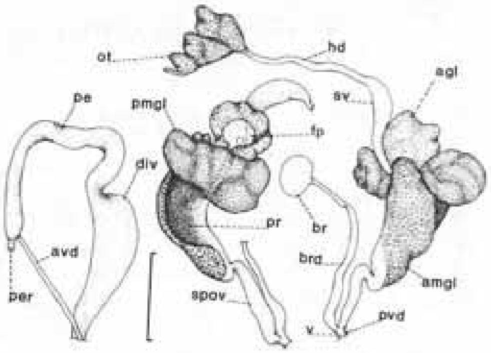


FIG. 146. *Pedipes ovalis,* reproductive system, Florida. Scale 1 mm.

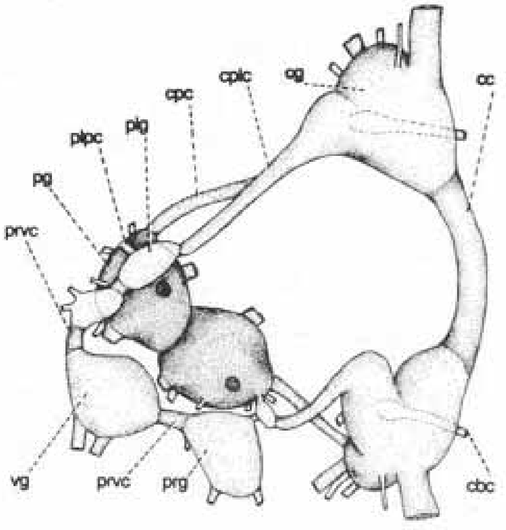


FIG. 147. *Pedipes ovalis,* central nervous system, Florida. Scale 1 mm.

systems, and counts of radular teeth are lower in *Pedipes ovalis.* On that basis, but mostly on the bases of the protoconch, the generally more disparate sizes of the columellar teeth, the shape of the outer lip tooth and the maximal size, *Pedipes ovalis* is considered distinct from *Pedipes mirabilis.* The resemblance of the two species can be interpreted as convergence due to adaptation to the same environmental pressures of the rocky shore. The gradation from the thick-shelled, rock-dwelling forms to the thin-shelled, mangrove-dwelling populations, together with the retention of the same pattern of protoconch and shape of the tooth on the outer lip, amply justify the inclusion of *Pedipes tridens, Pedipes naticoides* and *Pedipes insularis* as junior synonyms of *Pedipes ovalis.*

As stated under the remarks on the previous species, Gibson-Smith & Gibson-Smith (1985) described a *Pedipes mirandus* from the Early Miocene Cantaure Formation of Venezuela. The authors did not mention the shape of the protoconch, the decisive character for the separation of the Western Atlantic species. Judging from the accentuated difference in size of the columellar teeth, however, I consider *Pedipes mirandus* a jun-

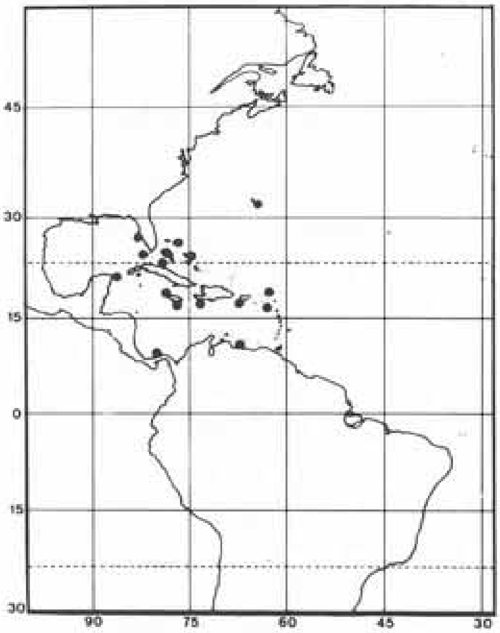


FIG. 148. *Pedipes ovalis*, geographic distribution.

ior synonym of *Pedipes ovalis*. The specimen of the latter species that I collected in Venezuela (Fig. 132) closely resembles the illustration of the holotype of *Pedipes mirandus* (Gibson-Smith & Gibson-Smith, 1985: 88, fig. 1).

Habitat: *Pedipes ovalis* often occurs with *Pedipes mirabilis* under rocks and in crevices at or just below the high-tide mark. The thinner-shelled forms are very common in mangroves under leaves, twigs and rocks at or just below high-tide mark. The juveniles venture farther into the intertidal zone than do any other West Indian ellobiid.

Range: Bermuda; Florida; West Indies; Mexico south to Panama and Venezuela (Fig. 148).

Specimens Examined: FLORIDA: Waveland (USNM 123531); Miami (ANSP 320358; USNM 159439, 330934); Ocean Beach (USNM 270714); Third Ragged Key above Sand Key (USNM 462738); Key Largo (USNM 597459); Tavernier Key (USNM 492504); Plantation Key (MCZ 188973, 291000, 291003); Ocean Dr., Plantation Key (A.M.); Upper Matecumbe Key (USNM 492492); Indian Key (MCZ 167889; USNM 492520); Indian Key Fill, N of Indian Key Channel (A.M.); Lignumvitae Key (ANSP 156683); Lower Matecumbe Key (MCZ 167893; USNM 492495); Long Key (ANSP 219860; A.M.); Grassy Key (ANSP 89560, 397279; MCZ 188970; A.M.); Crawl Key (MCZ 188972, 289998, 289999; A.M.); Bonefish Key (ANSP 227991); Knight Key (MCZ 188971); Bahia Honda (ANSP 104115; MCZ 188969); West Summerland Key (A.M.); Big Pine Key (ANSP 104114, 227999; MCZ 291104); W end of Kohen Avenue and Long Beach Drive, both on Big Pine Key (A.M.); Little Torch Key (MCZ 188974, 291108); Big Torch Key (ANSP 104112); Ramrod Key (MCZ 188975; USNM 599368); Sugarloaf Key (ANSP 89561, 104113; MCZ 188478); Boca Chica Key (MCZ 167892; USNM 270349); Key West (ANSP 22563; USNM 36017, 492494); SW channel, Dry Tortugas (USNM 492505); Garden Key, Dry Tortugas (USNM 590210); Flamingo Key (ANSP 294313); Cape Sable (MCZ 291103); Seminole Point (ANSP 105432); Sanibel Island (MCZ 84103); Tarpon Bay, Sanibel Island (MCZ 84339); Captiva Island (ANSP 149408); Starvation Key (ANSP 130059); Palmetto (A.M.); Mullet Key (USNM 652408, 653109; A.M.); Shell Key (USNM 466287); Tampa Bay (MCZ 239222; USNM 37598a); Anclote Key (ANSP 22564). MEXICO: Isla Cancún, Quintana Roo (ANSP 285534). BERMUDA: (ANSP 48597, 48600, 48601, 48602; MCZ 9952a, 74809, 314027; USNM 6523, 94438, 492496): Fairyland (ANSP 99077, 111096; USNM 208071); Flatts (USNM 171963); Shelly Bay (MCZ 225523); Old Road, Shelly Bay (A.M.); Coney Island (A.M.); N of Long Bird Bridge (A.M.); Nonsuch Island (MCZ 248274); Lover's Lake (ANSP 212176); Cooper's Island (ANSP 131648); Hungry Bay (A.M.); W of Somerset Bridge (A.M.); Ely's Harbour (A.M.); Mangrove Bay (A.M.). BAHAMA ISLANDS: BIMINI (ANSP 325624): East Well, East Bimini (ANSP 326449); N. end of Pigeon Cay, Bimini Lagoon (ANSP 326022; USNM 656173); S end of Pigeon Cay (ANSP 326017); Cavelle Pond, South Bimini (ANSP 325548); Tokas Cay (ANSP 325831); GRAND BAHAMA ISLAND: W of Eight Mile Rock (R.B.); Running Mon Canal (ANSP 369780); North Hawksbill Creek (ANSP 370569); Dead Mans Reef [Sandy Bevan's Cay] (ANSP 371226, 371285); Sweetings Cay (ANSP 374312); Riding Point (ANSP 371521); West End (ANSP 368763, 371933); GREAT ABACO ISLAND: West Point (ANSP 299478); Gorling Cay (ANSP 299549); ANDROS ISLAND: Morgan's Bluff (A.M.); South

Mastic Point (A.M.); Danlin Bay (USNM 180671); Mangrove Cay (ANSP 325639; USNM 180462); First island off Mintie Bar, SE end of South Bight (USNM 271784); NEW PROVIDENCE ISLAND: Delaporte Point (A.M.); E of Clifton Pier (A.M.); Clifton Bluff (MCZ 205367); Clifton Point (A.M.); Millars Road (A.M.); Malcolm Creek (A.M.); ROYAL ISLAND (MCZ 78360, 167901; USNM 468120); ELEUTHERA ISLAND: Governor's Harbor (MCZ 167995); EXUMA CAYS: Hog Cay (MCZ 225560, 225561); CAY SAL BANK: Salt Lagoon, Cay Sal (USNM 513429). CUBA (USNM 492498): Dimas (USNM 614603); Habana (ANSP 130744); Las Villas, Caibarién (USNM 608763). JAMAICA (MCZ 177348a, 177349, 177350, 185170a; USNM 90460, 94748): Falmouth (ANSP 397266); Robin's Bay (MCZ 167896a; USNM 441978a); Jack's Bay (MCZ 167895a; USNM 441836a); Port Morant (USNM 423674a); Palisadoes (USNM 442540a). HAITI: St. Louis (USNM 439397a); Port Salut (USNM 440000a); Bizoton (USNM 439843a). PUERTO RICO: San Juan (R.B.); Punta Arenas, N of Joyuda (A.M.); Cabo Rojo lighthouse (MCZ 188476b). VIRGIN ISLANDS: ST. CROIX (USNM 706775); ST. THOMAS (ANSP 22562). LESSER ANTILLES: ST. KITTS (MCZ 167935a; USNM 492491); GRENADA: Caliveny Harbor (ANSP 296716); ST. MARTIN (MCZ 250474). MEXICO: Isla Mujeres, Quintana Roo (R.B.). BELIZE: Twin Cays (USNM 841329); Drowned Cays (ANSP 284811). PANAMA: Devil's Beach, Fort Sherman (USNM 620532). CARIBBEAN ISLANDS: ST. ANDREWS ISLAND (ANSP 155415). VENEZUELA: Puerto Cabello (A.M.).

Genus *Creedonia* new genus

Type species: *Creedonia succinea* (Pfeiffer, 1854).

Description: Shell to 3.8 mm long, oval-elongate, fragile. Spire moderately high, truncated, with rounded apex; as many as four smooth, weakly convex whorls. Body whorl about 80% of shell length. Aperture oval-elongate, about 70% of body whorl length, posteriorly acuminate, rounded at base; columella somewhat oblique and twisted; columellar teeth two, posterior one stronger; parietal tooth a little stronger than posterior columellar tooth; outer lip sharp, smooth. Inner whorls not resorbed. Protoconch large, smooth, with nuclear whorls covered by first whorls of teleoconch.

Radula with about 45 teeth in a row; central tooth wide, with triangular base, small, unicuspid crown; lateral teeth with strong endocone; transitional teeth with two endocones; marginal teeth with as many as five endocones.

Animal whitish; tentacles long, pointed. Visceral mass coiled. Pallial cavity elongate; kidney long, thin. Hermaphroditic duct somewhat dilated in the middle; penis with long diverticulum. Nervous system with long cerebral commissure.

Remarks: The genus *Creedonia* is created for *Creedonia succinea* (Pfeiffer) upon the basis of shell, radular and anatomical characters. This new genus is closely related to *Pedipes* and *Marinula,* and the type species was formerly included in one or the other genus. *Creedonia,* like *Pedipes,* does not resorb its inner whorls and, like *Marinula,* has a smooth shell and a smooth outer lip. The three genera characteristically have two columellar teeth and one strong parietal tooth.

As stated above, *Creedonia succinea* formerly was considered to belong to the genus *Marinula.* Only twice have some species of *Marinula* been assigned tentatively to new genera. Swainson (1855) introduced the genus *Cremnobates* in which he included his three species *Cremnobates cornea, Cremnobates parva* and *Cremnobates solida,* all from Tasmania. Hedley & Suter (1910) noted that *Cremnobates cornea* is a junior synonym of *Ophicardelus australis* (Quoy & Gaimard, 1832) and that *Cremnobates solida* is conspecific with *Marinula patula* (Lowe, 1832). They therefore selected *Cremnobates parva* (Fig. 156) as type of the genus. Connolly (1915) considered *Cremnobates parva* allied to *Marinula xanthostoma* H. & A. Adams, 1855. Iredale (1936: 328) proposed *Maripythia* for *Marinula xanthostoma* H. & A. Adams on the basis of Connolly's opinion that that species "could not be classed under *Marinula.*" This is a misinterpretation of the statements of Connolly (1915: 118) who, after tracing the tortuous history of *Marinula xanthostoma,* concluded, "the typical form of *xanthostoma* is on the extreme borderland of *Marinula,*" but added that intermediate forms occurred in different localities, a fact making the connection with *Marinula* less doubtful.

Research on the anatomy of a *Marinula* cf. *xanthostoma* H. & A. Adams, conchologically related to *Cremnobates parva,* revealed a reproductive system similar to that of *Pedipes.*

The reproductive system of *Marinula pepita* King, 1832, the type species of the genus, differs considerably from that of the Adams' species, leading to the conclusion that they are at least subgenerically separated. The similarity of the radular teeth of *Marinula pepita* to those of *Marinula filholi* (Hutton, 1878) (Figs. 163–168), conchologically allied to *Marinula xanthostoma*, casts doubt upon their generic separation. Because I lacked an opportunity to examine the anatomy of *Cremnobates parva* to assess its relationship to *Marinula xanthostoma*, I think a decision about the synonymy of the names proposed by Swainson and Iredale is unwarranted.

The genus *Marinula* has been confused with *Ovatella* [Pythiinae] on the basis of the apparent similarity of the dentition of the inner lip. H. & A. Adams (1855b) created the subgenus *Monica* to include the Mediterranean *Monica firminii* (Payraudeau, 1826) [= *Ovatella firminii*], and the Madeiran *Monica aequalis* (Lowe, 1832) [= *Ovatella aequalis*] and *Monica gracilis* (Lowe) [= *Ovatella aequalis*]. The shells of *Marinula* are easily separated from those of *Ovatella* on the basis of their apertural teeth. *Marinula*, *Pedipes* and *Creedonia* all have two conspicuous columellar teeth, whereas *Ovatella* has only one columellar tooth. The parietal tooth of *Marinula* is the strongest of the three inner lip teeth, whereas in *Ovatella* the anterior parietal tooth is the strongest (Fig. 88). Connolly (1915) added as a diagnostic character of the genus the absence of teeth on the outer lip, but the Eastern Pacific *Marinula concinna* (C. B. Adams, 1852) and *Marinula brevispira* (Pilsbry, 1920) have a thick, ridge-like tooth opposite the parietal tooth. Anatomical research on these species is needed to ascertain their phylogenetic relationships, however.

Marinula is known from the Indo-Pacific and it is well represented along the Pacific coasts of Central and South America; it has been reported from the South Atlantic Islands and from South Africa as well (Connolly, 1915).

The new genus *Creedonia* differs from *Marinula* by having a thinner, smaller shell that is less than half the size of that of any species included in *Marinula*, with the possible exception of *Marinula mandroni* Velain, 1877, which Connolly (1915) suspected to have been named after a young specimen of *Marinula velaini* Connolly, 1915. In *Creedonia* the columella is twisted and oblique, instead of flat and straight, and the anterior columellar tooth is always conspicuous, whereas in *Marinula* it is very small (Figs. 155–157). The spire in *Creedonia* is more elevated, the apex is truncate and perforated (Fig. 158) instead of acuminate and obliterated as in *Marinula* (Fig. 159). As stated above, *Creedonia* animals do not resorb the inner whorls of the shell (Fig. 153), whereas those of *Marinula* species do.

The radula of *Creedonia succinea* differs from that of *Marinula* in its broad central and lateral teeth and in the very small number of teeth in a row (Table 3, Appendix). The marginal teeth have several endocones but no ectocones, whereas in the Neozealandic *Marinula filholi* (Hutton) and in *Marinula pepita* King there are one or two endocones and several ectocones (Figs. 163–168).

The genus *Creedonia* is named in honor of the Rev. Joseph Dennis Creedon, Pastor of Christ the King Church, Kingston, Rhode Island, as an expression of my gratitude for his support in this research and for his invaluable friendship.

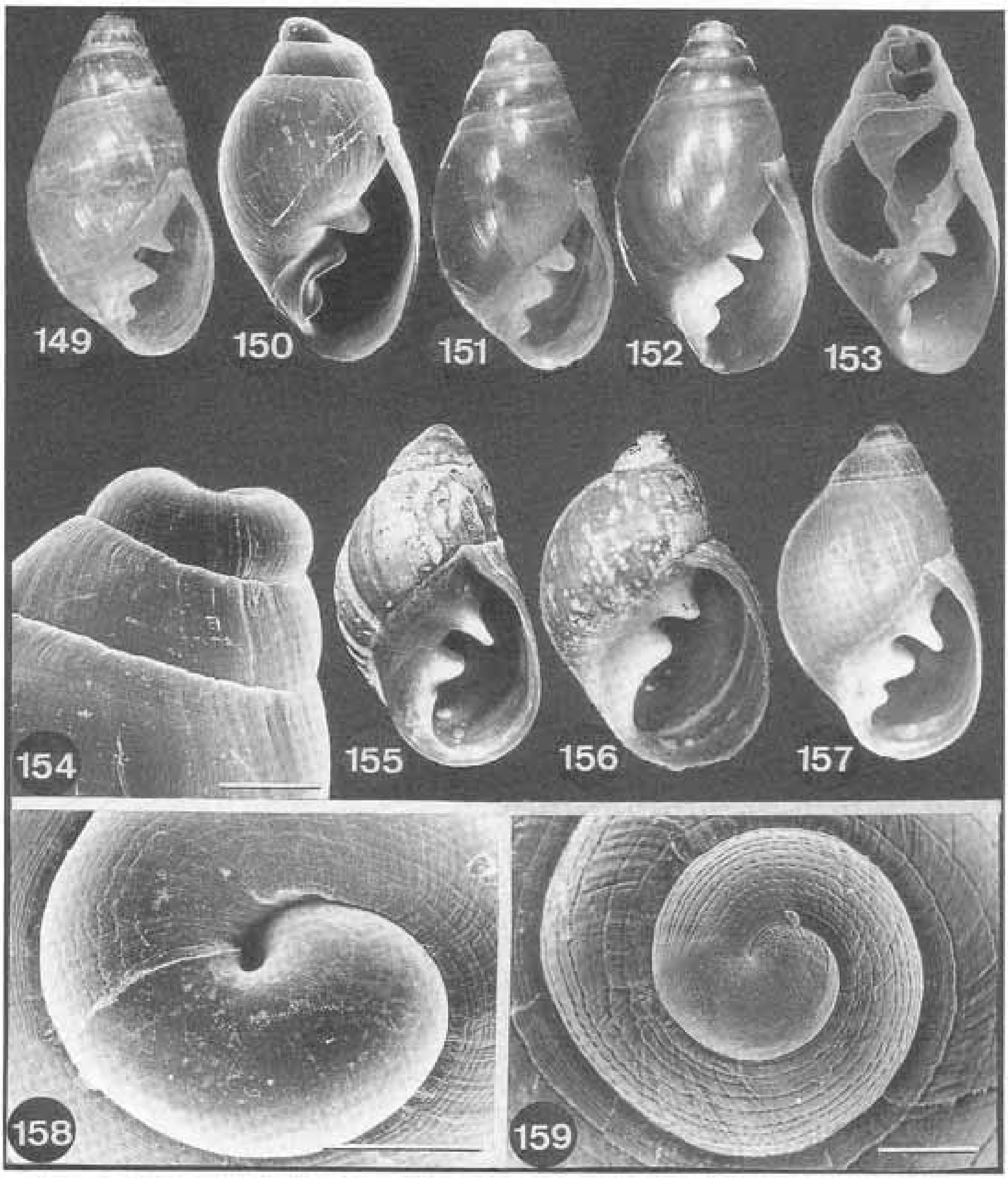
Creedonia succinea (Pfeiffer, 1854)
Figs. 149–154, 158, 160–162, 169–173

Leuconia succinea Pfeiffer, 1854b: 156 [Cárdenas, Cuba; location of type unknown]; Pfeiffer, 1856a: 157; Pfeiffer, 1876: 370; Arango y Molina, 1880: 61; Crosse, 1890: 260; H. & A. Adams, 1855b: 248.

Pedipes elongatus Dall, 1885: 279, pl. 18, fig. 4 [Marco, Florida; lectotype herein selected USNM 859012 (Fig. 149); five paralectotypes USNM 37599]; Dall, 1889: 92, pl. 47, fig. 4; Simpson, 1889: 60; Kobelt, 1900: 258, pl. 24, figs. 17, 18; Maury, 1922: 54; C. W. Johnson, 1934: 159; M. Smith, 1937, pl. 67, fig. 4 [pl. from Dall (1885)]; Emerson & Jacobson, 1976: 190, pl. 26, fig. 21.

Marinula succinea (Pfeiffer). Morrison, 1951b: 9; Morrison, 1958: 118–124 [habitat]; Abbott, 1974: 333, fig. 4100 [not fig. 4108]; Vokes & Vokes, 1983: 60, pl. 31, fig. 17.

Description: Shell (Figs. 149–154, 158) to 3.8 mm long, oval-elongate, fragile, shiny, translucent, pale yellow to golden brown. Spire truncate, with as many as four and one-half weakly convex, apparently smooth whorls; very fine spiral lines visible under high magnification, crossed by weak, irregularly spaced growth lines; spiral depression just below suture. Body whorl about 80% of shell length, smooth. Aperture oval-elongate,



FIGS. 149–159. *Creedonia, Marinula.* (149) *Pedipes? elongatus* Dall, lectotype (USNM 859012), Marco, Florida, sl 3.9 mm. (150) *C. succinea* (Pfeiffer), Crawl Key, Florida, sl 2.3 mm. (151) *C. succinea*, Big Pine Key, Florida, sl 3.3 mm. (152) *C. succinea*, Isla Mujeres, Yucatán, Mexico (R.B.), sl 4.3 mm. (153) *C. succinea*, Isla Mujeres, Yucatán, Mexico (R.B.), sl 3.3 mm. (154) *C. succinea*, lateral view of spire and protoconch, Crawl Key, Florida. (155) *M. pepita* King, syntype (BMNH 1968882), Chiloe Island, Chile, sl 10.1 mm. (156) *M. parva* (Swainson), New Zealand (USNM 98181), sl 6.4 mm. (157) *M. filholi* (Hutton), New Zealand, (USNM 681303), sl 5.4 mm. (158) *C. succinea*, top view of spire and protoconch, Crawl Key, Florida. (159) *M. filholi*, top view of spire and protoconch, New Zealand (USNM 681303). Scale 1 mm.

about 70% of length of body whorl, round at base; columella somewhat oblique, twisted; columellar teeth two, oblique toward base; anterior columellar tooth conspicuous, posterior columellar tooth twice the size of anterior; parietal tooth lamelliform, as large as or somewhat larger than posterior columellar tooth; outer lip sharp, smooth. Inner whorls not resorbed (Fig. 153). Protoconch large, smooth, whitish, translucent; nuclear whorls enveloped by first whorl of teleoconch, leaving pit in apex of shell (Figs. 154, 158).

Radula (Figs. 160–162, 169) with formula [12 + (2 + 12) + 1 + (12 + 2) + 12] × 80. Base of central tooth as wide as that of lateral teeth, rhomboidal, with anterior end much shorter than posterior, rounded; crown as wide as posterior end of base; mesocone small, triangular, with rounded tip; no ectocones. Lateral teeth eight to 12; base quadrangular, medially bent at half-length; crown as wide as posterior end of base, triangular, with rounded tip; endocone about half the length of mesocone, strong, weakly pointed. Transitional teeth two, with base wider than that of lateral teeth, with two subequal endocones. Marginal teeth 12 to 14; base becomes shorter and wider; mesocone becomes smaller as teeth approach lateral edge of radula; first marginal tooth with three subequal endocones; fourth endocone appears on fourth marginal tooth, fifth endocone on tenth marginal tooth.

Animal whitish, translucent; tentacles moderately long, somewhat pointed, translucent, with bulbous base. Foot transversely divided. Pallial cavity elongate; kidney broad, triangular, white.

Digestive system with salivary glands small, fusiform. Stomach globose, very muscular; gastric caecum conspicuous, membranous (Fig. 170). Digestive gland bilobed; anterior lobe covers most of stomach and empties into pouch-like posterior crop through dilated anterior diverticulum; intestine very dilated as it comes off the stomach.

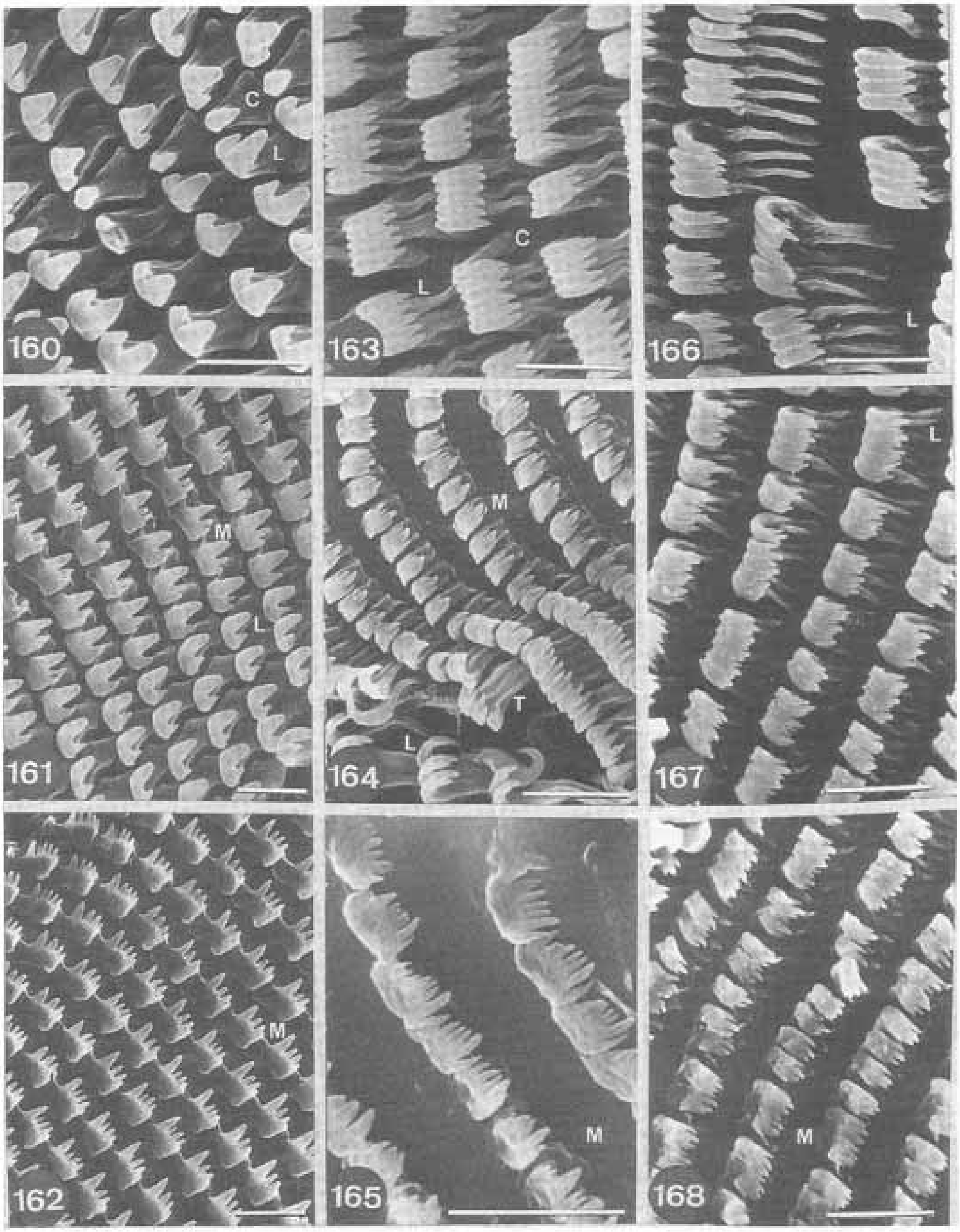
Reproductive system (Fig. 171) with ovotestis acinose, embedded in posterior lobe of digestive gland; hermaphroditic duct with irregularly dilated seminal vesicle; fertilization pouch bilobed, very conspicuous; albumen gland large, triangular; posterior mucous gland weakly convoluted; anterior mucous gland and prostate gland cover posterior half of spermoviduct. Bursa duct thick, shorter than spermoviduct; bursa elongate. Penis with several pouch-like dilations, with very long diverticulum wrapped around esophagus and salivary glands; short penial retractor attaches to columellar muscle; vas deferens short, free.

Nervous system (Fig. 172) with cerebral commissure just shorter than width of cerebral ganglion; left cerebropedal and cerebropleural connectives shorter than right ones; pedal commissure very conspicuous; cerebral ganglia large, elongate laterally; left pleural ganglion about one-fourth size of right one; left parietal ganglion about one-tenth size of right one; visceral ganglion largest of visceral ring, somewhat smaller than pedal ganglia.

Remarks: Creedonia succinea was originally assigned by Pfeiffer (1854b) to the genus *Leuconia* Gray [= *Auriculinella* Tausch, 1886]. The species appeared in the literature under this name until placed by Morrison (1951b) in the genus *Marinula* King, 1832, in which it has remained until now.

Dall (1885) apparently was not aware of Pfeiffer's species when he introduced *Pedipes elongatus* for specimens from Marco, Florida. *Creedonia succinea* is one of the few species of ellobiids that shows little morphological variation. It cannot be confused with any other West Indian species. The superficial similarity to the Mediterranean *Ovatella* was already pointed out in the remarks under the genus *Creedonia*. In *Creedonia* the columellar tooth is double and the parietal tooth is the strongest or at least as strong as the posterior columellar tooth. In *Ovatella* there is only one columellar tooth and the first parietal tooth is the strongest. The same applies to the introduced *Myosotella myosotis*, with the difference that in this species the posterior parietal tooth is either absent or weaker than the anterior parietal tooth. The spire of *Creedonia succinea* is truncate and the protoconch gives it a mucronate appearance. The elongate, smooth, translucent shell, with flat whorls, separates *Creedonia succinea* from the thin-shelled form of *Pedipes ovalis* with which it occurs. *Microtralia* and *Blauneria* also occur with *Creedonia;* the former differs from *Creedonia* in having a narrow aperture with much smaller inner lip teeth and a very short spire. *Blauneria* is sinistral, has a high spire and is white and transparent, whereas *Creedonia* is straw-colored to brown.

Connolly (1915: 105), in his monograph on the genus *Marinula*, apparently was not acquainted with Pfeiffer's species. He mentioned "*Pythia abbreviatus* Beck," criticizing Pfeiffer's (1856a) questionable attribution of it to *Marinula* in these terms: "whatever may be its true genus, as the shell is said to come from the Antilles it is quite unlikely to be a



FIGS. 160–168. *Creedonia*, *Marinula*, radular teeth. (160–162) *C. succinea*, Long Key, Florida, sl 3.0 mm. (163) *M. filholi*, New Zealand, sl 5.4 mm. (164) *M. filholi*, New Zealand, sl 5.5 mm. (165) *M. filholi*, New Zealand, sl 5.4 mm. (166–168) *M. tristanensis* Connolly [= *M. pepita* King], Gough Island (BMNH), sl 10.8 mm. Scale 50 µm.

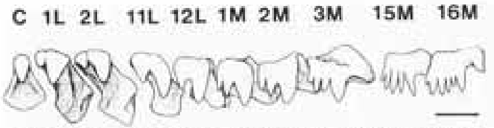


FIG. 169. *Creedonia succinea*, radula, Long Key, Florida. Scale 10 μm.

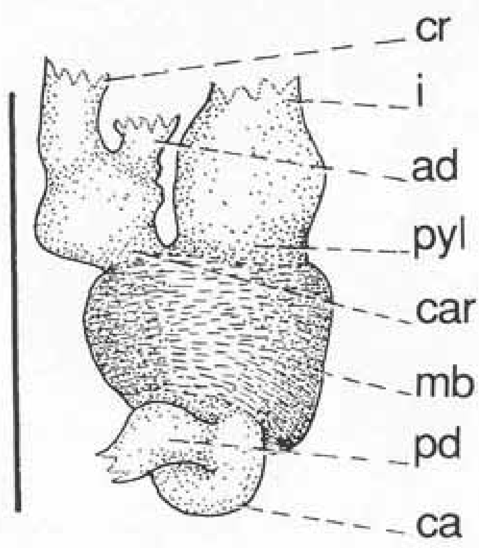


FIG. 170. *Creedonia succinea*, stomach, Crawl Key, Florida. Scale 1 mm.

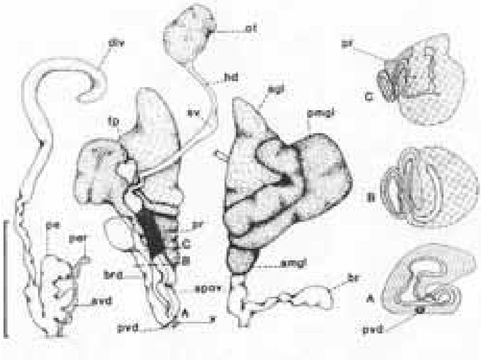


FIG. 171. *Creedonia succinea*, reproductive system, Crawl Key, Florida, sl 3.3 mm. A–C, transverse sections and their locations. Scale 1 mm.

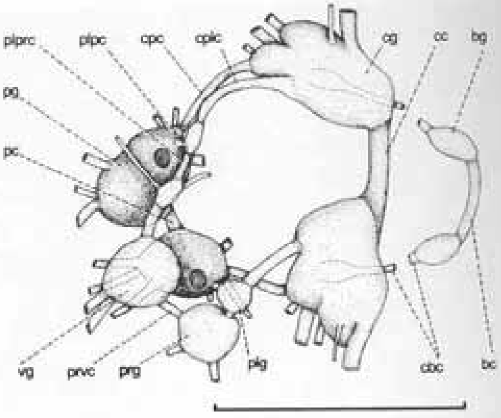


FIG. 172. *Creedonia succinea*, central nervous system, Crawl Key, Florida, sl 3.0 mm. Scale 1 mm.

Marinula." Beck (1837: 105) had listed, without description, a "*Pythia abbreviatus*" from the West Indies, placing the name after *Pythia aequalis* (Lowe, 1832) [= *Ovatella aequalis*] and *Pythia patulus*, which is questionably referred by Connolly (1915) to *Marinula xanthostoma* H. & A. Adams. Pfeiffer (1856a) did not see Beck's specimens but tentatively assigned *Pythia abbreviatus* Beck to *Marinula*, no doubt on the basis that Beck listed it between two species that Pfeiffer considered to be *Marinula*. The only other species in the Western Atlantic that at first glance could be confused with *Creedonia succinea* is *Myosotella myosotis*, which does not live in the West Indies. In spite of the fact that some circumstancial evidence seems to indicate that Beck's name refers to *Creedonia succinea*, *Pythia abbreviatus* Beck must remain a *nomen nudum*.

Habitat: Individuals of *Creedonia succinea* live about the high-tide mark, the juveniles venturing a short distance into the intertidal zone. They live within the sediment, sometimes 10 to 15 cm deep, and they occur frequently under half-buried rotting wood or rocks and on the roots of mangrove propagules, together with *Pedipes*, *Microtralia* and *Blauneria*.

Range: Georgia ?, Florida Keys and the Bahama Islands south to Cuba and Jamaica; Mexico (Fig. 173). The USNM record from Isle of Hope, Georgia, collected by Hubricht, is so distant from the normal range that it could be explained better as the result of accidental transportation by currents.

Specimens Examined: GEORGIA: Isle of Hope (USNM 663054). FLORIDA: S of Ocean Drive, Plantation Key (A.M.); Lignumvitae Key

(ANSP 156694); Long Key (A.M.); Grassy Key (A.M.); Crawl Key (A.M.); Big Pine Key (ANSP 293553); Long Beach Drive and W of Kohen Avenue, both Big Pine Key (A.M.); Newfound Harbor (USNM 272639); Big Torch Key (ANSP 104105); Sugarloaf Key (ANSP 89566, 104104); Ramrod Key (MCZ 235471a); Boca Chica Key (USNM 590597); Key West (USNM 450693); Seminole Point (ANSP 105410); Marco (ANSP 22578; USNM 37599, 859012); Captiva Island (ANSP 149409); Mullet Key (USNM 652409; A.M.); Mullet Key Bayway (USNM 653110). BAHAMA ISLANDS: GRAND BAHAMA ISLAND: South Hawksbill Creek (ANSP 371809); ANDROS ISLAND: South Mastic Point (A.M.). CUBA: Matanzas (MCZ 131760). JAMAICA: Kingston (USNM 442584). MEXICO: N end of Ascension Bay, Quintana Roo (USNM 736105); Isla Mujeres, Quintana Roo (R.B.).

Genus *Microtralia* Dall, 1894

Microtralia Dall, 1894: 117. Type species by monotypy: *Auricula* ? (*Microtralia*) *minuscula* (Dall, 1889) [= *Leuconia occidentalis* Pfeiffer, 1854].

Rangitotoa Powell, 1933: 148. Type species by monotypy: *Rangitotoa insularis* Powell, 1933.

Description: Shell to 3.8 mm long, subcylindric, fragile, translucent white. Spire low to moderately high, with as many as seven weakly convex whorls. Body whorl 80% of shell length. Aperture narrow, about 90% of body whorl length; inner lip with small, oblique columellar tooth; anterior parietal tooth very near columellar tooth, strong; posterior parietal tooth very small, about mid-length of aperture; outer lip thin, sharp. Protoconch smooth, globose; nuclear whorls deeply embedded in first whorl of teleoconch.

Radula with 55 to 79 teeth in a row. Central tooth at same level as lateral teeth; base broad, triangular, anteriorly emarginate; crown small, tricuspid. Base of lateral teeth quadrangular, weakly bent medially; crown less than half length of base, with large mesocone, small ectocone. Transitional teeth with one endocone. Marginal teeth wide, pectinate, with as many as six ectocones.

Animal whitish to rusty brown, translucent. Foot not divided transversely, posteriorly entire, round. Eyes lacking. Tentacles short, subcylindric. Hermaphroditic duct dilated anteriorly into a pouch-like seminal vesicle; anterior mucous gland covering posterior half of spermoviduct; vas deferens free from penis. Connectives of visceral ring very short.

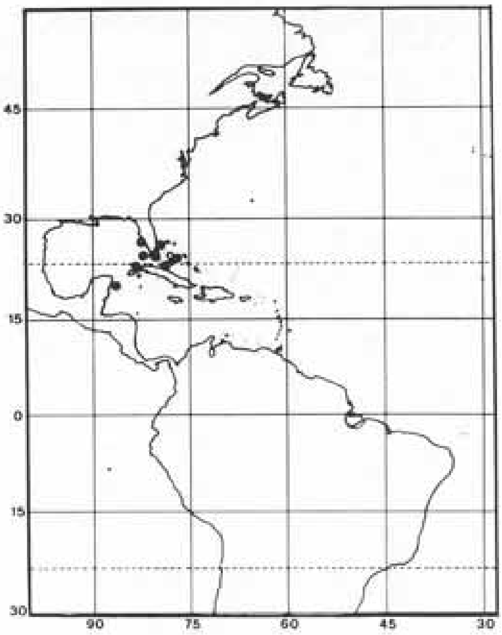


FIG. 173. *Creedonia succinea*, geographic distribution.

Remarks: Since its introduction by Dall (1894) the genus *Microtralia* has been considered to belong to very different taxonomic groups. Its uncertain taxonomic position is the result of the different weights given by different authors to the various taxonomic characters. The etymology of the word implies similarity to *Tralia*, a member of the Melampinae. Dall (1894) tentatively placed *Microtralia* in the genus *Auricula* [= *Ellobium*], a member of the Ellobiinae. Thiele (1931) considered *Microtralia* a subgenus of *Melampus*. Powell (1933), although recognizing the uniqueness of the genus, followed Odhner's (1925) radula-based classification and placed his *Rangitotoa*, here considered a junior synonym of *Microtralia*, in the Melampinae. Powell stressed the radular affinities of his genus with the Carychiinae. Morton (1955b), on the basis of anatomy and habitat preferences, placed *Rangitotoa* [= *Microtralia*] within the Pedipedinae. Zilch (1959) treated *Microtralia* as a subgenus of *Melampus*, and he considered *Rangitotoa* as a separate genus of the Melampinae. Abbott (1974) considered *Mi-*

crotralia a genus of the subfamily Cassidulinae.

Although the shell is not typical of the Pedipedinae, the dentition of the inner lip and the protoconch of *Microtralia* are similar to those of the more solid *Pseudomelampus* and *Sarnia* (Figs. 180, 181). The central and lateral teeth of the radula of this Eastern Atlantic genus closely resemble those of *Pedipes*, but the pectinate marginal teeth with as many as six ectocones are very similar to those of *Pseudomelampus* (Martins, personal observation). Analysis of the reproductive and nervous systems indicate the systematic position of *Microtralia* within the Pedipedinae.

The Neozealandic *Rangitotoa insularis* Powell, 1933, is quite similar to the West Indian *Microtralia occidentalis* (Pfeiffer, 1854), especially in shell and radular characters, and Climo (1982) considered them conspecific (Fig. 179).

Habitat: These animals live near the high-tide mark, under rocks partly buried in mud (Powell, 1933). In West Indian mangroves *Microtralia* lives in the black sediment at the high-tide mark, preferably under rotting, half-buried branches (Martins, personal observation).

Range: Sporadic records from Easter Island (Rehder, 1980), Hawaii (Pease, 1869), New Zealand (Powell, 1933), Japan (Habe, 1961) and South Africa (Turton, 1932) indicate an Indo-Pacific distribution. In the West Indian region the genus is represented by *Microtralia occidentalis* (Pfeiffer).

Microtralia occidentalis (Pfeiffer, 1854)
Figs. 174–178, 182–193

Leuconia occidentalis Pfeiffer, 1854b: 155 [Cárdenas, Cuba; location of type unknown]; H. & A. Adams, 1855b: 248; Pfeiffer, 1856a: 157; Pfeiffer, 1876: 370; Arango y Molina, 1880: 61; Crosse, 1890: 260.

Tralia (Alexia?) minuscula Dall *in* Simpson, 1889: 69 [Magill's Bay, Tampa, Florida, and Exuma Island, Bahamas, herein restricted to Magill's Bay, Tampa, Florida; lectotype herein selected USNM 61211 (Fig. 174); two paralectotypes USNM 859503].

Tralia minuscula Dall. Dall, 1889: 92.

Auricula ? (Microtralia) minuscula (Dall). Dall, 1894: 117, fig. 7 [Fig. 175].

Leucopepla occidentalis (Pfeiffer). Peile, 1926: 88.

Microtralia occidentalis (Pfeiffer). Pilsbry, 1927: 125; Morrison, 1951b: 10; Abbott, 1974: 334 [not figured; fig. 4105, erroneously referred to this species, represents *Myosotella myosotis*]; Jensen & Clark, 1986: 456 [fig. on page 456, wrongly stated to represent this species, is of *Myosotella myosotis*].

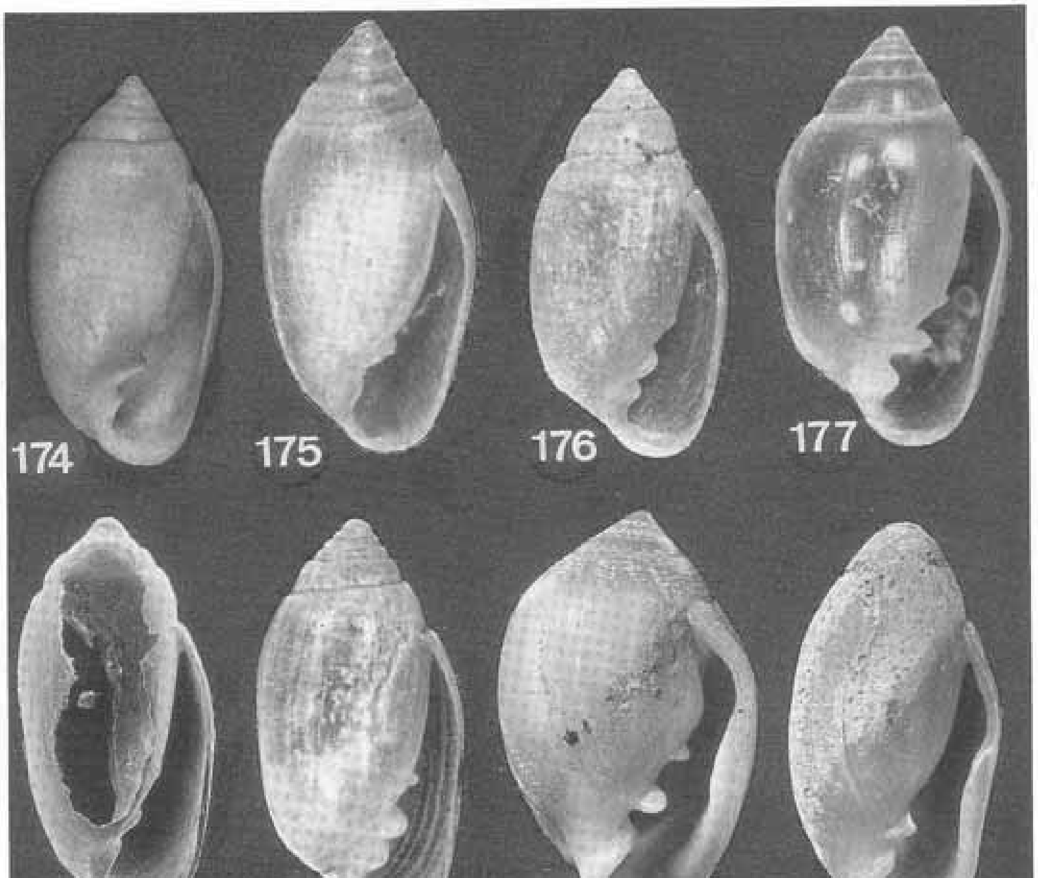
Auriculastrum (Microtralia) minusculum (Dall). C.W. Johnson, 1934: 159.

Auriculastra nana Haas, 1950: 197, pl. 22, figs. 1, 2 [Lover's Lake, St. George's Island, Bermuda; holotype FMNH 30169 (not seen); paratype ANSP 212177 (Fig. 176)].

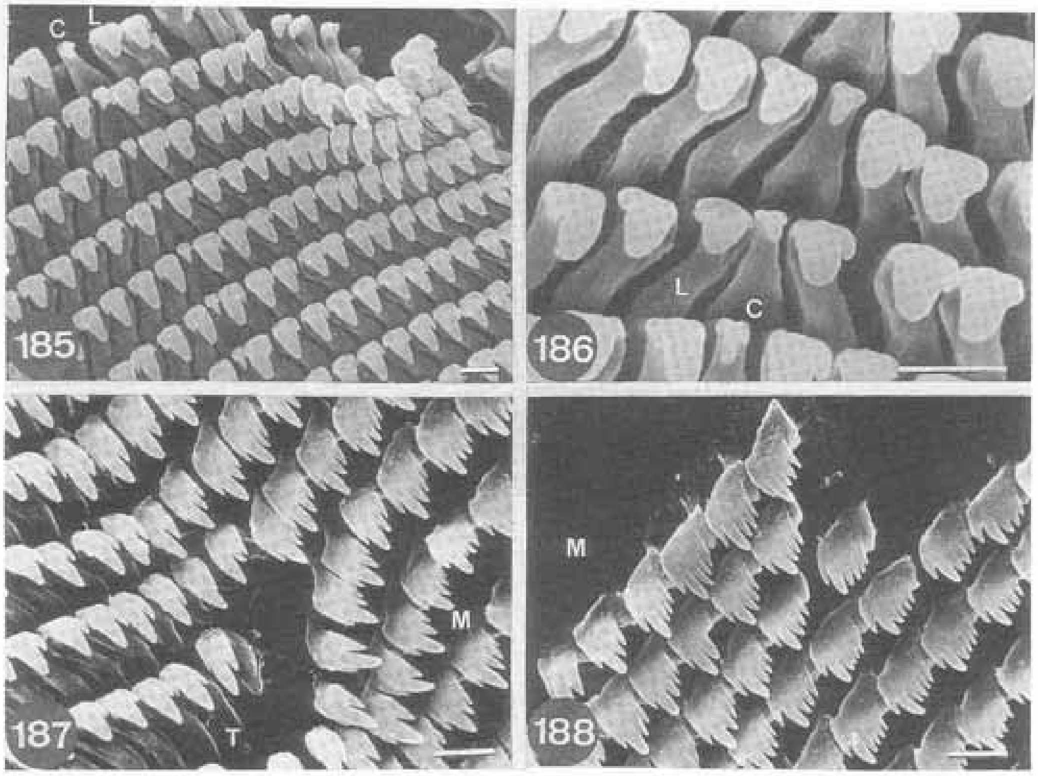
Melampus (Microtralia) minusculus (Dall). Zilch, 1959: 65, fig. 208.

Description: Shell (Figs. 174–178, 182–184) to 3.8 mm long, subcylindric, fragile, translucent, white to yellowish. Spire low to moderately high; whorls to five and three-fourths, weakly convex, sculptured with very fine, undulating spiral lines that extend over body whorl. Body whorl about 80% of shell length, crossed by faint, compact growth lines. Aperture about 90% of body whorl length, narrow; inner lip with three teeth on anterior half; columellar tooth small, oblique, twisted; anterior parietal tooth strong; posterior parietal tooth very small, sometimes reduced to a

FIGS. 174–184. *Microtralia, Rangitotoa, Pseudomelampus, Sarnia.* (174) *Tralia (Alexia?) minuscula* Dall, lectotype (USNM 61211), Magill's Bay, Tampa, Florida, sl 3.5 mm. (175) *Auricula? (Microtralia) minuscula* Dall, Atkins Island, Bahamas (USNM 127487), sl 2.3 mm; figured by Dall (1894, fig. 7). (176) *Auriculastra nana* Haas, paratype (ANSP 212177), Lover's Lake, Bermuda, sl 3.2 mm. (177) *M. occidentalis* (Pfeiffer), Hungry Bay, Bermuda, sl 3.5 mm. (178) *M. occidentalis*, Hungry Bay, Bermuda, sl 3.6 mm. (179) *R. insularis* Powell, paratype (ANSP 242319), Rangitoto Island, Auckland, New Zealand, sl 3.2 mm. (180) *P. exiguus* (Lowe), lectotype (BMNH 1875.12.31.109), Madeira, sl 5.8 mm. (181) *S. frumentum* (Petit), syntype? (BMNH 1843.11.24.58), Lima, Peru, sl 7.0 mm. (182) *M. occidentalis*, top view of spire and protoconch, Plantation Key, Florida. (183) *M. occidentalis*, Hungry Bay, Bermuda, sl 3.1 mm. (184) *M. occidentalis*, lateral view of spire and protoconch, Hungry Bay, Bermuda. Scale 1 mm.



FIGS. 174–184.



FIGS. 185–188. *Microtralia occidentalis*, radular teeth. (185) Hungry Bay, Bermuda, sl 3.9 mm. (186) Grassy Key, Florida. (187, 188) Hungry Bay, Bermuda, sl 3.9 mm. Scale 20 µm.

barely visible callus at mid-length of aperture; outer lip sharp, parallel to body whorl, sinuous. Inner wall of whorls occupying less than one-quarter of body whorl (Fig. 178). Protoconch globose; nuclear whorls deeply involuted in first whorl of teleoconch; only small portion of lip showing (Figs. 182, 184).

Animal whitish to rusty brown; tentacles short, subcylindric, with tip weakly pointed or somewhat flat and expanded. Eyes lacking. Mantle skirt whitish with brownish tinge along border. Pallial cavity somewhat elongate; kidney broadly triangular, anteriorly rounded, covering most of pallial cavity; pneumostomal and anal openings prolonged by a tube-like flap of mantle skirt; anal gill well developed.

Radula (Figs. 185–189) having formula [15 + (3 + 16) + 1 + (16 + 3) = 15] × 95. Crown of central tooth small, as wide as posterior end of base, tricuspid; mesocone small, blunt to weakly pointed; ectocones very small but well defined. Lateral teeth 12 to 18; crown wider than base, bicuspid; mesocone broadly rounded anteriorly, becoming more pointed and longer toward marginal teeth. Transitional teeth two to three, with small endocone, thinner and longer ectocone. Mar-

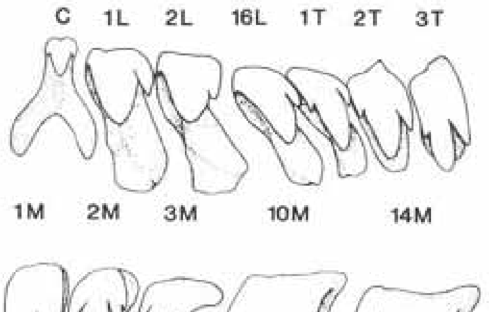


FIG. 189. *Microtralia occidentalis*, radula, Grassy Key, Florida. Scale 10 µm.

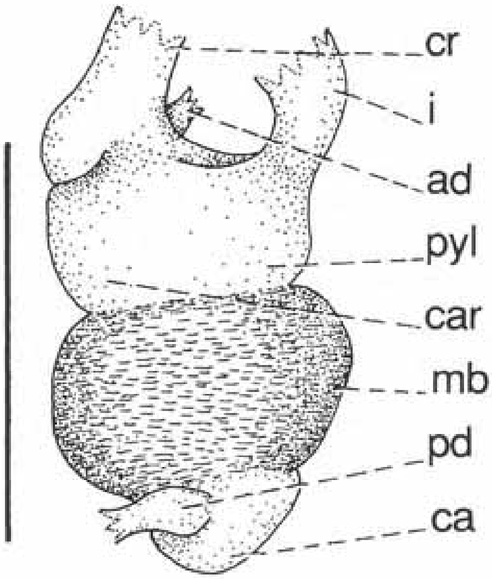


FIG. 190. *Microtralia occidentalis*, stomach, Bermuda. Scale 1 mm.

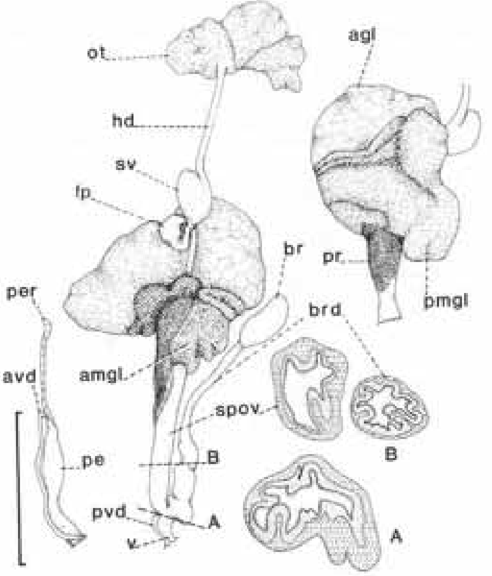


FIG. 191. *Microtralia occidentalis*, reproductive system, Hungry Bay, Bermuda. A, B, transverse sections and their locations. Scale 1 mm.

ginal teeth 13 to 19; base short and wide, with lateral flare, on which endocone of next tooth articulates; Crown gradually widening and mesocone gradually becoming shorter and thinner toward margin; first marginal tooth with two ectocones; additional ectocones appearing on fourth, eighth and twelfth marginal teeth; sometimes a sixth ectocone appears on twelfth marginal tooth in some rows.

Digestive system (Fig. 190) having digestive gland with two subequal lobes. Posterior crop dilated, receiving anterior diverticulum just before joining stomach. Anterior portion of stomach thin, with inner thickening between entrance of esophagus and exit of intestine; mid-stomach gizzard-like, thickly muscular; gastric caecum thin, dilated, receiving posterior diverticulum at junction with gizzard.

Reproductive system (Fig. 191) with ovotestis acinose, trilobed, conical, at posterior tip of visceral mass, covering stomach; hermaphroditic duct straight, with anterior, pouch-like seminal vesicle connecting with convoluted fertilization chamber; albumen gland and posterior mucous gland large; anterior mucous gland and prostate gland covering posterior half of spermoviduct; bursa duct as long as spermoviduct, thick, emptying near opening of vagina; bursa oval-elongate; vas deferens separates from oviduct near opening of vagina. Penis short, thick; associated vas deferens free, somewhat longer than penis; penial retractor about as long as penis, inserting on penis subapically, attaching to anterior portion of floor of pallial cavity.

Nervous system (Fig. 192) with cerebral commissure somewhat shorter than width of cerebral ganglion; left cerebropleural and cerebropedal connectives longer than right ones; connectives of visceral ring very short, causing agglomeration of ganglia; pedal commissure short but conspicuous. Cerebral ganglia largest; pleural ganglia well developed; left parietal ganglion very small; right parietal ganglion and visceral ganglion about same size. Penial nerve branching from medial lip nerve.

Remarks: Originally Pfeiffer (1854b) assigned *Microtralia occidentalis* to the genus *Leuconia* Gray, 1840, which, because it was preoccupied, was renamed *Leucopepla* by Peile (1926). Pilsbry (1927) showed that on the basis of shell characters *Microtralia occidentalis* could not be placed in *Leucopepla* [= *Auriculinella*]. The latter genus belongs in the Ellobiinae on the basis of its nervous and repro-

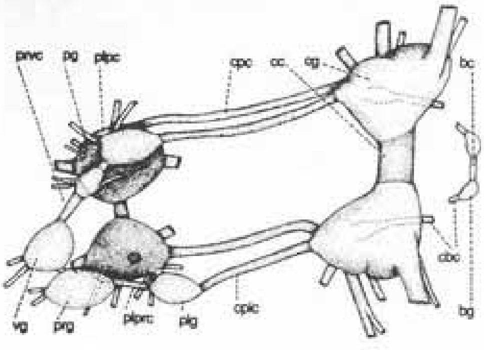


FIG. 192. *Microtralia occidentalis,* central nervous system, Hungry Bay, Bermuda. Scale 1 mm.

ductive systems, and *Microtralia* (see remarks under the genus) rightly belongs in the Pedipedinae.

Dall (1889), apparently unaware of Pfeiffer's name, described *Tralia (Alexia?) minuscula* (Fig. 174) for which he created, in 1894, the subgenus *Microtralia,* tentatively removing it to the genus *Auricula.* The odd combinations of names representing such different groups indicate the extent to which Dall was confused about the relationships of this small species.

Microtralia occidentalis shows some morphological variation within populations and across its geographical range. Bermudian specimens are brownish and have the tips of the tentacles somewhat flat and broad. Floridian specimens are usually whitish, sometimes yellowish brown, and the tentacles are subcylindrical with blunt or weakly pointed tips. Bahamian examples are rusty brown and the tips of the tentacles are intermediate in shape between Bermudian and Floridian specimens. The radulae of specimens from Bermuda have rounder and somewhat shorter cusps than do those from Florida, but otherwise show no other morphological differences. Intrapopulational variations in shell morphology, especially the height of the spire and the strength of the apertural teeth, occur throughout the range of the species.

Haas (1950) apparently was unaware of Pfeiffer's or Dall's names when he introduced *Auriculastra nana* from Bermuda, for he did not refer to either author in the original description. Haas' species (Fig. 176) does not differ from *Microtralia occidentalis* and it must therefore be considered a junior synonym of the latter.

Climo (1982), as noted under the remarks for the genus, synonymized *Rangitotoa insularis* Powell with *Microtralia occidentalis,* considering the former to have been introduced in New Zealand and possibly also in Rapa Iti Island and Easter Island. I concur with Climo's taxonomic decision about the genera, on the basis of the conchological and radular similarities; however, the widespread distribution of the genus (see the remarks for the genus) and the anatomical differences observed in *Microtralia alba* (Gassies, 1865) from Hong Kong (Martins, 1992), preclude an immediate synonymization of both species.

An anatomical peculiarity of *Microtralia occidentalis* is the absence of eyes, confirmed by histological examination. Concealment of the eyes under the skin has been reported for several species of the genus *Ellobium* (Pelseneer, 1894a: 75, note 1). In the West Indian species *Ellobium (A.) dominicense* the eyes, although covered by thick skin, are readily visible.

The shell of *Microtralia occidentalis* is not confused easily with that of any other West Indian ellobiid. It can resemble the very thin-shelled juveniles of some populations of *Tralia ovula,* however. *Microtralia* has a large, rounded protoconch, faintly incised, undulating lines on the spire and a posterior parietal tooth that is anterior to the mid-length of the aperture. In *Tralia ovula* the apex is mucronate, the spire has marked, pitted lines and the posterior parietal tooth is in the posterior half of the aperture.

Microtralia commonly occurs with *Pedipes ovalis, Laemodonta cubensis, Blauneria heteroclita* and *Creedonia succinea* and is readily distinguished from them. *Pedipes* is globose and has a rounded, strongly dentate aperture, *Laemodonta* is oval-elongate and hirsute and has a heavily dentate aperture, *Blauneria* has a sinistral shell and *Creedonia* has a truncated spire and very different inner lip dentition.

Habitat: Microtralia occidentalis lives at or above the high-tide mark, buried in the sediment sometimes 10 to 15 cm deep, in the company of *Blauneria heteroclita* and *Creedonia succinea.* The animals are quite common under partly buried, rotting wood or porous rocks, and on the roots of mangrove propagules, on which *Laemodonta cubensis* and *Pedipes ovalis* also abound.

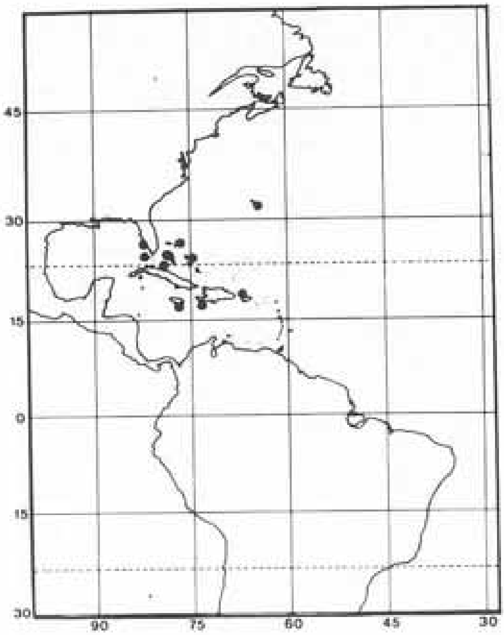


FIG. 193. *Microtralia occidentalis*, geographic distribution.

Range: Bermuda; Clearwater, Florida, south to the Florida Keys and the Greater Antilles (Fig. 193).

Specimens Examined: BERMUDA (USNM 250297); Fairyland (ANSP 99075; USNM 208069); Old Road, Shelly Bay (A.M.); Lover's Lake, St. George's (ANSP 212172); near St. George's (ANSP 1008220); Castle Harbour, near Harrington House (ANSP 143322); Cooper's Island (ANSP 131645); Hungry Bay (A.M.); S End of Ely's Harbour (A.M.); Mangrove Bay (A.M.). FLORIDA: N of Tavernier Creek, Key Largo (A.M.); S of Ocean Drive, Plantation Key (A.M.); Lignumvitae Key (ANSP 156682); Long Key (A.M.); Grassy Key (A.M.); Crawl Key (A.M.); Bahia Honda Key (ANSP 104108); Big Pine Key (ANSP 104102); W of Kohen Avenue, Big Pine Key (A.M.); Big Torch Key (ANSP 104001; A.M.); Sugarloaf Key (ANSP 89558); Boca Chica Key (ANSP 152503; USNM 270350); Seminole Point (ANSP 105409); Blue Hill, Hors Island (ANSP 99199); Captiva Island (ANSP 131836); McGill's Bay, near Tampa (USNM 61211, 859503); Boca Ciega Bay (ANSP 9571); Pinellas Point (USNM 83255); Clearwater Island (ANSP 9351). BAHAMA ISLANDS: GREAT ABACO ISLAND: Mores Island (MCZ 294207); ANDROS ISLAND: South Mastic Point (A.M.); Stafford Lake (ANSP 294338); Mangrove Cay (USNM 270214b); NEW PROVIDENCE ISLAND: W of Clifton Point (A.M.); E of Clifton Pier (A.M.); shore of Millars Road (A.M.); Bonefish Pond (A.M.); AKLINS ISLAND: Pinnacle Point (USNM 390857a); SAN SALVADOR (USNM 127487): Bob's Key, S. Ferdinand (USNM 360499). CUBA (ANSP 22482): near Habana (ANSP 130794). JAMAICA: Falmouth (ANSP 397269); Robin's Bay (USNM 441980, 442113); Kingston (USNM 395452b); Rio Cobre, Port Royal (USNM 426889); Hunt's Bay (USNM 441642); Rock Fort (USNM 467164). HAITI: Gonave Island (USNM 380184). DOMINICAN REPUBLIC: Rio Guayabin by Sabaneta Road (ANSP 160398). PUERTO RICO: Puerta de Tierra, San Juan (A.M.); Puerto Real (A.M.).

Genus *Leuconopsis* Hutton, 1884

Leuconopsis Hutton, 1884: 213. Type species by monotypy: *Leuconopsis obsoleta* (Hutton, 1878).

Apodosis Pilsbry & McGinty, 1949: 9. Type species by monotypy: *Apodosis novimundi* Pilsbry & McGinty, 1949.

Description: Shell to 4 mm long, oval-conic to oblong-conic, somewhat thin to solid. Spire low to moderately high, with as many as six and one-half flat, striated whorls. Body whorl about 80% of shell length. Aperture about 75% length of body whorl, approximately oval, posteriorly angulate; inner lip with strong submedian columellar tooth, usually with weak anterior secondary tooth; outer lip sharp. Protoconch smooth; nuclear whorls embedded in first whorl of teleoconch.

Radula with 87 to 111 teeth in a row. Base of central tooth widened anteriorly, sharply constricted posteriorly; crown thin, falciform; mesocone long, sharp. Base of lateral teeth abruptly bent medially at half length; crown as wide as base, with strong endocone. Transitional teeth lacking. Marginal teeth with strong mesocone, weaker endocone and ectocone.

Remarks: The genus *Apodosis* was created by Pilsbry & McGinty (1949) for the smallest and rarest West Indian ellobiid. In the original description the authors stated (p. 10) that they were "strongly inclined to treat *Apodosis* as a subgenus of the antipodal genus *Leuconopsis* Hutton." The shape of the shell, oblong-conic in the Atlantic species vs oval-conic in the type species (Fig. 217) the unimpressed suture and the inner thickening of the outer lip led them to establish a new genus. Examination of additional specimens of *Leuconopsis novimundi* revealed that the thickness of the outer lip varies with the thickness of the shell, and that the distinct thickened outer lip actually does not appear in some thin-shelled specimens. This variation was observed in *Leuconopsis manningi* n. sp. from Ascension Island and in *Leuconopsis rapanuiensis* Rehder, 1980, from Easter Island. The other characters mentioned by Pilsbry & McGinty are significant only at the specific level. The most obvious generic shell characters are the absence of a parietal tooth and the presence of a weak secondary columellar tooth just anterior to the primary submedian columellar tooth. This columellar structure is reminiscent of *Pedipes, Marinula* and *Creedonia.*

Powell (1933) illustrated the radula of *Leuconopsis obsoleta* (Hutton, 1878). The morphology of the teeth is very similar to that of the West Indian *Apodosis novimundi.* On the basis of shell and radular characters, *Apodosis* Pilsbry & McGinty must be considered a junior synonym of *Leuconopsis* Hutton.

Habitat: The genus lives intertidally under rocks (Hutton, 1884). Powell (1933: 150) found *Leuconopsis obsoleta* "in sheltered harbour bays towards high-tide, . . . and on cliffs, just above high-tide mark, in situations where fresh-water seepage occurs." I collected *Leuconopsis novimundi* on New Providence Island, Bahama Islands, in crevices of cliffs, just above high tide, but I did not see any indication of freshwater seepage.

Range: The genus *Leuconopsis* occurs in the Pacific in Australia, New Zealand and Easter Island. In the Atlantic it is represented by *Leuconopsis novimundi* (Pilsbry & McGinty) from the Florida Keys, Bahamas and Jamaica, and by *Leuconopsis manningi,* herein described, known only from Ascension Island. A possible third species from St. Thomas is left unnamed owing to lack of suitable material.

Leuconopsis novimundi
(Pilsbry & McGinty, 1949)
Figs. 194–204

Apodosis novimundi Pilsbry & McGinty, 1949: 10, pl. 1, fig. 1 [Clifton Bluff, New Providence, Bahamas; holotype ANSP 185474a (Fig. 194)]; Morrison, 1951b: 9; Zilch, 1959: 70, fig. 227; Franc, 1968: 525; Abbott, 1974: 334, fig. 4102. *Non* "Pilsbry & McGinty" Rosewater, 1975 [misindentification of *Leuconopsis manningi* Martins n. sp.].

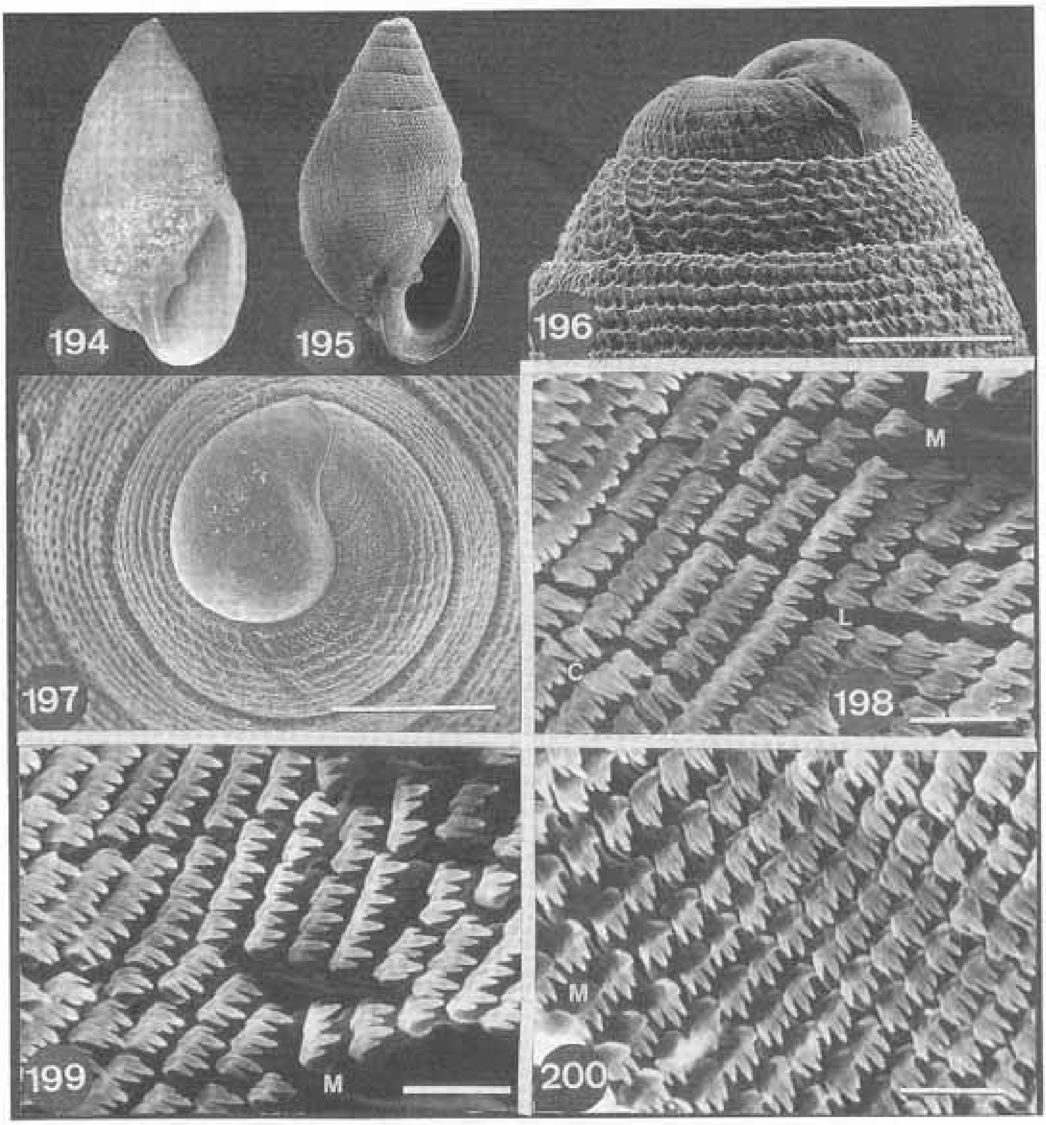
Description: Shell (Figs. 194–197) to 3.4 mm long, oblong-conic, solid, uniformly light yellow to pale brown. Umbilical area marked by shallow excavation. Spire moderately high, whorls as many as six and one-half, flat and heavily sculptured with numerous spiral cords, intersected by compact axial, somewhat regularly spaced, fine growth lines, giving shell a matte appearance. Body whorl convex, about 75% of shell length and with same sculpture as spire. Aperture about 70% body whorl length, subaxial, narrowly ovate; inner lip with partly hidden tooth at point of juncture of columella and parietal wall; occasionally secondary columellar tooth present as faint callosity just anterior to columellar tooth; outer lip sharp. Protoconch oblong, smooth, transparent, with sinuous lip (Fig. 197).

Animal whitish gray; foot dirty white, transversely divided; tentacles short, transparent, subcylindric, with rounded tip; mantle skirt slightly lighter than rest of animal.

Radula (Figs. 198–201) having formula $(33 + 10 + 1 + 10 + 33) \times 75+$. Base of central tooth with quadrangular anterior half, round at tip; width of posterior half abruptly reduced to half; crown as wide as posterior half of base, falciform; mesocone just over half length of base, pointed. Lateral teeth bicuspid; mesocone sharp, as long as, but stronger than, that of central tooth; endocone sharp, almost as long and strong as mesocone. Marginal teeth tricuspid; ectocone becoming as long as endocone; mesocone becoming smaller, but remaining the strongest cusp.

Digestive system with posterior crop wide, with strong internal folds; stomach very muscular, with gastric caecum where posterior diverticulum empties.

Reproductive system (Fig. 202) semidiaulic, with vas deferens separating from oviduct almost at half-length of pallial gonoduct; anterior mucous gland covers spermoviduct nearly to separation of vas deferens; bursa duct empties near female opening. Penial complex dilated, pouch-like in mid-section; posterior section thinner, coming out of pouch as blunt diverticulum; penial retractor



FIGS. 194–200. *Leuconopsis novimundi* (Pilsbry & McGinty), Clifton Bluff, New Providence, Bahamas. (194) Holotype (ANSP 185474a), sl 3.36 mm. (195) Shell length 2.73 mm. (196) Lateral view of spire and protoconch. (197) Top view of spire and protoconch. (198) Central, lateral and marginal teeth of radula. (199) Marginal teeth of radula. (200) Marginal teeth of radula. Scale, Figs. 196, 197, 1 mm; Figs. 198–200, 20 µm.

multifid, short, attaching to end of posterior section of penis subapically; vas deferens free, entering penis at base of thinner posterior section.

Nervous system (Fig. 203) with cerebral ganglia largest; left pleural ganglion larger than right one; left parietal ganglion much smaller than right one; visceral ganglion

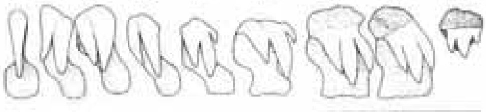


FIG. 201. *Leuconopsis novimundi*, radula, Clifton Bluff, New Providence, Bahamas. Scale 10 µm.

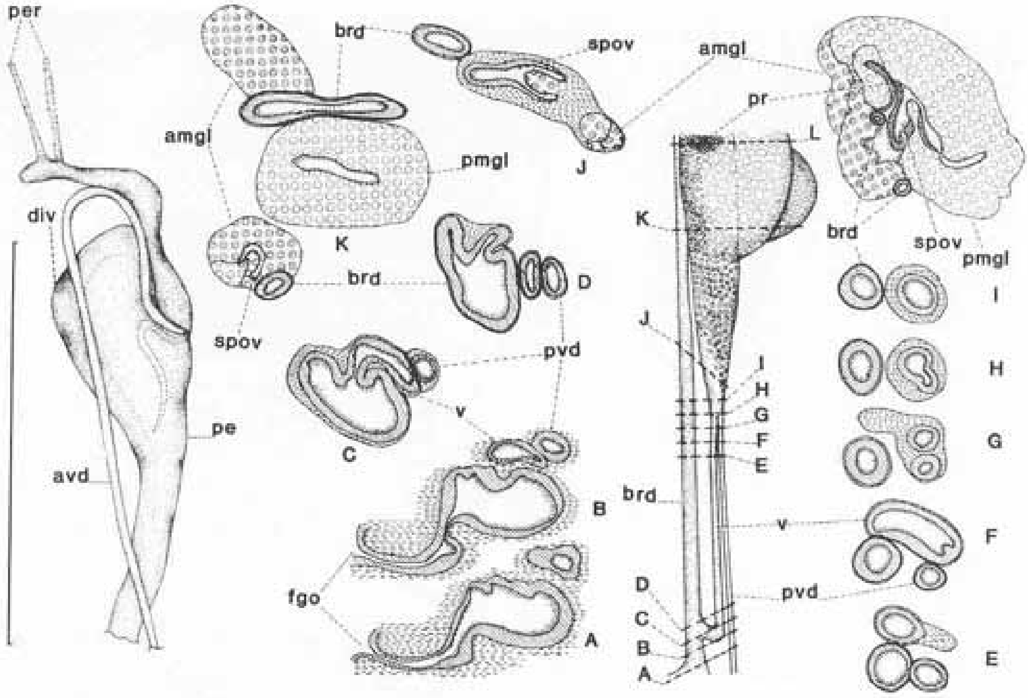


FIG. 202. *Leuconopsis novimundi*, reproductive system, Clifton Bluff, New Providence, Bahamas. Penis drawn under camera lucida, pallial gonoducts reconstructed from histological sections. A-L, transverse sections and their locations. Scale 1 mm.

about as large as right parietal ganglion. Cerebral commissure somewhat longer than width of cerebral ganglion; right and left cerebropedal and cerebropleural connectives roughly equal; left pleuroparietal connective very small; all other visceral ring connectives equal, about half length of cerebropleural connectives.

Remarks: Leuconopsis novimundi shows some anatomical deviations from typical members of the Pedipedinae such as *Pedipes* and *Creedonia* (see the remarks under the subfamily). The origin of the vas deferens from the mid-section of the spermoviduct-vaginal tract was unexpected in this species because Morton (1955b) stated that the separation of the vas deferens from the spermoviduct in *Leuconopsis obsoleta* occurs at the vaginal opening, as in *Ovatella* [*sensu Myosotella*]. Nevertheless, *Leuconopsis novimundi* is placed in the Pedipedinae on the basis of the presence of the double columellar tooth in the aperture, the shape of the crown of the central and lateral teeth, the prostate and anterior mucous gland not reaching the female opening, and the relatively short visceral nerve ring, as compared to that of the Pythiinae or Ellobiinae.

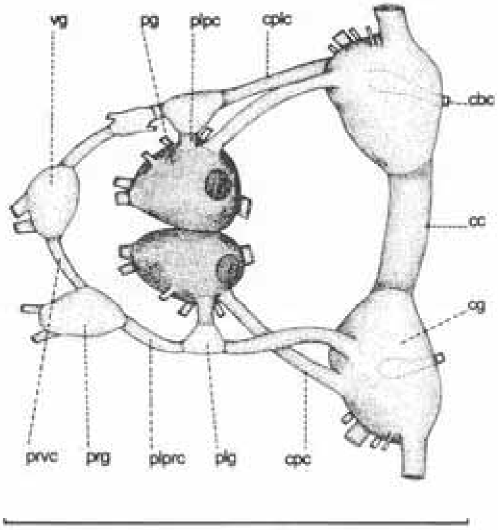


FIG. 203. *Leuconopsis novimundi*, central nervous system, Clifton Bluff, New Providence, Bahamas. Scale 1 mm.

Rosewater (1975) erroneously identified a small *Leuconopsis* from Ascension Island as *Apodosis novimundi*. These specimens (USNM 735149, 859015) differ from *Leuconopsis novimundi* in the differently sculptured shell that lacks the matte appearance and in the readily visible secondary columellar tooth. They represent a previously undescribed species that is introduced as *Leuconopsis manningi* n. sp. in this report (Figs. 205, 206). The protoconch of *Leuconopsis novimundi* is very similar to that of *Leuconopsis manningi* in having a sinuous lip (Figs. 207, 208), a characteristic lacking in *Leuconopsis rapanuiensis* (Fig. 216).

Leuconopsis novimundi is readily distinguished from all other Western Atlantic ellobiids by its oval-elongate shell that has a matte appearance and by its lack of parietal teeth in the aperture.

Habitat: The two specimens collected by R. Robertson in 1964 on Pigeon Cay, Bimini, in algae on mangrove roots were probably the first ones to be collected alive. All other specimens in museum collections, including those of Pilsbry and McGinty, seem to have been obtained from beach drift. Despite thorough field work and patient rock-combing, all but one of the specimens I found alive came from a cave at the western tip of Clifton Bluff (Clifton Pt.), New Providence Island, Bahamas, kindly indicated to me by T. L. McGinty. The cave formed from a double crack in the coral bed, running from sea to shore. It is open above, so direct sunlight illuminates it a few hours a day. At high tide water enters the main opening from the ocean, as well as the bottom of the double crack. One specimen was found among stones that had collected in one such crack, just above high-tide mark. Eight others were found in the crevices as deep as 20 cm in the wall and were obtained by chipping away the wet layers of coral in a band about 15 cm wide just above the black zone. The animals apparently feed on the detritus that collects in these crevices. The eight specimens were found within a radius of about 20 cm, together with *Pedipes ovalis*, *Laemodonta cubensis* and young *Melampus (D.) monile*. The other live specimen was found at Morgan's Bluff, Andros Island, Bahamas, under stones at the high-tide mark of a tidal pool.

Range: Florida Keys, Bahamas, Jamaica (Fig. 204).

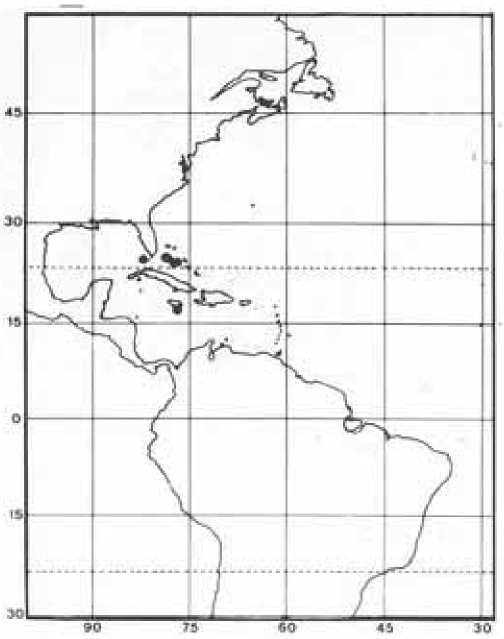


FIG. 204. *Leuconopsis novimundi*, geographic distribution.

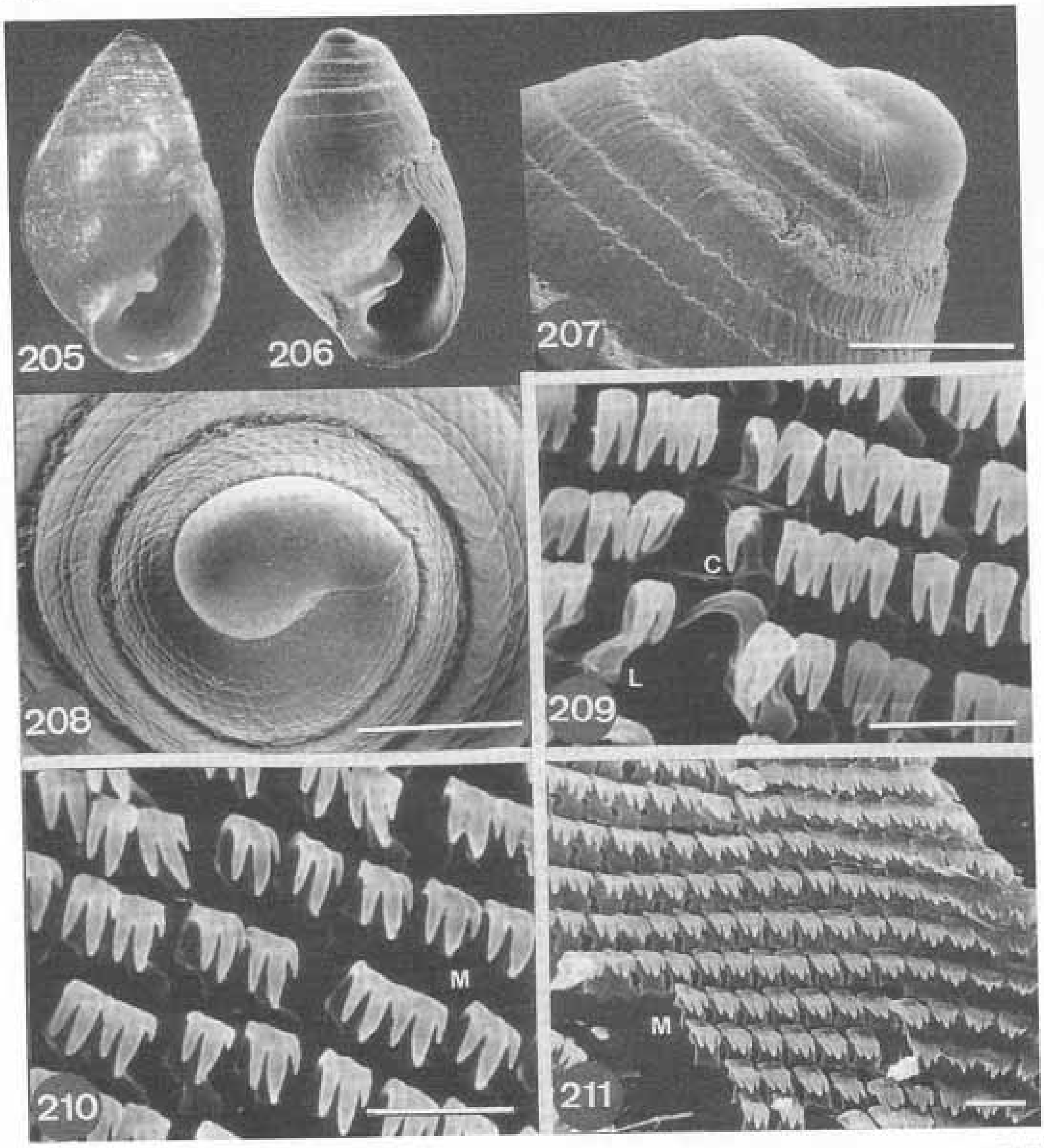
Specimens Examined: FLORIDA: Indian Key (USNM 492557a). BAHAMA ISLANDS: GRAND BAHAMA ISLAND: Gold Creek (ANSP 369338); Hepburn Town, Eight Mile Rock (ANSP 370409); Caravel Beach [John Jack Point], Freeport (ANSP 370225); BIMINI ISLANDS: N end of Pigeon Cay (ANSP 329623); ANDROS ISLAND: Morgan's Bluff (A.M.); Mangrove Cay (USNM 180462b); First island off Mintie Bar, SE of South Bight (USNM 271888); NEW PROVIDENCE ISLAND: Clifton Bluff (ANSP 185474; A.M.). JAMAICA: Jack's Bay (USNM 441915).

Leuconopsis manningi n. sp.

Figs. 120, 205–212

Apodosis novimundi Pilsbry & McGinty. [Type locality: English Bay, Ascension Island; holotype USNM 859015 (Fig. 205); 11 paratypes USNM 859015 (Fig. 206)].Rosewater, 1975: 23. *Non* Pilsbry & McGinty, 1949.

Description: Shell (Figs. 205–208) to 2.1 mm long, ovate, solid, uniformly pale to dark brown, smooth, shiny. Umbilical excavation very weak. Spire short, whorls as many as five and one-fourth, flat, sculptured with two



FIGS. 205–211. *Leuconopsis manningi* n. sp., English Bay, Ascension Island. (205) Holotype (USNM 859015), sl 2.02 mm. (206) Paratype (USNM 859015), sl 1.58 mm. (207) Lateral view of spire and protoconch. (208) Top view of spire and protoconch. (209) Central and lateral teeth of radula. (210) Marginal teeth of radula. (211) Marginal teeth of radula. Scale, Figs. 207, 208, 1 mm; Figs. 209–211, 20 µm.

to seven incised spiral lines on shoulder in adults, juveniles often spirally striated on entire length; growth lines very faint. Aperture 75% of body whorl length, ovate; inner lip with strong posterior columellar tooth about mid-length of aperture, with conspicuous but much smaller anterior secondary tooth; outer lip sharp. Protoconch oblong, smooth, transparent, dark brown, with sinuous lip.

Radula (Figs. 209–212) having formula $(32+11+1+11+32)\times 70+$. Radular morphology as in *Leuconopsis novimundi*.

Animal unknown.

Remarks: Leuconopsis manningi was first mentioned in the literature by Rosewater (1975), who misidentified it as *Apodosis novimundi*. This new species differs from

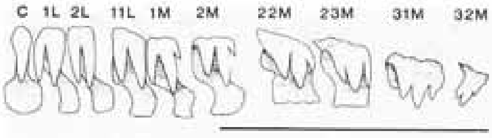


FIG. 212. *Leuconopsis manningi*, radula, Ascension Island. Scale 10 μm.

Leuconopsis novimundi in the ovate shape of the shell, the proportionately longer, nonmatte body whorl that usually has two incised lines on the shoulder, the larger aperture and the conspicuous secondary columellar tooth. *Leuconopsis manningi* is closely related to *Leuconopsis rapanuiensis* Rehder, 1980, from Easter Island (Figs. 214–216). The secondary columellar fold of the latter is farther foreward than in *Leuconopsis manningi,* the protoconch is stouter and has a rounded instead of sinuous lip.

The single radula studied was obtained by breaking the shell of a dried animal; the apex of the shell was used for the SEM study of the protoconch.

Following the suggestion of the late J. Rosewater I name this species for R. B. Manning, who collected the specimens in 1971.

Habitat: Intertidal pools, subtidal rocky shore, with some coarse sand (from USNM label).

Range: English Bay, Ascension Island (Fig. 120).

Leuconopsis sp.
Fig. 213

Description: Shell (Fig. 213) 4 mm long, oval-conic, solid, white. Spire moderately high, with about six weakly convex whorls. Body whorl 77% of shell length. Aperture semilunate, 67% of body whorl; inner lip with moderately strong, horizontal columellar tooth just anterior to mid-length of aperture; obvious secondary tooth somewhat anterior to previous one; outer lip sharp.

Remarks: A single specimen from St. Thomas, Virgin Islands, originally from the Swift collection (now ANSP 22599), differs from the other Atlantic species of *Leuconopsis* in its wider body whorl, in its anteriorly less expanded outer lip, which gives the aperture a semilunate aspect, and in its conspicuous secondary columellar tooth at some distance anterior to the primary tooth. The example is undoubtedly a beach specimen, a fact that might account for the absence of any visible sculpture.

I am reluctant to erect a new species upon a single worn specimen; the naming of this probably new species must await collection of more material.

Subfamily Melampinae Pfeiffer, 1853

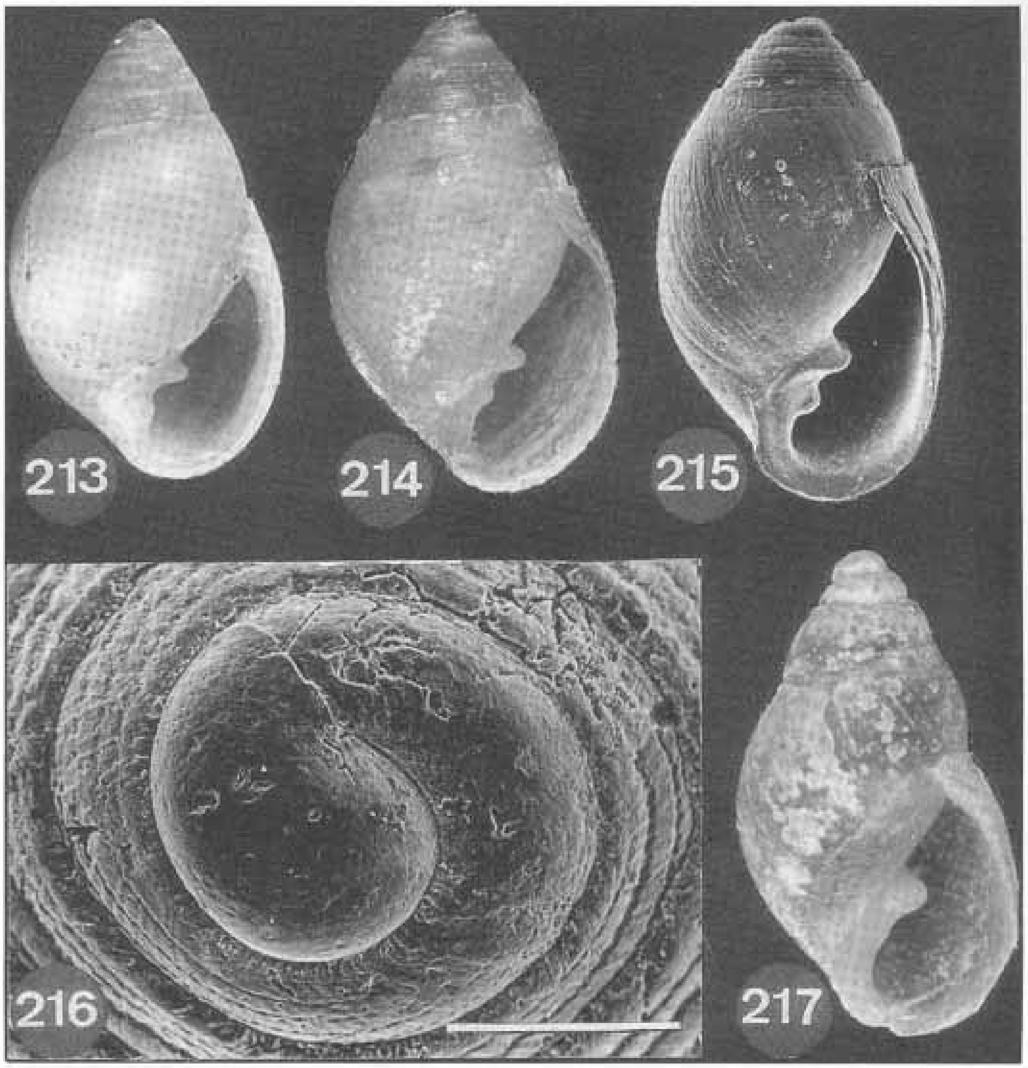
Melampinae Pfeiffer, 1853a: 8 [corrected from Melampea by H. & A. Adams, 1855b].
Melampodinae Fischer & Crosse, 1880: 5 [unjustified emendation].

Description: Shell to 23 mm long. Spire low to high. Body whorl usually more than 75% of shell length. Aperture elongate, narrow; one columellar tooth; one to five parietal teeth; outer lip internally smooth or with as many as 18 riblets. Protoconch nipple-like, smooth, with spiral axis perpendicular to columellar axis of teleoconch; nuclear whorls only partly covered by first whorl of teleoconch.

Animal white to black, generally brown; foot transversely divided, bifid posteriorly.

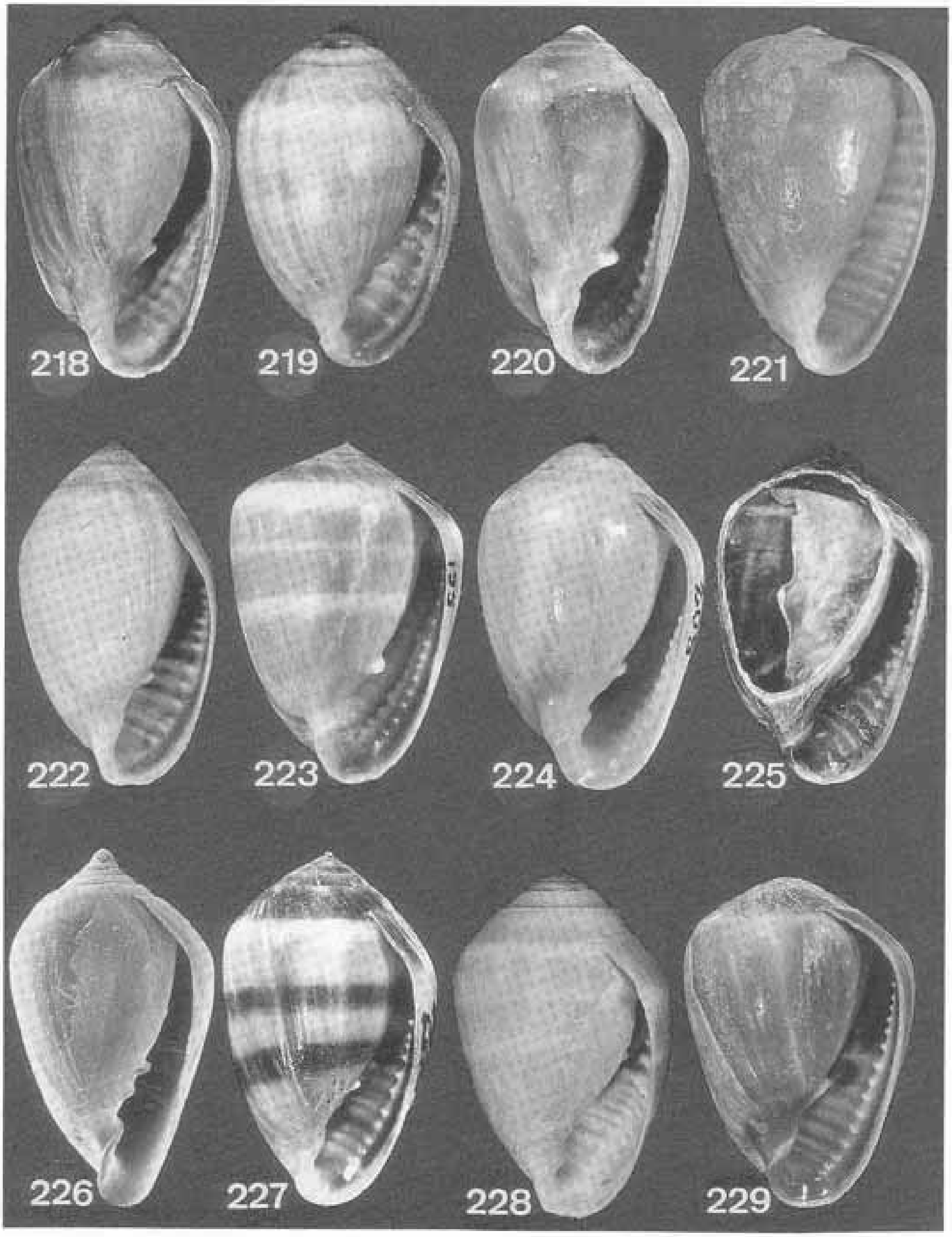
Radula with central tooth posterior to lateral teeth, triangular, with base deeply indented; crown with narrow, sharp mesocone, ectocones very small or absent. Base of lateral teeth rectangular, medially bent in shape of boomerang, with medial node on inner surface; crown with strong mesocone pointing laterally, sometimes with endocone or ectocone. Transitional teeth with shorter base, crown more elongate posteriorly and extra denticle on ectocone. Marginal teeth with very strong mesocone, one or two denticles on endocone and one to eight denticles on ectocone; base and crown gradually become shorter from innermost to outermost teeth and denticles of ectocone gradually advance to same level, becoming subequal in size.

Digestive system having mandible tripartite, of numerous longitudinal fibers; stronger central portion lining upper lip and folded, tapering extremities lining lateral lips. Salivary glands yellowish to white, long, fusiform. Esophagus with internal, longitudinal folds, ending posteriorly in a wide crop that receives anterior diverticulum of digestive gland; a thin muscular strand secures posterior crop to posterior portion of muscular band of stomach. Digestive gland brown to dark orange, bilobed; anterior lobe very large, composed of several lobules that empty into wide anterior diverticulum; posterior lobe small, located



FIGS. 213–217. *Leuconopsis*. (213) *Leuconopsis* sp., St. Thomas, Virgin Islands (ANSP 22599), formerly in Swift collection, sl 4.04 mm. (214) *L. rapanuiensis* (Rehder), holotype (USNM 756790), Easter Island, sl 2.87 mm. (215) *L. rapanuiensis*, paratype (USNM 756238) Easter Island, sl 2.34 mm. (216) *L. rapanuiensis*, top view of spire and protoconch. (217) *L. obsoleta* (Hutton), Takapuna, Auckland, New Zealand (USNM 681309), sl 2.50 mm. Scale 1 mm.

partly beneath ovotestis, covering posterior left portion of stomach and emptying into small posterior diverticulum. Stomach globular, tripartite; anterior portion thin, weakly muscular at cardiac aperture; middle portion surrounded by thick band of muscle around pyloric region; posterior portion of caecum thin, receiving posterior diverticulum at anterior border, just posterior to muscular band and near attachment of muscular strand; stomach attached to mantle by muscular fibers extending from region opposite opening of posterior diverticulum. Intestine dilates as it leaves the stomach anteriorly just right of esophagus, and has several convolutions in midst of digestive gland; rectum parallels right edge of pallial cavity; anal opening lateral to pneumostome, on mantle lappet. Anal gill bilobed, flanking rectum just posterior to anus.



FIGS. 218–229. *Melampus (M.) coffeus* (Linnaeus). (218) Lectotype (LSL), sl 18.8 mm. (219) Paralectotype (LSL), sl 11.0 mm. (220) *Auricula biplicata* Deshayes, holotype (MNHNP), sl 20.0 mm. (221) *M. coffea* var. *microspira* Pilsbry, holotype (ANSP 61471), Progreso, Yucatán, Mexico, sl 12.8 mm. (222) Bermuda (USNM 11421), sl 15.2 mm. (223) Grand Bahama Island, Bahamas (MCZ 116679), sl 17.3 mm. (224) Anegada, Virgin Islands (MCZ 229004), sl 18.3 mm. (225) Isla Matica, Dominican Republic (R.B.), sl 10.4 mm. (226) Juvenile, Puerto Real, Puerto Rico, sl 3.6 mm. (227) Tucacas, Venezuela, sl 10.5 mm. (228) Bahia [San Salvador], Brazil (AMNH 22434), sl 12.0 mm. (229) Boa Viagem, Brazil (MCZ 219130), sl 19.5 mm.

Reproductive system of advanced semidiaulic type, the short spermoviduct separating into long, thin vagina and vas deferens shortly after passing posterior mucous gland; posterior mucous gland large, spiral, covering only small portion of spermoviduct; prostate gland beneath posterior mucous gland, not discrete; anterior mucous gland absent; vagina running posteriorly, turning abruptly and following columellar muscle anteriorly; elbow of vagina attached by muscle fibers to left corner of insertion of columellar muscle. Bursa with short peduncle, at or very near proximal end of vagina. Penis long, usually simple; anterior vas deferens long, thin, entering penis apically; penis and posterior vas deferens run beneath upper tentacle retractors, over cerebral commissure and under right tentacular nerve.

Nervous system having cerebral commissure short; cerebropleural connectives about same length as cerebropedal connectives; pleuroparietal and parietovisceral connectives very short.

Remarks: Baker (1963) showed that, although the word *Melampus* has its origin in the Greek, meaning "black foot," it was Latinized and used by the Romans in the genitive case, "melampi." Hence Melampinae must be used instead of Melampodinae.

During growth the radula changes considerably in shape and number of teeth (Table 4, Appendix). In very young animals the inner edge of the arms of the base of the tricuspid central tooth bears conspicuous prominences. The first lateral tooth can be either tricuspid or bicuspid. The marginal teeth have an ectocone that becomes serrate, carrying as many as eight subequal cusps. As the animal grows, certain characteristics are retained, such as the splitting of the endocone and ectocone. Others are enhanced, such as the serrations on the lateral edge of the crown of the marginal teeth of young *Melampus s. s.* before the ectocone becomes a distinct cusp. Some characteristics, such as the ectocone and endocone of the lateral teeth, become lost in most species. Even in adults the same tooth in adjacent rows might be inconsistent. The characteristics given in the description must be considered as the general pattern in adult individuals.

In all animals examined the stomach agrees with Koslowsky's (1933) and Marcus & Marcus' (1965a) descriptions, rather than with Morton's (1955c) account, which did not record the presence of the caecum and posterior diverticulum. No evidence was found to support Marcus & Marcus' statement that the stomach of *Melampus gundlachi* Pfeiffer, 1853 [= *Melampus (M.) bidentatus* Say, 1822] is radically different from that of other West Indian Melampinae.

Only two genera compose the subfamily Melampinae: *Melampus* Montfort and *Tralia* Gray. *Melampus* is easily distinguished from *Tralia* on the basis of its shell. *Melampus* has a much narrower aperture than does *Tralia*, the dentition of the inner lip is restricted to the anterior half, the anterior parietal tooth, when present, is very small and the outer lip is usually interiorly ribbed. *Tralia* has a strong anterior parietal tooth and always has another conspicuous parietal tooth on the posterior half of the aperture. The outer lip is sinuous and has only one ridge-like riblet opposite the posterior parietal tooth. Zilch (1959) listed *Rangitotoa* Powell in this subfamily, but results of this study led me to conclude with Climo (1982) that *Rangitotoa* is a junior synonym of *Microtralia* Dall, which Zilch had listed as a subgenus of *Melampus*. The genus *Microtralia* belongs to the Pedipedinae by reason of the morphology of the reproductive and nervous systems.

The Melampinae are separated from the other ellobiid subfamilies on the basis of radula, reproductive system and nervous system. The serration of the ectocones of the marginal teeth of the radula has some parallel only in *Microtralia*. The nonglandular pallial gonoducts, the proximal position of the bursa duct and the long, generally thin penis are unique. The concentration of ganglia has some parallel in the Pedipedinae, but in the Melampinae the cerebral commissure is relatively shorter and the cerebropleural and the cerebropedal connectives are much longer.

A planktonic veliger has been reported for several Melampinae (Morrison, 1959; Russell-Hunter et al., 1972; Berry, 1977). This condition is considered primitive, retained from the estuarine habit of the ancestors of the ellobiids.

Habitat: The Melampinae are the most common ellobiids in the Western Atlantic, living mostly in salt marshes and in mangroves. They can occur in zones of very low salinity such as along the banks of rivers some miles inland [*Melampus (M.) bidentatus*, *Melampus (D.) floridanus*], or under rocks exposed to high-tide surf [*Melampus (D.) monile, Tralia (T.) ovula*]. They are among the common gastropods found in Stephenson & Stephenson's (1950) upper intertidal gray zone.

Range: Worldwide distribution, except in the Mediterranean region. In the Western Atlantic the Melampinae extend from Newfoundland to southern Brazil. Species are especially numerous in the West Indian region.

Genus *Melampus* Montfort, 1810

Melampus Montfort, 1810: 319. Type species by monotypy: *Melampus coniformis* (Bruguière, 1789) [= *Melampus coffeus* (Linnaeus, 1758)]. *Non* Gray, 1865 [Mammalia].

Conovulus Lamarck, 1816, pl. 459, fig. 2 a. b., Liste, p. 12. Type species herein designated, *Conovulus coniformis* (Bruguière, 1789) [= *Melampus coffeus* (Linnaeus, 1758)].

Melampa "Draparnaud" Montfort. Schweigger, 1820: 739 [unjustified emendation of *Melampus*].

Conovula Lamarck. Schweigger, 1820: 739 [in synonymy; unjustified emendation of *Conovulus*].

Conovulae Lamarck. Férussac, 1821: 104 [unjustified emendation of *Conovulus*].

Conovolus Lamarck. Sowerby, 1839b: 10 [error for *Conovulus*].

Conovulum Lamarck. Sowerby, 1842: 119 [unjustified emendation of *Conovulus*].

Maelampus Montfort. Reeve, 1877, pl. 1 [in synonymy; error for *Melampus*].

Description: Shell ovoid, white to dark brown, uniform or with light spiral bands or axial stripes. Aperture high, narrow, with widest point above columellar tooth; first parietal tooth reduced or absent; outer lip sharp, with lirae.

Animal grayish blue to black; tentacles subcylindric, pointed.

First lateral tooth of radula with or without ectocone, always lacking endocone.

Salivary glands attaching to ventral portion of esophagus, right one in front of left one. Esophagus heavily pigmented.

Reproductive system having ovotestis of dark yellow radiating tubules with or without dark brown spots, shallow-conic to leaf-like, rounded or lobed at base, deeply split on right side; gonadial artery entering ovotestis from left, bifurcates and radiates, covering lower surface of gland. Hermaphroditic duct brown, moderately long, forming very convoluted seminal vesicle, passing beneath posterior diverticulum. Albumen gland spiral. Posterior end of short, nonglandular spermoviduct with pouch-like prevaginal caecum; bursa large, banana-shaped, located partly against mucous gland, partly embedded in digestive gland, beneath heart. Penis simple, thin; penial retractor usually running beneath albumen gland, entering between two major bundles of columellar muscle and inserting together with muscle attachment; often penial retractor attaches to floor of lung, bifurcates or runs on top of columellar muscle.

Free-swimming veliger larva present.

Remarks: Ignorance of the specific habitat of the supralittoral pulmonate genus *Melampus* Montfort led to taxonomic misplacement of the group. Some early workers tried to incorporate habitat information in their classification schemes and therefore early 19th century nomenclatorial history of this genus is related not only to shell characters but also to knowledge of the habitats of species.

Montfort (1810) separated *Melampus coniformis* (Bruguière) [= *Melampus coffeus* (Linnaeus)] from *Bulimus* Bruguière on the basis of apertural details, and from *Auricula* Lamarck [= *Ellobium* Röding] and *Scarabus* Montfort [= *Pythia* Röding] on the basis of its conical shape. *Bulimus* Bruguière was a large, heterogeneous assemblage of mostly terrestrial and fluviatile mollusks. Montfort (1810: 320) seems to have had reliable information about the marine habitat of *Melampus (M.) coffeus,* for he specified (1810: 20), "Ce mollusque est marin, il vit sur les côtes de Cayenne, et principalement contre le rocher du Conétable, qui est en avant de la rade." It is also probable that Montfort had access to live or preserved material, although in the description he did not mention the external appearance of the animal. Only such an observation would justify the choice of the appropriate name *Melampus,* meaning black foot, a conspicuous characteristic of the type species.

Lamarck, apparently unaware of Montfort's work, also used shell shape and habitat in his classification. In 1812 he used the vernacular Conovule, Latinized by him in 1816 to *Conovulus,* for those fluviatile shells with the outer lip simple and sharp, which he previously had included under *Auricula.* Upon being informed that the animals in question were terrestrial, however, Lamarck (1822: 136) suppressed *Conovulus,* reuniting those species with *Auricula.* Nevertheless, the name *Conovulus* continued to be used occasionally, either emended or as originally spelled (Beck, 1837; Anton, 1839; Gray, 1840; Clark, 1850, 1855).

Lowe (1832) was convinced that the genus *Melampus* Montfort should be included within the marine pectinibranchs, and he stated, wrongly, that his *Melampus aequalis* [= *Ovatella aequalis*] had branchial respiration. Lowe knew of Montfort's comments on the marine habitat of the type species, *Melampus (M.) coffeus,* but he listed the latter species, without justification, among *Species incertae: huc forsan referendae* [Uncertain species; perhaps to be referred to this place]. It was this misidentification that led Gray (1847a) to consider Lowe's use of *Melampus* Montfort distinct and thus erroneously to designate a type species.

The genus *Melampus* is the predominant West Indian ellobiid group because of the number of species and abundance of individuals. Of the 18 recognized ellobiid species belonging to ten genera, seven are in *Melampus.* The very numerous individuals in salt marshes (Morrison, 1951a; Martins, personal observation) and in mangroves (Martins, personal observation) makes them very conspicuous occupants of those habitats.

Only two subgenera are recorded for the Western Atlantic, *Melampus s. s.* and *Detracia* Gray, which can be separated on the basis of apertural morphology. In *Melampus s. s.* the columellar tooth is small and the upper parietal tooth is the largest of the teeth on the inner lip. In *Detracia* the columellar tooth is largest, usually strongly twisted, and the upper parietal tooth is small and hidden. Anatomical differences reside mainly in the comparatively longer separation of the foot from the visceral mass in *Detracia,* with consequent elongation of the pallial and anterior reproductive ducts. In *Detracia* the mantle organ is conspicuously pouch-like, rather than rounded and conforming to the general shape of the mantle cavity.

The anatomical differences are related to the degree of resorption of the inner whorls of the shell. In *Melampus s. s.* resorption is so extensive that less than half of the partition of the body whorl remains (Figs. 225, 267), whereas in *Detracia* at least 75% of that partition remains (Figs. 302, 316, 340, 361). In *Detracia* the parietal teeth appear on the inner whorl as two conspicuous lamellae and the region near the columellar tooth forms a cavity that is occupied by the pouch-like mantle organ.

Habitat: Ubiquitous in those habitats mentioned for the Melampinae.

Range: Worldwide. Most of the Western Atlantic species live in the West Indies, but the genus extends from Newfoundland to southern Brazil.

Subgenus *Melampus s.s.*

Description: Shell oval-conic, spire low, eight to 12 whorls; posterior parietal tooth stronger than columellar tooth. Animal brownish to uniform black or with white markings. Medial edge of arms of base of central tooth of radula smooth or with very faint medial nodes. Visceral mass separated from foot by half a whorl; mantle organ round, not pouch-like.

Remarks: Beck (1837) used *Melampus* B [Beck (*sic*)] as a subgenus of *Melampus* Montfort. In listing the species, however, he did not include *Melampus (M.) coffeus,* the type of the nominate genus, which he had listed under the subgenus *Conovulus* B [Beck (*sic*)]. Gray (1847a) considered Beck's *Melampus* a valid taxonomic name and he erroneously designated *Melampus lineatus* Say [= *Melampus (M.) bidentatus* Say] as type species.

Melampus s. s. is represented in the Western Atlantic by only two species: *Melampus (M.) coffeus* (Linnaeus) and *Melampus (M.) bidentatus* Say. In Florida, Bermuda and the Greater Antilles, in which they overlap, the two species show a wide range of variation in shape and color, sometimes making their separation difficult. *Melampus (M.) bidentatus* can be recognized by the presence of at least one, usually two or three marked spiral grooves on the whorls of the spire and on the shoulder of the body whorl. In *Melampus (M.) coffeus* these grooves occur only on the first four whorls (Figs. 230, 232, 233). In addition, *Melampus (M.) coffeus* is conical, whereas *Melampus (M.) bidentatus* is more ovoid. Although variable in color, *Melampus (M.) coffeus* characteristically has as many as five dark, olive-green bands on the body whorl and usually it has a pinkish to purple patch covering the columellar fold and the tip of the columella. In *Melampus (M.) bidentatus* the bands are usually brownish and the columella is white. Anatomical differences occur, as in the nervous system, in which the right parietovisceral connective is shorter than that in *Melampus (M.) coffeus;* also in this species the vagina is twice the length of the posterior vas deferens, whereas in *Melampus (M.) bidentatus,* although variable, both ducts are much more alike in length.

Habitat: Melampus (M.) bidentatus is a common inhabitant of the North American salt marshes and of the mangroves of the Florida Keys, Bermuda and the Bahama Islands. *Melampus (M.) coffeus* lives in mangroves from Florida to Brazil. This species has not been reported from salt marshes and it overlaps with the former species only in mangroves.

Range: The subgenus *Melampus* has a worldwide distribution, not being restricted, as are most ellobiid groups, to the tropics. In the Western Atlantic the subgenus extends from Newfoundland, Canada, to Brazil.

Melampus (Melampus) coffeus

(Linnaeus, 1758)

Figs. 218–256

Bulla coffea Linnaeus, 1758: 729 [type locality unknown, herein designated to be Barbados, West Indies; lectotype herein selected, Linnaean collection, LSL (Fig. 218)].

Voluta coffea (Linnaeus). Linnaeus, 1767: 1187; Gmelin, 1791: 3438; Dillwyn, 1817: 505.

Bulimus coniformis Bruguière, 1789: 339 [American coast, herein restricted to Barbados, West Indies; location of type unknown].

Melampus coniformis (Bruguière). Montfort, 1810: 319; Lowe, 1832: 292; C. B. Adams: 1849: 42; C. B. Adams, 1851: 186; Shuttleworth, 1858: 73; Franc, 1968: 525.

Conovulus coniformis (Bruguière). Lamarck, 1816, pl. 459, figs. 2, a. b., Liste p. 12.

Auricula coniformis (Bruguière). Férussac, 1821: 105; Lamarck, 1822: 141; Menke, 1830: 36; Gould, 1833: 67; Potiez & Michaud, 1838: 202; Jay, 1839: 59; Sowerby, 1839b: 10, fig. 298: Sowerby, 1842: 77, fig. 298; Küster, 1844: 31, pl. 4, figs. 14–17; Reeve, 1877, pl. 7, fig. 57.

Pedipes coniformis (Bruguière). Blainville, 1824: 245; Blainville, 1825: 325 [425], pl. 37 bis, fig. 4 [erroneously listed in plate caption as Tornatelle coniforme].

Auricula biplicata Deshayes, 1830: 91 [type locality unknown, herein designated to be Barbados, West Indies; holotype MNHNP (Fig. 220)]; Pfeiffer, 1854b: 148.

Melampus (Conovulus) biplicatus (Deshayes). Beck, 1837: 106.

Melampus (Conovulus) coffeus (Linnaeus). Beck, 1837: 106.

Auricula (Conovulus) coniformis (Bruguière). Anton, 1839: 48.

Auricula conoidalis (Bruguière). Sowerby, 1839b: 63, fig. 298; Sowerby, 1842: 187, fig. 298 [referred to in text as *coniformis*].

Conovulus coffee (Linnaeus). Gray, 1840: 20 [error for *coffea*].

Auricula coniformis Férussac. Orbigny, 1841: 187, pl. 12, figs. 4–7 [plate caption incorrect; should be 4–7, not 1–3].

Auricula coniformis Lamarck. Reeve, 1842: 106, pl. 187, fig. 7.

Auricula olivula "Moricand" Küster, 1844: 33, pl. 3, figs. 11–33 [Bahía, Brazil; location of type unknown].

Melampus coffea (Linnaeus). Mörch, 1852: 38; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 28; Binney, 1860: 4; Binney, 1865: 13, fig. 15; Tryon, 1866: 8, pl. 18, figs. 7, 8; Pfeiffer, 1876: 306; Mörch, 1878: 5; Fischer & Crosse, 1880: 23, pl. 34, figs. 10, 10a; Crosse, 1890: 258; Hinkley, 1907: 71; Bequaert & Clench, 1933: 538.

Melampus coniformis (Lamarck). Shuttleworth, 1854b: 101.

Melampus coffeus (Linnaeus). H. & A. Adams, 1854: 9; H. & A. Adams, 1855b: 243, pl. 82, figs. 7, 7a; Binney, 1859: 162, pl. 75, figs. 21, 25; Poey, 1866: 394; Nevill, 1879: 219; Arango y Molina, 1880: 59; Dall, 1885: 280, pl. 18, fig. 3; Dall, 1889: 92, pl. 47, fig. 3; Maury, 1922: 54; Peile, 1926: 88; M. Smith, 1937: 146, pl. 55, fig. 7, pl. 67, fig. 3 [pl. 67 copied from Dall (1885: pl. 18)]; Perry, 1940: 117, pl. 39, fig. 286; Broek, 1950: 80; Morrison, 1951b: 8; Dodge, 1955: 64–68 [history of nomenclature]; Perry & Schwengel, 1955: 197, pl. 39, fig. 286; Morris, 1958: 228, pl. 40, fig. 14; Coomans, 1958: 103; Morrison, 1958: 118–124 [habitat]; Nowell-Usticke, 1959: 88; Holle & Dineen, 1959: 28–35, 46–51 [shell morphometry]; Golley, 1960: 152–155 [ecology]; Warmke & Abbott, 1961: 153 [pl. 28, fig. n is of *Melampus (Detracia) monile* (Bruguière)]; Marcus &

Marcus, 1963: 41–52 [early life history]; Marcus, 1965: 124–128 [systematics]; Marcus & Marcus, 1965a: 19–82, figs. 1–18 [distribution, ecology, anatomy]; Natarajan & Burch, 1966: 114 [chromosomes]; Scarabino & Maytia, 1968: 276–278; Coomans, 1969: 82; Rios, 1970: 138; Vilas & Vilas, 1970: 91, pl. 10, fig. 21; Princz, 1973: 183; Morris, 1973: 273, pl. 74, fig. 11; Abbott, 1974: 332, fig. 4088; Humphrey, 1975: 196, pl. 22, fig. 27 [figured dorsal view looks very much like *Melampus (D.) monile* (Bruguière)]; Rios, 1975: 158, pl. 48, No. 764; Emerson & Jacobson, 1976: 192, pl. 26, fig. 26; Berry, 1977: 181–226; Cosel, 1978: 215; Rosewater, 1981; 161; Rehder, 1981: 646, fig. 362; Heard, 1982: 20, fig. 15; Mahieu, 1984: 314; Jensen & Clark, 1986: 457, figured.

Melampus (Tralia) olivula (Küster). H. & A. Adams, 1854: 11.

Melampus olivula (Küster). Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 23; Pfeiffer, 1876: 304; Lange de Morretes, 1949: 122; Morrison, 1951b: 8.

Melampus biplicatus (Deshayes). Pfeiffer, 1856a: 21; Pfeiffer, 1876: 303.

Melampus caffeus (Lamarck) (Linnaeus). Dall, 1883: 322 [misspelling].

Melampus caffeus (Linnaeus). Simpson, 1889: 68 [misspelling].

Melampus coffea, var. *microspira* Pilsbry, 1891: 320 [Progreso, Yucatán, Mexico; holotype ANSP 61471 (Fig. 221)].

Melampus (Melampus) coffeus (Linnaeus). Dall & Simpson, 1901: 368, pl. 53, fig. 13; Thiele, 1931; 467; Zilch, 1959: 65, fig. 211; Vokes & Vokes, 1983: 6, pl. 22, fig. 13.

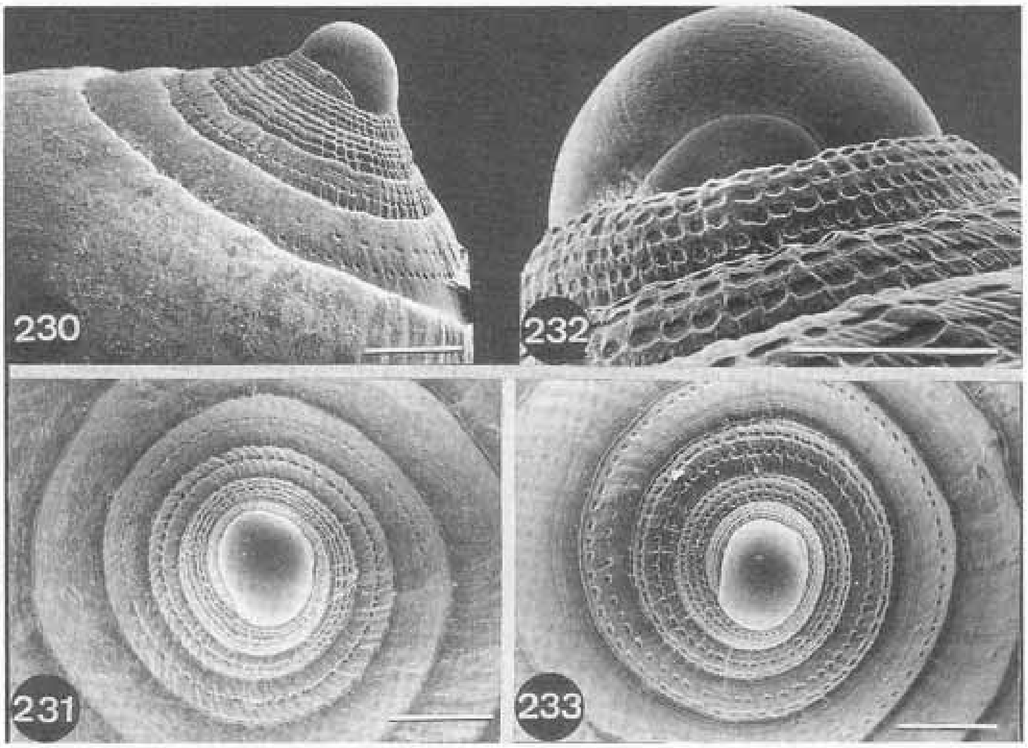
Melampus coffeus coffeus (Linnaeus). C.W. Johnson, 1934: 159.

Melampus (Melampus) coffea (Linnaeus). Altena, 1975: 86, pl. 8, fig. 8; Gibson-Smith & Gibson-Smith, 1982: 116, fig. 1.

Description: Shell (Figs. 218–233) to 23 mm long, ovate-conic, solid, shiny to dull, whitish to dark brown with olive tones, sometimes monochrome, rarely with irregular axial markings, generally with as many as five olive green to brown bands on body whorl, the one just below shoulder markedly consistent; pinkish to dark brown patch usually covering tip of columella and columellar tooth. Umbilical excavation visible in large specimens. Spire low, whorls nine to 12, flat; the first three and one-half to four whorls of teleoconch dark brown, spirally pitted; four rows of pits in first whorl, gradually disappearing at a rate of about one a whorl; remaining whorls smooth or marked with very fine superficial cords, not related to the preceding pits; body whorl about 90% of total length, carinate at shoulder, near its broadest point, smooth except around columella, which is striated. Aperture narrow, broadening anteriorly, subaxial, averaging 93% of body whorl length; inner lip with small, oblique columellar tooth, two parietal teeth, posterior one moderately strong, perpendicular to columellar axis, anterior one minute, sometimes fused with posterior one, sometimes absent; rarely with additional parietal denticles above posterior parietal tooth; outer lip sharp, with 13 to 18 even, white internal riblets not reaching edge. Inner whorls greatly resorbed, partition extending into only half of body whorl (Fig. 225). Protoconch smooth, translucent, brownish (Figs. 230–233).

Radula (Figs. 234–251) with formula [32 + (1 + 26) + 1 +(26 + 1) + 32] × 113. Base of central tooth approximately same width as that of lateral teeth, triangular, laterally constricted on first third; crown small, posterior edge with medial depression; mesocone small, sharp; ectocones very small or absent. Lateral teeth 20 to 36; crown strong, broadly triangular, one-third of total length of tooth; irregularities on crown give it tricuspid appearance, but distinct endocone or ectocone not present. Marginal teeth 28 to 38; mesocone large, triangular, pointing medially; endocone small, sometimes divided into as many as five small denticles that can give a serrated appearance; ectocone appearing as serrate edge in crown of first marginal tooth; denticles becoming distinct around seventh to tenth marginal tooth; from about 20th marginal tooth onward, ectocone becomes cteniform with as many as eight denticles.

Animal (Fig. 252) brownish, mottled to uniform black. Mantle skirt broad, with numerous mucous cells; right and left margins posteriorly fused to form pointed lappet of posterior aperture canal. Pallial cavity deep, not covering entire body whorl, opening to outside through semicircular pneumostome on right side of mantle skirt. Rectum delimits right side of pallial cavity; bilobed anal gill flanking rectum just posterior to anus. Long, weakly developed hypobranchial gland just to left of rectum. Kidney contiguous with hy-

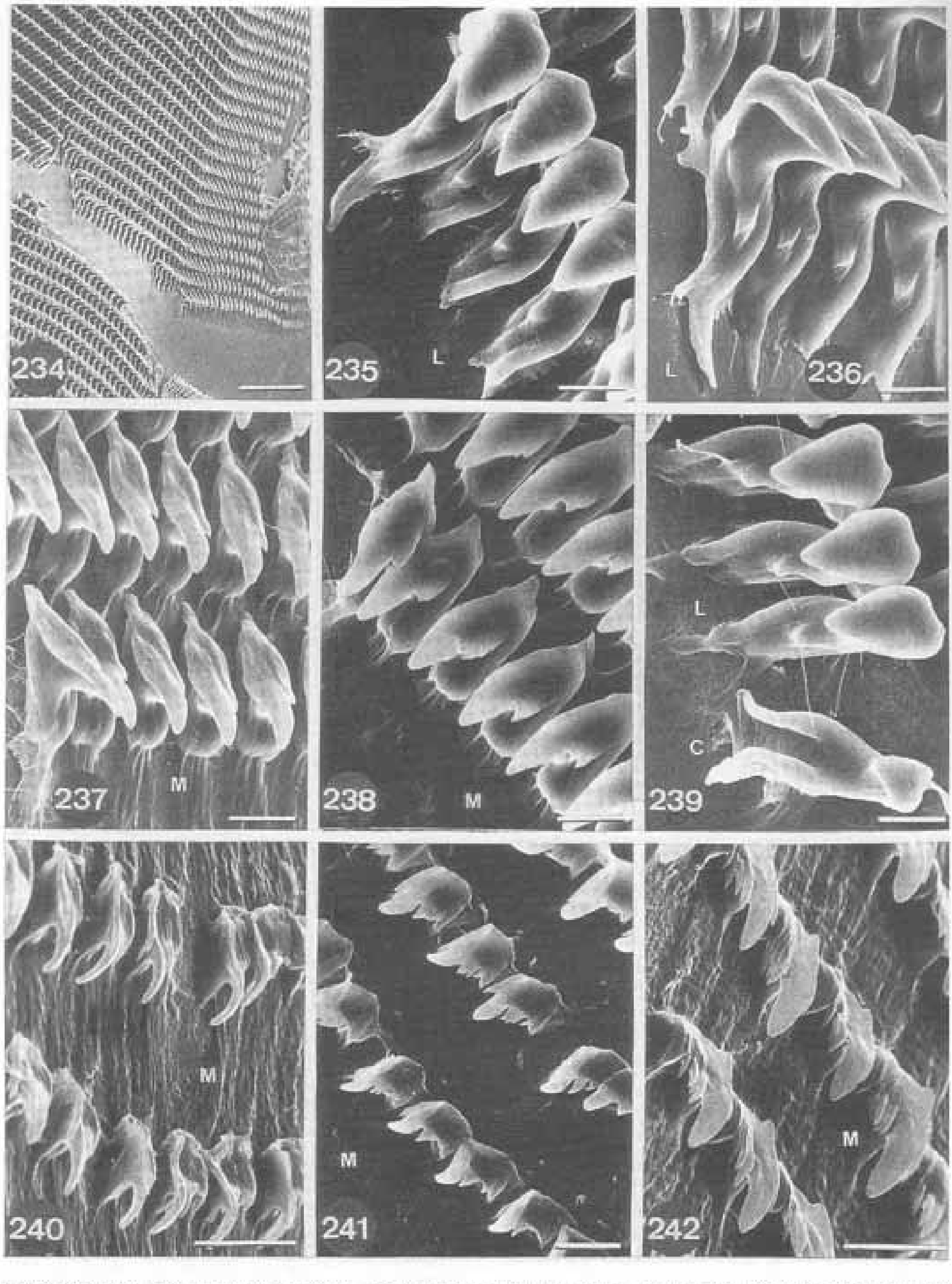


FIGS. 230–233. *Melampus (M.) coffeus,* lateral and top views of spire and protoconch. (230, 231) South Mastic Pt., Andros Island, Bahamas. (232, 233) Tucacas, Venezuela. Scale, Fig. 231, 500 µm; all others, 1 mm.

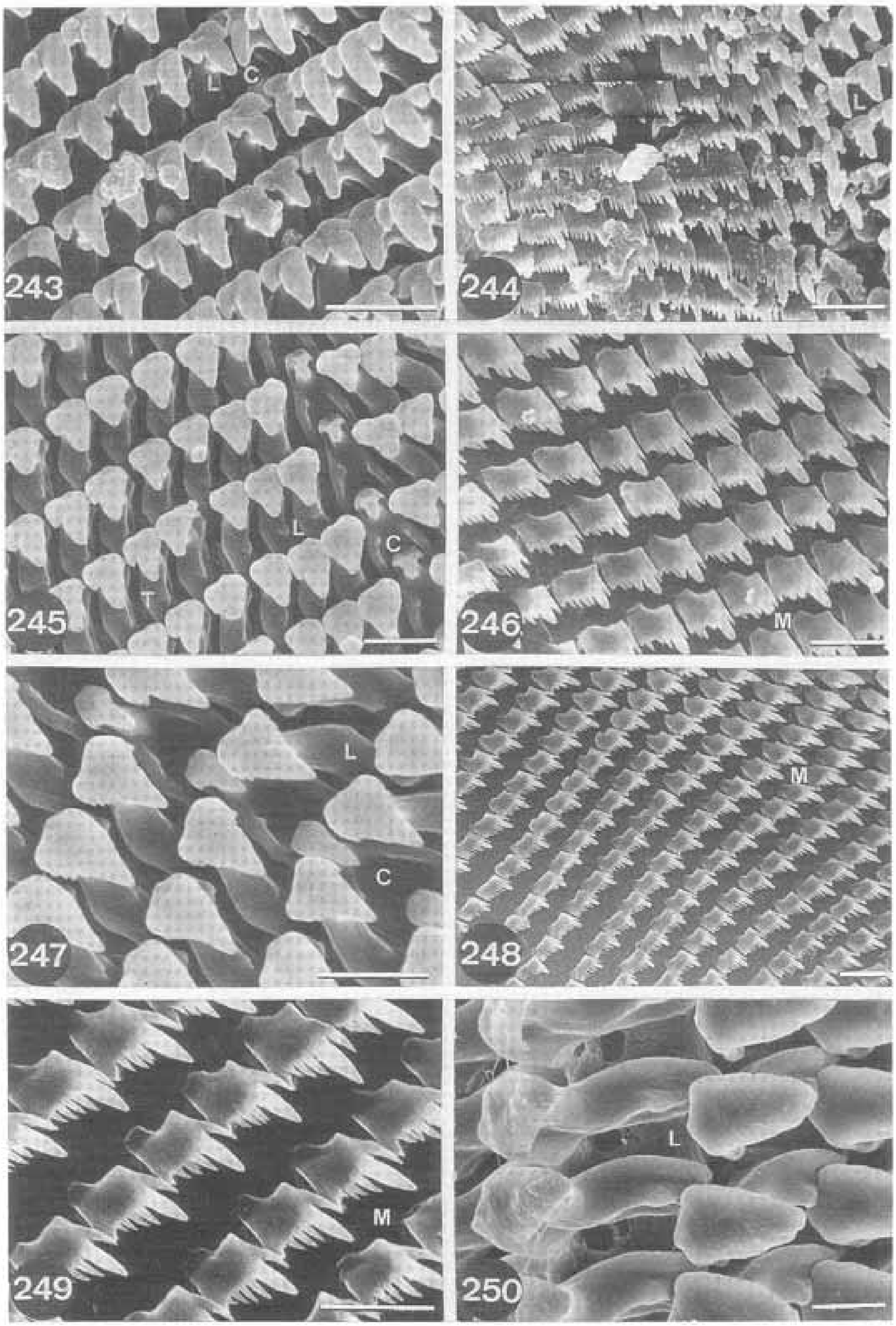
pobranchial gland, white, long, narrow, with incomplete transverse foldings forming longitudinal medial atrium; kidney opening papillose, emptying into mantle cavity just posterior to dorsal pneumostomal gland. Grayish, white-spotted pneumostomal glands in front of kidney, one on roof, other on floor of pallial cavity. Mantle organ in anterior left corner, well developed, dark brown to black. Heart transparent, posterior to kidney and mantle organ; posterior ventricle gives off short aorta that branches anteriorly and posteriorly; anterior aorta large, passing beneath crop, crossing to right over columellar muscle and under right parietovisceral connective, and emptying into large pedal sinus; posterior aorta branches to digestive gland, intestine, stomach and ovotestis; some blood collects in wide circular vein of mantle skirt and passes to pulmonary vein that opens into auricle; rest of blood passes through kidney and mantle organ, joining pulmonary vein at entrance of auricle. Stomach (Fig. 253) as in subfamily.

Reproductive system (Fig. 254) basically as described under *Melampus s. l.;* vagina about one and one-half times length of body whorl; posterior vas deferens about half the length of vagina.

Nervous system (Fig. 255) having cerebral ganglia joined by thick cerebral commissure, usually heavily wrapped in connective tissue; cerebral commissure shorter than width of a single cerebral ganglion. Ten pairs of nerves originate on cerebral ganglia; from anterior to posterior, they are: large tentacular nerve innervating tentacles; ocular nerve to eyes; peritentacular nerve going to base of tentacles; anterior labial nerve innervating sides of mouth; thicker medial labial nerve with one branch to sole of labial palps and two branches to lips and right medial labial nerve sends a branch to penis (penial nerve); posterior labial nerve innervating ventral portions of mouth; long cerebrobuccal connective; thick cerebropedal connective; thin statocyst nerve; and thick cerebropleural connective.



FIGS. 234–242. *Melampus (M.) coffeus*, radula, Hungry Bay, Bermuda, sl 14.1 mm. (234) General view, left half. (235, 236) Left lateral teeth. (237, 238) First left marginal teeth. (239) Central and first right lateral teeth. (240, 241) Last left marginal teeth. (242) Last right marginal teeth. Scale, Fig. 241, 500 µm; all others, 50 µm.



FIGS. 243–250.

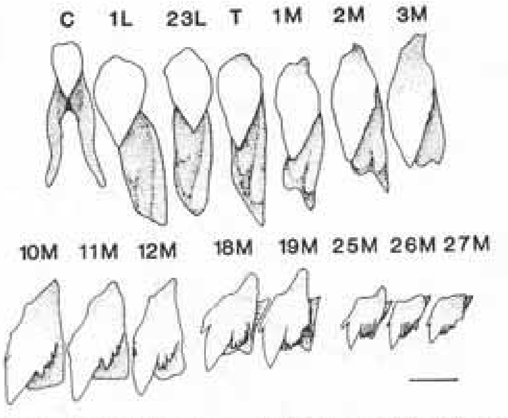


FIG. 251. *Melampus (M.) coffeus*, radula, Mullet Key, Florida. Scale 10 µm.

Buccal ganglia small, joined by short, thin buccal commissure from which unpaired pharyngeal nerve leaves, embedding into buccal bulb just anterior to radular sac; a pair of esophageal nerves leave medial anterior portion of ganglia, splitting immediately into anterior and posterior esophageal nerves, the latter running posteriorly on sides of esophagus; cerebrobuccal connectives securely attached to sides of buccal bulb, at which they emit a lateral buccal nerve; the salivary gland nerve branches off cerebrobuccal connectives and enters salivary ducts near junction with buccal bulb.

Pleural ganglia small, lacking nerves directly associated with them other than cerebropleural, cerebropedal and pleuroparietal connectives; thin cutaneous lateropleural nerve extends from lower posterior portion of pleuropedal connective to lateral mid-foot region; left pleural ganglion about 30% of size of right pleural ganglion; left pleuroparietal connective twice length of right one.

Parietal ganglia unequal. Left ganglion half size of right one, with fewer nerves; mantle skirt artery nerve leaving ganglion anteriorly, entering mantle skirt on left side, running along artery, sending branch into dorsal portion of mucous gland; thin external pallial nerve going to posteroventral section of mantle skirt; parietocutaneous nerve with branch to origin of posterior left bundle of columellar muscle; internal pallial nerve to mantle skirt, bifurcating to left side and to posteroventral portion. Nerves from right parietal ganglion are: external pallial nerve originating ventrally near pleural ganglion, crossing beneath other right parietal nerves and ramifying in floor of lung; thick pneumostomal nerve following floor of pneumostome and branching to innervate lips of pneumostome; medial pallial nerve arising above pneumostomal nerve and branching into mantle skirt; internal pallial nerve arising above pneumostomal nerve and branching into mantle skirt; internal pallial nerve, closely associated with pneumostomal nerve, going to roof of mantle cavity; and aortic nerve innervating wide aorta.

Visceral ganglion about same size as right parietal ganglion, giving off these nerves: thick pallial cutaneous visceral nerve crosses from left to right to innervate mantle lappet; thinner anal nerve goes to lower pneumostomal gland and anal region; genital nerve gives off thin branch to columellar muscle, extends along posterior vas deferens, sends branch to albumen and mucous glands and continues to ovotestis; and thinner columellar muscle nerve arises to right of genital nerve and penetrates columellar muscle.

Pedal ganglia united in front by pedal commissure and posteriorly by thin subpedal commissure. There are seven pairs of pedal nerves: anteromedian pedal nerve goes forward to mid-ventral foot; anterolateral pedal nerve runs laterally and anteriorly; anterior and posterior cutaneous pedal nerves go midlaterally to wall of foot; posterolateral pedal nerve runs posterolaterally; posteromedian pedal nerve goes to posterior midventral section; and posteropedal nerve goes to posterior ventral portion of foot. Thick cerebropedal and thinner pleuropedal connectives insert close to each other on anterior and lateral margins of ganglion respectively; thin statocyst nerve inserts just above cerebropedal commissure; thin left pharyngeal retractor muscle nerve originates posterior to

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FIGS. 243–250. *Melampus (M.) coffeus*, radula. (243) Laguna Rincón, Bahía de Boquerón, Puerto Rico, sl 2.33 mm; central tooth hidden by tricuspid first lateral teeth. (244) Laguna Rincón, Bahía de Boquerón, Puerto Rico, sl 2.33 mm. (245, 246) Laguna Rincón, Bahía de Boquerón, Puerto Rico, sl 3.48 mm. (247–249) Shore of Millars Road, New Providence, Bahamas, sl 4.63 mm. (250) Left lateral teeth, with articulation of medial node of base of one tooth with crown of next tooth, Punta Arenas, Puerto Rico, sl 19.9 mm. Scale 50 µm.

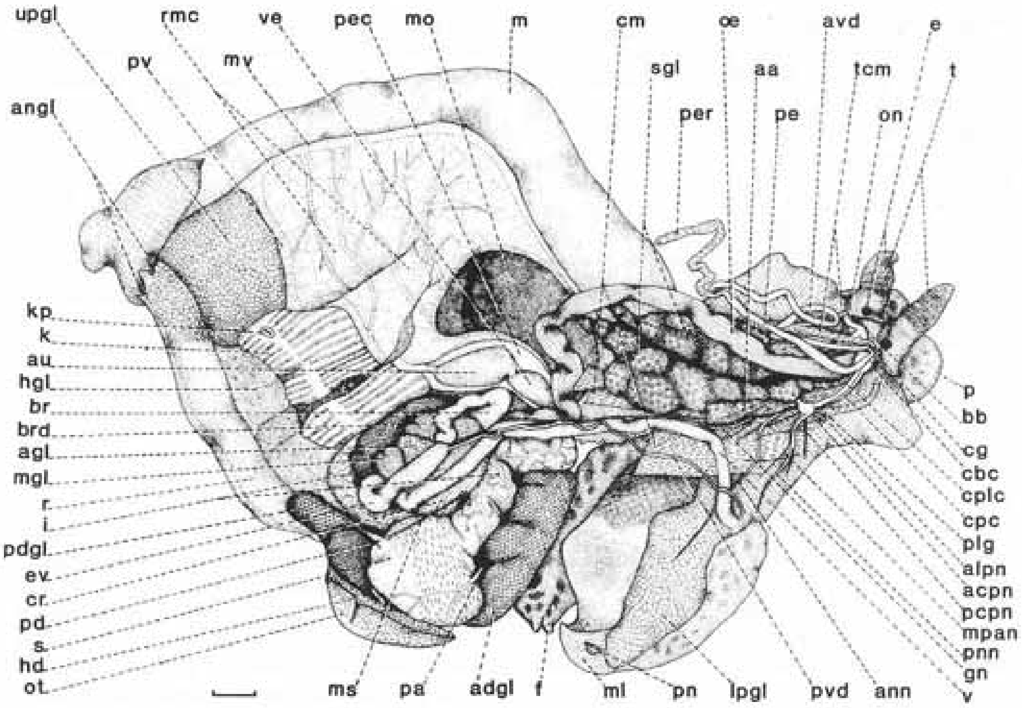


FIG. 252. *Melampus (M.) coffeus*, anatomy. Right and anterior sides of mantle cavity cut, roof of lung reflected to left; neck incised longitudinally, neck skin reflected laterally; insertion of penial retractor muscle, columellar muscle and anterior aorta cut; floor of mantle removed, organs cleaned of connective tissue and slightly separated. Scale 1 mm.

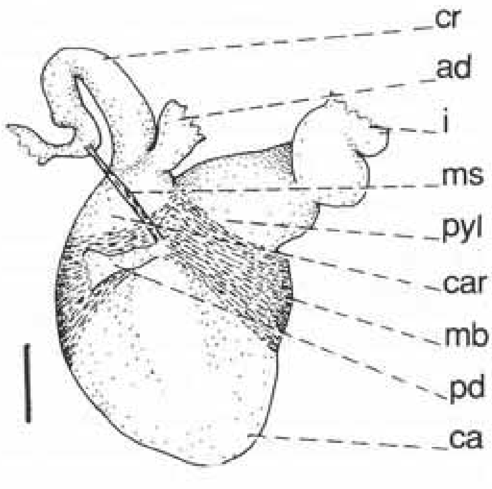


FIG. 253. *Melampus (M.) coffeus*, stomach, Florida. Scale 1 mm.

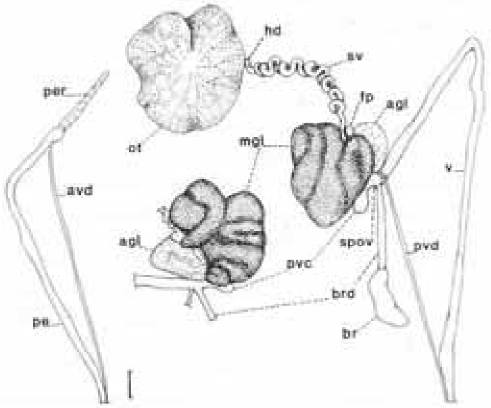


FIG. 254. *Melampus (M.) coffeus*, reproductive system, Grassy Key, Florida. Scale 1 mm.

statocyst nerve, follows the latter forward and, halfway, turns posteriorly and inserts in radular muscle; wide sheet of connective tissue wraps connectives associated with pedal ganglia, statocyst nerve and proximal portion of radular muscle nerve; right pharyngeal retractor muscle nerve and associated connective tissue attach to posterior right side of buccal bulb. Round statocyst with numerous

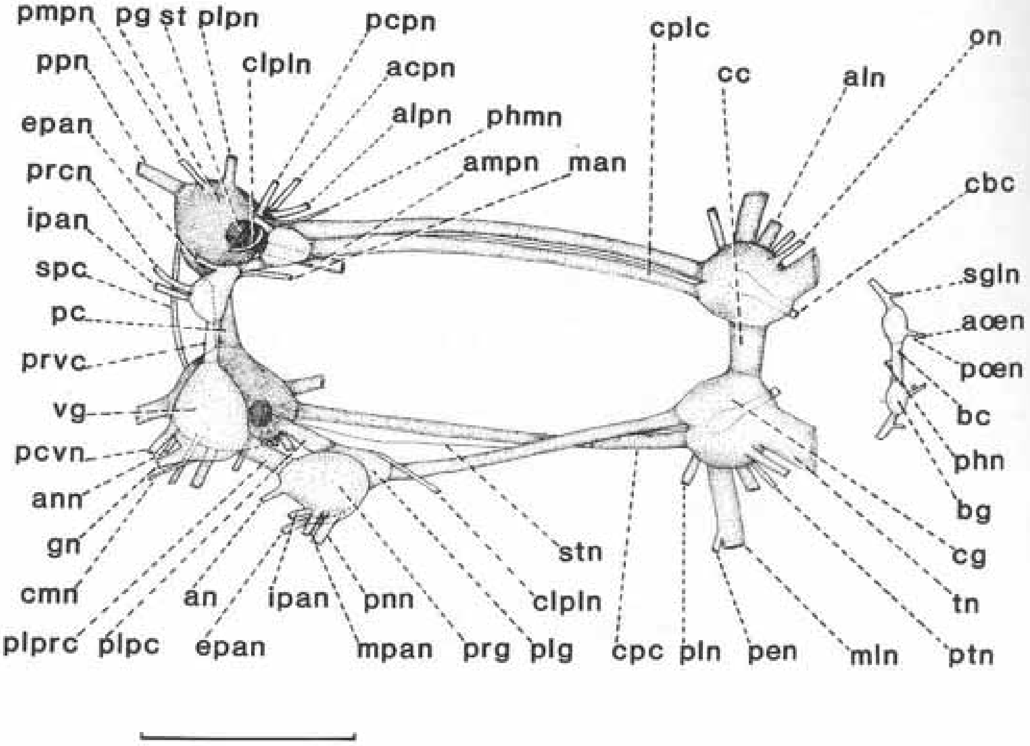


FIG. 255. *Melampus (M.) coffeus*, central nervous system, Grassy Key, Florida. Scale 1 mm.

statocones on anterodorsal surface of each pedal ganglion.

Remarks: Dodge (1955) gave a detailed account of the nomenclatorial history of *Melampus (M.) coffeus* (Linnaeus). The description provided by Linnaeus (1758) was so brief and general that it could be applied to almost any species of *Melampus*. The specific characters mentioned were the aperture dentate on both sides and conical shell, characters common among ellobiid species. A synonymy was not given, references to any illustration were not cited, and the locality was unknown. In his copy of the twelfth edition of the *Systema* Linnaeus added a manuscript reference to Lister (1770: fig. 59) (Dodge, 1955). Although the abbreviation "Barb" [for Barbados] is written between figures 59 and 60, plate 834, of Lister, the sketchy representation of the outer lip in figure 59, chosen by Linnaeus, suggests a species of the Indo-Pacific genus *Cassidula*. Such was the interpretation of Hanley (1855: 214), who regarded it as being *Bulimus auris-felis* Bruguière [= *Cassidula aurisfelis*] "or some closely allied congener." Also according to Hanley, *Cassidula aurisfelis* was not present in the Linnaean collection although Linnaeus asserted that he owned the specimen he used for the description of his *Bulla coffea*.

The history of the interpretation of the name *Bulla coffea* exemplifies the confusion of the various authors about the identity of Linnaeus' species. One of the illustrations cited in early works for the Linnaean species is a dorsal view of the *Auricula Midae nonfimbriata, bidens* of Martini (1773, 2: 126, pl. 43, fig. 445). Although Martini's description and figure are rather sketchy and inaccurate, he cited in synonymy Petiver's (1770) species No. 493, *Persicula barbadensis fasciatus*. The locality, Barbados, is within the range of the species and agrees with Lister's note. Chemnitz [1786, 9(2): 45, figs. 1043, 1044] also illustrated and described under the name *Voluta coffea Linnaei* his concept of Linnaeus' species, referring to the tenth and twelfth editions of the *Systema*. Chemnitz criticized Martini's illustration as a "small, unimportant and unrecognizable figure of the present much larger and impressive shell." The Chemnitz definition and illustration are equally incorrect, however; the former mentions fine transverse striae, the latter closely resembles *Cassidula aurisfelis* (Bruguière, 1789). An indication that Chemnitz was confused about the true identity of Linnaeus' species is the reference to the size. *Cassidula aurisfelis* easily reaches 30 mm whereas *Melampus (M.) coffeus* rarely surpasses 20 mm in length.

Probably with the intention of clarifying the existing confusion Bruguière (1789) introduced the name *Bulimus coniformis*, for which he provided a fairly accurate description. He cited in the synonymy Lister's figure 59, Linnaeus (1758, 1767) and Martini's figure 445. He rejected, however, Chemnitz' figure, which shows an apertural view.

The thirteenth edition of the *Systema naturae* (Gmelin, 1791: 3438) also failed to resolve adequately the question of the identity of *Melampus (M.) coffeus* (Linnaeus). Gmelin listed *Voluta coffea*, and the references to the synonymy included Lister's figure 59, Favanne's (1780) figure H7 [miscited as fig. 47], Martini's figure 445 and Chemnitz' figures 1043, 1044. Two pages before (p. 3436) Gmelin introduced *Voluta minuta*, for which he cited the same references to Lister and Martini. He described two color patterns, dark with two to six white bands, or white with four alternating yellow and coffee-colored bands. These features are not surprising, considering the variation in color that characterizes the group. Reference to the "three ribs on the outer lip" raises doubt about the relationship of *Voluta minuta* to *Melampus (M.) coffeus*, because the latter species has many (13–18) riblets inside the outer lip. *Voluta minuta* has been cited frequently as junior synonym of *Melampus (M.) coffeus*. Given both the impossibility of identifying Gmelin's species from the original description, and the ambiguity of the illustrations cited in the synonymy, however, the name *Voluta minuta* of Gmelin must be treated as a *nomen dubium*.

Röding (1798: 106) introduced the names *Ellobium inflammatum* and *Ellobium barbadense* and referred both to *Voluta coffea* (Linnaeus). No locality was given for the "Banded Midas ear," *Ellobium inflammatum*, and the additional references are the Lister figure 59 and the Chemnitz figures 1043, 1044, already discussed and considered inconclusive. The only reference given for *Ellobium barbadense* was the unidentifiable Martini figure 445. Röding did not provide any description and, as noted, the references given are inconclusive. For this reason, *Ellobium inflammatum* and *Ellobium barbadense* are to be considered *nomina dubia*.

According to Dodge (1955) *Melampus (M.) coffeus* is not described in the *Museum Ulricae*, and specimens of it are not in the Queen's collection at Uppsala. Inspection of the type material at the Linnaean Society of London revealed a mixed lot of 12 specimens representing two species. A label note by S. P. Dance from 1963 attributes to Hanley the selection of these 12 unmarked specimens. Seven specimens are *Melampus (D.) monile* (Bruguière), four represent a smaller form of *Melampus (M.) coffeus* (Linnaeus) (Fig. 219) and the twelfth specimen, nearly twice the size of any of the others, conforms to *Melampus (M.) coffeus* (Linnaeus) of all authors (Fig. 218).

With all the inconsistencies in the descriptions and figures applied by the early authors to *Bulla coffea* Linnaeus, this name, as Dodge (1955: 67) remarked, would be treated as *nomen dubium* were it not for the existence in the Linnaean collection of a specimen that must be considered the ostensible type. Equally important is the fact that the name *Melampus (M.) coffeus* has been in general use since 1854 and to remove this well-established name would create unnecessary confusion in the literature. To prevent further confusion, the large specimen in the LSL (Fig. 218) is herein designated lectotype.

Another source of confusion was the failure of some authors to distinguish between *Melampus (M.) coffeus* (Linnaeus) and *Melampus (M.) bidentatus* Say. The geographical ranges of these two species overlap in Bermuda, most of Florida, the Gulf of Mexico and the western Greater Antilles. *Melampus (M.) bidentatus* is highly variable, sometimes resembling the highest-spired *Melampus (M.) coffeus* in shape, size and color. The most distinctive characteristic, as noted by Morrison (1958, 1964), is the absence of incised lines on the shoulder of the body whorl of *Melampus (M.) coffeus*. This characteristic can be used only in individuals having more than four whorls. In fact, the first three and one-half to four whorls of both species have incised lines and are indistinguishable in this regard (Figs. 230–233). Binney (1859) and Tryon (1866) perceived this difference, describing *Melampus (M.) coffeus* as having microscopic revolving lines, as opposed to *Melampus (M.) bidentatus*, which has revolving striae. Lines are very weak cords whereas striae are finely impressed spiral depressions. The lines in *Melampus (M.) coffeus* are not incised and they do not correspond to the continuation of the striations or rows of pits on the first whorls.

Failure to distinguish between *Melampus (M.) coffeus* and *Melampus (M.) bidentatus* is obvious in the work of Holle & Dineen (1959). One of their conclusions is the hypothesis that *Melampus (M.) coffeus* and *Melampus (M.) bidentatus* are but subspecies. Natarajan & Burch (1966), on the basis of chromosomal counts, stated that these species hybridize. I doubt, however, that they were dealing with both species, but rather with two forms of the variable *Melampus (M.) bidentatus*. The supposed *Melampus coffeus* used in their research was from Jekyll Island, Georgia. Inspection of four major museum collections of the east coast of the United States failed to yield any record of *Melampus (M.) coffeus* north of Florida. It is doubtful, therefore, that this species was involved and the suggestion that *Melampus (M.) bidentatus* and *Melampus (M.) coffeus* hybridize is probably untenable.

Deshayes (1830) introduced *Auricula biplicata*, of unknown locality. Beck (1837) reported Deshayes' species as living in America and Binney (1859), probably on account of Beck's reference to the name *biplicata*, treated *Auricula biplicata* as a synonym of *Melampus (M.) bidentatus*, without comment. In the original description Deshayes (1830: 91) stressed that his species should not be confused with those under the section of the Conovules. In comparing *Auricula biplicata* with *Auricula coniformis* (Bruguière) [= *Melampus (M.) coffeus*], Deshayes pointed out that, although comparable in size [22 × 12 mm], his species differed from Bruguière's species in color, shape and apertural dentition. The holotype of *Auricula biplicata* (Fig. 220) lacks the incised grooves on the shoulder of the body whorl, characteristic of *Melampus (M.) bidentatus*. The uniform brownish color, the slender shape, the strong, whitish posterior parietal tooth and the greatly reduced anterior parietal tooth are well within the range of variation that I have observed in *Melampus (M.) coffeus*. I collected in Florida specimens that conform with Deshayes' species. I have designated herein Barbados as the type locality for *Auricula biplicata* Deshayes to avoid confusion with a large form of *Melampus (M.) bidentatus*, also found in Florida, which Pfeiffer (1853b) described as *Melampus gundlachi* (Fig. 271).

Melampus olivula (Küster) is a Brazilian morph of *Melampus (M.) coffeus* characterized by the absence of the first parietal tooth (Fig. 228). Although Küster (1844: 33) referred to an alleged publication by Moricand in "Mémoir de la Société de Genève. VIII", I failed to see such a reference in the place indicated. Accepting Pfeiffer's (1856a) authority, who attributed *Auricula olivula* to Moricand "*ex citationibus auctorum*," one can conclude that Moricand's publication of the name is doubtful or obscure, and Küster (1844) is to be credited for its introduction.

As pointed out under the remarks for the subgenus, the radular morphology of *Melampus* changes considerably during the early growth of the animal (Figs. 243–249). Among the most noticeable differences are the wide base of the central tooth bearing conspicuous nodes on the inner edge of the arms and the clearly tricuspid first lateral tooth with ectocone and endocone that becomes serrated in larger juveniles. In juveniles, as in adults, the transitional tooth is characterized by a shortening of the base and the presence of an ectocone. The marginal teeth also have an endocone. The number of cusps on the ectocone can vary from row to row in the same positional tooth.

A unique feature of the Melampinae is the mantle organ. This squarish, black structure was first mentioned by Koslowsky (1933: 178) for *Melampus boholensis* H. & A. Adams, and by Marcus & Marcus (1965a: 31) for *Melampus (M.) coffeus*. Although of unknown function, this highly vascularized organ probably is excretory or lymphatic, according to the latter authors.

Another structure, here called the bilobed anal gill, was described by Koslowsky (1933) and by Marcus & Marcus (1965a) as a pair of anal glands. It consists of two small, profusely ciliated tubular structures flanking the anus and isolated from the pallial cavity. According to Marcus & Marcus (1965a: 38) this structure, consisting of epithelial cells and subepithelial secretory cells, probably secretes some mucilaginous substance that helps in holding the fecal pellets together and in lubricating the anal groove. Renault (1966) described the same structure in *Cassidula la-*

brella Deshayes, but considered it a gill. In the Pythiinae, to which *Cassidula* belongs, and in the Pedipedinae I observed it to be a single, well-developed, highly folded structure, closely resembling a gill. Renault noted that this structure is at the bottom of a depression in the mantle-skirt groove and concluded that such a depression is comparable to a reduced pallial cavity, seen in the ontogeny of some pulmonates and retained in adult ellobiids. Although not denying its glandular character, I am inclined to consider this structure in *Melampus (M.) coffeus* as a gill because of its homology with identical organs in the Pedipedinae and Pythiinae.

The connectives of the visceral nerve ring are short, but readily identifiable and of unequal length. In this respect Marcus & Marcus' illustration (1965a, pl. 2, fig. 7) of the central nervous system of *Melampus (M.) coffeus* is inaccurate in not showing evidence of those connectives, a condition never found in the ellobiids.

Habitat: Melampus (M.) coffeus, an inhabitant of mangroves, lives at and above the high-tide mark but can also occur intertidally, commonly gathering on mangrove roots and propagules above water level at high tide, but descending to the muddy ground at low tide. They prefer shady places (Marcus & Marcus, 1965a) and seem to be more active at night (Golley, 1960).

Range: Bermuda; Florida to West Indies; Gulf of Mexico, Central America south to Brazil (Fig. 256). Scarabino & Maytia (1968) reported this species from Uruguay, where four beach specimens were collected; the authors suggested that they might have been carried by currents from nearby Brazil.

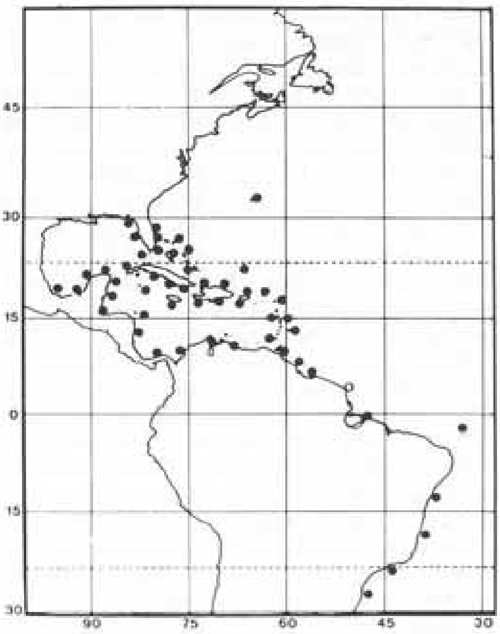


FIG. 256. *Melampus (M.) coffeus*, geographic distribution. Open circle, locality from literature.

Specimens Examined: FLORIDA (ANSP 56829): Indian River (USNM 758220); S of Sebastian Inlet (MCZ 143993); Coconut Grove (MCZ 291328, 291330; USNM 603112); Miami (USNM 700802); Biscayne Bay (USNM 603116); Brickell Hammock, Biscayne Bay (MCZ 291325); Homestead (MCZ 291097); Card Sound (ANSP 84403); Turner River, Card Sound (ANSP 93430); Barnes Sound (MCZ 291095); Middle Key (USNM 338339); McGinty Key (ANSP 139532); Key Largo (ANSP 194009; MCZ 246700, 291324; USNM 529249, 603118); Tavernier (ANSP 325296; MCZ 201659); Tavernier Creek (USNM 667400; A.M.); Tavernier Key (USNM 492563); Snake Creek (MCZ 291012); Snake Key (ANSP 1054); Plantation Key (MCZ 199340, 291016; A.M.); Windley Key (USNM 603103); Indian Key Fill (A.M.); Lignumvitae Key (ANSP 156326); MCZ 75605); Matecumbe Key (USNM 822252); Lower Matecumbe Key (USNM 700764); Rabbit Key (ANSP 88135); Long Key (MCZ 176170; A.M.); Grassy Key (MCZ 201673; A.M.); Crawl Key (MCZ 291020; A.M.); Key Vaca (MCZ 201672); Marathon (MCZ 153253); Knight Key (A.M.); Bahia Honda Key (ANSP 89551;USNM 269777b); No Name Key (MCZ 142470); Little Pine Key (USNM 681643); Big Pine Key (ANSP 89552; MCZ 201651; USNM 597455; A.M.); Ramrod Key (MCZ 291021); Pavilion Key (ANSP 93431); Pelican Key (MCZ 3967; USNM 39829); Key West (MCZ 201666; USNM 60754, 668244); Marquesas Key (ANSP 73711); Mangrove Key (ANSP 365478); Flamingo Key (ANSP 294311; MCZ 235501, 275576, 291098; USNM 672441); Cape Sable (ANSP 56825; USNM 603117); East Cape, Cape Sable (MCZ 291017); Sandy Key (USNM 603121); Lossman River (ANSP 132368); Everglades City (MCZ 291096); Seminole Point (ANSP 105431); Horr's Island, Ten Thousand Islands (USNM 381325); Fakahatchee Key (ANSP 88139);

Royal Palm Hammock (MCZ 257250; USNM 492561); Marco Island (MCZ 201687, 291011; USNM 381332); Blue Hill Island, near Goodland Point (ANSP 88134); Little Marco (ANSP 93429); Gordon Pass (USNM 603098); Naples (MCZ 178104, 201661; USNM 667406); Bonita Springs Beach (MCZ 201680, 291015); Bonita Beach (USNM 334075); Cayo Tuna, S. Carlos Bay (ANSP 106299); Carl E. Johnson Park, Little Carlos Pass (A.M.); Mound Key, 2 km N of south end of Estero Island (MCZ 201657); Dog Key, 1.5 km NW of middle of Estero Island (MCZ 201648); Starvation Key (ANSP 130057); Fort Myers (ANSP 183181); Punta Rassa (ANSP 45075, 56826, 140849; MCZ 84097, 291018; USNM 37601, 513900, 492573, 700853; A.M.); Sanibel Island (ANSP 91378, 170651; MCZ 13702, 55773, 201655, 291024; USNM 611799); Wulfert, Sanibel Island (MCZ 13703, 13803); Pine Island (ANSP 93387); Pineaire, Pine Island (MCZ 291023); Bokeelia (MCZ 291025; A.M.); Captiva Island (MCZ 291013; USNM 513901); Blind Pass, Captiva Island (MCZ 201658); Boca Grande, Gasparilla Island (ANSP 142272); Little Gasparilla Island (ANSP 131405); Punta Gorda (ANSP 45076); Charlotte Harbor (USNM 592308); Nokomis (ANSP 180747); Siesta Key (USNM 669348); Sarasota (MCZ 201679; USNM 30625, 487314a); 4.5 km N of Sarasota (ANSP 294315); Long Boat Key (MCZ 201686); between Palma Sola and Cortez (MCZ 291014); Palmetto (A.M.); Manatee River (ANSP 56832; MCZ 3968, 201664; USNM 492566); Big Bend Road [Rt. 672] (A.M.); Tampa Bay (MCZ 55757, 70569, 201645, 201654, 201664; USNM 37602, 73210, 193362, 196349a, 504481, 711484); Small Island (MCZ 91358); Mullet Key (ANSP 76699; USNM 652406; A.M.); Tierra Verde (MCZ uncatalogued); Shell Key (USNM 466206, 466288a); key 2 km S of Pass-a-grille (MCZ 56177); Pass-a-grille (ANSP 148522; MCZ 138939, 162640); Bird Key (ANSP 134318; MCZ 71009, 71595, 104946; USNM 36896, 37600); Terra Ceia (MCZ uncatalogued; USNM 124285); Pinellas Point (MCZ uncatalogued); St. Petersburg (USNM 341721a, 466195, 663066); SE of Gulfport (MCZ 201665); Gulfport (MCZ 88789); Bocca Key (USNM 75409); Boca Ciega Bay (ANSP 9568; MCZ 291329); Sand Key (ANSP 128525); Clearwater Island (ANSP 9354, 176363; MCZ 105461; USNM 611786); island in Clearwater Bay (ANSP 149851); Anclote River (A.M.); Cedar Key (ANSP 362803; MCZ 201660; USNM 27918). BERMUDA (ANSP 158807; USNM 11421, 94432a, 173642, 228686): inlet E of biological station, St. George's (MCZ 64705); Hungry Bay (ANSP 85712; MCZ 24247; A.M.); BAHAMA ISLANDS (ANSP 56830): GRAND BAHAMA ISLAND (ANSP 374525): Gold Rock Creek (ANSP 369339); Running Mon Canal (ANSP 369778); Eight Mile Rock (ANSP 173255); Hawksbill Creek (ANSP 176351; MCZ 116679); GREAT ABACO ISLAND (ANSP 362802, 362804; MCZ 201683; USNM 492564, 492591): Witch Point (ANSP 299482); Bootle Bay (ANSP 371879); Cherokee Sound (MCZ 133101); BIMINI ISLANDS: Alicetown, North Bimini (MCZ 144186); BERRY ISLANDS (MCZ 291332); ANDROS ISLAND (USNM 492572): South Mastic Point (A.M.); Stafford Creek (ANSP 189566); Mangrove Cay (ANSP 94525; MCZ 24137, 24138; USNM 269861, 269968b); Lisbon Point, Mangrove Cay (USNM 269599); Linder Key (USNM 270483a); NEW PROVIDENCE ISLAND (ANSP 184850; MCZ 85768): Nassau (USNM 160765, 467072, 568412); Old Fort (MCZ 107792); Dick's Point (MCZ 107797, 113101, 291333); Adelaide (USNM 603873); Millars Sound (A.M.); Millars Road (A.M.); Bonefish Pond (USNM 618597; A.M.); Fox Hill, South Beach (MCZ 107770); ELEUTHRA ISLAND: Schooner Cays (ANSP 359332); Millars Beach (ANSP 359351); ROYAL ISLAND (MCZ uncatalogued; USNM 468114); CAT ISLAND (ANSP 173256): Russell Creek (ANSP 173260; MCZ 63384); Orange Creek (ANSP 173254; MCZ 63385); Arthurstown (ANSP 173661; MCZ 107832); Dumfries (MCZ 107752); EXUMA CAYS: Hog Cay (ANSP 285755); SAN SALVADOR ISLAND: Riding Rock (USNM 360311); LONG ISLAND: Salt Pond, Clarencetown (ANSP 189565; MCZ 113099; USNM 589832, 590247); Brett's Hill (MCZ 113336, 142299); Glenton's (ANSP 173253; MCZ 113100; Cape Sta. Maria (MCZ 113329). CUBA (ANSP 56791; USNM 10967, 59724, 121518, 492569, 492581): Bahia de Santa Rosa (USNM 492556, 492568); Cape Cajón (USNM 492571a); Los Arroyos (USNM 492558); Cayo Rapado (MCZ 201652); Dimas (USNM 492559a); Bahia Honda (USNM 492560); Mariel (MCZ 131922; USNM 169938); Marianao (ANSP 77006; MCZ 131953); Rio San Juan (MCZ 127825); Cayo Cristo (MCZ 291321); Cárdenas (MCZ 87886); Rio Yumurí (ANSP 87920, 167219; MCZ 83311, 131913, 131941, 201684); Cayo de las Cinco Léguas

(ANSP 158050); Rancho Veloz, Sagua la Grande (MCZ 201682); Caibarién (MCZ 131914, 131920, 131940); Cayo Francés (MCZ uncatalogued); Muelles (MCZ 131915); Cayo Salinas, Buena Vista Bay (MCZ 201681); Cayo Conuco (MCZ uncatalogued); Isla de Cobos (MCZ uncatalogued); Punta Alegre (ANSP 149212); Isla Turigano (MCZ uncatalogued); Terraplen, Isla Turigano (USNM 385661); S of Central Ramon (USNM 391797); Gibara (USNM 381469, 603096); Bañes (MCZ 59623); Penon el Fraile, Fraile, Santa Cruz del Norte (USNM 807577); Playa Cajio, Guira del Melena (USNM 803401); Guantánamo Bay (MCZ 92675); Santiago (USNM 373225, 603114); Tarallones de Arena, near Santiago (ANSP 182935); Rio Cauto (USNM 682787); Santa Cruz del Sur (MCZ 131919, 201662); Finca, Sabanalmar (MCZ uncatalogued); Cienfuegos Bay (ANSP 106093); Alto del Caracol (ANSP 222629); Cienfuegos Bay, 1 km E of La Milpa (MCZ uncatalogued); Cayo Blanco (ANSP 157942); Batabanó (ANSP 93714; USNM 603115); La Coloma (MCZ 84884, 131949); Punta de Llana (MCZ 201668); Isla de Pinos (MCZ 48079, 48080). JAMAICA (ANSP 56822; MCZ 291233, 291318, 291322; USNM 94743, 492562, 492570): Green Island Harbor (USNM 440805); Fort Clarence (USNM 433433); Montego Bay (ANSP 329154; MCZ 17452); Port Morant (USNM 375739); Cow Bay (USNM 440974); Kingston (USNM 442610); Palisadoes (USNM 442466a); Port Royal (USNM 395452c, 427004, 442268); Hunt's Bay (USNM 441673); Rock Fort (USNM 374232); Phillipsfield (USNM 402222); Old Harbor (441009); Portland (USNM 375680); near Portland Light, Portland Hills (MCZ uncatalogued); Little River (USNM 128066); Great Goat Island (ANSP 344216); Little Goat Island (MCZ 291326); Black River (USNM 441356); Savanna la Mar (MCZ uncatalogued). HAITI: Fort Liberté (USNM 426365); St. Louis (USNM 439390); Morne Rouge (USNM 402680, 402715); Gonave Island (MCZ 82119; USNM 492531); Port-au-Prince (MCZ 183920; USNM 403109, 403408, 440460, 440610, 442923); Miragoane (MCZ 82072); Anse-à-Maissons, Grand Cayamite (MCZ 82100); Île-à-Vache, Soulette Bay (USNM 439191, 442850); Torbeck (USNM 383068, 403363, 439667, 439695b); Les Cayes (USNM 439742a); Aquin (USNM 367358, 402839, 403255, 403561, 440163); Bizoton (USNM 439832). DOMINICAN REPUBLIC: Monte Cristi (MCZ 57752, 291334); 19 km E of Monte Cristi (USNM 471542); Sanchez (USNM 307261); Rio Tapion, Puerto Libertador (USNM 618639); Puerto Plata (MCZ 90785, 291317, 291320); Santa Bárbara de Samaná (ANSP 173257; MCZ 57754); Sanchez (ANSP 173252; MCZ 57338); Isla La Matica, Playa Boca Chica, E of Santo Domingo (R.B.). PUERTO RICO: San Juan (USNM 161160, 169885); Cayo Maguey (MCZ uncatalogued); Cabo Rojo lighthouse (MCZ 242179); Laguna Rincón (A.M.); Boquerón Beach (A.M.); Puerto Real (A.M.); Punta Arenas (A.M.); La Parguera (USNM 622804); Santurce (ANSP 175624); Piñones (A.M.); Culebra Island (USNM 360536). VIRGIN ISLANDS: ST. THOMAS (ANSP 56824, 56827; MCZ 89651, 291319; USNM 6363, 6385a): Benner Bay (USNM 702725). ST. JOHN'S (MCZ uncatalogued). TORTOLA (USNM 6484). ANEGADA ISLAND (ANSP 249494; MCZ 229004). ST. CROIX (ANSP 56831): Altons Lagoon (USNM 621394); Salt River (MCZ 110325). LESSER ANTILLES: ST. MARTIN'S (ANSP 56821). ANTIGUA (ANSP 109156; USNM 215049); Fitches Creek (USNM 809739). GUADELOUPE (MCZ uncatalogued). MARTINIQUE (MCZ 56464): between Le Vauclin and Le François (ANSP 253289; MCZ 229358). BARBADOS (MCZ 148628). TOBAGO: Pigeon Point (USNM 682273). TRINIDAD: S of Shoran Site (USNM 608786); Caroni Swamp (MCZ uncatalogued); Blue River (R.B.). CURAÇAO: Schotteghat, near Willemstad (ANSP 133971). CARIBBEAN ISLANDS: GRAND CAYMAN ISLAND: 5 km N of Georgetown (ANSP 209765). OLD PROVIDENCE ISLAND (USNM 687818): N of Ironwood Point (ANSP 313209; USNM 678832, 678833; MCZ 270624). MEXICO: Tampico (USNM 219997); Vera Cruz (USNM 769426); Rio Vinasco, Vera Cruz (USNM 675266); Tuxpan, Vera Cruz (MCZ uncatalogued); SE of Tuxpan, Vera Cruz (USNM 675271); Mandinga Lagoon, Vera Cruz (USNM 791711); Boca del Rio, Vera Cruz (MCZ 155429); Isla de Carmen (USNM 809096); Ciudad del Carmen (USNM 702910); Rio Champotón (MCZ 59747); Silam (ANSP 61470); Progreso (ANSP 61469, 61471); Rio Lagartos (USNM 618635); Isla Cancún, Quintana Roo (ANSP 285520); N end of Ascension Bay, Quintana Roo (USNM 736142, 736691, 738632); Allen Point, Ascension Bay, Quintana Roo (USNM 736695, 736892). BELIZE: Ambergris Cay (ANSP 284797); Belize (ANSP 294323); Botanical Garden, Belize (USNM 426007);

Blackadore Cay (ANSP 282031); Robinson Point (ANSP 281579); N of Punta Gorda (ANSP 282494). GUATEMALA: Puerto Barrios (MCZ 88877). NICARAGUA: Wounta (ANSP 97591; USNM 181854); Wounta River, near Wounta (MCZ 14804); 16 km S of Wounta (MCZ 137227). PANAMA (USNM 46182): Galeta Island (USNM 703195, 732922, 732949); Toro Point, Limon Bay (USNM 732885); Colón (ANSP 107258; MCZ 45058); Porto Bello (USNM 218173). COLOMBIA: Sabanilla (USNM 103175); Cartagena (MCZ 192431); Coveñas, Bolívar (USNM 364336). VENEZUELA (MCZ 291327): S of Porlamar, Isla Margarita (ANSP 240007; USNM 707796); Punta Mangle, ESE of Punta Piedras, Isla Margarita (MCZ 273661); La Orchila Island (USNM 656031); Carenero (784775); Tucacas (A.M.). GUYANA: Demerara (MCZ 177296). SURINAME: 16 km WNW of Paramaribo (MCZ uncatalogued); Nickerie Strand, Zeedijk (MCZ uncatalogued); Bigisanti (USNM 635225). BRAZIL: Boa Viagem (MCZ 219130); Urumajó, Bragança, Pará (ANSP 244096); Praia de Búzios, 20 km S of Natal, Rio Grande do Norte (ANSP 300442); Praia Upanema, Areia Branca, Rio Grande do Norte (ANSP 300320); Rio Pirangi (ANSP 300343); Baía (AMNH 22434; USNM 119506,157674, 465525); Victória (MCZ uncatalogued); Rio de Janeiro (ANSP 56828; MCZ 89650); Pinheiro Island, Rio de Janeiro (USNM 598337). ATLANTIC ISLANDS: FERNANDO NORONHA (MCZ uncatalogued).

Melampus (Melampus) bidentatus
Say, 1822
Figs. 257–289

Melampus bidentatus Say, 1822: 245 [East Florida, herein restricted to mouth of St. John's River; type material presumed lost (Baker, 1964); neotype herein designated USNM 859014 (Fig. 257)]; Jay, 1839: 59; H. & A. Adams, 1854: 10; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 45; Say *in* Binney, 1858: 84; Binney, 1859: 156, pl. 75, fig. 23; Binney, 1860: 4; Binney, 1865: 10, figs. 11, 12; Tryon, 1866: 8, pl. 18, fig. 5; Gould, 1870: 467, fig. 721; Binney & Bland, 1870: 286, fig. 7 [radula figured]; Pfeiffer, 1876: 316; Nevill, 1879: 219; Dall, 1883: 322; Whiteaves, 1901: 207; Morse, 1921: 21, pl. 7, fig. 46, pl. 9, figs. 46, 46a [external anatomy and morphology]; Peile, 1926: 88; Pilsbry, 1927: 125–126; Hausman, 1932: 541–545 [ecology]; Hausman, 1936: 127; M. Smith, 1937: 146, pl. 55, fig. 11, pl. 67, fig. 12 [pl. 67 copied from Dall (1885: pl. 18)]; Morton, 1955c: 127–168 [anatomy, evolution]; Holle & Dineen, 1957: 90–95 [life history]; Morrison, 1958: 118–124 [habitat]; Morris, 1958: 40, fig. 15; Holle & Dineen, 1959: 28–35, 46–51 [shell morphometry, taxonomy]; Baker, 1964: 151; Russell-Hunter & Brown, 1964: 143; Russell-Hunter & Meadows, 1965: 409 [physiology]; Russell-Hunter & Apley, 1966, 392–393 [early life history]; Apley et al. 1967: 455–456 [annual reproductive turnover]; Coomans, 1969: 82; Apley, 1970: 381–397 [life history]; Jacobson & Emerson, 1971: 64, text fig.; Russell-Hunter et al., 1972: 623–656 [early life history]; Grandy, 1972: 106–109 [winter distribution]; Morris, 1973: 273, pl. 74, fig. 8; Abbott, 1974: 331, fig. 4087; Lesser et al., 1976: 69–77 [population density]; Emerson & Jacobson, 1976: 192, pl. 26, fig. 25; Orton, 1976: 1–57 [ecology]; Andrews, 1977: 181, figured [common name coffee *Melampus* erroneously applied]; Price, 1977: 295–312 [central nervous system]; Fitzpatrick & Sutherland, 1978: 23–28 [population density]; Moffett, 1979: 306–319 [locomotion]; Andrews, 1981: 77, text fig.; Rehder, 1981: 645, fig. 361; Heard, 1982: 19, fig. 15; Moffett, 1983: 950; Ridgway, 1983: 950; Thompson, 1984: 44–53 [diet]; Jensen & Clark, 1986: 457, figured.

Melampus bidentatus var. *lineatus* Say, 1822: 246 [Coasts of Maryland and New Jersey, herein restricted to Bivalve, New Jersey, type material presumed lost (Baker, 1964); neotype herein designated USNM 859013 (Fig. 259)]; Say *in* Binney, 1858: 85; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 46.

Melampus obliquus Say, 1822: 377 [South Carolina; type material lost (Binney, 1859)]; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 30; Say *in* Binney, 1858: 27; Binney, 1860: 4; Pfeiffer, 1876: 306; Mazÿck, 1913: 2.

Auricula cornea Deshayes, 1830: 90 [New York; location of type unknown]; Jay, 1839: 59.

Melampus (Melampus) lineatus Say. Beck, 1837: 107.

Melampus (Melampus) obliquus Say. Beck, 1837: 107.

Melampus (Melampus) corneus (Deshayes). Beck, 1837: 107.

Auricula bidentata (Say). Gould, 1841: 197, fig. 130; De Kay, 1843: 57, pl. 5, figs. 92, 1–3; Küster, 1844: 41, pl. 6, figs. 7–11.

Auricula jaumei Mittré, 1841: 67 [Hampton, Virginia; location of type unknown].

Auricula obliqua (Say). De Kay, 1843: 58.

Melampus lineatus Say. Gray, 1847a: 179; Dall, 1885: 282, pl. 18, figs. 9, 12; Dall, 1889: 92, pl. 47, figs. 9, 12; Apgar, 1891: 181, figs. 46–48; Mazÿck, 1913: 2; C.W. Johnson, 1915: 178; Maury, 1922: 55; C.W. Johnson, 1934: 159; Webb, 1942, pl. 11, fig. 20; La Rocque, 1953: 262; Coomans, 1958: 103; Bousfield, 1960: 14, pl. 1, fig. 10; Coomans, 1962: 90; Baker, 1964: 152; Baranowski, 1971: 143.

Melampus corneus Stimpson. Stimpson, 1851: 51; Porter, 1974: 301.

Melampus gundlachi Pfeiffer, 1853b: 126 [Cayo Blanco, Cuba: location of type unknown]; Pfeiffer, 1854a: 147; Pfeiffer, 1856a: 20; Pfeiffer, 1876: 303: Arango y Molina, 1880: 59; A.E. Smith, 1884: 277; Crosse, 1890: 258; Kobelt, 1900: 229, pl. 29, figs. 1, 2; Pilsbry, 1900b: 504; Morton, 1955c: 9; Holle & Dineen, 1959: 28–35, 46–51.

Melampus redfieldi Pfeiffer, 1854a: 112 [Bermuda; location of type unknown]; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 33; Binney, 1859: 170; Pfeiffer, 1876: 308; Kobelt, 1900: 232, pl. 29, figs. 8, 9; Pilsbry, 1900b: 504.

Melampus ? jaumei (Mittré). Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 25.

Melampus bidentatus var. *borealis* "Conrad" Pfeiffer, 1856a: 46 [Georgia; type in Cuming collection, *fide* Pfeiffer, not found at BMNH].

Auricula gundlachi (Pfeiffer). Reeve, 1877, pl. 6, fig. 50. *Non* Gassies, 1869.

Auricula redfieldi (Pfeiffer). Reeve, 1877, pl. 7, fig. 52.

Auricula bidenta (Say). Reeve, 1877, pl. 7, fig. 54 [error for *bidentata*, corrected in the Index].

Melampus spiralis "Pfeiffer" Melvill, 1881: 155–173 [misidentification]. *Non* Pfeiffer, 1855.

Melampus coffeus var. *gundlachi* Pfeiffer. Davis, 1904: 126, pl. 4, fig. 9; Maury, 1922: 55; Peile, 1926: 88.

Melampus coffeus var. *redfieldi* Pfeiffer. Davis, 1904: 126, pl. 4, fig. 10; Peile, 1926: 88.

Melampus coffeus var. *bishopi* Davis, 1904: 127, pl. 4, fig. 13 [Bermuda; lectotype selected by Baker (1964) ANSP 86925 (Fig. 262)].

Melampus coffeus var. *verticalis* Davis, 1904: 127, pl. 4, fig. 12 [Bermuda; lectotype selected by Baker (1964) ANSP 86927 (Fig. 263)].

Melampus coffeus var. *alternatus* Davis, 1904: 127, pl. 4, fig. 11 [Bermuda; lectotype selected by Baker (1964) ANSP 86926 (Fig. 264)].

Melampus coffeus gundlachi Pfeiffer. C.W. Johnson, 1934: 159; Perry, 1940: 177.

Melampus bidentatus corneus (Deshayes). Morrison, 1951b: 8.

Melampus bidentatus lineatus Say. Morrison, 1951b: 8; Burch, 1960a: 177–208, pl. 1, fig. 1, pl. 4, fig. 62 [chromosomes]; Burch, 1960b: 454, fig. 5 [chromosomes]; Natarajan & Burch, 1966: 111, figs. 8, 13 [chromosomes].

Melampus bidentatus bidentatus Say. Morrison, 1951b: 8;

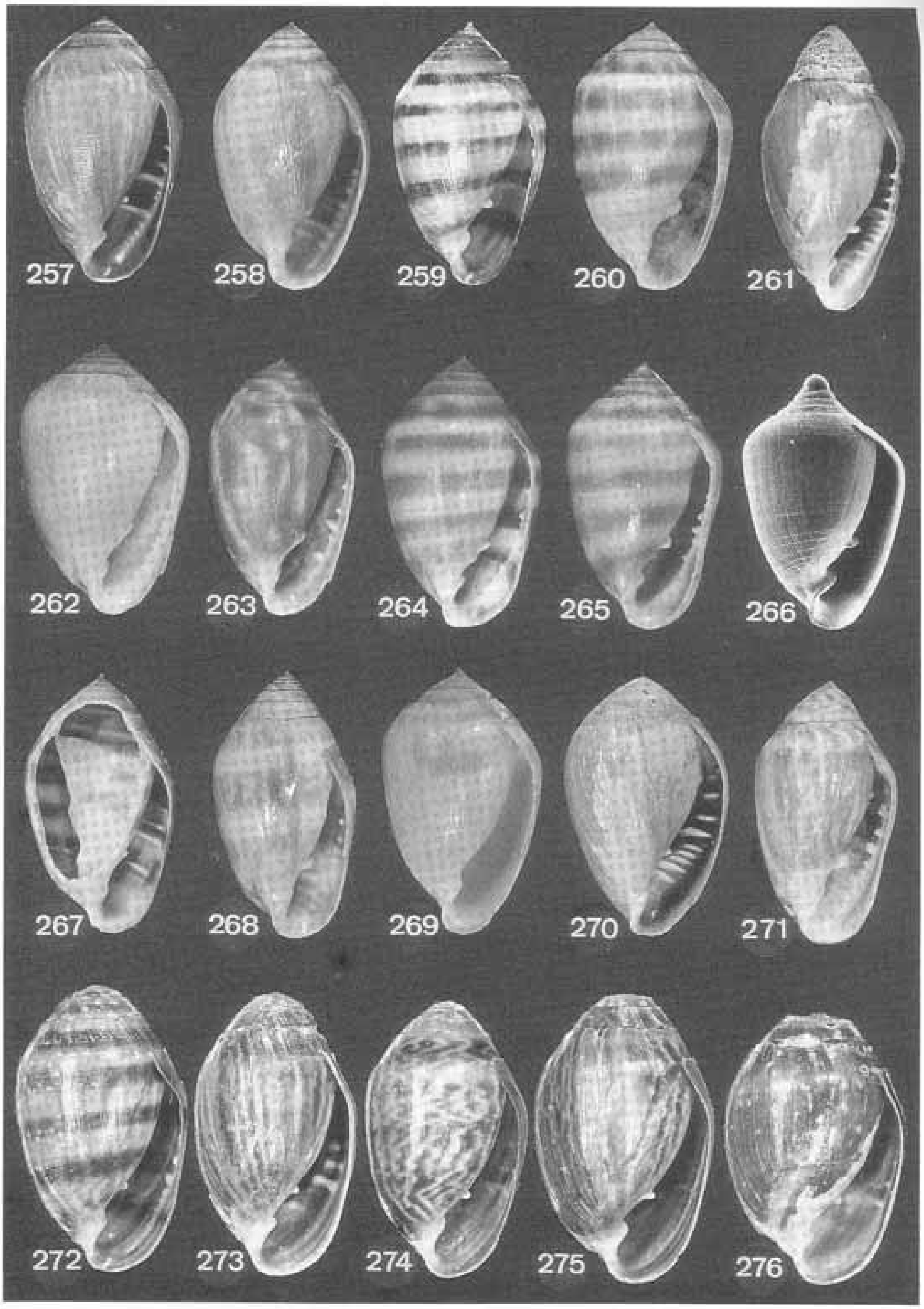
Melampus bidentatus redfieldi Pfeiffer. Morrison, 1951b: 8

Melampus (Micromelampus) bidentatus Say. Morrison, 1959: 25.

Melampus bidentus Say. Porter, 1974: 300 [error for *bidentatus*].

Melampus (Melampus) bidentatus Say. Vokes & Vokes, 1983: 60, pl. 22, fig. 12.

Description: Shell (Figs. 257–280) to 20 mm long, ovate-conic to elongate-oval, solid to thin, shiny to dull, often whitish, commonly a uniform yellowish to dark brown, with irregular axial markings or with as many as five transverse brown bands on body whorl. Umbilical excavation present. Spire low to moderately high, whorls eight to 11, flat, spirally pitted or grooved; apex frequently eroded. Body whorl about 85% of total length, striated, with one, usually two or more incised striae on round shoulder. Aperture subaxial, about 90% body whorl length, narrow, with base moderately broadening; inner lip with small, oblique columellar tooth and two parietal teeth, the posterior strongest, perpendicular to columellar axis, anterior one minute, often absent; additional parietal denticles sometimes present; outer lip sharp, internal lamellae uneven, white, as many as 17, not reaching edge and only three or four ex-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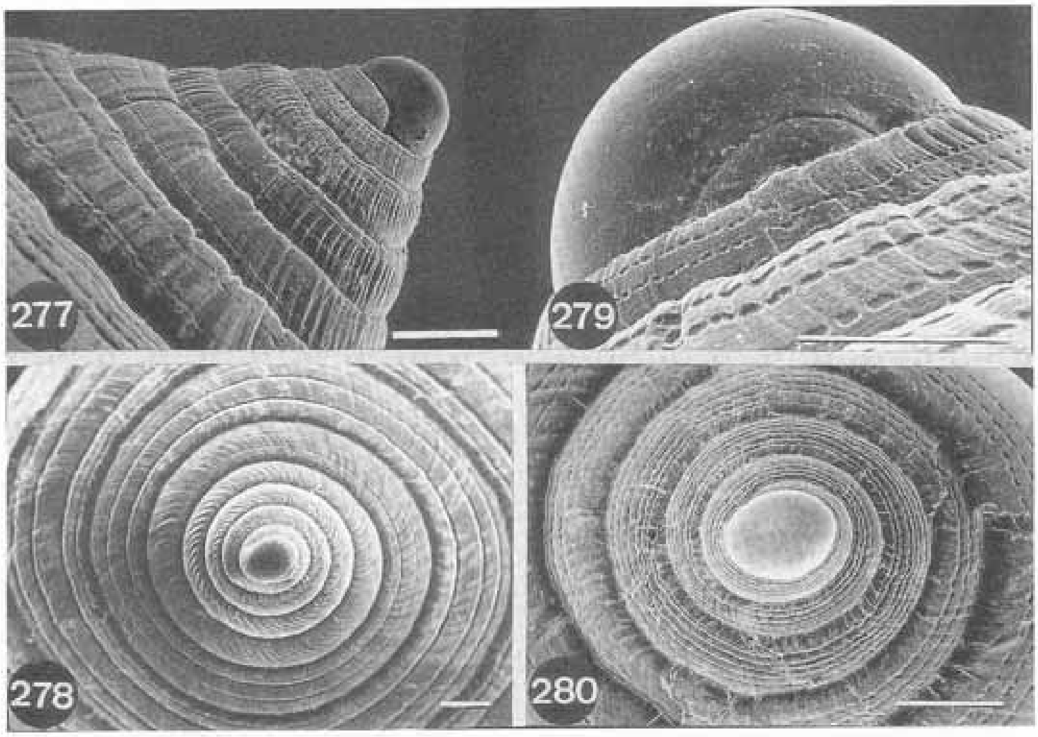
FIGS. 257–276.



FIGS. 277–280. *Melampus (M.) bidentatus*, lateral and top views of spire and protoconch. (277) Hudson, Florida. (278) Jekyll Island, Georgia. (279) Long Key, Florida. (280) South Mastic Pt., Andros Island, Bahamas. Scale, Fig. 279, 500 µm; all others, 1 mm.

tend inward. Resorption of inner whorls extensive, remaining internal partition less than half a turn (Fig. 267). Protoconch smooth, translucent, brownish (Figs. 277–280).

Radula (Figs. 281–285) with formula $[26 + (1 + 17) + 1 + (17 + 1) + 26] \times 100$. Radular morphology the same as that of *Melampus (M.) coffeus*.

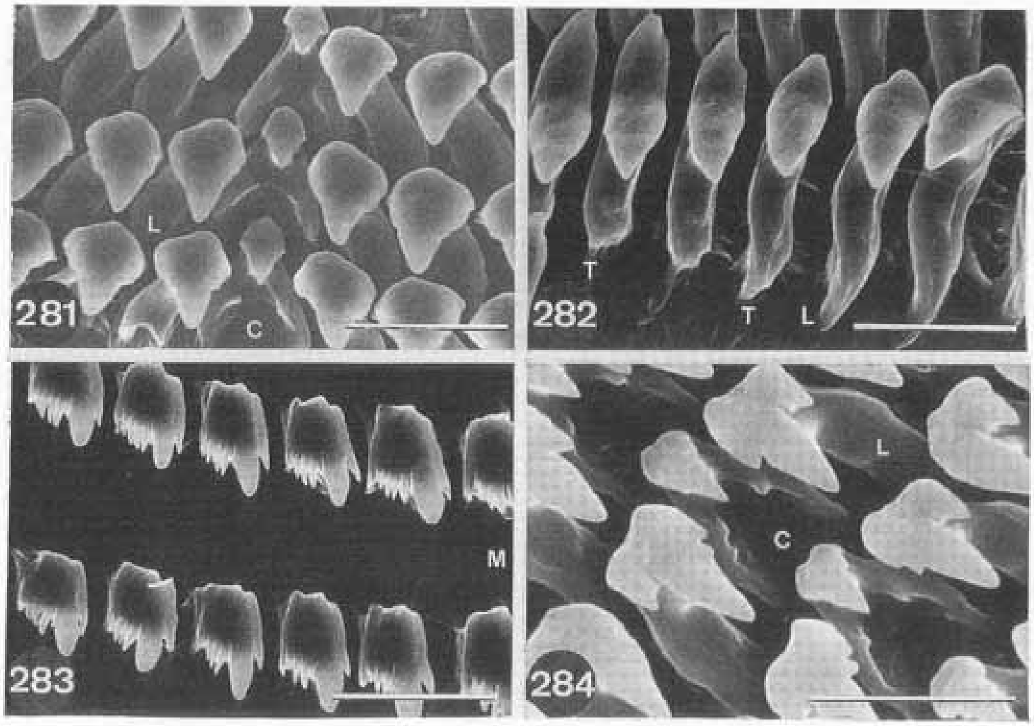
Animal as in *Melampus (M.) coffeus*.

Stomach (Fig. 286) as in subfamily.

Reproductive system basically as described under *Melampus s.l.;* posterior vas deferens about 70% of vagina length (Fig. 287).

Nervous system (Fig. 288) with left parietal ganglion one-fourth size of right one; visceral ganglion slightly larger than right parietal ganglion. Length of cerebral commissure

FIGS. 257–276. *Melampus (M.) bidentatus* Say. (257) Neotype (USNM 859014), from Smith collection, St. John's River, Florida, sl 9.2 mm. (258) Specimen figured by Binney (1865:10, fig. 11) (USNM 39818), sl 14.8 mm. (259) *M. bidentatus* var. *lineatus* Say, neotype (USNM 859013), Bivalve, New Jersey, sl 8.1 mm. (260) Specimen figured by Binney (1865:10, fig. 12) (USNM 39818), sl 12.6 mm. (261) Cedar Island, North Carolina, sl 18.2 mm. (262) *M. coffeus* var. *bishopi* Davis, lectotype (ANSP 86925), South Shore, Bermuda, sl 12.1 mm. (263) *M. coffeus* var. *verticalis* Davis, lectotype (ANSP 86927), South Shore, Bermuda, sl 11.2 mm. (264) *M. coffeus* var. *alternatus* Davis, lectotype (ANSP 86926), South Shore, Bermuda, sl 11.6 mm. (265) Specimen figured by Binney (1859, pl.75, fig. 30) as "*Melampus floridanus* Shuttleworth" (USNM 39835), sl 6.8 mm. (266) Crawl Key, Florida, sl 2.15 mm. (267) Knight Key, Florida, sl 14.8 mm. (268) Belize (USNM 426007a), sl 12.0 mm. (269) Tampico, Mexico (USNM 219997a), sl 8.8 mm. (270) Myrtle Grove, Louisiana (USNM 628753), sl 15.0 mm. (271) Long Key, Florida (USNM 193363), sl 18.8 mm. (272) Narrow River, Wakefield, Rhode Island, sl 10.1 mm. (273) Narrow River, Wakefield, Rhode Island, sl 12.6 mm. (274) Narrow River, Wakefield, Rhode Island, sl 9.3 mm. (275) Narrow River, Wakefield, Rhode Island, sl 10.7 mm. (276) Narrow River, Wakefield, Rhode Island, sl 10.0 mm.



FIGS. 281–284. *Melampus (M.) bidentatus*, radular teeth. (281) Narrow River, Rhode Island, sl 11.1 mm. (282, 283) Hungry Bay, Bermuda, sl 14.4 mm. (284) Skidaway Island, Georgia, sl 2.3 mm. Scale, Fig. 284, 50 µm; all others, 100 µm.

equals width of one cerebral ganglion; left pleuroparietal connective twice length of right pleuroparietal; left parietovisceral connective about half the length of right parietovisceral. Internal pallial nerve crosses pneumostomal nerve to right, anastomoses with branch of medial pallial nerve, follows floor of pneumostome toward aperture and turns up to roof of mantle cavity, just to left of upper pneumostomal gland; pneumostomal nerve branches to mantle skirt, runs to pneumostomal aperture, sending branches along the way to mucous gland of mantle skirt, splitting to innervate lips of pneumostome.

Remarks: Melampus (M.) bidentatus Say is more variable than any other Western Atlantic ellobiid. The shape of the shell (Figs. 257–276) varies from almost globose to moderately high spired and oval-elongate. The thickness of the shell shows a geographic gradient, increasing toward the warmer parts of the range; *Auricula cornea* from New York, described by Deshayes (1830), exemplifies the much thinner-shelled northern variety of *Melampus (M.) bidentatus*. The intergrading color pattern ranges from monochromic to axially striped to discretely banded, the latter pattern being common among juveniles. In some populations the size of some individuals reaches that of some gerontic *Melampus (M.) coffeus*. The latter consistently has an accentuated conic shape as opposed to the slender profile of comparably-sized *Melampus (M.) bidentatus*. The number of riblets on the outer lip also shows geographical gradation with a tendency toward higher counts in the warmer parts of the range. These riblets are of unequal size and only four or fewer large ones penetrate deep into the aperture.

As noted in the synonymy above, *Melampus lineatus* and *Melampus obliquus*, proposed by Say (1822: 246, 377, respectively), are here considered to be *Melampus (M.) bidentatus*. The name *Melampus bidentatus* was applied to the thin, monochromic east Florida specimens, *Melampus lineatus* to the smaller, banded variety of *Melampus (M.) bidentatus* from Maryland and New Jersey and

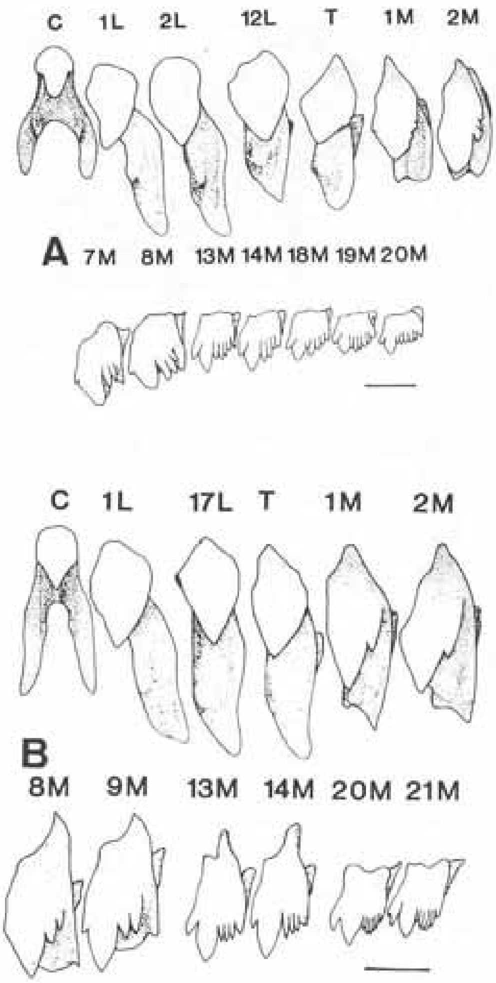


FIG. 285. *Melampus (M.) bidentatus*, radula. A, Woodville, North Carolina; B, Hudson, Florida. Scale 10 µm.

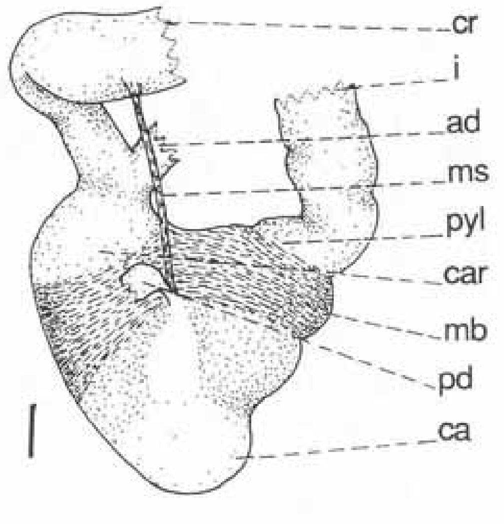


FIG. 286. *Melampus (M.) bidentatus*, stomach, North Carolina. Scale 1 mm.

Melampus obliquus to the rather thick form with a very oblique columellar tooth from South Carolina.

Binney (1859: 159), who had access to the type material of *Melampus bidentatus* and *Melampus lineatus*, noted the variability of the species and wrote about the latter name, "I have met with none sufficiently marked to form a variety, much less a distinct species." Nevertheless, the name *Melampus lineatus* has been used to designate a subspecies or, erroneously, to substitute for *Melampus (M.) bidentatus* Say (Dall, 1885). The reasons for the use of *Melampus lineatus* resided in the misplacement of *Auriculinella (Leucophytia) bidentata* (Montagu, 1801) in the genus *Melampus*, which would have constituted a case of secondary homonymy. Dall's confusion arose from Binney's contention (1865) that the animal of *Myosotella myosotis* from America was apparently similar to *Melampus (M.) bidentatus* Say, and that it did not agree with the illustration of *Alexia* given by H. & A. Adams (1855b, pl. 82, fig. 5). Binney did not say in what way they differed, however. Besides the color, the main difference between the animal of *Myosotella myosotis* (Draparnaud) and that of *Auriculinella (L.) bidentata* (Montagu, 1801) is that the foot of the latter species is transversely divided (Morton, 1955b). Because *Melampus* has this same characteristic, Dall probably assumed that the *Alexia myosotis* referred to by Binney, like *Melampus*, would have a transversely divided foot. The shells of *Myosotella myosotis* and of *Auriculinella (L.) bidentata* can be confused easily and Dall's (1885: pl. 18, fig. 13) illustration of *Melampus (Leuconia) bidentata* (Montagu) is a facsimile of Binney's (1865: 4, fig. 4) representation of *Alexia myosotis*.

Say's last name, *Melampus obliquus*, was applied to a form similar to *Melampus (D.) monile* (Bruguière, 1789). Say (1822: 377) added that in the collection of the Academy of Natural Sciences of Philadelphia there were specimens from the West Indies which conformed with his description of *Melampus obliquus*. Binney (1859: 167), who had seen

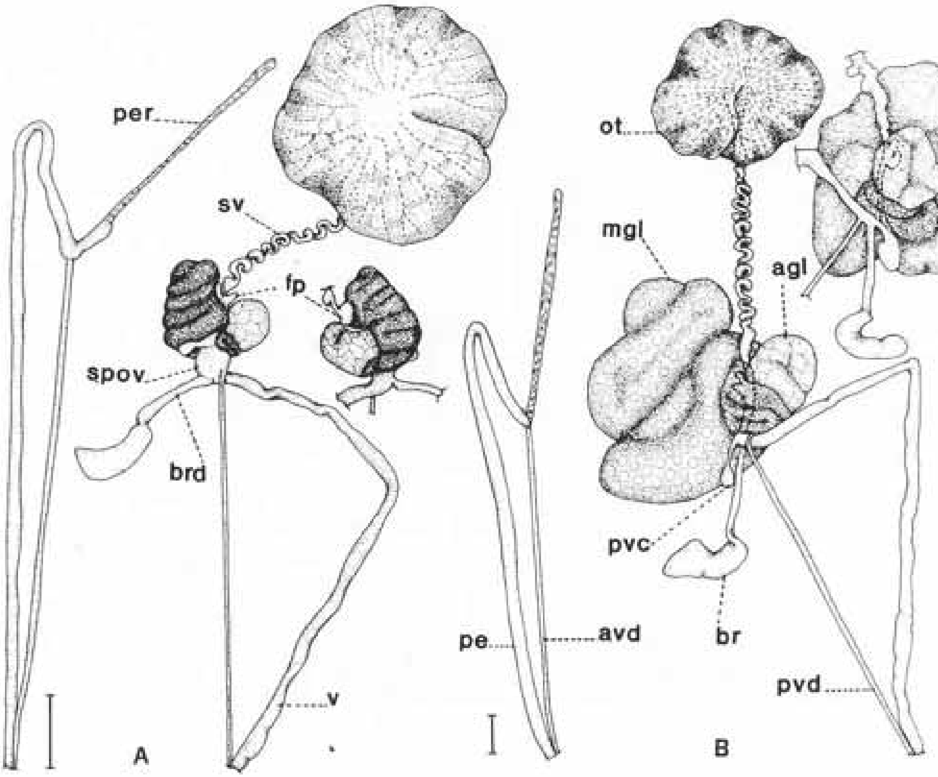


FIG. 287. *Melampus (M.) bidentatus*, reproductive system. A, Narrow River, Rhode Island; B, Cedar Island, North Carolina; C, New Smyrna, Florida; D, Hungry Bay, Bermuda. Scale 1 mm.

specimens belonging to the first two of Say's names, noted, "It is not known what shell Say had in view when the above description was written. No authentic specimen was preserved, and no author has seen any shell from that locality answering to the characters laid down." In 1865 Binney relegated Say's *Melampus obliquus* to his "Spurious species of *Melampus*." On Cedar Island, North Carolina, however, I found specimens of *Melampus (M.) bidentatus* that fit Say's description of *Melampus obliquus* (Fig. 261). *Melampus obliquus* Say must, then, be treated as a junior synonym of *Melampus (M.) bidentatus* Say.

Pfeiffer introduced several species that should be related to *Melampus (M.) bidentatus*. In his comments on *Melampus gundlachi* from Cayo Blanco, Cuba, Pfeiffer (1853b) noted that their juveniles were much more brightly colored than those of *Melampus (M.) coffeus* and he did not mention incised grooves. The elliptic-ovate shape of the shell, however, indicates to me that Pfeiffer's name can be treated as a synonym of *Melampus (M.) bidentatus* Say.

Another of Pfeiffer's (1854a) introductions, *Melampus redfieldi* from Bermuda, was distinguished from *Melampus (M.) coffeus* by the presence of very compressed riblets in the outer lip. Because it occurs in the latter species (personal observation), this condition is not a useful character. The fact that Pfeiffer referred to the striations on the shell suggests that he was actually describing a specimen of *Melampus (M.) bidentatus*.

Pfeiffer (1854b, 1856a) erroneously identified a variety of *Melampus (M.) bidentatus* Say with *Melampus borealis* (Conrad) [= *Myosotella myosotis* (Draparnaud)]. Neither Pfeiffer's description nor the locality given (Georgia) agrees with those of Conrad (1832). Pfeiffer (1876: 316) later explained that he was referring to a museum label in the Cuming collection, rather than to Conrad (1832).

In 1841 Mittré described *Auricula jaumei*

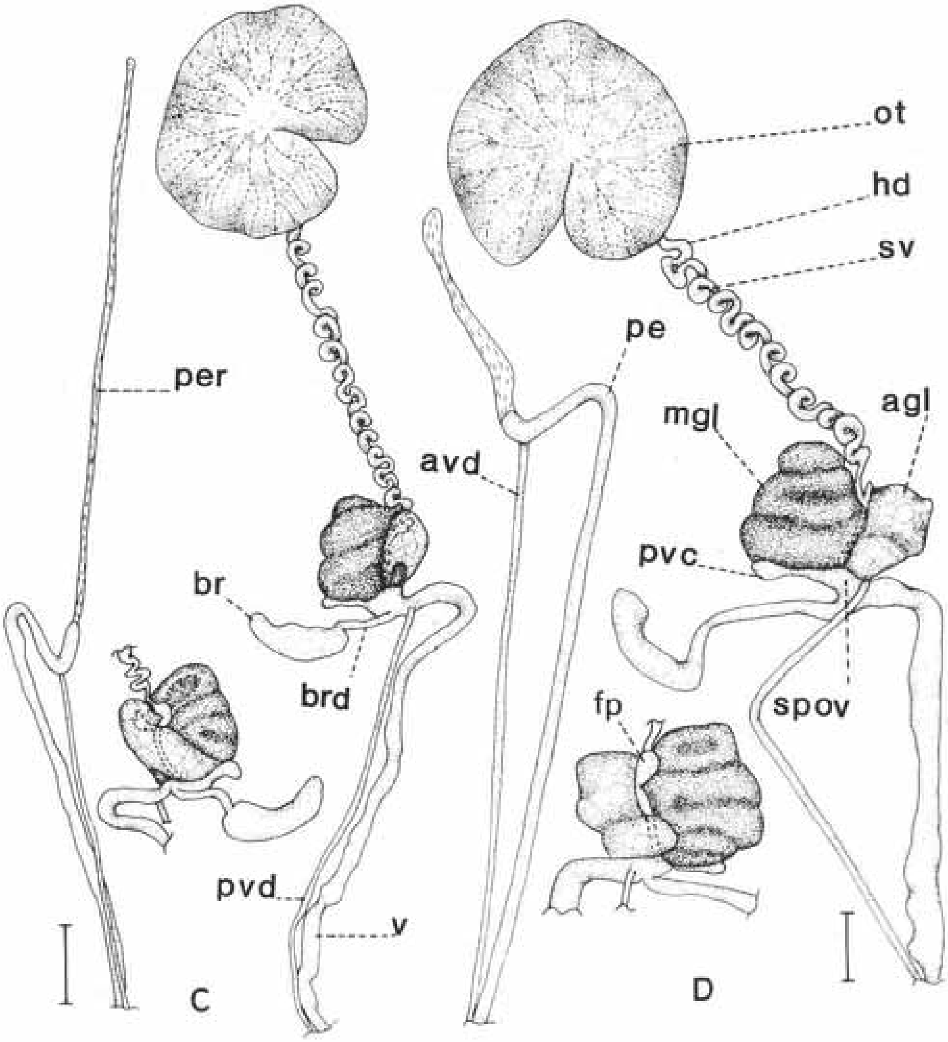


FIG. 287.

from Hampton, Virginia. It was said to differ from Deshayes' *Auricula cornea* in having the inside of the outer lip consistently ribbed. *Melampus (M.) bidentatus* is highly variable in this respect (Holle & Dineen, 1959) and this character is therefore unreliable for taxonomy. *Auricula jaumei* is conspecific with *Melampus (M.) bidentatus*.

Melvill (1881) mentioned *Melampus spiralis* Pfeiffer from Cedar Keys, on the western coast of Florida. Pfeiffer (1856a), however, in his observations on *Melampus spiralis*, noted that this species was made known to him by Cuming as *Melampus pallescentis* Sowerby, 1839. Because Sowerby provided an incomplete description of the latter taxon, Pfeiffer, based on Sowerby's figure (1839a *in* Beechy: pl. 38, fig. 28), thought that *Melampus pallescentis* Sowerby should be referred to *Melampus luteus* Quoy & Gaimard, 1832, from the Philippines. It appears, then, that the *Melampus spiralis* of Pfeiffer was not based on West Indian material. Melvill's citation (1881) of "*Melampus spiralis* Pfeiffer" should be treated as a misidentification of *Melampus (M.) bidentatus*.

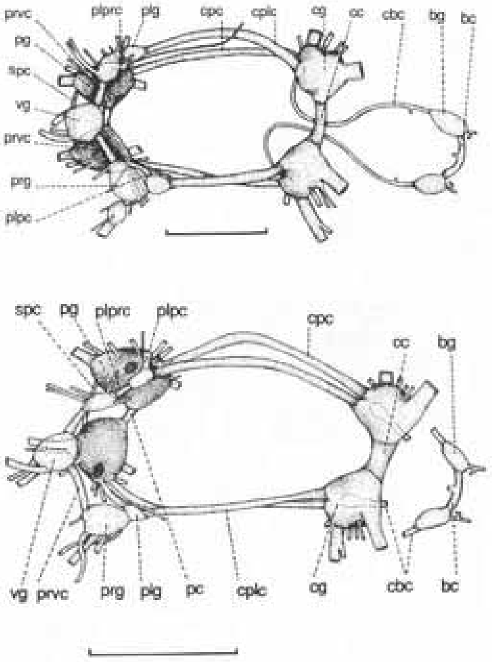


FIG. 288. *Melampus (M.) bidentatus*, central nervous system. A, Narrow River, Rhode Island; B, New Smyrna, Florida. Scale 1 mm.

Morrison (1951b) recognized several subspecies of *Melampus (M.) bidentatus: M. b. corneus* from Prince Edward Island, Canada, to Staten Island, New York; *M. b. lineatus* from New Jersey to North Carolina; *M. b. bidentatus* from South Carolina to Florida, Texas and the West Indies; and *M. b. redfieldi* from Bermuda. The latter supposed subspecies also lives in Florida (Pfeiffer, 1876, with a question mark; personal observation) and shows as much variation as the other forms of *Melampus (M.) bidentatus.* Shell thickness and color seem to be linked to temperature, the thinner and paler forms being typical of colder regions. This link would account for the similarities between shells from Bermuda and those from Florida (see the remarks under *Myosotella myosotis*). Holle & Dineen (1959) reported the continuous variation in shell characters along the range of the species, thus rendering Morrison's treating the morphs as subspecies unjustifiable.

Morrison (1951b, 1964) placed *Melampus (M.) bidentatus* in the subgenus *Micromelampus* Möllendorff, 1898, which had been erected, according to Zilch (1959), to include the small *Melampus.* Only anatomical study of the type species, *Melampus nucleolus* Martens, 1865, from Amboina, will allow an objective decision concerning the taxonomic status of this subgenus. In any case, the observed wide range of size in *Melampus (M.) bidentatus* does not justify its inclusion in the subgenus *Micromelampus* and my anatomical study strongly favors its inclusion in *Melampus s.s.*

It appears that Say's type material, to which Binney referred (1859), is not in the Academy of Natural Sciences of Philadelphia and was presumed lost (Holle & Dineen, 1959; Baker, 1964). Because of documented confusion between *Melampus (M.) bidentatus* and *Melampus (M.) coffeus,* neotypes that conform to original descriptions and accepted usage are herein designated for *Melampus bidentatus* and *Melampus lineatus.* Inspection of material from South Carolina present in the collections of the various museums did not provide any specimens that could be identified with Say's *Melampus obliquus.* As noted above, I found on Cedar Island, North Carolina, a colony of *Melampus (M.) bidentatus* that agree with Say's description of *Melampus obliquus.* Without adequate material from the type locality, South Carolina, and with the disuse into which Say's name has fallen, it is inappropriate and unnecessary to designate a neotype for *Melampus obliquus.*

Habitat: The salt-marsh snail, *Melampus (M.) bidentatus,* is very common in the high-tide fringe of salt marshes and mangroves. Its habits have been studied only in the New England area, in which this mollusk lacks congeneric competitors. When Say described this species (1822) he noted its abundance and he considered it an important item in the diet of marsh birds.

Although dependent upon the rhythm of the tides, the salt-marsh snails are more active during the low tides at twilight. Their diet includes diatoms and detritus of vegetal and animal origin (Hausman, 1936; Thompson, 1984). The animals gather to spend the winter in partial hibernation (Grandy, 1972).

Apley (1970) and Russell-Hunter et al. (1972) provided detailed studies of the early life-history of this species. The snails become sexually mature at a shell length of 5 to 6 mm and have a life span of three to four years. Copulation and hatching of veliger larvae are closely synchronized with spring tides. Gelatinous masses of eggs are laid within one

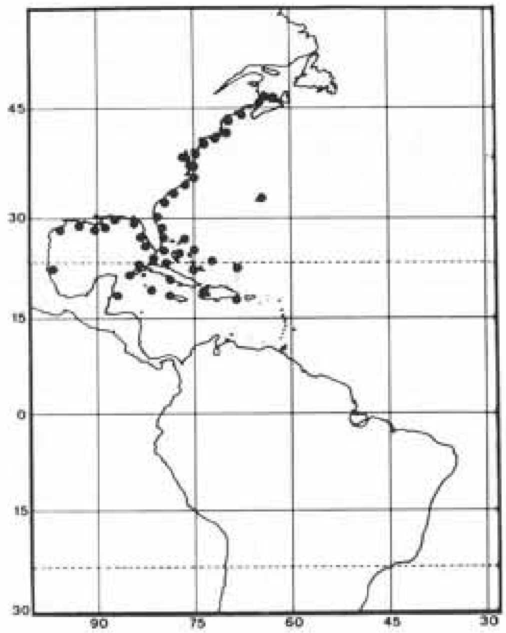


FIG. 289. *Melampus (M.) bidentatus*, geographic distribution.

day after copulation. About 13 days later free-swimming veligers hatch and spend about six weeks in the plankton before settling.

In the mangroves *Melampus (M.) bidentatus* commonly lives under fallen leaves and debris at the high-tide fringe, and is abundant on the margins of sheltered inland lagoons. In this habitat it coexists with *Melampus (M.) coffeus*.

Range: New Brunswick, Canada, to the Florida Keys, the Gulf coast of the United States south to Belize; Bermuda; Bahamas, Cuba, Jamaica, Hispaniola, Tortola (Fig. 289). The Tortola record is suspect and has not been confirmed by recent collections.

Specimens Examined: NEW BRUNSWICK: Buctouche Bay (MCZ 200471). PRINCE EDWARD ISLAND (MCZ 34048): Mount Stuart (ANSP 106545); Bunbury (ANSP 106678, 106938). NOVA SCOTIA: Windsor (ANSP 326060); West Peswick, Halifax (MCZ 297898). MAINE: Newmeadows River (MCZ 104992); Middle Bay (MCZ 294188); Cape Elizabeth (USNM 129331, 190466); Biddeford (ANSP 22370, 77421, 242121; MCZ 34049, 34810); USNM 492528). NEW HAMPSHIRE: Jackson's Landing, Durham (MCZ 193855); Sagamore Creek (MCZ 275395). MASSACHUSETTS (MCZ 201644): Ipswich (MCZ 147833); Gloucester (ANSP 102400; MCZ 201639; USNM 159104); Bass Rocks, Gloucester (USNM 408730); Goodharbor Beach, East Gloucester (MCZ 199906); Manchester (USNM 398130); Danvers (MCZ 3963, 34052, 61508, 133195; USNM 504484); Salem (MCZ 201633, 201636; USNM 73424); Lynn (MCZ 34053; USNM 224905); Revere (ANSP 89557); Revere Beach (MCZ 147714, 199909); Magazine, Cambridgeport (MCZ 141058; USNM 590055, 600303); Charles River, Boston (ANSP 56837); Boston Harbor (MCZ 141060); Neponset River, Milton (MCZ 142330); East Milton (MCZ 55146); Cohasset, North Scituate (MCZ 139271); Duxbury (MCZ 14884, 163165, 201638; USNM 492523, 492525, 492535); Gurnet Lights, Plymouth (MCZ 199905); Barnstable (ANSP 44599, 56840; USNM 34404, 159105, 487652); Sandy Neck (MCZ 182392); Truro (USNM 603101); Playground Beach, Hyannis (ANSP 176264); Wellfleet (R.B.); Provincetown (ANSP 134441; MCZ 147715, 199911; USNM 159108, 307158, 341102, 341104, 492532, 492533, 492536); Buzzard's Bay (MCZ 199913); Eastham (MCZ 199907, 201632); Pleasant Bay (MCZ 80561); Chatham (MCZ 34054); Eel Pond, South Chatham (MCZ 18812); South Dennis (MCZ 14547; USNM 492526); Grand Cove, South Dennis (MCZ 14548); Point Gammon, West Yarmouth (MCZ 112213); Lewis Bay (MCZ 200027); Nobska Point (MCZ 140811); Briar Neck (MCZ 199904); Vineyard Sound (USNM 159107); Nantucket (MCZ 34047); SE of Coskatee, Nantucket (MCZ 167949); South Beach, Nantucket Harbor (MCZ 167450); Popponesset Beach (MCZ 182391); Waquoit (ANSP 46678); Naushon Island (ANSP 163469; USNM 159110); Great Pond, Falmouth (USNM 660507); Woods Hole (MCZ 34051, 199908; USNM 159106); Bathing Beach, Woods Hole (USNM 340981, 340983, 340984; Little Sippewisset Marsh, Falmouth (MCZ 294115; A.M.); West Falmouth (ANSP 76171); Wareham (MCZ 34050, 199910); Piney Point, Marion (MCZ 178105); New Bedford (ANSP 56846; MCZ 201635). RHODE ISLAND: Newport (ANSP 56838; USNM 39814, 159109); Nayatt (MCZ 71268, 199914; Jamestown, Conanicut Island (A.M.); Seekonk River (ANSP 243912; MCZ 199912); Pawtuxet (MCZ 68940); Buttonwoods (MCZ 199915; USNM 492530); Apponaug (MCZ 151930; USNM

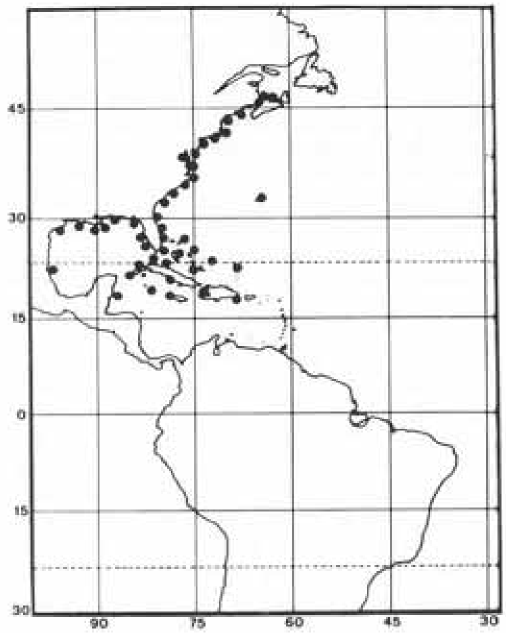


FIG. 289. *Melampus (M.) bidentatus*, geographic distribution.

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Range: New Brunswick, Canada, to the Florida Keys, the Gulf coast of the United States south to Belize; Bermuda; Bahamas, Cuba, Jamaica, Hispaniola, Tortola (Fig. 289). The Tortola record is suspect and has not been confirmed by recent collections.

Specimens Examined: NEW BRUNSWICK: Buctouche Bay (MCZ 200471). PRINCE EDWARD ISLAND (MCZ 34048): Mount Stuart (ANSP 106545); Bunbury (ANSP 106678, 106938). NOVA SCOTIA: Windsor (ANSP 326060); West Peswick, Halifax (MCZ 297898). MAINE: Newmeadows River (MCZ 104992); Middle Bay (MCZ 294188); Cape Elizabeth (USNM 129331, 190466); Biddeford (ANSP 22370, 77421, 242121; MCZ 34049, 34810); USNM 492528). NEW HAMPSHIRE: Jackson's Landing, Durham (MCZ 193855); Sagamore Creek (MCZ 275395). MASSACHUSETTS (MCZ 201644): Ipswich (MCZ 147833); Gloucester (ANSP 102400; MCZ 201639; USNM 159104); Bass Rocks, Gloucester (USNM 408730); Goodharbor Beach, East Gloucester (MCZ 199906); Manchester (USNM 398130); Danvers (MCZ 3963, 34052, 61508, 133195; USNM 504484); Salem (MCZ 201633, 201636; USNM 73424); Lynn (MCZ 34053; USNM 224905); Revere (ANSP 89557); Revere Beach (MCZ 147714, 199909); Magazine, Cambridgeport (MCZ 141058; USNM 590055, 600303); Charles River, Boston (ANSP 56837); Boston Harbor (MCZ 141060); Neponset River, Milton (MCZ 142330); East Milton (MCZ 55146); Cohasset, North Scituate (MCZ 139271); Duxbury (MCZ 14884, 163165, 201638; USNM 492523, 492525, 492535); Gurnet Lights, Plymouth (MCZ 199905); Barnstable (ANSP 44599, 56840; USNM 34404, 159105, 487652); Sandy Neck (MCZ 182392); Truro (USNM 603101); Playground Beach, Hyannis (ANSP 176264); Wellfleet (R.B.); Provincetown (ANSP 134441; MCZ 147715, 199911; USNM 159108, 307158, 341102, 341104, 492532, 492533, 492536); Buzzard's Bay (MCZ 199913); Eastham (MCZ 199907, 201632); Pleasant Bay (MCZ 80561); Chatham (MCZ 34054); Eel Pond, South Chatham (MCZ 18812); South Dennis (MCZ 14547; USNM 492526); Grand Cove, South Dennis (MCZ 14548); Point Gammon, West Yarmouth (MCZ 112213); Lewis Bay (MCZ 200027); Nobska Point (MCZ 140811); Briar Neck (MCZ 199904); Vineyard Sound (USNM 159107); Nantucket (MCZ 34047); SE of Coskatee, Nantucket (MCZ 167949); South Beach, Nantucket Harbor (MCZ 167450); Popponesset Beach (MCZ 182391); Waquoit (ANSP 46678); Naushon Island (ANSP 163469; USNM 159110); Great Pond, Falmouth (USNM 660507); Woods Hole (MCZ 34051, 199908; USNM 159106); Bathing Beach, Woods Hole (USNM 340981, 340983, 340984; Little Sippewisset Marsh, Falmouth (MCZ 294115; A.M.); West Falmouth (ANSP 76171); Wareham (MCZ 34050, 199910); Piney Point, Marion (MCZ 178105); New Bedford (ANSP 56846; MCZ 201635). RHODE ISLAND: Newport (ANSP 56838; USNM 39814, 159109); Nayatt (MCZ 71268, 199914; Jamestown, Conanicut Island (A.M.); Seekonk River (ANSP 243912; MCZ 199912); Pawtuxet (MCZ 68940); Buttonwoods (MCZ 199915; USNM 492530); Apponaug (MCZ 151930; USNM

568388); Wakefield, Pettaquamscutt River [Narrow River] (A.M.); Westerly (MCZ 14550; USNM 492541, 590089). CONNECTICUT: Stonington (ANSP 91947; MCZ 3965, 56902, 133196; USNM 858073; A.M.); Long Beach (MCZ 231486); Oxecoset Brook (A.M.); Guilford (USNM 478030, 568440); Pine Orchard (MCZ 166061, 201630); Branford (MCZ 34055, 34925, 199916); New Haven (MCZ 291293; USNM 404295); Lighthouse, New Haven (USNM 380818); Greenwich (ANSP 154660). NEW YORK: Harlem River (MCZ 156659, 167630; USNM 492538); Long Island (MCZ 201637, 230929; USNM 307157, 492527, 492542); Greenport (MCZ 161271; USNM 407784); Sand's Point (ANSP 145457); Sea Cliff (ANSP 43785); Oyster Bay (USNM 307154); Cold Spring (USNM 504486); Towo Point (USNM 694036); Orient (ANSP 133707, 218373; MCZ 124210); Shelter Island (ANSP 362811); East Patachogue (MCZ 288109); Freeport (MCZ 248224); Coney Island (ANSP 362808); Far Rockaway (MCZ 54518, 139569); Sheepshead (MCZ 156658); Staten Island (ANSP 132043; MCZ 78422, 201631; USNM 59725, 307159, 492500b). NEW JERSEY: Raritan Bay (USNM 608377); Union Beach, Raritan Bay (USNM 606609); E of Nantuxant Point, Newport (ANSP 162143); Point Pleasant (ANSP 65200); Harvey Cedars, Long Beach Island (ANSP 106527); Beach Haven (ANSP 155518); Shrewsbury River (ANSP 99006); Brigantine Island (ANSP 195015, 328333; USNM 611523); Atlantic City (ANSP 56843; MCZ 188902; USNM 492524); Ventnor (ANSP 99155); Margate City (ANSP 45192); Great Egg Harbor Bay (ANSP 326220; A.M.); Avalon (ANSP 354825); Wildwood Beach (ANSP 78982, 194600); Cape May (ANSP 45098, 65201, 106229, 110131, 117532; USNM 119503, 124603, 406309, 504479); Cape May Harbor (ANSP 182641); Carson's Inlet (ANSP 133907); Bivalve (ANSP 113465; A.M.); Dividing Creek (A.M.); Fortescue (ANSP 113466). DELAWARE: Woodland Beach (USNM 522267); Rockhall (ANSP 112612); S of Fort Miles (USNM 621420); Indian River Inlet (MCZ 198052); N end of Cedar Neck, S side of Indian River Bay (USNM 621418, 621419); Mouth of Cedar Creek (USNM 406310); Assawoman Wildlife Area (ANSP 302221). MARYLAND: Mayo Beach (USNM 522288); Galesville (USNM 595602); Chesapeake Beach (USNM 191595, 473893); Parkers Creek (USNM 521920, 536709); near Triton Beach (758314); Piney Island (USNM 667267); Patuxent River (ANSP 396602; MCZ 139263); Carrolls Bank, mouth of Patuxent River (USNM 363927); Broome Island (USNM 473465); N of Solomons Island (USNM 600765); Solomons Island (USNM 424040); Millstone Landing (USNM 512876); Benedict (USNM 473456); St. Marys River (USNM 379539); Smiths Creek (USNM 518853); Cobb Island (USNM 499519, 522921); Island Creek (USNM 252064); Hope House, N of Easton (USNM 602855); Huggins Point, S of Leonard Town (MCZ 216712); Town Point (ANSP 132462; MCZ 46420, 52344); Church Creek, Cambridge (MCZ 200468); Parsons Creek (MCZ 211150); Bishops Head (MCZ 139264); Ocean City, Sinepuxent Bay (USNM 601744, 601747); E of Dames Quarter (USNM 618922); SE of Chance Island (USNM 473331); Deal Island (USNM 468283); Crisfield (USNM 595598); near Snow Hill, Chincoteague Bay (USNM 605563); West Bay, Chincoteague Bay (USNM 591783). VIRGINIA: Chincoteague Island (MCZ 199443; USNM 530826, 533596); Oyster (USNM 407459); Magotha (ANSP 275980; USNM 422297); Smiths Island (USNM 153352, 225965, 422294, 422295); Dameron Marsh, Balls Creek and Ingram Bay (ANSP 305137); Fisherman Island (USNM 422293); Brighton (USNM 171118); Assateague Island (ANSP 352439; USNM 809536); Toms Cove, Assateague Island (USNM 209268); Watts Bay (USNM 701629); Fairport (USNM 103258); Potomac Beach (USNM 473900); Wicomico Church (USNM 269147); Bretton Bay (USNM 628900); Greenvale Creek near Rappahannock (MCZ 214466, 291314); Sweetheart Island (USNM 269077); Fleeton (USNM 308939); Severn River (USNM 679373); Chisman Creek (USNM 603690); Poropotank, York River (USNM 679375); Goodwin Island (USNM 679374); Yorktown (USNM 474077); Norfolk (MCZ 46542; USNM 407588, 504483, 539235, 667497); Granby and Lakewood bridge, Norfolk (ANSP 219145; MCZ 221231; USNM 653497); Boissevain Avenue, Norfolk (ANSP 263386; MCZ 186692); Lamberts Point (ANSP 263388); Elizabeth River (MCZ 186696); Lafayette Park, on bank of Lafayette River (MCZ 186691). NORTH CAROLINA: Bodie Island (MCZ 105478); Pee Island (USNM 488826); Hatteras Island (USNM 637152); Cedar Island (A.M.); North River, Woodville (A.M.); Williston (A.M.); Oyster Creek (A.M.); Beaufort (ANSP 56839, 145683; USNM 380566, 382982, 433203, 523610, 523620); Mullet Pond, Beaufort (USNM 380565); Brackish Pond (MCZ 141059); North

River (ANSP 179830; MCZ 81930); Newport River (A.M.); Wrightsville (USNM 492540); Southport (ANSP 113647, 227028; MCZ 176143); Smith Island, Cape Fear (ANSP 95602); Cape Fear River (MCZ 175210). SOUTH CAROLINA: Pawleys Island (MCZ 201642); Bull Island (USNM 543341); Sullivans Island (USNM 492537); Charleston (ANSP 56884; USNM 26571, 26574, 39823, 307156); Folly Beach (ANSP 300432); Edisto Island (USNM 474096); Edisto Beach (ANSP 180786); Yemassee (USNM 492539; A.M.); Lobeco (A.M.); Pocataligo (USNM 603106); N of McClellanville (USNM 758249). GEORGIA (ANSP 56835): Skidaway Island (A.M.); Coxboro Island (USNM 622491); Savannah (MCZ 200467; USNM 610311, 665761, 665762); Jones Island, Savannah River (ANSP 164988); Crescent (A.M.); Valona (A.M.); Fort King George, Darien (USNM 707263); Sea Island (ANSP 56847); Saint Simons Island (ANSP 123529); Brunswick (ANSP 183414; MCZ 186697; USNM 425961; A.M.); Jekyll Island (A.M.). FLORIDA: Fernandina (MCZ 201208); St. John's River (USNM 307155); Mayport (ANSP 56844, 76095); Jacksonville (ANSP 56841; USNM 39815); St. Augustine (ANSP 45077, 66965, 140731; MCZ 186695; USNM 36014, 39825a, 492529); Fort Marion, St. Augustine (ANSP 9523); Matanzas (USNM, 672437); Indian River (MCZ 186699, 291315; USNM 758221); Ormond Beach (MCZ 82493); New Smyrna Beach (MCZ 291026; A.M.); Oak Hill (ANSP 22362; MCZ 201640; USNM 87624); Titusville (MCZ 143992); Banana River (MCZ 201643); Grant (MCZ 105475); Lake Worth (ANSP 69851; MCZ 291287; USNM 253538); Fort Dallas (USNM 39817, 119502); Haulover Canal, head of Indian River (ANSP 62720); Miami (ANSP 77506, 82844, 145885); Biscayne Bay (MCZ 291305); Sands Key (MCZ 291309); Virginia Key, Biscayne Bay (ANSP 189570); Coconut Grove (MCZ 291299, 291300; USNM 603111); Waveland (USNM 103495, 123532); Madero Bay (MCZ 291289); Soldier Key (MCZ 174457); Middle Key, Barnes Sound (USNM 405985); McGinty Key (ANSP 189572; MCZ 103303); Pumpkin Key (USNM 355115); Tavernier (MCZ 294246); Key Largo (ANSP 294318; MCZ 291281, 291302, 291313, 294228; USNM 603119); Tavernier Creek (USNM 667401; A.M.); Tavernier Key (USNM 492549, 492552); Snake Creek (MCZ 294234); Plantation Key (MCZ, 294230, 294231; A.M.); Windley Key (USNM 603104); Indian Key (USNM 26423, 27917, 462894a); Indian Key Fill (A.M.); Lignumvitae Key (ANSP 156327, 189571); Lower Matecumbe Key (MCZ 291294; USNM 492553); Long Key (ANSP 76700; MCZ 291296, 291031; USNM 193363, 492578; A.M.); Grassy Key (MCZ 291288; A.M.); Crawl Key (MCZ 174458, 291032, 291033, 294235; A.M.); Marathon, Key Vaca (ANSP 189584); Knight Key (A.M.); Bahia Honda Key (ANSP 104095; USNM 269777a, 270310); West Summerland Key (A.M.); Newfound Harbor (USNM 272688a); Little Pine Key (USNM 681642); Big Pine Key (ANSP 104092, 104093; MCZ 291029, 291034, 294237, 294243; USNM 597453; A.M.); Big Torch Key (ANSP 104096; A.M.); Howe Key (USNM 681641); Ramrod Key (MCZ 291028, 291045, 294232, 294233); Sugarloaf Key (ANSP 104094); Big Coppit Key (USNM 603102); Boca Chica Key (ANSP 104091, 152501; USNM 270326, 511180); Stock Island (ANSP 149993; MCZ 59993; USNM 270269); Key West (ANSP 294309; MCZ 9947; USNM 27730, 529557, 596787, 667405, 670450); Shark Key (USNM 696979, 711532); Boca Grande Key (USNM 270262); Flamingo Key (ANSP 294312; MCZ 291038, 294236, 294244); Cape Sable (MCZ 291035); Lossman River (ANSP 132369); Everglades City (USNM 683928); Marco Island (MCZ 294249); Little Marco (USNM 511210); Naples (ANSP 189568; MCZ 291316); Sanibel (ANSP 170640; MCZ 13278, 13279, 294239, 294248); Pineaire, Pine Island (MCZ 291030); Bokeelia (MCZ 294245; A.M.); Matlacha Key (MCZ 291311); Starvation Key (ANSP 294320); Captiva Island (MCZ 294250); Punta Gorda (USNM 492577); between Fort Myers and Punta Gorda (USNM 531133); Charlotte Harbor Bay (USNM 407410); Boca Grande, Gasparilla Island (ANSP 142272); Little Gasparilla Island (ANSP 189592); Sarasota (USNM 159254, 487213, 487314); 5 km N of Sarasota (ANSP 195406); Long Boat Key (MCZ 294252); between Palma Sola and Cortez (MCZ 291037); Anna Maria Key (MCZ 291027); Palmetto (A.M.); Manatee River (MCZ 3969; USNM 61052); Small Island, mouth of Manatee River (MCZ 291282); Big Bend Road [Rt. 672] (A.M.); Tampa (ANSP 56836, 294317, 362807; MCZ 201649, 291284, 294238; USNM 36061, 37609, 193361, 196349, 492574, 504487); Young Lagoon, Tampa (USNM 37610); Hillsborough River (USNM 100693); Palm River (MCZ 201647); Mullet Key (A.M.); Shell Key (USNM 466206a, 466288); S of Pass-a-grille (MCZ 201685, 291285, 294241); Pass-a-grille

(ANSP 294321); Pinellas Point (MCZ 294190; USNM 194730); St. Petersburg (ANSP 132371, 132372, 132373, 132374; USNM 341721, 466194); Bird Key (ANSP 43568); Gulfport (MCZ 294242); Boca Ciega Bay (ANSP 189574; USNM 341722); Clearwater (ANSP 189569, 294319, 294322; MCZ 294247; USNM 611786a); Anclote River (A.M.); Hudson (A.M.); Aripeka (ANSP 73902, 151138, 151257); Little Blind Creek (ANSP 149525); Cedar Key (ANSP 56842, 194040, 194227, 362810; MCZ 199316, 201653, 201656, 291279; USNM 36012, 36013, 61700); Suwannee (ANSP 88138; MCZ 199315); Jena (USNM 484844); Adams Beach (MCZ 186701); St. Marks (ANSP 56814, 56816); Panacea (MCZ 91696; USNM 706611); St. Andrews Bay (ANSP 83641; USNM 667402, 667403, 667404); Anderson's Bayou, St. Andrews Bay (ANSP 83653); Ochlockonee (MCZ 199317); Port St. Joe Bay (MCZ 29130, 291297); Panama City (MCZ 235949). ALABAMA: Cedar Point (MCZ 186702); Heron Bay (ANSP 315710); Dauphin Island (USNM 701860); Coden Beach (USNM 422364); St. Anthony Bay (ANSP 365474). MISSISSIPPI: Boat Harbor at Ocean Springs (MCZ uncatalogued). LOUISIANA: Chandeleur Islands (USNM 189168); Grand Isle (MCZ 186700; USNM 603100); Cherniere-au-Tigre (ANSP 145106); Fort Pike, Orleans Parish (MCZ 251101); Houma (USNM 653314); Grand Lake, Calcasieu (USNM 160814, 467015); Myrtle Grove (USNM 628753); Cameron (USNM 177952). TEXAS: Galveston (ANSP 69414, 71522, 73692); East Lagoon, Galveston (MCZ 217872); Seabrook (ANSP 105895); Clearlake (MCZ 217874); Quitano Beach (MCZ 227841; USNM 600177); Freeport (ANSP 254824); Matagorda (USNM 125534); La Vaca, La Vaca Bay (MCZ 223041; USNM 126755); Sand Point, Keller Bay (USNM 464802, 465269, 465278); Indianola (USNM 26425, 26572, 39832); Rockport (MCZ 217875); Carancahua Bay (USNM 134435); Aransas Pass (ANSP 322151; USNM 603108); Ransom Island (MCZ 200470); Ransom Island, Redfish Bay (MCZ 198174); Port Aransas (ANSP 284785); Mustang Island (MCZ 217873); Corpus Christi (MCZ 294191; USNM 603107); Port Isabel (ANSP 80044; MCZ 193910; USNM 603109, 603110); Brownsville (ANSP 351204); Callo del Oro (USNM 473355). MEXICO: Tampico (USNM 219997a); N end of Ascension Bay, Quintana Roo (USNM 735992, 735993, 736143); near Allen Point, Ascension Bay, Quintana Roo (USNM 736693). BELIZE: Belize (ANSP 96583); Botanical Garden (USNM 426007a). BERMUDA (ANSP 56815, 56817, 56819, 56823, 77905; MCZ 3972, 9949, 201106, 201663, 201667, 201674, 201676, 291290, 291303, 291307, 291312; USNM 6540, 11420, 37605, 39805, 94432, 94433, 98152, 173643, 173644, 173645, 173646, 173647, 492582, 492584): Fairyland (ANSP 99053); Hamilton Island (MCZ 201105); Hungry Bay (ANSP 85712; MCZ 10381, 24248, 48123, 291306; USNM 492578, 492583; A.M.); South Shore (ANSP 86925, 86926, 86927; MCZ 53060, 53061, 53062; USNM 109557, 109558, 109559); Ely's Harbour (A.M.). BAHAMA ISLANDS (MCZ 54619): GRAND BAHAMA ISLAND: Bootle Bay (ANSP 371880); North Hawksbill Creek (ANSP 370567); GREAT ABACO ISLAND: Witch Point (ANSP 359151; USNM 492565, 492580b); Mastic Point Creek (USNM 618607); Angelfish Point (MCZ 116711); BIMINI: Mangrove Creek (ANSP 325614); Mosquito Point (ANSP 326148); BERRY ISLANDS (MCZ 294251); ANDROS ISLAND: Morgan's Bluff (A.M.); South Mastic Point (A.M.); Mangrove Cay (ANSP 189587; USNM 269477, 269855, 269968a, 270214d, 270216); Linder Key (USNM 269360, 270483); NEW PROVIDENCE ISLAND: Nassau (USNM 160766); Dick's Point (MCZ 291280); South Beach, Fox Hill (MCZ 294240); Bonefish Pond (USNM 618645; A.M.); Millars Sound (A.M.); Millars Road (A.M.); ROYAL ISLAND (USNM 468115); ELEUTHERA ISLAND: Rock Sound (MCZ 135932); CAT ISLAND: Russell Creek (ANSP 294330; MCZ 291278, 294229); Arthurstown (MCZ 291295); EXUMA CAYS: Hog Cay (ANSP 285755); LONG ISLAND: Brett's Hill (MCZ 113332, 291283, 291286); Clarencetown (ANSP 173261); Glenton's (ANSP 189573; MCZ 291291); Pinder's (MCZ 113330); Salt Pond, Clarencetown (USNM 595950); AKLINS ISLAND: Pinnacle Point (USNM 390856, 392237); Rooker Cay (USNM 390674); CAY SAL BANK: CAY SAL (MCZ 291331). TURK'S & CAICOS: TURK'S ISLAND: (USNM 492474a). CUBA (ANSP 56794, 56795, 56820, 189584): Bahia de Santa Rosa (USNM 492556a); Dimas (USNM 492559); Cayo de las Cinco Léguas (ANSP 294325); Cayo Perro, Cárdenas (ANSP 189589); Marianao (ANSP 294324); Cayo Maya, near Cayo Santa Maria (MCZ 294187); Cayo Juan Garcia (MCZ 291308); Isla de Cobos (MCZ 294186); Cayo Romano (MCZ 291309); Gibara (USNM 603097); Finca, Sabanalmar (MCZ 294189); Punta de los Colorados, Bahia de Cienfuegos (MCZ 291292); Alto del Caracol, Caracoles, S of Pinar del Rio (MCZ 201675); Isla de Pinos (MCZ 48079; USNM 130028). JAMAICA (ANSP 56793): Green Island Harbor (USNM 440805a); Palisadoes (USNM 713079). HAITI: Gonave Island (USNM 492531a). DOMINICAN REPUBLIC: Isla La Matica, Playa Boca Chica, E of Santo Domingo (R.B.). VIRGIN ISLANDS: ? TORTOLA (USNM 6485).

Subgenus *Detracia* Gray, 1840

Detracia Gray, 1840: 20. Type species by monotypy: *Detracia bullaeoides* (Montagu, 1808) [unjustified emendation of *bullaoides*].

Tifata H. & A. Adams, 1855b: 245. Type species herein designated: *Tralia (Tifata) globulus* (Orbigny, 1837).

Ensiphorus Conrad, 1862: 571. Type species by monotypy: *Melampus (Ensiphorus) longidens* Conrad, 1862 [Miocene].

Eusiphorus Conrad. Zilch, 1959: 65 [error for *Ensiphorus;* in synonymy].

Description: Shell globose to oval-oblong to fusiform; spire low to high, whorls ten to 13; aperture very narrow; columellar tooth oblique and stronger than parietal teeth; partition of inner whorls occupying almost all of body whorl, parietal teeth continuing on wall of inner whorl as conspicuous lamellae. Animal grayish blue to dirty white, sometimes mottled with dark brown spots. Conspicuous medial nodes on base of central radular tooth. Visceral mass separated from foot by a length equivalent to about one and one-half whorls; mantle organ forming conspicuous pouch; pallial gonoducts and cephalopedal reproductive organs elongate.

Remarks: Detracia was created by Gray (1840) for the West Indian species *Melampus bullaoides* (Montagu) because it was said to have only the columellar tooth on the inner lip. Careful inspection of *Melampus (D.) bullaoides* reveals a hidden parietal tooth midway on the inner lip and a long, vertical, callous anterior parietal tooth. The most obvious diagnostic feature is the very strong, oblique columellar tooth.

The genus *Tifata* was introduced by H. & A. Adams (1855b) as a subgenus of *Tralia* and was characterized by having two spiral, elevated, lamellar plates at the forepart of the inner lip. The genus *Tralia* had been introduced by Gray (1840) on account of the shape of the outer lip, but H. & A. Adams (1855b), followed by Binney (1865), used the incorrect anatomical feature, "foot posteriorly acute," to separate this taxon from *Melampus* (Fischer & Crosse, 1880; Dall, 1885). This led to the erroneous inclusion of *Tifata* within the genus *Tralia.* The pattern of dentition of the inner lip used by the Adams brothers to characterize *Tifata* is not conspicuous in the first two originally included species, *Tralia cingulata* (Pfeiffer, 1840) [= *Melampus (D.) bullaoides* (Montagu, 1808)] and *Tralia floridana* (Pfeiffer, 1856) [= *Melampus (D.) floridanus*]. In those species the first parietal tooth is usually a broad, longitudinal callosity, and the lamellar second parietal tooth is too far posterior in the aperture to be considered in the "forepart" of the inner lip. In the next species listed, *Tralia globulus* (Orbigny, 1837) [= *Melampus (D.) globulus*], the longitudinal callosity is less pronounced, resembling more an oblique lamella (Keen, 1971: fig. 2402). This agreement with the original description justifies my choice of *Tralia globulus* as type species of the subgenus *Tifata;* to clarify further the taxonomy, I hereby select a lectotype for this species (Fig. 320). Nevertheless, all species originally included in *Tifata* H. & A. Adams, including *Tralia pulchella* (Petit, 1843), should be placed in *Detracia* on the basis of the strong, oblique columellar fold.

Morrison (1951b, 1964) considered *Melampus (D.) monile* (Bruguière, 1789) to belong to *Pira* H. & A. Adams, 1855, which he elevated to generic rank. *Pira* was characterized as having three teeth on the inner lip. The type species, *Auricula kuesteri* (Krauss MS) Küster, 1844 [= *Melampus fasciatus* (Deshayes, 1830)], was illustrated by Küster (1844: 34–35, pl. 4, figs. 10–13), who noted the conspicuous twisted columellar tooth. Its relative prominence is evident in his figure 13, which represents Küster's variety A of that species. Although a decision on the systematic status of *Pira* is at present unwarranted owing to lack of anatomical data for comparisons, *Melampus monile* (Bruguière) should be included in *Detracia* on the basis of shell and anatomical characters.

Conrad (1862) introduced *Ensiphorus* for a Miocene species from Yorktown, Virginia, that was characterized by its elongate, slightly curved columellar tooth directed obliquely upwards, a characteristic of *Melampus (D.) morrisoni.* The type species, *Ensi-*

phorus longidens, illustrated by Conrad (1866, pl. 4, fig. 12), resembles in its size and shape a small *Melampus (D.) bullaoides* or a *Melampus (D.) floridanus,* hence justifying putting Conrad's name in synonymy with *Detracia.*

Anatomical comparison of *Detracia* with *Melampus* does not justify their generic separation. Thus *Detracia* is treated as a subgenus of *Melampus* [see the remarks under *Melampus s. l.*].

The subgenus *Detracia* is represented in the West Indian region by five species, which can be distinguished on the basis of shell morphology. The type species, *Melampus (D.) bullaoides,* is usually high spired, oval-elongate and without any indication of a carina on the shoulder of the body whorl. The spire has axial ribs and incised spiral grooves, and in juveniles it is hirsute. The spire of juvenile *Melampus (D.) monile* is also hirsute (Figs. 341, 345), but the shell is ovate-conic and the middle riblets of the outer lip are the strongest, whereas in *Melampus (D.) bullaoides* the anteriormost riblet of the outer lip is strongest. Some high-spired specimens of North American *Melampus (D.) floridanus* resemble *Melampus (D.) bullaoides,* but can be distinguished from them by the absence of axial ribs and hairs on the spire, as well as by the conspicuous parietal callus that occupies the site of the anterior parietal tooth. This latter character also distinguishes *Melampus (D.) floridanus* from its South American counterpart, *Melampus (D.) paranus,* which lacks the parietal callus. In addition, the South American species never has more than three riblets in the outer lip, whereas the North American species has four to eight riblets. Also included in this subgenus is *Melampus (D.) morrisoni,* a species that has certain characteristics of *Melampus s. s.,* such as the readily visible upper parietal tooth and a discrete anterior parietal tooth. Placement in *Detracia* is based upon the strong columellar tooth, narrow aperture, long pallial gonoducts and the pouch-like mantle organ.

Habitat: The West Indian species of *Detracia* characteristically live farther from the water than do the species of *Melampus s.s.* with which they can occur. *Melampus (D.) monile* is an exception in preferring the area of the high-tide mark, in which it is very common among piles of rocks frequently covered by waves at high tide. *Melampus (D.) morrisoni* prefers inland lagoons and, along with *Melampus (D.) bullaoides,* lives in areas reached only by spring tides. The North American *Melampus (D.) floridanus* and the South American *Melampus (D.) paranus* are very closely related. Morrison (1951a) interpreted this similarity as a case of parallel evolution. The North American species lives in inland salt marshes of low salinity and curiously it is absent from mangroves, whereas its South American counterpart is a supratidal estuarine species, living in mangroves (Marcus & Marcus, 1965a).

Range: The subgenus *Detracia* is mostly tropical and occurs in the Indo-Pacific and the West Indies. In the Western Atlantic it ranges from New Jersey to southern Brazil.

Melampus (Detracia) bullaoides
(Montagu, 1808)
Figs. 290–314

Voluta bullaoides Montagu, 1808: 102, pl. 30, fig. 4 [Lincoln, England (error), herein corrected to St. Vincent's, West Indies; location of type unknown].

Auricula multivolvis Jeffreys, 1833: 518 [Scarborough, England (error), herein corrected to St. Vincent's, West Indies; holotype USNM 55308 (Fig. 290)].

Tornatella bullaoides (Montagu). Férussac, 1821: 108.

Melampus bulla Lowe, 1832: 280 [unnecessary new name for *Voluta bullaoides* Montagu].

Melampus (Melampus) bulla Lowe. Beck, 1837: 108.

Detracia bullaeoides (Montagu). Gray, 1840: 20 [unjustified emendation for *bullaoides*].

Auricula cingulata Pfeiffer, 1840: 251 [Cuba; location of type unknown]; Küster, 1844: 40, pl. 6, figs. 4–6; Reeve, 1877, pl. 6, fig. 46.

Auricula oliva Orbigny, 1841: 189, pl. 12, figs. 8–10 [Outskirts of Havana, Cuba; lectotype herein selected BMNH 1854.10.4. 109 (Fig. 291)].

Melampus cingulatus (Pfeiffer). C. B. Adams, 1849: 42; C. B. Adams, 1851: 186; Shuttleworth, 1854b: 102; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 17; Binney, 1859: 161, pl. 75, figs. 12, 13; Binney, 1860: 4; Poey, 1866: 394; Pfeiffer, 1876: 301; Nevill, 1879: 219; Arango y Molina, 1880: 58; Crosse, 1890; 258.

Conovulus bullaoides (Montagu). Forbes & Hanley, 1852: 197.

Melampus poeyi Pfeiffer, 1853b: 126 [Cuba; location of type unknown]; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 17; Pfeiffer, 1876: 301.

Melampus (Tralia) cingulatus (Pfeiffer). H. & A. Adams, 1854: 11.

Melampus (Tifata) cingulata (Pfeiffer). H. & A. Adams, 1855b: 245.

Melampus bullaoides (Montagu). Pfeiffer, 1856a: 18; Kobelt, 1901: 277, pl. 33, figs. 6–8.

Melampus oblongus Pfeiffer, 1856b: 393 [Bermuda; lectotype herein selected BMNH 1968848 (Fig. 292)].

Tralia cingulata (Pfeiffer). Binney, 1865: 18, fig. 19; Tryon, 1866: 9, pl. 18, fig. 10; Fischer & Crosse, 1880: 22; Dall, 1883: 323.

Melampus ? bullaoides (Montagu). Pfeiffer, 1876: 301.

Melampus (Detracia) bulloides (Montagu). Dall, 1885: 285, pl. 18, fig. 7; Dall, 1889: 92, pl. 47, fig. 7; Simpson, 1889: 68; Maury, 1922: 56 [misspelling of *bullaoides*].

Melampus bulimoides (Montagu). Verrill, 1901: 35 [error for *bullaoides*].

Melampus bulloides (Montagu). Davis, 1904: 126, pl. 4, fig. 4 [error for *bullaoides*].

Melampus (Detracia) bullaoides (Montagu). Peile, 1926: 88.

Melampus (Detracia) bullaeoides (Montagu). Thiele, 1931: 467; Zilch, 1959: 65, fig. 207 [error for *bullaoides*].

Detracia bulloides (Montagu). M. Smith, 1937: 147, pl. 55, fig. 1; pl. 67, fig. 7 [pl. 67 copied from Dall (1885, pl. 18)]; Perry, 1940: 178: Coomans, 1958: 103; Porter, 1974: 300 [error for *bullaoides*].

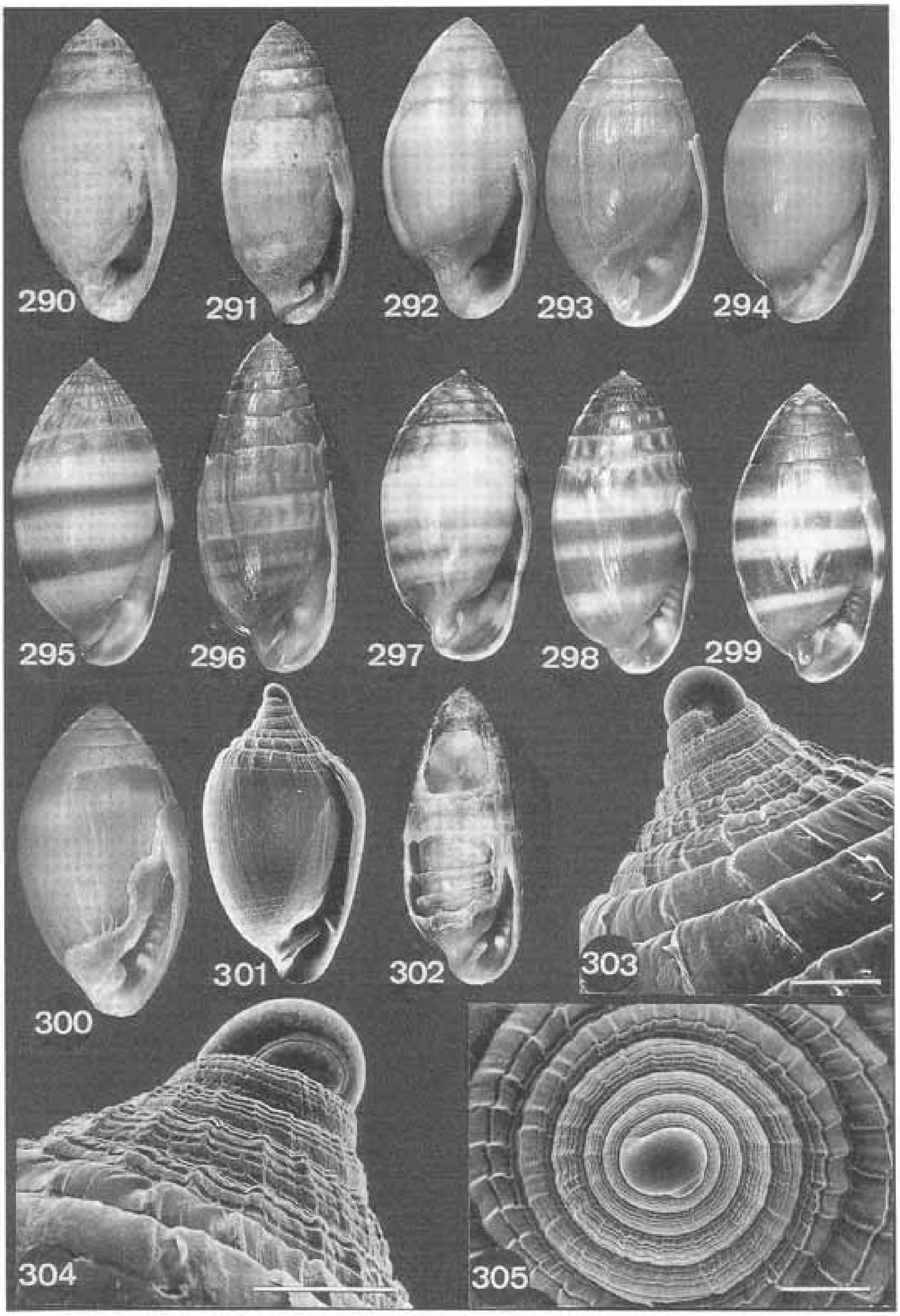
Detracia bullaoides (Montagu). Morrison, 1951a: 18, figs. 1, 5 [systematics]; Morrison, 1951b: 9; Perry & Schwengel, 1955: 198, pl. 53, fig. 359; Morrison, 1958: 118–124 [ecology]; Warmke & Abbott, 1961: 153, pl. 28, fig. o; Coomans, 1969: 82; Morris, 1973: 274, pl. 74, fig. 13; Abbott, 1974: 332, fig. 4092; Humphrey, 1975: 196, pl. 22, fig. 26; Emerson & Jacobson, 1976: 190, pl. 26, fig. 22; Rehder, 1981: 648, fig. 349; Gibson-Smith & Gibson-Smith, 1982: 117; Vokes & Vokes, 1983: 60, pl. 22, fig. 15; Jensen & Clark, 1986: 457, figured.

Detracia roquesana Gibson-Smith & Gibson-Smith, 1982: 117, fig. 6 [Isla de los Roques, Venezuela; holotype USNM 784718 (Fig. 300)].

Description: Shell (Figs. 290–305) to 15 mm long, globose to fusiform, solid, shiny, uniform whitish, yellow to brown or with as many as three, rarely more, white, unequally wide bands on body whorl; body whorl frequently with axial zigzag markings or with combination of bands and markings. Deep umbilical groove sometimes present in gerontic specimens. Spire high, mucronate, whorls as many as 13, flat and sculptured with well-marked spiral grooves, axial ribs and a spiral row of laterally compressed, short periostracal hairs. Body whorl 70% of total length, oval, smooth or with very faint spiral lines, without carina on shoulder. Aperture length about 80% of body whorl, very narrow, angulated anteriorly, with base sometimes broad and round in gerontic specimens; inner lip with a strong, oblique, twisted columellar tooth and a small, oblique, hidden parietal tooth just posterior to conspicuous longitudinal parietal callus; area posterior to parietal tooth excavated, with anterior border weakly raised to plait-shaped; in the latter case, corresponding riblet of outer lip becomes stronger, forming wall of narrow anal canal; outer lip sharp, rarely smooth within, with one strong riblet opposite columellar tooth, usually followed posteriorly by as many as eight riblets that do not reach the edge of the lip, gradually becoming smaller towards posterior end of aperture. Inner partition of whorls occupying entire body whorl; connection of posterior visceral mass space with aperture very narrow (Fig. 302). Protoconch translucent, whitish to slightly brown (Figs. 303–305).

Animal bluish gray; foot dirty white; top of neck dark brown to black; tentacles subcylindric, pointed, translucent in first quarter, abruptly changing to dark gray or black; mantle skirt light gray. Pallial cavity long; mantle organ dark brown, well developed, forming very conspicuous pouch; kidney long.

Radula (Figs. 306–310) having formula [24 + (1 + 14) + 1 + (14 + 1) + 24] × 100. Base of central tooth twice width of base of lateral teeth, triangular, with very conspicuous prominences on inner surface of arms; crown smaller than that of lateral teeth, with medial depression at posterior edge; mesocone small, sharp; ectocones not defined. Lateral teeth ten to 18; crown strong, broadly trian-



FIGS. 290–305.

gular, half total length of tooth; mesocone sharp, pointing laterally; no distinct endocone or ectocone. Transitional tooth with base partly reduced, crown weakly projecting posteriorly, with small ectocone or serrate edge on ectocone site. Marginal teeth 20 to 31 with reduced base and elongated crown; mesocone strong and sharp, gradually becoming rounded toward the edge of the radular ribbon; appearance of ectocones inconsistent from row to row.

Stomach (Fig. 311) as in subfamily.

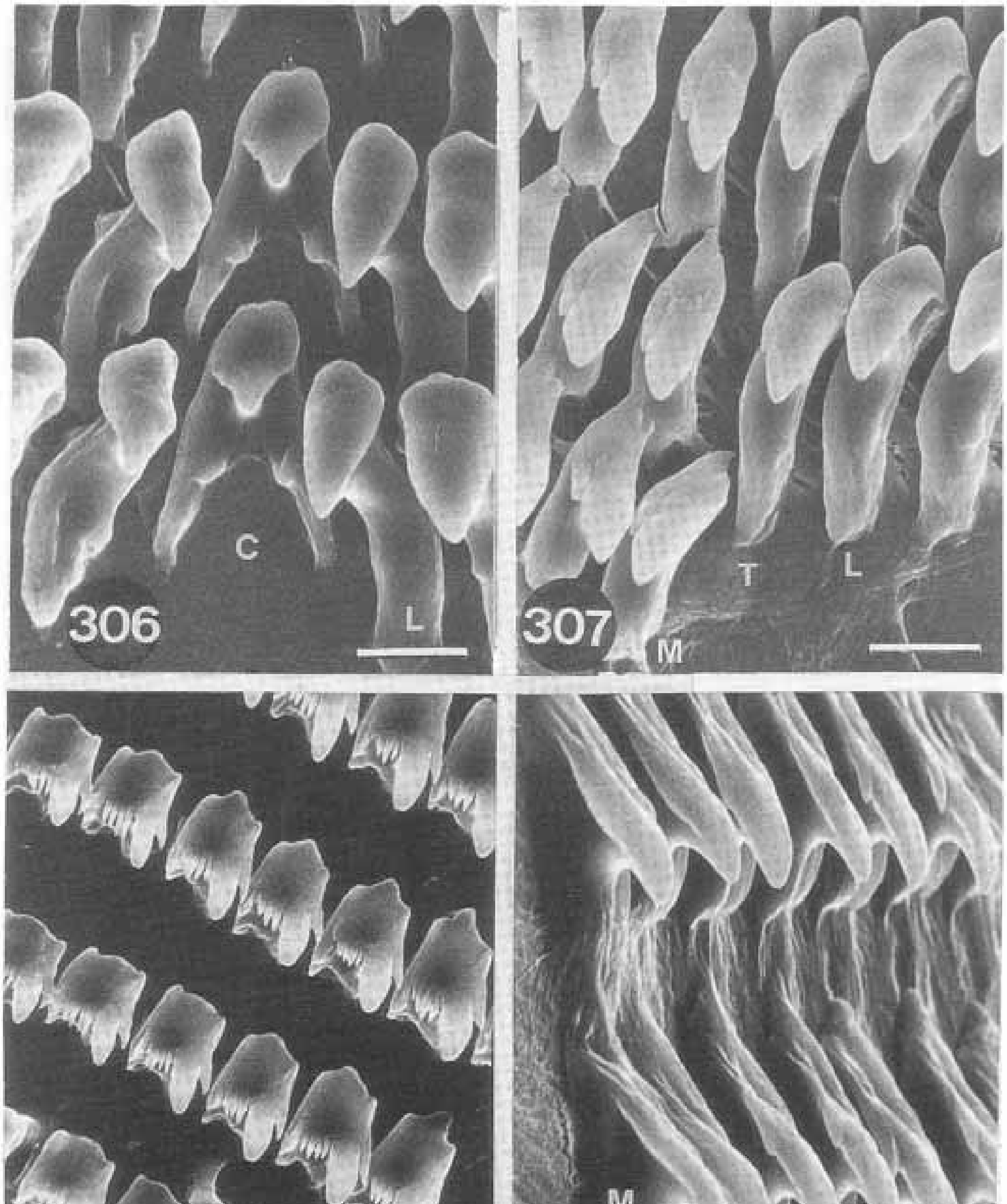
Reproductive system (Fig. 312) with ovotestis conical, dark brown; mucous gland spiral, conical; prevaginal caecum very conspicuous; bursa duct thick, enters vagina opposite to exit of posterior vas deferens; bursa large, approximately oval; vagina thin, about one and four-fifths times length of body whorl; penis thin, long; penial retractor inserting with columellar muscle.

Nervous system (Fig. 313) having cerebral commissure about as long as width of cerebral ganglion; left parietovisceral connective twice the length of right one.

Remarks: Melampus (D.) bullaoides originally was stated to belong to the British fauna although Montagu (1808) doubted its origin. He reported it as from Lincoln, because this was the locality given on the lot label in the Portland collection, from which the shell had been purchased. Lowe (1832) repeated the original information when, for no apparent reason, he renamed Montagu's species *Melampus bulla*. Beck (1837) erroneously reported Lowe's species from "Atlantic Ocean, Boreal Africa." The shell, however, became well known in European collections, allowing Gray (1840: 21) to remark, "it is one of the most common shells in the small boxes from the West Indies." Jeffreys (1869: 109) also noted that "*Voluta bullaoides* of Montagu (my *Auricula multivolvis*) [Fig. 290] is a rather common West Indian species." He also stated that a specimen had been found at Scarborough and that the species had been reported from Croisic in the Loire-Inferieure. Morrison (1951a) explained those odd occurrences as inclusions in ballast picked up by ships in the West Indies and dumped along the coast of England.

The high degree of variability that characterizes the genus *Melampus* is also noticeable in *Melampus (D.) bullaoides* and caused the introduction of most of the names here considered synonyms. In Pfeiffer's three major revisions of the family (1854b, 1856a, 1876), the name *Melampus bullaoides* appears only in the last two, indeed with a query in the last one. Pfeiffer (1856a) noted that Forbes & Hanley (1852) had treated his *Melampus cingulatus* from Cuba as a junior synonym of Montagu's species. Although he admitted that they were very closely related, Pfeiffer was reluctant to synonymize them solely on the basis of Montagu's figure, leaving the problem, in his words, to the consideration of the experts. Almost at the same time Pfeiffer described *Melampus cingulatus*, Orbigny (1841) described and nicely illustrated *Auricula oliva* from Cuba (Fig. 291). Presumably Orbigny was not aware of Pfeiffer's publication, because the two descriptions are very similar. The second of Pfeiffer's supposed species, *Melampus poeyi*, also from Cuba, is intermediate between *Melampus bullaoides* and Pfeiffer's *Auricula cingulata*, according to Pfeiffer's observation (1856a). The last of Pfeiffer's names, *Melampus oblongus*, was applied to a Bermudian specimen (Fig. 292) that Pfeiffer (1856b) thought was more closely allied to *Melampus angiostomus* (Deshayes, 1831) than to his *Auricula cingulata*. The Bermudian specimens have a quasi-smooth outer lip, and some populations have only the characteristic strong riblet opposite the columellar tooth (Figs. 293–296). Comparison of individuals from Bermuda with specimens from Florida

FIGS. 290–305. *Melampus (D.) bullaoides* (Montagu). (290) *Auricula multivolvis* Jeffreys, holotype (USNM 55308), Scarborough, England, sl 7.5 mm. (291) *Auricula oliva* Orbigny, lectotype (BMNH 1854.10.4.109), Cuba, sl 11.0 mm. (292) *M. oblongus* Pfeiffer, lectotype (BMNH 1968848), Bermuda, sl 11.1 mm. (293) Somerset Bridge, Bermuda, sl 8.1 mm. (294) Hungry Bay, Bermuda, sl 10.6 mm. (295) Hungry Bay, Bermuda, sl 10.3 mm. (296) Hungry Bay, Bermuda, sl 11.2 mm. (297) Crawl Key, Florida (R.B.), sl 9.0 mm. (298) Big Pine Key, Florida, sl 9.4 mm. (299) South Mastic Pt., Andros Island, Bahamas, sl 9.1 mm. (300) *Detracia roquesana* Gibson-Smith & Gibson-Smith, holotype (USNM 784718), Isla de los Roques, Venezuela, sl 10.6 mm. (301) Long Key, Florida, sl 2.4 mm. (302) Grassy Key, Florida, sl 13.7 mm. (303) Lateral view of spire and protoconch, Somerset Bridge, Bermuda. (304) Lateral view of spire and protoconch, Long Key, Florida. (305) Top view of spire and protoconch, Somerset Bridge, Bermuda. Scale 1 mm.



FIGS. 306–309. *Melampus (D.) bullaoides*, radular teeth, Somerset Bridge, Bermuda, sl 9.0 mm. (306) Central and lateral teeth. (307) Transitional and lateral teeth. (308) Marginal teeth. (309) Lateral view of marginal teeth in preceding figure. Scale 50 μm.

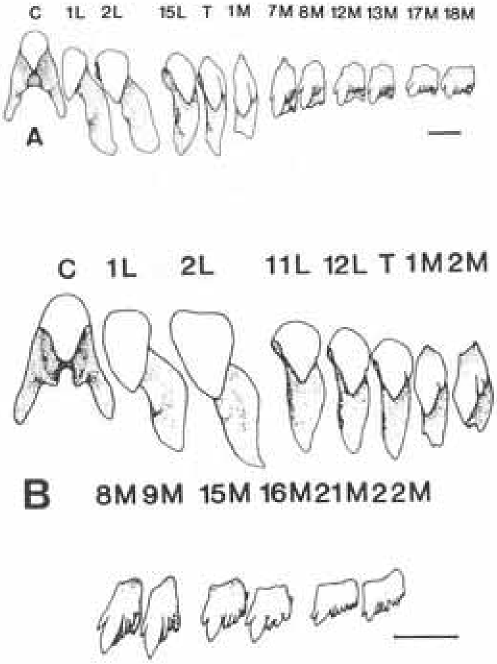


FIG. 310. *Melampus (D.) bullaoides,* radula. A, Somerset Bridge, Bermuda; B, Big Pine Key, Florida. Scale 10 µm.

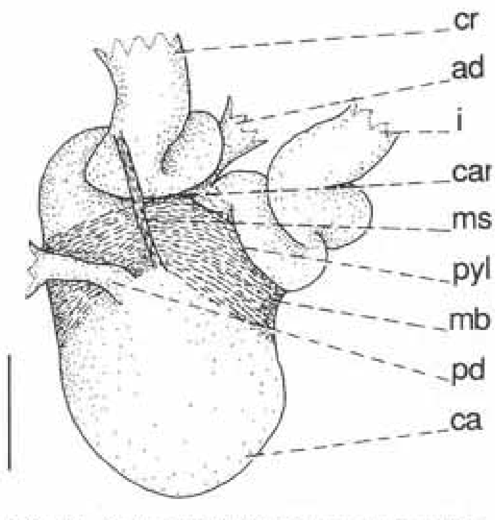


FIG. 311. *Melampus (D.) bullaoides,* stomach, Florida. Scale 1 mm.

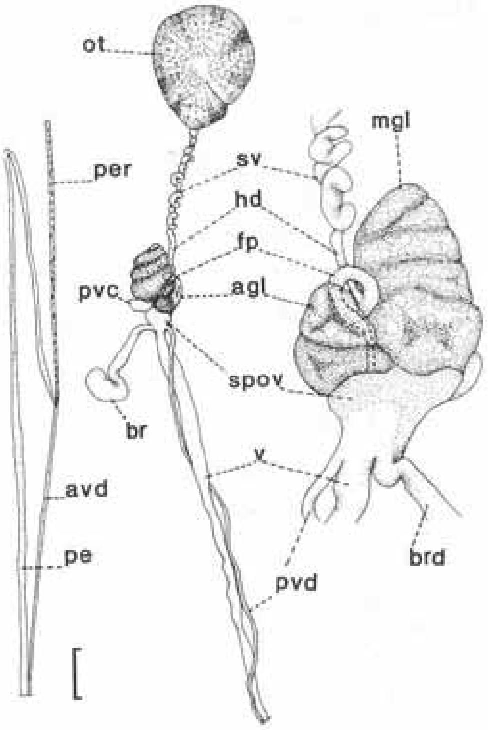


FIG. 312. *Melampus (D.) bullaoides,* reproductive system, Grassy Key, Florida. Scale 1 mm.

and Bahamas, however, revealed overlap in characters of the apertural dentition (Figs. 297–299, 301, 302). One must conclude that, owing to its variable expression, the apertural dentition in this species is not a reliable taxonomic character and that *Melampus oblongus* Pfeiffer from Bermuda is conspecific with *Melampus (D.) bullaoides.*

Very recently Gibson-Smith & Gibson-Smith (1982), on the basis of six beach specimens, described *Detracia roquesana* from Islas de los Roques, off Venezuela (Fig. 300). The Bermudian specimens in my collection, which I refer to Pfeiffer's *Melampus oblongus,* as well as those from the Bahamas, fit the description of Gibson-Smith & Gibson-Smith. The brown protoconch, so common in Bermudian shells, also occurs in certain specimens from Florida, although in the latter specimens the aperture is narrower and more dentate. Analysis of protoconch, radula and anatomy of the Bermudian forms did not yield any differences between specimens from Florida and those from the Bahamas. These facts led me to consider *Detracia roquesana* Gibson-Smith & Gibson-Smith a junior synonym of *Melampus (D.) bullaoides* (Montagu).

Melampus (D.) bullaoides is very easily distinguished from *Melampus (D.) floridanus* by

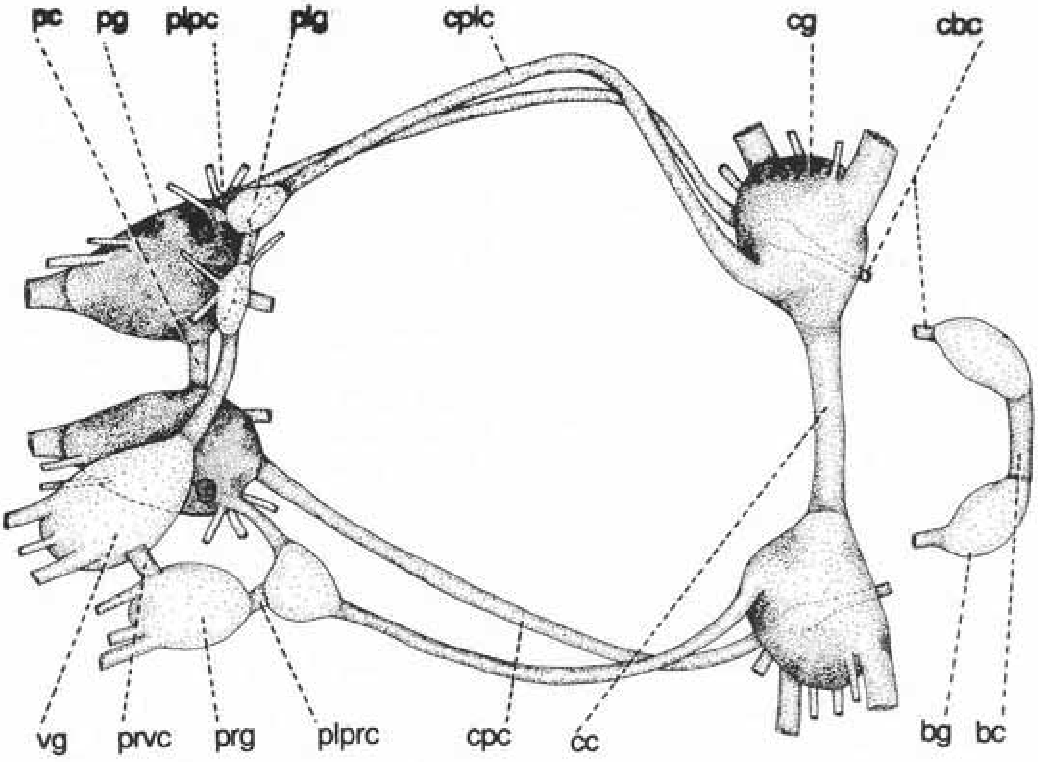


FIG. 313. *Melampus (D.) bullaoides*, central nervous system, Grassy Key, Florida. Scale 1 mm.

the presence of ribs on its spire and by its protruding, mucronate apex. The spire is constricted toward the apex and broadens suddenly toward the base. The juveniles have a crown of periostracal hairs. The last whorl shows a wide range of color patterns, and frequently young specimens are brightly colored. In *Melampus (D.) floridanus* the spire is regularly conical, glabrous, and the body whorl has as many as three chestnut-brown bands.

Habitat: Melampus (D.) bullaoides is a common inhabitant of the mangroves and can be very abundant in some localities. The species prefers the supralittoral zone and it frequently lives on the edges of inland tidal lagoons, sometimes in relatively dry places, in which they aggregate under rocks, pieces of wood, cardboard and other decaying trash.

Range: Bermuda; Florida, West Indies to Suriname (Fig. 314).

Specimens Examined: FLORIDA (USNM 27914, 39833, 39838, 39839, 1524268, 492459): Fernandina (USNM 492544); Lake Worth at Boynton (ANSP 194770); Miami (ANSP 91284; USNM 153399, 492460); Coconut Grove (MCZ 82497, 291238, 291258); Virginia Key (MCZ 46880); Bear's Cut, Key Biscayne (MCZ 153116); Soldier Key (MCZ 174459); Third Ragged Key, above Sands Key (USNM 462736); Sands Key, Biscayne Bay (MCZ 291269); Elliot Key (ANSP 160894); Key Largo (ANSP 56813; MCZ 56473, 291255, 291264; USNM 68130, 492546, 597456); Tavernier (MCZ 153121); N of Tavernier Key (A.M.); Tavernier Key (USNM 492550); Snake Creek (MCZ 291058); Plantation Key (MCZ 199343, 291057); S of

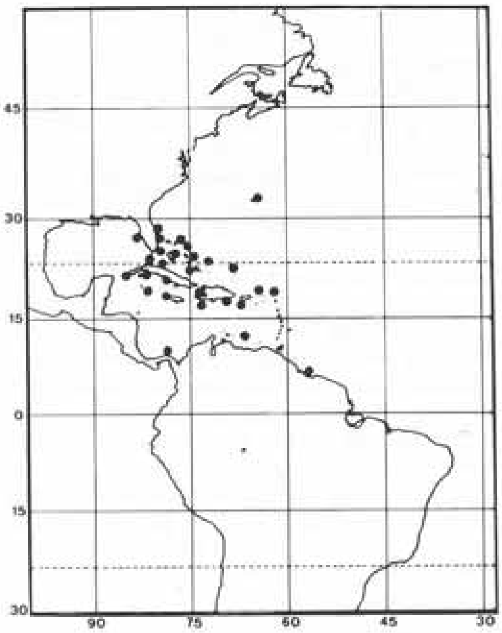


FIG. 314. *Melampus (D.) bullaoides*, geographic distribution.

Ocean Drive, Plantation Key (A.M.); Indian Key (USNM 462895, 492547); Indian Key Fill, N of Indian Key Channel (A.M.); Little Duck Key (MCZ 291061); Lower Matecumbe Key (USNM 700771); N end of Long Key (A.M.); Bonefish Key (MCZ 291059); Upper Grassy Key (MCZ 291051); Grassy Key (MCZ 291064; A.M.); Crawl Key (MCZ 174470, 199342, 291046, 291047; A.M.); Key Vaca (ANSP 181137); Marathon (MCZ 153258); Knight Key (A.M.); Bahia Honda Key (ANSP 88030, 88132, 104098, 189562; USNM 269780); Howe Key (USNM 681640, 706766); Big Pine Key (ANSP 89549, 104099, 189559; MCZ 250733, 291048, 291049, 291517; USNM 597454); Long Beach Drive, Big Pine Key (A.M.); W end of Kohen Avenue, Big Pine Key (A.M.); Big Torch Key (ANSP 104100; A.M.); Little Torch Key (MCZ 291053); Ramrod Key (MCZ 291050, 291247); Sugarloaf Key (ANSP 9635, 22475, 89550, 189560); Lower Sugarloaf Key (USNM 672440); Summerland Key (USNM 270318); West Summerland Key (MCZ 291084; A.M.); Military Key (MCZ 291055); Pavilion Key (ANSP 93434); Boca Chica Key (ANSP 104097, 152502, 189561; MCZ 162638; USNM 270327); Cow Key (USNM 596786); Stock Island (ANSP 149994; USNM 270280); Key West (ANSP 56812, 100848, 174635, 264540, 294310; USNM 36015, 36965, 61101, 153076, 270363, 338357); Snake Key (ANSP 105461); Seminole Point (ANSP 105437); Boca Grande Key (USNM 272834); Flamingo Key (MCZ 291060); Cape Sable (MCZ 291062); Marco Key (USNM 381333); mouth of Henderson Creek, 5 km N of Marco (MCZ 294215); Little Marco (ANSP 93435); Bonita Springs (MCZ 291063); Carl E. Johnson Park, Little Carlos Pass (A.M.); Mound Key (MCZ 291270); Punta Rassa (MCZ 13705, 291056); Sanibel Island (ANSP 179352; MCZ 291052); Tarpon Bay, Sanibel Island (MCZ 13704, 55961); Turner's Pond, Sanibel Island (MCZ 232526); E of St. James, Pine Island (ANSP 93433); Captiva Island (ANSP 149406; MCZ 60186, 236852, 291054); Osprey (ANSP 88078); Mullet Key (USNM 652407; A.M.); Pinellas Point (MCZ 294209); Bayou off Gulfport (MCZ 138942); St. Petersburg (MCZ 291242; USNM 343843, 366191, 466193); Maximo Point, St. Petersburg (ANSP 167540); Shell Bay, off St. Petersburg (USNM 466207, 466289); Sand Key (ANSP 129249; USNM 338365); Harts Bayou, Boca Ciega Bay (MCZ 291266); Indian Rocks (ANSP 167541); Clearwater Island (ANSP 189558); Clearwater (USNM 611785); Cedar Key (MCZ 291246; USNM 36895, 37611, 37612). BERMUDA: (ANSP 85590; MCZ 24246, 291240, 291253, 291260, 291262, 292267; USNM 6529, 94435, 98153, 173651, 492543); Hamilton (ANSP 182551; USNM 152145, 171960); Fairyland (ANSP 99058, 111095); N end of Long Bird Bridge (A.M.); Hungry Bay (ANSP 88581; A.M.); S end of Ely's Harbour (A.M.); W side of Somerset Bridge (A.M.); Mangrove Bay (A.M.); Ireland Island (USNM 712379); Pond W of Evans Bay (A.M.); Riddell's Bay (USNM 621666). BAHAMA ISLANDS (MCZ 24141): GRAND BAHAMA ISLAND: Dead Mans Reef [Sandy Bevan's Cay] (ANSP 371222); Riding Point (ANSP 371520, 375562); 4 km NW of Sweetings Cay Light (ANSP 307628); GREAT ABACO ISLAND: Witch Point (ANSP 299481, 359153; USNM 492580c); Crossing Bay (ANSP 173189); McLeans Town (ANSP 369066); Running Mon Canal (ANSP 369777); North Hawksbill Creek (ANSP 370565); BIMINI ISLANDS: Alicetown, North Bimini (USNM 598841); opposite Cat Tail Pond, South Bimini (ANSP 325782); BERRY ISLANDS: Chub Cay (ANSP 359148); Frazier, Hog Cay (ANSP 194182, 195213); ANDROS ISLAND (ANSP 226713; USNM 269844); Stafford Creek (ANSP

151848, 151930); Mangrove Cay (MCZ 24102; USNM 180518); Bastion Point, Mangrove Cay (USNM 269226, 269252); Rocky Point, Mangrove Cay (USNM 270214, 270215); Solomon Pond, Mangrove Cay (USNM 269968); 5 km from mouth of Lisbon Creek, Lindsey Creek (USNM 270234); First island off Mintie Bar, SE of South Bight (USNM 271785); Long Bay Key (USNM 269323); PARADISE ISLAND (A.M.); NEW PROVIDENCE ISLAND (ANSP 18485, 299646; USNM 124376): Nassau (MCZ 107498; USNM 160767, 467111); Bar Point (A.M.); Delaporte Point (A.M.); W of Rock Point (A.M.); Clifton Point (A.M.); Clifton Pier (A.M.); shore off Millars Road (A.M.); Millars Sound by Bacardi Road (A.M.); Bonefish Pond (A.M.); South Beach (MCZ 291268); Malcolm Creek (A.M.); Dick's Point (MCZ 291518); ROYAL ISLAND (MCZ 184098, 280395; USNM 343844, 366190, 468116); ELEUTHERA ISLAND (USNM 465988): Tarpon Bay (MCZ 135934, 175921); Great Oyster Pond (MCZ 291265); BRIGADINE KEY (USNM 270034); CAT ISLAND: Arthurstown (MCZ 291237); LONG ISLAND: Simms (MCZ 291251); Galloway's Landing (MCZ 291241); Pinders (MCZ 113328); AKLINS ISLAND: Pinnacle Point (USNM 390857); ROOKER KEY (USNM 390663, 390674a); GREAT INAGUA: Matthewstown (MCZ 291263); 5 km SE of Matthewstown (MCZ 190050); CAY SAL BANK: Cay Sal, (MCZ 291256); Salt Lagoon, Cay Sal (USNM 513426). TURK'S & CAICOS: CAICOS ISLAND: Bell Cay (USNM 391323). CUBA (ANSP 56810, 567800; MCZ 31418, 291257, 294214; USNM 10966, 39840, 55727, 336072, 492461): Cayo Juan Garcia (MCZ 291271); La Habana (MCZ 291259); Cayo Birricu, N. of Habana (ANSP 362823); Cayo Blanco, Cárdenas Bay (ANSP 157955); Playa del Bellamar (MCZ 291239, 291243); Cayo Cristo (MCZ 292559); Caibarién (MCZ 291248, 294213); Dimas (USNM 492559b); Cayo Romano (MCZ 291272); Punta de Piedra (MCZ 291252); Santa Cruz del Sur (MCZ 131939, 291254); Santa Maria Key (MCZ 291261); Cochinos Bay (USNM 492548); Cayo de las Cinco Léguas (ANSP 158053); Finca, Sabanalmar (MCZ 294210); Isla de Pinos (MCZ 48081). JAMAICA (ANSP 56811; MCZ 291245; USNM 94746, 374270a, 492462, 492551): Montego Bay (ANSP 359146); Kingston (USNM 442736); Harbor Head, Kingston (USNM 617127); Hunt's Bay (USNM 441719); Cow Bay (USNM 440985); Palisadoes (USNM 442465); Port Royal (USNM 442419); Rock Fort (USNM 374243); Great Goat Island (ANSP 359156). HAITI (ANSP 146738): St. Louis (USNM 439392); Gonave Island (MCZ 82118; USNM 380256); near Port-au-Prince (USNM 403034, 403035, 440610a); Île-à-Vache, Soulette Bay (USNM 439169a, 439169b, 442850a); Port Salut (USNM 403760); Aquin (USNM 403256, 403573, 440170); Bizoton (USNM 439828). DOMINICAN REPUBLIC: Monte Cristi (MCZ 291249). PUERTO RICO: Punta Arenas, N of Joyuda (A.M.). VIRGIN ISLANDS: ST. CROIX (ANSP 56809). LESSER ANTILLES: ANGUILLA BANKS (MCZ 294216); ANTIGUA: Fitches Creek (USNM 809737); BARBUDA (USNM 735816). CARIBBEAN ISLANDS: CAYMAN ISLANDS: Cayman Brac (MCZ 294212); Georgetown Barcadero, Grand Cayman (ANSP 209770). COLOMBIA (MCZ 291273). VENEZUELA: Islas de los Roques (USNM 784718). SURINAME: Paramaribo (MCZ 274063).

Melampus (Detracia) floridanus
Pfeiffer, 1856
Figs. 315–318, 321–332

Melampus (Tralia) floridianus Shuttleworth. H. & A. Adams, 1854: 11 [*nomen nudum*].

Melampus floridanus Shuttleworth. Pfeiffer, 1854b: 147 [*nomen nudum*].

Tralia (Tifata) floridana Shuttleworth. H. & A. Adams, 1855b: 245 [*nomen nudum*].

Melampus floridanus "Shuttleworth" Pfeiffer, 1856a: 35 [Florida, herein restricted to Myakka River; location of type unknown]; Binney, 1860: 4; Nevill, 1879: 219; Dall, 1885: 281, pl. 18, fig. 2; Dall, 1889: 92, pl. 47, fig. 2; Simpson, 1889: 68; Kobelt, 1898: 213, pl. 24, fig. 14; Hinkley, 1907: 71; Maury, 1922: 55; C. W. Johnson, 1934: 159; M. Smith, 1937: 146, pl. 55, fig. 5, pl. 67, fig. 2 [pl. 67 from Dall (1885)].

Melampus floridianus Shuttleworth. Binney, 1859: 165 [error for *floridanus;* pl. 75, fig. 30 is of *Melampus (M.) bidentatus* Say (Fig. 265)].

Tralia floridana (Shuttleworth) (Pfeiffer). Binney, 1865: 16 [fig. 17 is of *Melampus (M.) bidentatus*]; Tryon, 1866: 9 [pl. 18, fig. 11 copied from Binney (1859) shows *Melampus (M.) bidentatus*].

Detracia floridana (Pfeiffer). Morrison, 1951a: 17, figs. 4, 7 [description, habitat]; Morrison, 1954: 15–16 [egg masses]; Morrison, 1959: 25 [early life history]; Burch, 1960a: 182, pl. 1, figs. 2, 91 [chromosomes]; Abbott, 1974: 332 [Fig. 4093 copied from Binney (1859) is of *Melampus (M.) bidentatus*]; Emerson & Jacobson, 1976: 191, pl. 26, fig. 23; Heard, 1982: 20, fig. 16.

Detracia floridana (Shuttleworth). Morrison, 1951b: 8.

Melampus floridanus Pfeiffer. Holle & Dineen, 1959: 50 [systematics].

Description: Shell (Figs. 315–318, 321–323) to 7 mm long, globose to fusiform, thin, smooth to corrugated, dark brown with grayish tones, with as many as three chestnut-brown bands on upper half of body whorl. Spire moderately high, mucronate, with as many as 10.25 flat, compressed whorls, with fine, spirally arranged pits. Body whorl 70% of total length, oval to subcylindric, lacking carina on shoulder, smooth or with very faint spiral lines. Aperture narrow, about 90% of length of body whorl, weakly canaliculate at base; inner lip with oblique columellar tooth, conspicuous parietal callus and, above it and hidden inside, small horizontal parietal tooth; outer lip sharp, with as many as ten subequal riblets, not reaching edge. Inner partition of whorls occupying entire body whorl (Fig. 316). Protoconch raised, smooth, translucent, dark brown (Figs. 321–323).

Animal bluish gray; foot paler; tentacles subcylindric, pointed, darker toward tip; mantle skirt grayish. Mantle organ dark brown, well developed, forming conspicuous pouch.

Radula (Figs. 324–328) having formula $[14 + (1 + 12) + 1 + (12 + 1) + 14] \times 100$. Central tooth with base wider than that of lateral teeth, with conspicuous medial prominences; crown half length and width of that of lateral teeth, rounded posteriorly; mesocone sharp; ectocones well marked, small. Lateral teeth 11 to 16; crown strong, half total length of tooth; mesocone sharp, pointing laterally; ectocone well developed in all lateral teeth. Transitional tooth with very weak endocone. Marginal teeth 13 to 17, with reduced base and elongate crown; mesocone becoming shorter and thinner; endocone and second cusp of ectocone in first marginal tooth; outer edge of base assuming configuration of denticle around third marginal tooth, first cusp of ectocone becoming smaller and third cusp of ectocone appearing; second cusp of endocone appearing on fifth to sixth marginal tooth; eighth to tenth marginal teeth without additional cusps; last two marginal teeth rudimentary.

Digestive system as in *Melampus s. s.;* stomach elongate, muscular band thick (Fig. 329).

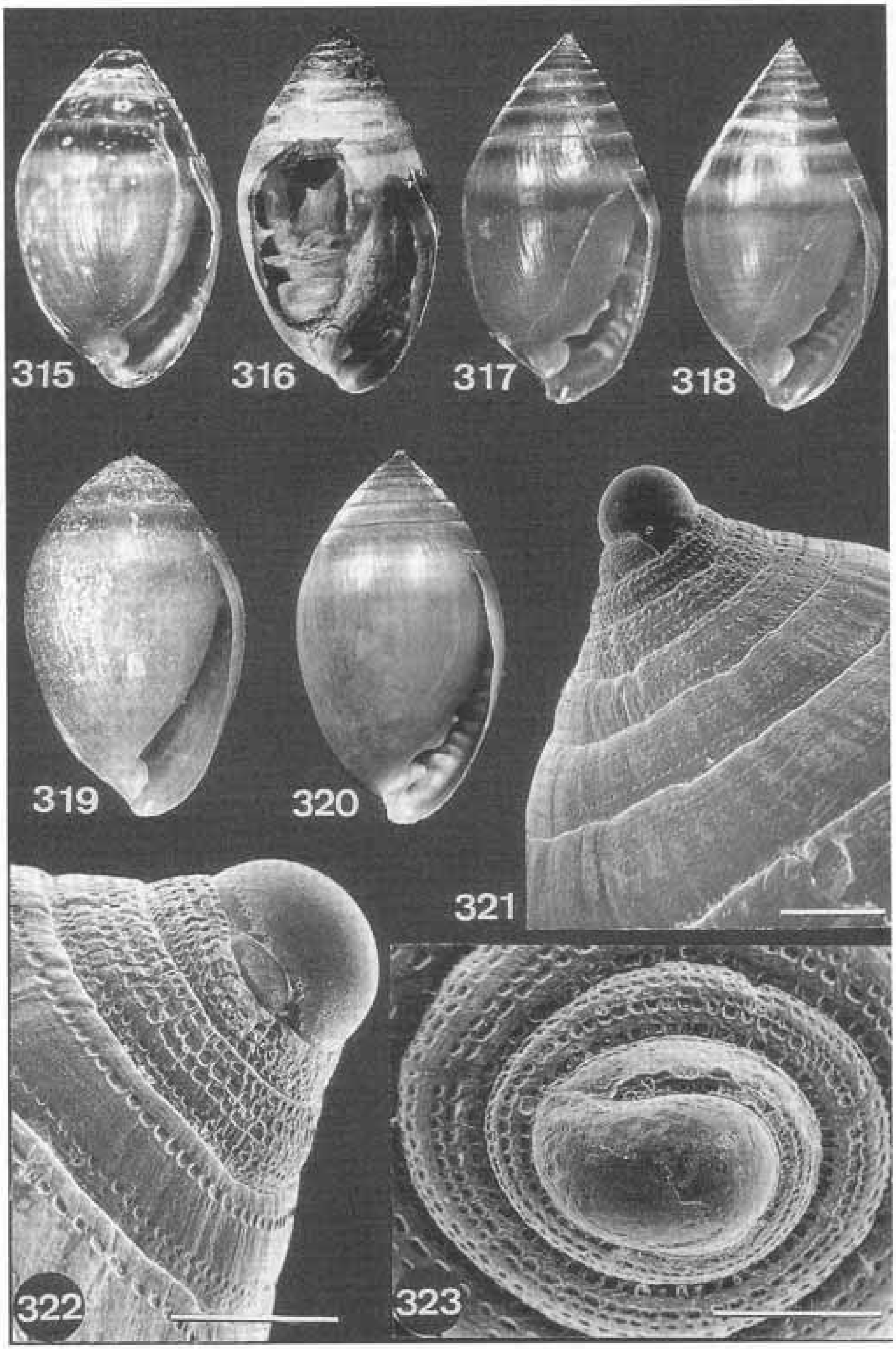
Reproductive system (Fig. 330) with ovotestis shallow-conical, dark brown; albumen gland spiral, conical; fertilization chamber forming double pouch; vagina and associated vas deferens muscular, long; bursa duct entering vagina opposite exit of posterior vas deferens; penis muscular, long; length of anterior vas deferens 75% that of penis.

Nervous system (Fig. 331) having cerebral commissure about as long as width of cerebral ganglion; left pleuropedal connective very short; left parietovisceral connective longer than right one.

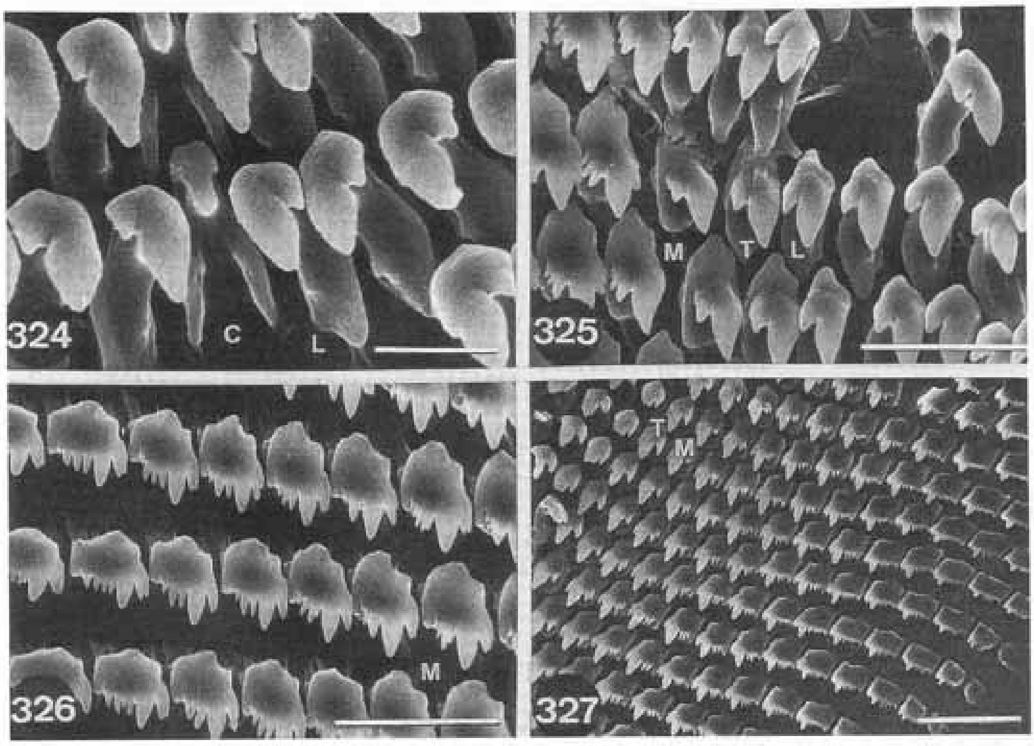
Remarks: The name *Melampus floridanus* appeared in published lists for several years before Pfeiffer (1856a) validated it with a description in his *Monographia.* Holle & Dineen (1959) stated that the original specimens had been collected in Florida by a Mr. Rugel for Shuttleworth, who deposited them in the Cuming collection under his manuscript name. Pfeiffer (1856a) probably had seen these specimens marked as *Auricula floridana* by Shuttleworth, and also the specimens in the Albers collection marked as *Auricula rugeli* by Charpentier. Both names are referred to as manuscript names in Pfeiffer's description. He gave the measurements of the specimen he used for the description, however, mentioning that it was Nr. 15 of his collection. The type material therefore should include only the specimen in Pfeiffer's collection, because there is no assurance that Pfeiffer used other collections in writing the description. Most authors have given credit erroneously to Shuttleworth for introduction of *Melampus (D.) floridanus* but in accord with the ICZN Pfeiffer must be credited with this name, for it is he who validly introduced it.

According to Morrison (1951a), Binney (1859), using shells collected by Bartlett from the Florida Keys, wrongly illustrated this species by using an example of a dwarf *Melampus (M.) bidentatus* (Fig. 265). Several subsequent authors, including Abbott (1974), perpetuated Binney's mistake by copying that figure. Morrison (1951a), Emerson & Jacobson (1976) and Heard (1982) correctly illustrated *Melampus (D.) floridanus,* however.

Melampus (D.) floridanus can be distin-



FIGS. 315–323.



FIGS. 324–327. *Melampus (D.) floridanus*, radular teeth. (324–326) Myakka River, Florida, sl 6.7 mm. (327) Woodville, North River, North Carolina, sl 5.3 mm. Scale, Fig. 324, 50 µm; all others, 100 µm.

guished from *Melampus (M.) bidentatus*, with which it commonly associates, by its smaller size, stronger columellar tooth, the callus on the site of the first parietal tooth, its narrower aperture and more numerous whorls. The specimens of *Melampus (D.) floridanus* from southern and western Florida are smooth and sometimes brightly colored, and usually retain all the whorls of the spire, whereas northern specimens are thinner and corrugated, with the apex greatly eroded.

Habitat: Melampus (D.) floridanus lives in salt marshes and freshwater riverbanks on which it often occurs with *Melampus (M.) bidentatus*. The Floridian salt-marsh snail prefers that zone of the marsh rarely flooded by spring tides. The animals frequently live half-buried in the sediment, against the base of the stems of *Spartina, Juncus* and other marsh plants. Very common in some places, they were estimated by Morrison (1951a) to attain a density of about four billion individuals in a square mile.

Range: New Jersey to Florida, and along the Gulf Coast to Vera Cruz, Mexico (Fig. 332). I have not observed specimens from the Florida Keys.

Specimens Examined: NEW JERSEY: Dividing Creek (A.M.); Newport (ANSP 294331). DELAWARE: Woodland Beach (USNM 522268); Bombay Creek (USNM 473356,

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FIGS. 315–323. *Melampus (Detracia)*. (315) *M. (D.) floridanus* Pfeiffer, Woodville, North River, North Carolina, sl 5.2 mm. (316) *M. (D.) floridanus*, Woodville, North River, North Carolina, sl 5.5 mm. (317) *M. (D.) floridanus*, Myakka River, Florida, sl 6.7 mm. (318) *M. (D.) floridanus*, Myakka River, Florida, sl 5.7 mm. (319) *Detracia parana* Morrison, holotype (USNM 594591), Pará, [Belém], Brazil, sl 6.5 mm. (320) *Auricula globulus* Orbigny, lectotype (BMNH 1854.12.4.243), Guayaquil, Ecuador, sl 8.1 mm. (321–323) *M. (D.) floridanus*, lateral and top views of spire and protoconch, Myakka River, Florida. Scale 1 mm.

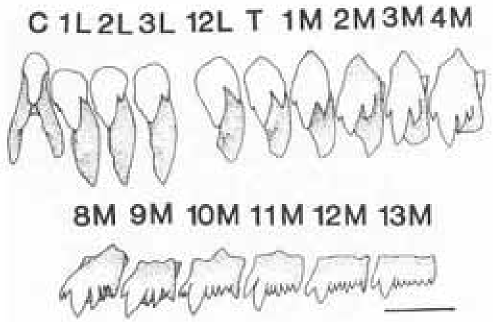


FIG. 328. *Melampus (D.) floridanus*, radula, Crescent, Georgia. Scale 10 µm.

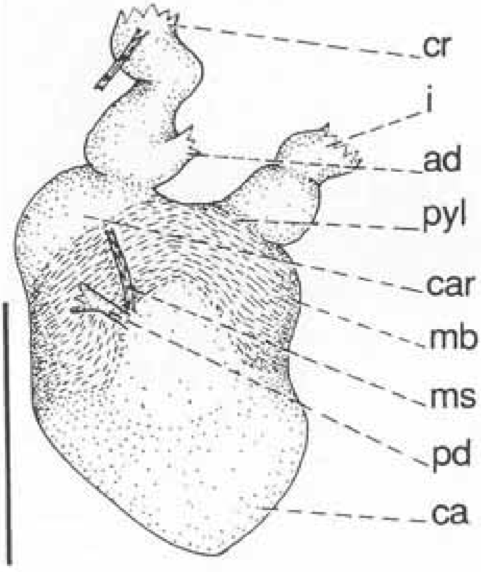


FIG. 329. *Melampus (D.) floridanus*, stomach, Georgia. Scale 1 mm.

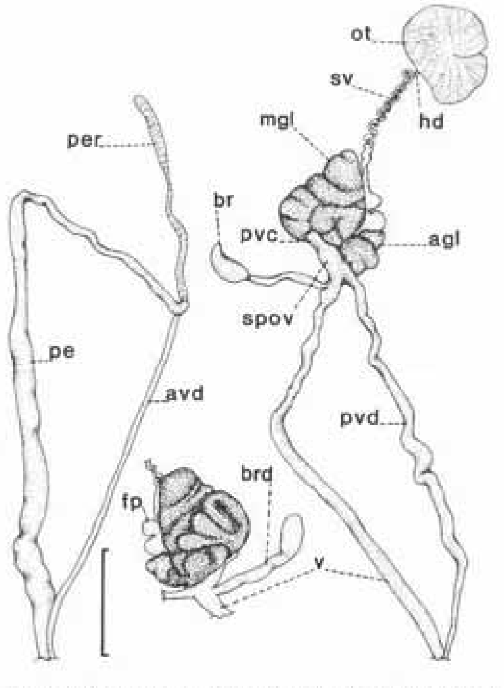


FIG. 330. *Melampus (D.) floridanus*, reproductive system, Sapelo Island, Georgia. Scale 1 mm.

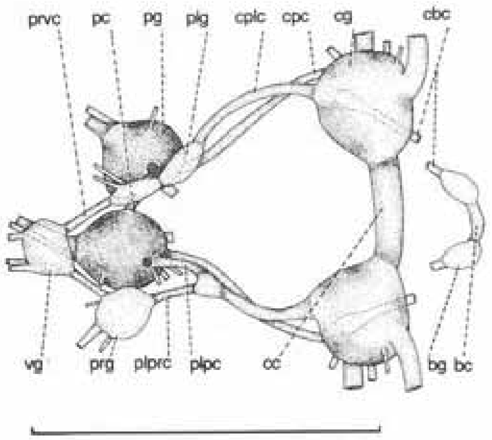


FIG. 331. *Melampus (D.) floridanus*, central nervous system, Sapelo Island, Georgia. Scale 1 mm.

628864, 628865, 628866); Augustine Pier (ANSP 89556; MCZ 294219; USNM 492587). MARYLAND: Morgan Creek, Charlestown (MCZ 200469); Mayo Beach (USNM 522289); Galesville (USNM 595601); Chesapeake Beach (USNM 473812); Parkers Creek (USNM 536708); N of Benedict, Patuxent River (USNM 473459, 473460, 473461); Benedict (USNM 473463); Kepplers, Broomes Island (USNM 473466); Helen Creek, N of Solomons Island (USNM 600764); Solomons Island (USNM 4240410; Millstone Landing, mouth of Patuxent River (USNM 521877); Cobb Island, Potomac River (USNM 473565, 473566, 499520, 522920); Bretton Bay, Potomac River (USNM 628901); Chapel Point, Potomac River (USNM 758317); opposite Chestertown (ANSP 106973); Town Point (MCZ 46419); Head of Little Choptank River, Cambridge (USNM 348955); Cambridge (MCZ 52355, 291275); Dailsville (ANSP 1332468, 303357; MCZ

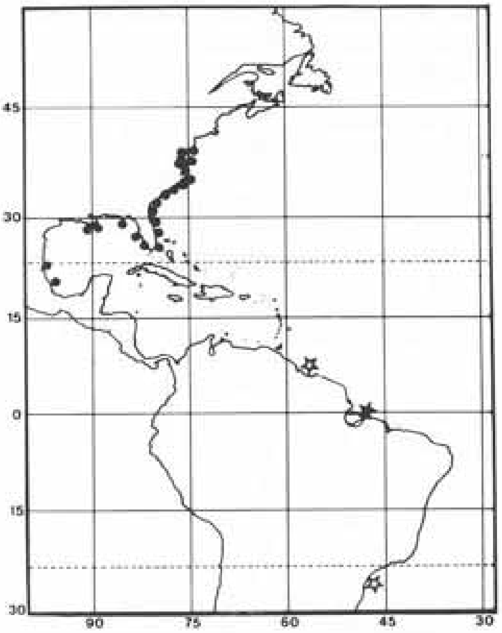


FIG. 332. Geographic distributions, *Melampus (D.) floridanus* (circles), *Melampus (D.) paranus* (stars). Open symbols, localities from literature.

55922); Chambers Farm, Dailsville (ANSP 65100); Whitehaven (MCZ 291276); East of Dames Quarter (USNM 618923). VIRGINIA: Colonial Beach, Potomac River (USNM 473890, 473891); Potomac Beach (USNM 473901, 473902, 473903); Poropotank River (USNM 679376); 2 mi NE of Bartlett (USNM 595938); Yorktown (USNM 474078); Norfolk, Lafayette River (USNM 667496). NORTH CAROLINA: Cedar Island (A.M.); Williston (A.M.); Woodville, North River (A.M.); Beaufort (MCZ 294261; USNM 678946); Morton's Hill, near Beaufort (USNM 621431). SOUTH CAROLINA: Yemassee (A.M.). GEORGIA: Crescent (A.M.); Fort King George, at Darien (USNM 628867). FLORIDA: Jacksonville (ANSP 132461); Clear Lake (MCZ 294218; USNM 30210); Miami (ANSP 77039; USNM 153403); Everglades fork of Miami River (ANSP 82852); Biscayne Bay (USNM 492586); Seminole Point (ANSP 293554); Flamingo Key (MCZ 291041); Cape Sable (MCZ 291039); Turner River, near Chokoloskee (ANSP 93436); Everglades City (MCZ 291040, 294262); Naples (MCZ 291041); Fort Myers (ANSP 62805; MCZ 291277; USNM 492585); Little Gasparilla Island (ANSP 142169); Myakka River (A.M.); Sarasota Bay (ANSP 294332; USNM 30624); Big Bend Road, Tampa Bay (A.M.); Tampa (ANSP 76114; MCZ 70562; USNM 37608, 504488); Ballast Point, Tampa (MCZ 13815); Hudson (A.M.); Tributary to Hudson Bayou (USNM 487336); Aripeka (ANSP 73901; USNM 149953); Little Blind Creek, below mouth of Chassahowitzka River (ANSP 148526); Tarpon Springs (MCZ 291274); Suwannee River (ANSP 189567); St. Marks (ANSP 56815, 56816). ALABAMA (USNM 492588): SE of Heron Bay (ANSP 315714); Mobile (MCZ 68065); Coden Beach (USNM 422365). MISSISSIPPI: Point Cadet, Biloxi (USNM 518640); Davis Bayou, Ocean Springs (USNM 778280); Escatawpa River (ANSP 315718). LOUISIANA: New Orleans (USNM 119495). MEXICO: Tampico (ANSP 46584); Rio Vinazco (USNM 675265); SE of Tuxpan, Vera Cruz (USNM 675272).

Melampus (Detracia) paranus
(Morrison, 1951)
Figs. 319, 332, 333

Detracia parana Morrison, 1951a: 19, fig. 3 [Amazon River at Pará, Brazil; holotype USNM 594591 (Fig. 319); three paratypes USNM 32090]; Morrison, 1951b: 9; Marcus & Marcus, 1965a: 42–51, figs. 19–21, 23–25 [distribution, ecology, anatomy]; Rios, 1970: 138; Rios, 1975: 158, pl. 48, fig. 766.

Melampus (Detracia) paranus (Morrison). Altena, 1975: 86.

Description: Shell (Fig. 319) to 7 mm long, globose to fusiform, thin, smooth, yellowish brown with one to three darker brown bands on body whorl, the one nearest suture more conspicuous. Spire low, with as many as ten flat whorls, dark brown with lighter band. Body whorl 80–90% of shell length, fusiform to subcylindric, without hint of carina on shoulder. Aperture 85–90% of length of body whorl, narrow, weakly canaliculate at base; inner lip with strong, oblique columellar tooth and small, horizontal parietal tooth hidden inside aperture; outer lip sharp, usually with one riblet opposite columellar tooth, sometimes with none, rarely with two or three.

Animal with tentacles bulbous at base; eyes surrounded by unpigmented skin. Visceral mass separated from foot by one whorl, with corresponding extension of mantle cavity; mantle organ forming funnel-shaped pouch.

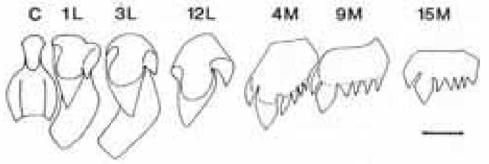


FIG. 333. *Melampus (D.) paranus* (Morrison), radula, Cananeia, Brazil; redrawn from Marcus & Marcus (1965a). Scale 10 µm.

Radula (Fig. 333) having formula [16 + 16 + 1 + 16 + 16] × 100. Base of central tooth weakly concave, not emarginate; crown rounded posteriorly; mesocone small, rounded; ectocones absent. Mesocone of lateral teeth about half of length of tooth, with conspicuous ectocone. Endocone appearing on second marginal tooth; as many as five ectocones on marginal teeth.

Remarks: Melampus (D.) paranus was described by Morrison (1951a) on the basis of four specimens in the United States National Museum of Natural History, collected in Brazil before 1885. Only the type specimens were available to me and they constitute the basis for my description of the shell. All data on the animal and its anatomy were taken from Marcus & Marcus (1965a). In their study of 174 specimens from Cananeia, Brazil, Marcus & Marcus observed the aperture length to be barely 75% of the length of the body whorl, an important difference from the few specimens that constitute the type material. I observed similar variation in the North American companion species *Melampus (D.) floridanus*.

According to Morrison (1951a) the strong similarities between *Melampus (D.) paranus* and *Melampus (D.) floridanus* suggest that both species underwent closely parallel evolution. The former differs from the North American species by its lack of a callosity above the columellar tooth and by the number of riblets inside the outer lip. Marcus & Marcus (1965a) observed that *Melampus (D.) paranus* commonly had one riblet, seldom none and rarely two, and only one of the 174 specimens examined had three riblets inside the outer lip. *Melampus (D.) floridanus* has four to ten riblets inside the outer lip.

Habitat: According to Marcus & Marcus (1965a), *Melampus (D.) paranus* is a supralittoral estuarine species that lives in mangroves together with *Melampus (M.) coffeus.*

Range: Suriname (Altena, 1975), south to Cananeia, Brazil (Marcus & Marcus, 1965a) (Fig. 332).

Specimens Examined: BRAZIL: Pará [Belém], on the Amazon River (USNM 32090, 594591).

Melampus (Detracia) monile
(Bruguière, 1789)
Figs. 334–354

Bulimus monile Bruguière, 1789: 338 [West Indies, herein restricted to San Juan, Puerto Rico; location of type unknown]; Dillwyn, 1817: 506 [erroneously stated as a probable variety of *Voluta flava* Gmelin, 1791]; Cuvier, 1817: 414.

Melampa monile (Bruguière). Schweigger, 1820: 739.

Auricula monile (Bruguière). Férussac, 1821: 105; Lamarck, 1822: 141; Küster, 1844: 30, pl. 4, figs. 7–9.

Auricula monile Lamarck. Menke, 1830: 36; Gould, 1833: 67; Jay, 1839: 59; Reeve, 1842: 106, pl. 187, fig. 8.

Melampus monile Schweigger. Lowe, 1832: 292.

Conovulus monile (Bruguière). Deshayes, 1836: 71, pl. 27, figs. 5, 5a.

Melampus (Melampus) monile (Bruguière). Beck, 1837: 108.

Auricula monile Férussac. Potiez & Michaud, 1838: 202.

Melampus coronatus C. B. Adams, 1849: 41 [Jamaica; lectotype chosen by Johnson & Boss (1972) MCZ 186029 (Fig. 342); C. B. Adams, 1851: 186; Pfeiffer, 1854b: 147; Pfeiffer: 1856a: 51; Johnson & Boss, 1972: 196, pl. 41, fig. 5 [lectotype figured].

Melampus flavus Gmelin of authors. C. B. Adams, 1849: 42; C. B. Adams, 1851: 186; H. & A. Adams, 1854: 9; Pfeiffer, 1854b: 147; Pfeiffer, 1856a: 21; Binney, 1859: 167, text fig.; Binney, 1860: 4; Binney, 1865: 12, fig. 14; Tryon, 1866: 8, pl. 18, fig. 6; Poey, 1866: 394; Pfeiffer, 1876: 303; Mörch, 1878: 5; Arango y Molina, 1880: 59; Dall, 1883: 322; Dall, 1885: 281, pl. 18, fig. 1; Dall, 1889: 92, pl. 47, fig. 1; Simpson, 1889: 68; Crosse, 1890: 258; Davis, 1904: 126, pl. 4, fig. 5; Peile, 1926: 88; Maury, 1922: 55; C. W. Johnson, 1934: 159; M. Smith, 1937: 146, pl. 55, fig. 12, pl. 67, fig. 1 [pl. 67 copied from Dall (1885)]; Holle & Dineen, 1959: 28–35, 46–51. *Non* Gmelin, 1791.

Melampus torosa Mörch, 1852: 38 [Antilles; location of type unknown].

Melampus fusca Mörch, 1852: 35 [Antilles; location of type unknown].

Melampus coronulus C. B. Adams. H. & A. Adams, 1854: 10 [error for *coronatus*].

Melampus monilis Lamarck. Shuttleworth, 1854b: 102; Shuttleworth, 1858: 73 [unjustified emendation of *monile*].

Melampus monile Lamarck. Mörch, 1878: 5.

Melampus flavus (Gmelin?) Binney. Dall & Simpson, 1901: 368, pl. 54, fig. 9. *Non* Gmelin, 1791.

Melampus flavus var. *purpureus* Davis, 1904: 126, pl. 4, fig. 6 [Bermuda, herein restricted to South Shore; lectotype selected by Baker (1964) ANSP 86922 (Fig. 336).

Melampus flavus var. *albus* Davis, 1904: 126, pl. 4, fig. 7 [Hungry Bay, Bermuda; lectotype selected by Baker (1964) ANSP 86924 (Fig. 337)].

Pira monile (Bruguière). Morrison, 1951b: 8; Morrison, 1958: 118–124 [ecology]; Nowell-Usticke, 1959: 88; Morrison, 1964: 119–121 [systematics].

Melampus monile (Bruguière). Warmke & Abbott, 1961: 153, pl. 28, fig. p; Rios, 1970: 138; Morris, 1973: 273, pl. 74, fig. 9; Emerson & Jacobson, 1976: 192, pl. 26, fig. 27; Rehder, 1981: 647, fig. 363.

Melampus (Pira) monilis (Bruguière). Abbott, 1974: 332, fig. 4090: Rios, 1975: 158, pl. 48, fig. 765; Gibson-Smith & Gibson-Smith, 1982: 116, figs. 2, 3; Vokes & Vokes, 1983: 60, pl. 22, fig. 14.

Melampus (Pira) monile (Bruguière). Humphrey, 1975: 196, pl. 22, fig. 23 [shell figured seems to be *Melampus coffeus*].

Melampus monilis (Bruguière). Cosel, 1978: 216; Mahieu, 1984: 314; Jensen & Clark, 1986: 457, figured.

Description: Shell (Figs. 334–345) to 16 mm long, ovoid to fusiform, solid, shiny, usually a uniform purplish brown or with as many as three narrow white bands, rarely uniformly white or yellowish. Excavated umbilical groove sometimes present in gerontic specimens. Spire low to moderately high, with as many as 11.25 flat whorls, with two or three well-marked spiral grooves on first two whorls, one or two rows of elongated pits on remaining whorls; spiral row of short, laterally compressed periostracal hairs, often running along spiral row of pits in adult specimens; location of hairs does not correspond to that of pits. Body whorl averaging 83% of shell length, conic to ovoid, smooth or with pitted and sometimes carinate shoulder. Aperture about 90% length of body whorl, narrow, anteriorly angulate; inner lip with strong, oblique, twisted columellar tooth, conspicuous parietal callus and, just posterior to it, deep parietal tooth; outer lip sharp, with as many as ten subequal riblets not reaching edge. Inner partition of whorls occupying two-thirds of body whorl (Fig. 340). Protoconch translucent, brownish (Figs. 343–345).

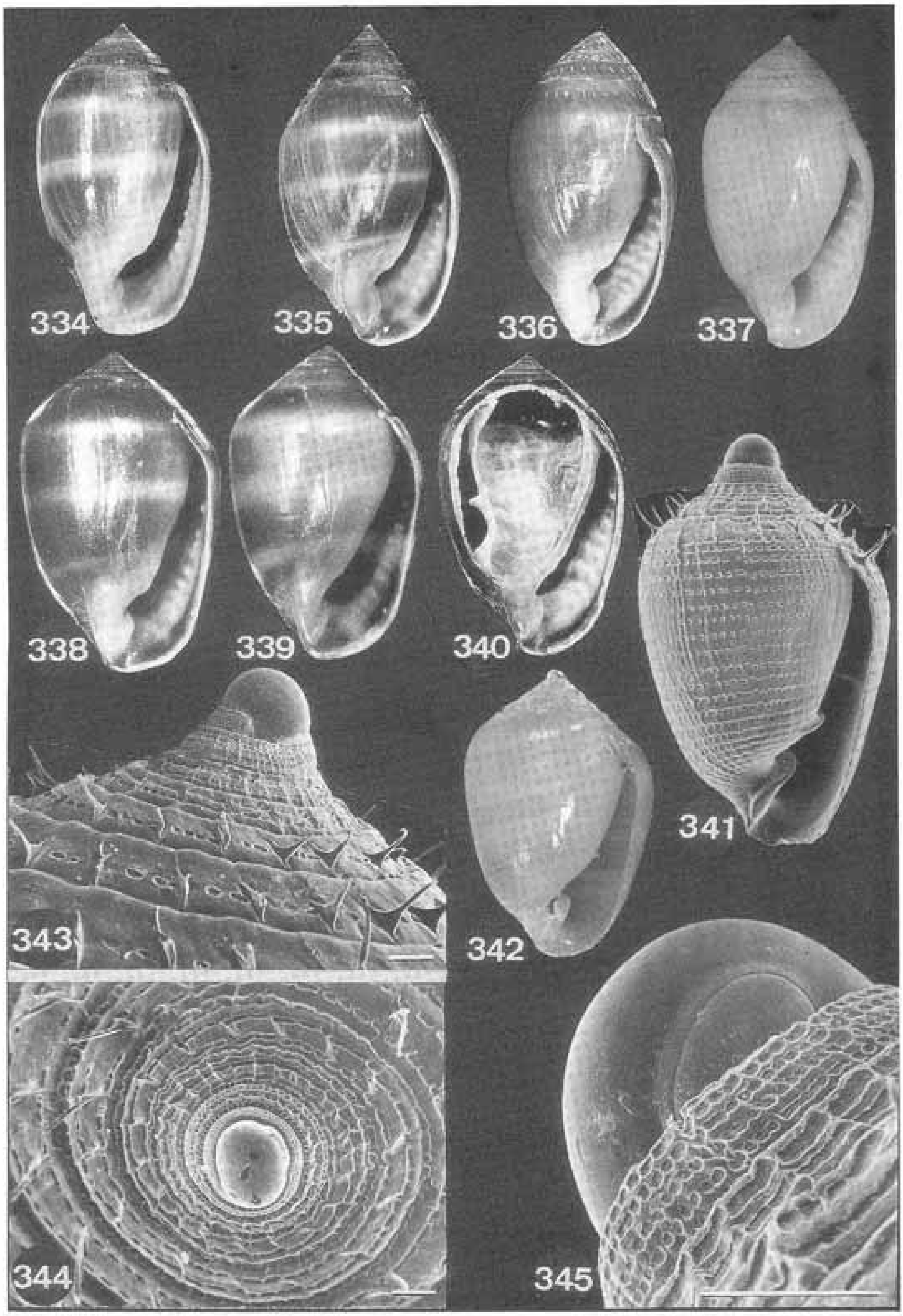
Animal bluish gray; foot whitish; top of neck blackish; tentacles subcylindric, pointed, translucent in first quarter, changing sharply to dark gray or black; mantle skirt light gray. Pallial cavity elongate; mantle organ forming conspicuous pouch; kidney very elongate.

Radula (Figs. 346–350) having formula $[29 + (1 + 15) + 1 + (15 + 1) + 29] \times 113$. Central tooth base twice width of lateral teeth base, triangular, with conspicuous prominences on inner surfaces of arms; crown narrower and smaller than that of lateral teeth, with posterior edge straight or with weak medial depression; mesocone small, pointed; very weak ectocones sometimes present. Lateral teeth 14 to 17; crown broadly triangular, half total tooth length; mesocone sharp, pointed laterally; first lateral tooth with medial posterior part of crown elongate, with weak endocone; remaining lateral teeth without endocone, posterior edge of crown with medial prominence, medial posterior part of base flaring, cusp-shaped; no ectocone. Transitional tooth with weak ectocone. Marginal teeth 24 to 32; base reduced, crown very elongate in first teeth, gradually becoming smaller; mesocone strong, sharp, gradually becoming rounded at tip.

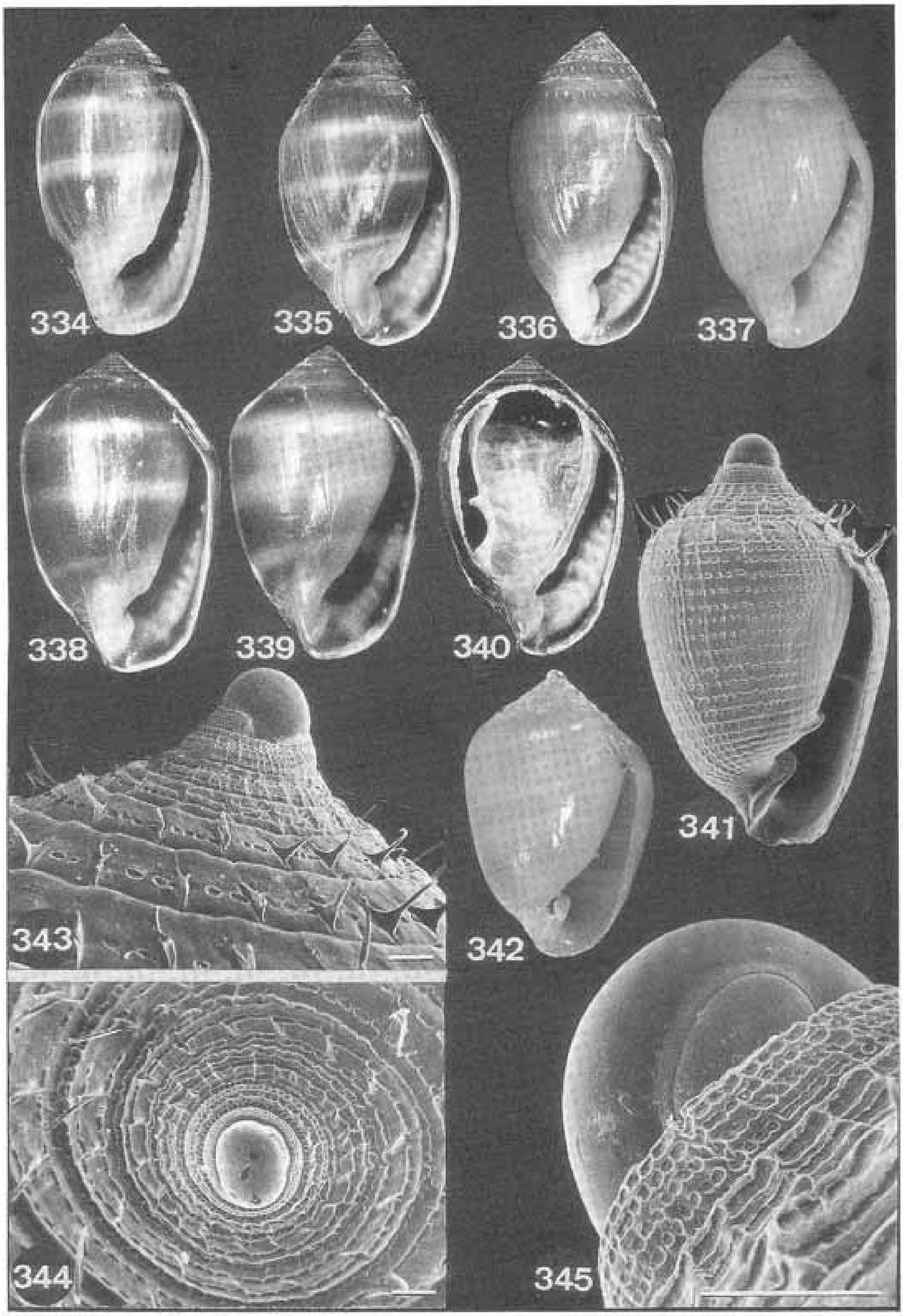
Digestive system as in *Melampus s. s.;* stomach (Fig. 351) as in subfamily.

Reproductive system (Fig. 352) with ovotestis leaf-like, round, dark brown; albumen gland spiral; prevaginal caecum conspicuous; bursa duct connecting with vagina opposite exit of posterior vas deferens; bursa large, oval-elongate; vagina thin, long, about same size as posterior vas deferens; penis thin, long; anterior vas deferens about 65% of penis length; penial retractor attaching together with columellar muscle.

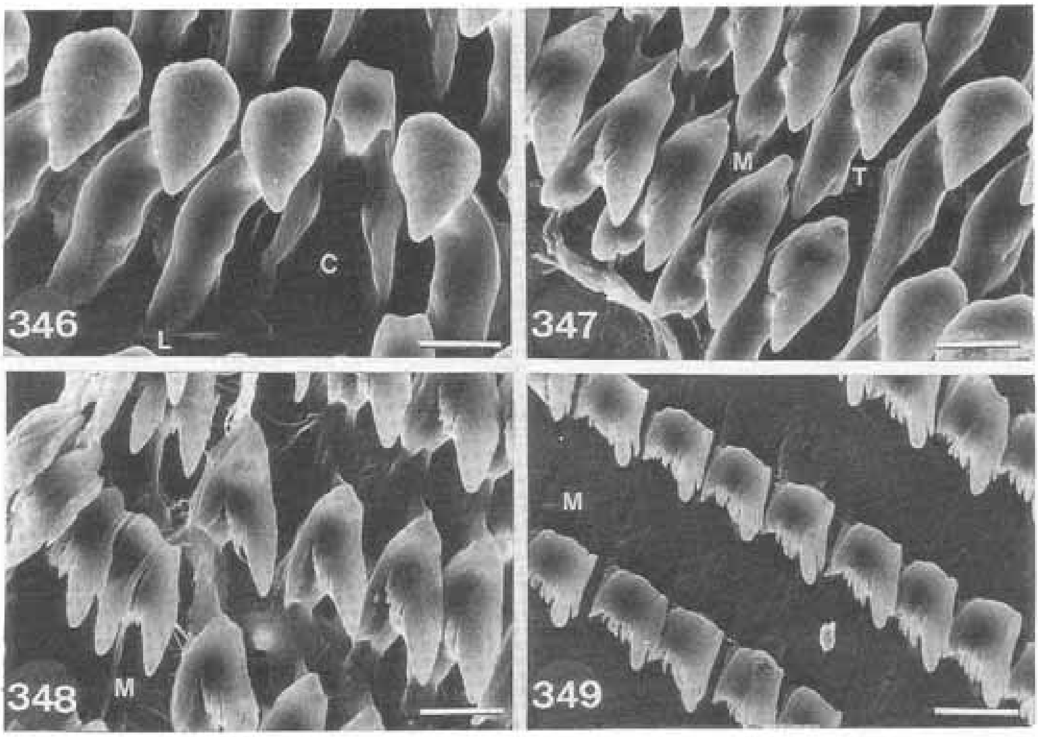
Nervous system (Fig. 353) having cerebral commissure narrower than width of cerebral ganglion; left parietovisceral connective twice the length of right one.



FIGS. 334–345.



FIGS. 334–345.



FIGS. 346–349. *Melampus (D.) monile*, radular teeth, Shelly Bay, Bermuda, sl 11.2 mm. (346) Central and lateral teeth. (347) Transitional and marginal teeth. (348,349) Marginal teeth. Scale 50 µm.

Remarks: Bruguière (1789) clearly stated that his *Bulimus monile* was from the West Indies, but the works he cited refer to both the West Indies (Lister, 1770: pl. 834, figs. 60, 61, Barbados) and East Indies (Martini, 1773: 2, p. 126, pl. 43, fig. 444, East Indies). It was probably this discrepancy that led Dillwyn (1817) to suggest that Bruguière's *Bulimus monile* was only a variety of *Voluta flava* Gmelin, 1791. This, in turn, led to the general confusion of *Bulimus monile* with *Voluta flava* and the general use of the latter name for the West Indian species. Gmelin (1791: 3431), however, under *Voluta flava* referred only to figure 444 of Martini (1773), which definitely represents an East Indian species.

Another explanation for the confusion of the two species, besides common reference to Martini's fig. 444, might reside in the variable color pattern of the West Indian species. The juveniles of *Melampus (D.) monile*, like those of *Melampus flavus*, are often golden or golden brown, as seen in C. B. Adams' *Melampus coronatus* [= *Melampus (D.) monile*, juvenile]. Bruguière (1789) in the original description stated that his specimens of *Melampus (D.) monile* were not fully grown, because they lacked the inner dentition of the outer lip, a feature reported by Lister (1770) and Martini (1773). This might explain his statement about the "very light yellow" color.

Binney (1859), using the name *Melampus flavus* Gmelin, 1791, for the West Indian species, listed *Melampus torosa* Mörch and

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FIGS. 334–345. *Melampus (D.) monile* (Bruguière). (334) Specimen perhaps figured by Binney (1859:167, fig. IV) (USNM 39827), sl 12.8 mm. (335) Shelly Bay, Bermuda, sl 14.4 mm. (336) *M. flavus purpureus* Davis, lectotype (ANSP 86922), South Shore, Bermuda, sl 10.0 mm. (337) *M. flavus albus* Davis, lectotype (ANSP 86924), South Shore, Bermuda, sl 8.6 mm. (338) San Juan, Puerto Rico, sl 12.6 mm. (339) San Juan, Puerto Rico, sl 12.5 mm. (340) San Juan, Puerto Rico, sl 12.2 mm. (341) Juvenile, Maravén, Venezuela, sl 1.67 mm. (342) *M. coronatus* C. B. Adams, lectotype (MCZ 186029), Jamaica, sl 3.0 mm. (343,344) Lateral and top views of spire and protoconch, Indian Key Fill, Florida. (345) Detail of spire and protoconch of specimen of Fig. 341. Scale 500 µm.

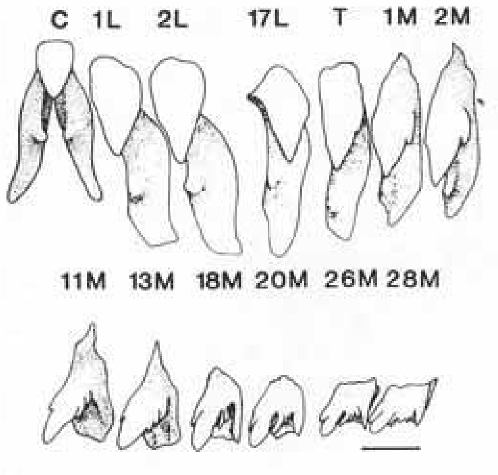


FIG. 350. *Melampus (D.) monile*, radula, Shelly Bay, Bermuda. Scale 10 μm.

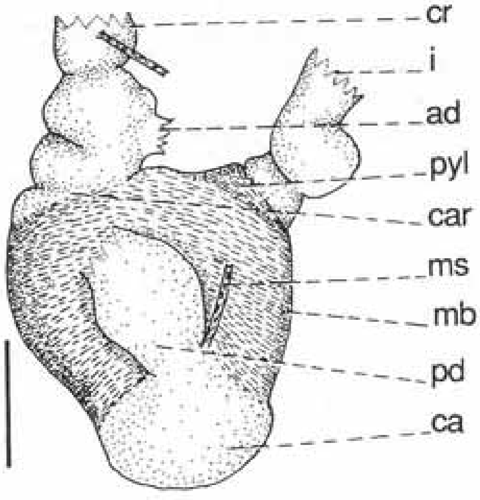


FIG. 351. *Melampus (D.) monile*, stomach, Bermuda. Scale 1 mm.

Melampus (D.) monile (Bruguière) as synonyms. Under *Melampus torosa*, Mörch (1852) cited figure 444 of Martini (1773), included *Voluta flava* Gmelin in the synonymy and mentioned the Antilles as the locality. It appears, then, that Mörch also confused *Melampus flavus* (Gmelin) with *Melampus (D.) monile* (Bruguière) and Mörch's name must be treated as a synonym of *Melampus (D.) monile* (Bruguière, 1789).

Another name listed in Mörch's (1852) *Yoldi Catalogue* is *Melampus fusca* from the Antilles. In the synonymy he cited Martini (1773, pl. 43, fig. 445), *Voluta minuta* Gmelin, 1791, which prompted Binney (1859) to include *Melampus fusca* as a synonym of *Melampus (M.) coffeus*, and *Voluta monile*. Figure 445 of Martini, upon which *Voluta*

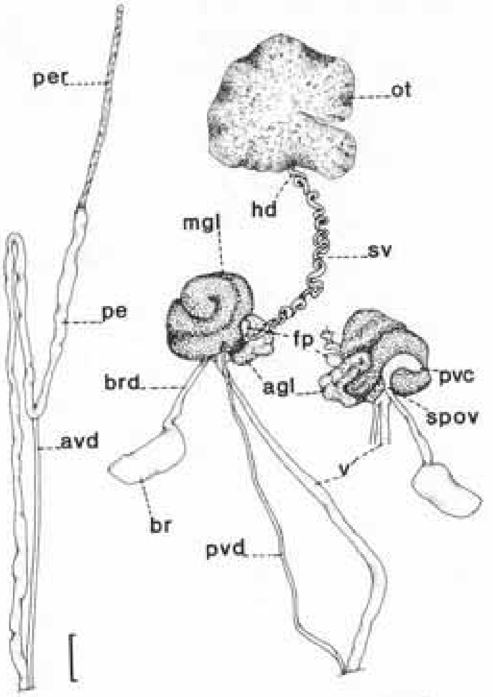


FIG. 352. *Melampus (D.) monile*, reproductive system, Clifton Pt., New Providence, Bahamas. Scale 1 mm.

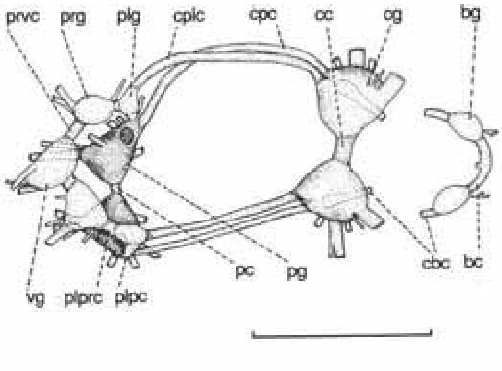


FIG. 353. *Melampus (D.) monile*, central nervous system, Clifton Pt., New Providence, Bahamas. Scale 1 mm.

minuta Gmelin was based, has already been shown to be unidentifiable [see the remarks for *Melampus (M.) coffeus*]. Thus, the only citation under *Melampus fusca* that can support the name is *Voluta monile,* of which *Melampus fusca* Mörch must be considered a synonym.

Dall & Simpson (1901) found it difficult to separate *Melampus (D.) monile;* erroneously listed as *Melampus flavus,* from *Melampus (M.) coffeus,* owing to similarities in shape and color. They noted that the apertural dentition is the most reliable distinguishing character. Bruguière (1789) for *Melampus (D.) monile* mentioned two teeth, a small, oblique columellar tooth and a smaller parietal tooth. Usually *Melampus (M.) coffeus* has one small, more or less oblique columellar tooth, and two readily visible parietal teeth, the posterior one the largest of the three. Sometimes, however, the anterior parietal tooth is either very small or absent, hence the source of confusion. The twisted columellar tooth, the much smaller, hidden parietal tooth and the hairs (noticed by Shuttleworth in 1858) or pits on the shoulder of the body whorl and spire unmistakeably distinguish *Melampus (D.) monile* from *Melampus (M.) coffeus, Melampus (M.) bidentatus* and *Melampus (D.) morrisoni.* It differs from *Melampus (D.) bullaoides* in its more conical shape, longer aperture and evenness of the riblets on the outer lip. The hairs and general aspect of the spire are similar to those of the latter species, but *Melampus (D.) monile* has a more regular, lower conical spire.

Melampus (D.) monile was placed by Morrison (1951b) within the genus *Pira* H. & A. Adams. The reasons that I do not accept that decision are discussed in the remarks for *Detracia. Melampus (D.) monile* is placed in the subgenus *Detracia* on the basis of shell, radular and anatomical characters. The strong, twisted columellar tooth, the medial prominences on the base of the central radular tooth, the pouch-like mantle organ and the greater separation between foot and visceral mass are all typical characters of *Detracia.*

Habitat: Melampus (D.) monile is unique among species of *Detracia* in its preference for living much closer to the high-tide mark than do any other species of the subgenus, which usually live farther inland. *Melampus (D.) monile* commonly lives under boulders above the high-tide mark along open rocky shores, together with *Tralia (T.) ovula* and *Pedipes mirabilis.* It can also occur in mangroves, but always near the high-tide mark.

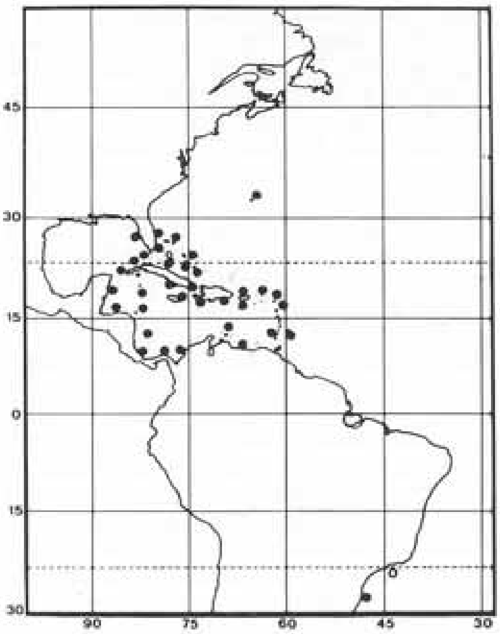


FIG. 354. *Melampus (D.) monile*, geographic distribution. Open circle, locality from literature.

Range: Bermuda; Florida; West Indies, Central America to Guanabara Bay, Brazil (Rios, 1975) (Fig. 354).

Specimens Examined: FLORIDA: Indian River (MCZ 201670); Miami (ANSP 47603, 294316; USNM 492589); Coconut Grove (MCZ 201093, 291380, 294258); Brickell Hammock, Biscayne Bay (MCZ 291382); 6 km S of Tavernier, Key Largo (MCZ 291385); Tavernier Key (USNM 492549a); Plantation Key (MCZ 294255); S of Ocean Drive, Plantation Key (A.M.); Tea Table Key (MCZ 291009); Indian Key Fill, N of Indian Channel (A.M.); Long Key (MCZ 291010; A.M.); Grassy Key (A.M.); Crawl Key (MCZ 294256; A.M.); Knight Key (A.M.); West Summerland Key (MCZ 291388; A.M.); Big Torch Key (ANSP 189590); Key West (ANSP 56804; 174363; USNM 36062a, 596785); Boca Grande, Gasparilla Island (ANSP 142273). TEXAS: Port Maria (USNM 711207). BERMUDA (ANSP 56790, 85587; MCZ 24155, 24249, 24250; USNM 11421a, 94432b, 173648, 173649, 173650, 228688): Fairyland (ANSP 99082); N of Shelly Bay Beach (A.M.); Coney Island

(A.M.); Ferry Reach Park (R.B.); N end of Long Bird Bridge (A.M.); St. George's Island (USNM 621572); Castle Harbor (ANSP 143319); Hungry Bay (USNM 171939, 492555; A.M.); Agar's Island, Hungry Bay (MCZ 48124, 106521; A.M.); South Shore (ANSP 86922, 86924; MCZ 53063, 53064; USNM 109560, 109561); Boat Bay (USNM 621691); S end of Ely's Harbour (A.M.); W side of Somerset Bridge (A.M.); Mangrove Bay (A.M.). BAHAMA ISLANDS (ANSP 56799; MCZ 9946; USNM 37607): GRAND BAHAMA ISLAND (ANSP 374527): Running Mon Canal (ANSP 369779); Eight Mile Rock (ANSP 173262; MCZ 116712); Caravel Beach [John Jack Point], Freeport (ANSP 370226); Dead Mans Reef [Sandy Bevan's Cay] (ANSP 371225); McLeans Town (ANSP 369067); GREAT ABACO ISLAND (MCZ 24140; USNM 492580): Hope Town Harbor (ANSP 299391); Little Harbor (USNM 180520); Witch Point (ANSP 299483, 359150); Matt Lowes Cay (ANSP 299248); Marsh Harbor (MCZ 275572); BIMINI ISLANDS: Alicetown, North Bimini (MCZ 144132); opposite Cat Tail Pond, South Bimini (ANSP 325784); ANDROS ISLAND (MCZ 66755, 71633): Morgan's Bluff (A.M.); Mastic Point (USNM 359884); South Mastic Point (A.M.); First island off Mintie Bar, SE end of South Bight (USNM 271785b); Mangrove Cay (USNM 269968c); Lisbon Point, Mangrove Cay (USNM 269599a); Bastion Point, Mangrove Cay (USNM 269260); Long Bay Key (USNM 269304); PARADISE ISLAND: (A.M.); NEW PROVIDENCE ISLAND (USNM 603913): Nassau (USNM 160765a); Culbert Point, 10 km ESE of Nassau (MCZ 107793); Bar Point (A.M.); Delaport Point (A.M.); W of Rock Point (A.M.); Clifton Point (A.M.); Clifton Pier (A.M.); shore off Millars Road (A.M.); Malcolm Creek (A.M.); Coral Harbor (USNM 679136); ROYAL ISLAND (USNM 468115a); CAT ISLAND: Arthurstown (MCZ 107833); 6 km E of Arthurstown (MCZ 107825); RUM CAY (MCZ 87849); LONG ISLAND: 3 km NE of O'Neill's (ANSP 173265; MCZ 113102); Simms (MCZ 294259); Clarencetown (MCZ 113339); GREAT INAGUA: Matthewstown (MCZ 291384). TURK'S & CAICOS: TURK'S ISLAND (MCZ 201098; USNM 492474, 509960). CUBA (ANSP 56801, 56802; USNM 492478): Jaimanitas (MCZ 294198); Habana (ANSP 93653); Cayo Birricu, N of Habana (ANSP 362824); Cojimar (ANSP 45089; MCZ 131921, 131955); Matanzas (ANSP 87896; MCZ 294192); La Playa (MCZ 92045, 131950, 189818, 294260); Versalles (MCZ 291381); Cayo Cristo (MCZ 291389); Varadero (ANSP 110604; MCZ 201677; USNM 598261); Cayo Galindo, Cárdenas Bay (ANSP 157578); Cayo Francès (MCZ 42106, 131951); Siboney (USNM 533912); Aguadora, Santiago (USNM 391879); Guantánamo (ANSP 313059); Cabo Cruz (MCZ 87887); Rancho Alma, Cienfuegos (MCZ 291386). JAMAICA (ANSP 56803; MCZ 186029, 201094, 294254, 294257; USNM 6385, 94744, 492475, 492477, 492480): Montego Bay (USNM 441488); Falmouth (ANSP 397268); Robin's Bay (USNM 442026, 442092); Jack's Bay (USNM 441926); Buff Bay (USNM 441196); Port Antonio (USNM 440855); Priestmans River (USNM 492479); Manchioneal (R.B.); Rock Fort (USNM 374242); Kingston (USNM 374270, 442730); Harbor Head, Kingston (USNM 375579); Palisadoes (USNM 442466); Runaway Bay (USNM 202658); Little River (USNM 128046). HAITI: Gonave Island (492531a); Île-à-Vache, Soulette Bay (USNM 439191a); Port Salut (ANSP 226701; MCZ 183912); Les Cayes (USNM 439742); Baïe Anglaise, near Aquin (USNM 439548a); Saltrou (USNM 439342, 442819); Bizoton (USNM 439832a). DOMINICAN REPUBLIC: Monte Cristi (MCZ 57591, 57750, 291383); Puerto Plata (MCZ 291379, 291387); Santa Bárbara de Samaná (ANSP 173263; MCZ 57757); Cayo Chico, E of Santa Bárbara de Samaná (MCZ 57776); Cayo de Tamiso (MCZ 57812); Isla La Matica, Playa Boca Chica, E of Santo Domingo (R.B.). PUERTO RICO: E of San Juan (USNM 683107); Puerta de Tierra, San Juan (A.M.); Punta Cerro Gordo (USNM 683012); Punta Agujereada (MCZ 233338); Arecibo (MCZ 291391); Punta Arenas, N of Joyuda (A.M.); Lighthouse, Cabo Rojo (MCZ 294194; Ensenada Honda, Culebra Island (USNM 161161). VIRGIN ISLANDS: ST. THOMAS (ANSP 56789; MCZ 294196; USNM 256035); ST. CROIX (ANSP 56788; USNM 621396). LESSER ANTILLES: ANTIGUA (MCZ 71511): off Falmouth (USNM 502116); North Bay, Guana Island (MCZ 88870; ANSP 351799); GUADELOUPE (MCZ 294197; USNM 492481): Anse-Dumont, Gosier (USNM 758065); ST. VINCENT: (USNM 492473); Villa (USNM 487000); BARBADOS: (ANSP 56797; MCZ 291390; USNM 502108, 502109); Bridgetown (USNM 502115); Pelican Island (USNM 502110, 502112); Needham Point (USNM 502113); off Telegraph Station (USNM 502114); Maxwell's Coast (USNM

603784); San Blas (ANSP 56796); GRENADA: Prickly Bay (ANSP 297189); off Hardman Bay (ANSP 296483); TRINIDAD (MCZ 294193). CARIBBEAN ISLANDS: SWAN ISLAND (MCZ 22938, 36611); CAYMAN ISLANDS: Cayman Brac (ANSP 296178; MCZ 294195); OLD PROVIDENCE ISLAND: N of Ironwood Point (USNM 678831); ST. ANDREWS ISLAND (ANSP 154359; MCZ 88689); CURAÇAO: Port Marie & Daaibooi Baai (R.B.). MEXICO: Isla Mujeres, Yucatán (ANSP 284638); Ascension Bay, Quintana Roo (USNM 736381, 736718). BELIZE: North Spot (ANSP 281604); Belize (USNM 150281). HONDURAS: Utila Island (USNM 61185); Roatan Island (USNM 364701). COSTA RICA: Portete, Limón (USNM 702853, 706403). PANAMA: Limón Bay (USNM 732871, 734073); Fort Sherman, Devil's Beach, 9 km N of Colón (USNM 620529). COLOMBIA: Sabanilla (USNM 103467, 193611). VENEZUELA: Cayo Punta Brava, Parque Nacional de Morrocoy, Tucacas (A.M.); El Palito (A.M.); Borburata (USNM 784776); Maravén, Borburata, E of Puerto Cabello (A.M.).

Melampus (Detracia) morrisoni
new name
Figs. 355–376

Detracia clarki Morrison, 1951a: 18, figs. 2, 6 [Key West, Florida; holotype USNM 594588 (Fig. 355)]; Morrison, 1951b: 9; Morrison, 1958: 118–124 [habitat]; Abbott, 1974: 332; Emerson & Jacobson, 1976: 191, pl. 26, fig. 24 [dubious illustration]; Vokes & Vokes, 1983: 60, pl. 22, fig. 16. *Non Melampus clarkii* White, 1895.

Description: Shell (Figs. 355–367) to 17.7 mm long, ovate-conic to subcylindric, solid, shiny; uniformly white to dark brown or with as many as five spiral brown bands or with irregular yellowish axial markings on body whorl. Spire short to moderately high, with as many as 13.25 spirally grooved or pitted whorls. Body whorl about 80% of total length, with incised spiral lines on shoulder. Umbilical excavation sometimes present. Aperture about 90% of body whorl length, very narrow; inner lip with very strong, oblique, upcurved columellar tooth; posterior parietal tooth strong, sometimes upcurved, anterior parietal tooth sometimes fused with posterior one; outer lip with as many as 18 uneven internal riblets, not reaching edge; when numerous, not more than five riblets extend inside aperture. Partition of inner whorls occupying about 75% of body whorl (Fig. 361). Protoconch smooth, translucent, brownish (Figs. 365–367).

Animal whitish, mottled with irregular brown spots, or uniformly black becoming lighter toward yellowish gray foot; tentacles subcylindric, pointed, discolored at base, dark toward tip; mantle skirt yellowish gray.

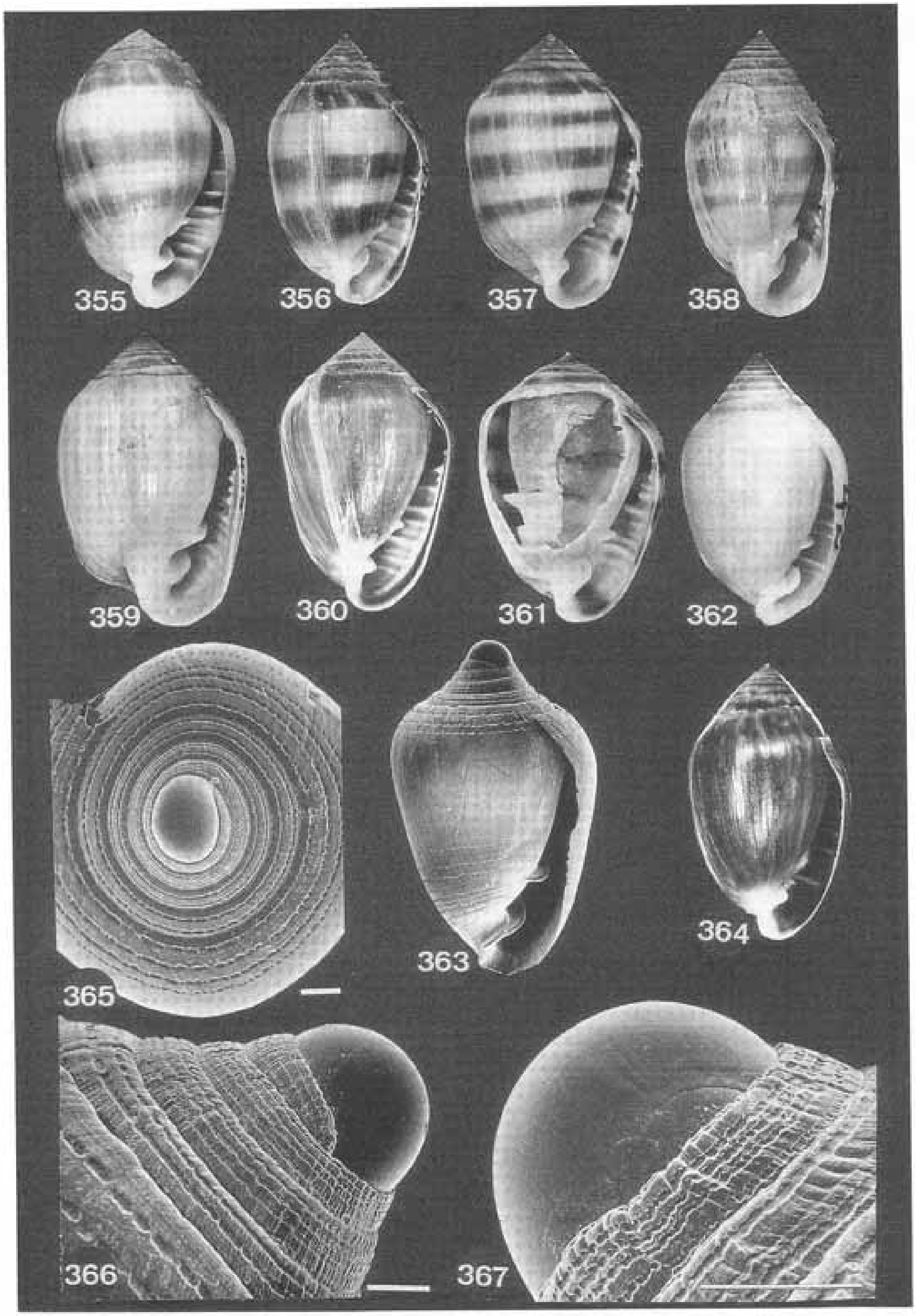
Radula (Figs. 368–372) having formula $[29 + (1 + 20) + 1 + (20 + 1) + 29] \times 110$. Base of central tooth wider than that of lateral teeth, triangular, weakly constricted laterally, with small medial prominence on inner surface of arms; crown length half of lateral teeth; mesocone small, sharp; ectocones very small or lacking. Lateral teeth 15 to 28; crown strong, cuneiform, half total length of tooth; mesocone sharp, pointed laterally; no distinct ectocone or endocone. Transitional tooth with elongate crown, with either weak ectocone or serrated edge at site of ectocone. Marginal teeth 23 to 42, with reduced base; crown high; mesocone very strong, sharp, rapidly becoming round at tip; first marginal tooth with ectocone, becoming bicuspid on second marginal tooth and tricuspid on third; fourth cusp appears on seventh or eighth marginal tooth; endocone visible on fourth marginal tooth; outer edge of base gradually shortening posteriorly, fusing with crown and assuming shape of denticle stronger than ectocone cusps.

Digestive system as in *Melampus s.s.;* stomach (Fig. 373) as in subfamily.

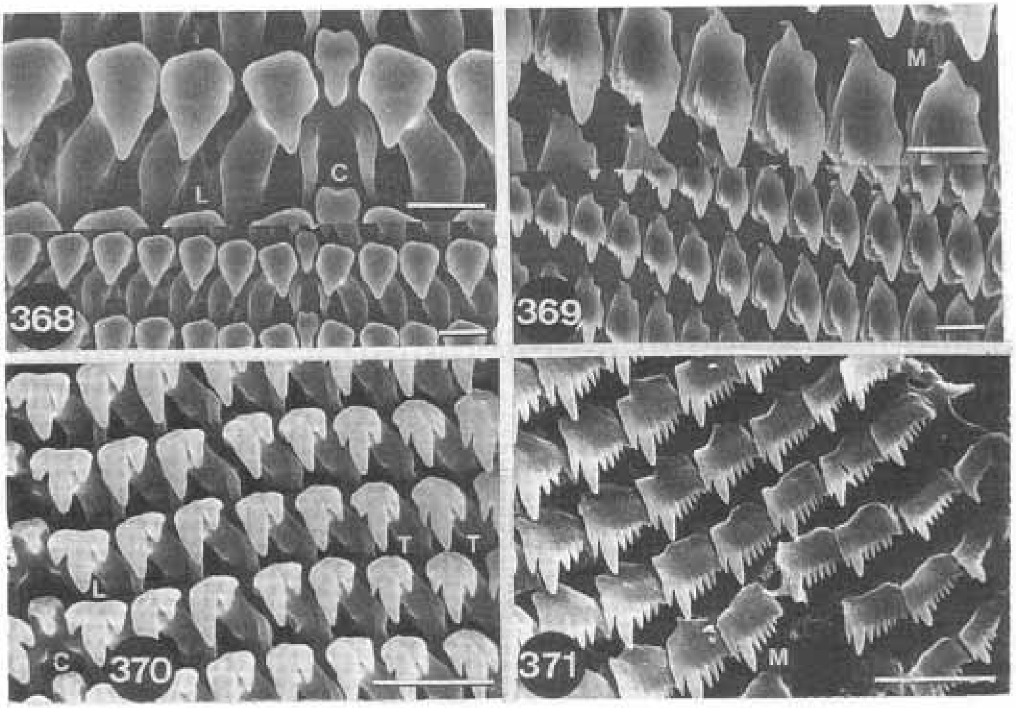
Reproductive system (Fig. 374) with ovotestis leaf-like, circular, dark brown; albumen gland spiral, conical; prevaginal caecum very conspicuous; bursa duct connecting with vagina just before exit of posterior vas deferens; bursa elongate; vagina thin, with length corresponding to nearly one and one-fifth the length of body whorl; penis thin, slightly longer than associated vas deferens.

Nervous system (Fig. 375) with cerebral commissure about as long as width of cerebral ganglion; left parietovisceral connective slightly larger than to twice size of right one.

Remarks: Morrison (1951a) described this species as *Detracia clarki*. The anatomy of *Detracia*, however, does not justify generic rank and this taxon is here considered a subgenus of *Melampus* (see the remarks for *Melampus s. l.*). The name *Melampus clarki* was used by White (1895) for a fossil shell,



FIGS. 355–367.



FIGS. 368–371. *Melampus (D.) morrisoni*, radular teeth, Plantation Key, Florida. (368) Central and lateral teeth, sl 12.9 mm. (369) Marginal teeth, sl 12.9 mm. (370) Central and lateral teeth of juvenile, sl 1.8 mm. (371) Marginal teeth of juvenile, sl 1.8 mm. Scale 50 µm.

later chosen as the type species of the genus *Melampoides* Yen, 1951. The inclusion of *Detracia* as a subgenus of *Melampus* creates a case of secondary homonymy. A new name is necessary and I hereby rename the species *Melampus (Detracia) morrisoni*, in honor of J. P. E. Morrison and in appreciation for his work on the Ellobiidae.

Melampus (D.) morrisoni is unusual among members of this subgenus in having a conspicuous parietal tooth. In the other members of the group this tooth is not readily visible owing to its being deep within the aperture. The strong columellar tooth, the greater length of the pallial gonoducts, the pouch-like mantle organ and the medial nodes on the base of the central tooth of the radula justify removing this species from

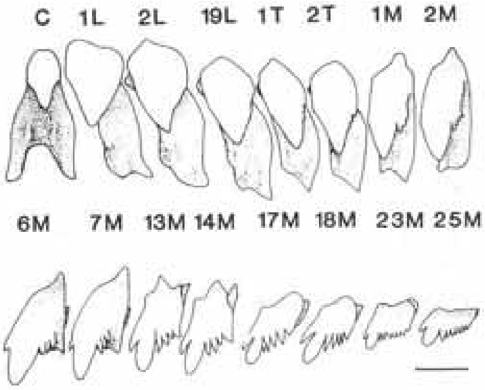


FIG. 372. *Melampus (D.) morrisoni*, radula, Plantation Key, Florida. Scale 10 µm.

FIGS. 355–367. *Melampus (D.) morrisoni*, new name. (355) *Detracia clarki* Morrison, holotype (USNM 594588), Key West, Florida, sl 12.5 mm. (356) Grassy Key, Florida, sl 13.6 mm. (357) Grassy Key, Florida, sl 14.0 mm. (358) Grassy Key, Florida, sl 17.7 mm. (359) Grassy Key, Florida, sl 15.7 mm. (360) Grassy Key, Florida, 14.2 mm. (361) Plantation Key, Florida, sl 12.8 mm. (362) Key Largo, Florida, sl 12.7 mm. (363) Juvenile, Long Key, Florida, sl 2.15 mm. (364) Millars Sound, New Providence, Bahamas, sl 13.8 mm. (365–367) Lateral and top views of spire and protoconch, Long Key, Florida. Scale 500 µm.

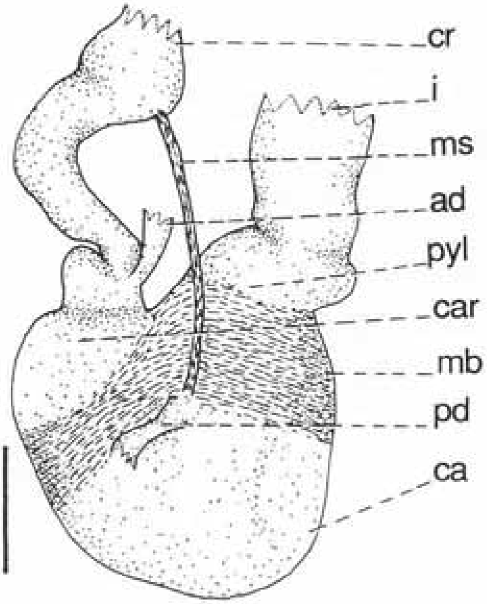


FIG. 373. *Melampus (D.) morrisoni*, stomach, Florida. Scale 1 mm.

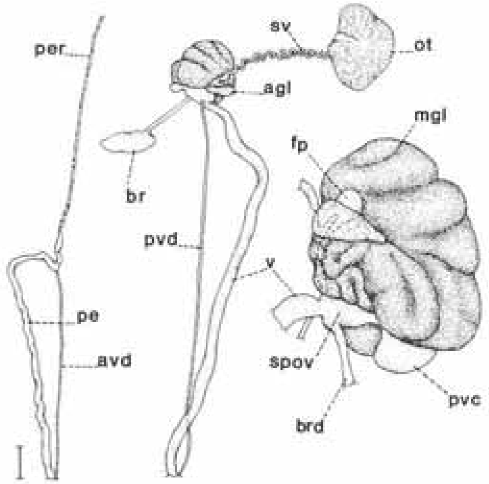


FIG. 374. *Melampus (D.) morrisoni*, reproductive system, Grassy Key, Florida. Scale 1 mm.

Melampus s. s. and placing it in *Detracia*, however.

Melampus (D.) morrisoni can be confused with *Melampus (M.) bidentatus* because they converge in shape and color and are similar in their variability. In its typical form, *Melampus (D.) morrisoni* is readily distinguished by its very narrow shell aperture, well-developed, upcurved columellar tooth, numerous whorls and its more globose shape. Some populations from inner lagoons, in which they occur with *Melampus (M.) bidentatus*, show gradation to an average-sized columellar tooth and a common ovoid shape (Fig. 364). In such cases anatomical studies are helpful. The combination of a greater value of vagina length/body whorl length and the slightly higher number of whorls/shell length characterizes *Melampus (D.) morrisoni*. The latter species also can resemble the morphs of *Melampus (M.) coffeus* that have a less pronounced carina on the shoulder of the body whorl. The strong, curved columellar tooth, the presence of striae on the shoulder of the body whorl, the narrow aperture and the uneven outer lip riblets of *Melampus (D.) morrisoni* clearly separate this species from *Melampus (M.) coffeus*.

As do other members of the genus, *Melampus (D.) morrisoni* undergoes a change in radular morphology with age (Figs. 370, 371). The central tooth has weak but distinct ectocones. The first lateral tooth, deeply tricuspid in very young individuals, becomes bicuspid, then unicuspid, with serrated edges on the sites of the endocone or ectocone, or both. The transitional tooth develops an endocone, which remains through the marginal teeth. The marginal teeth have more ectocone cusps in the juvenile than in the adult. The radula of juveniles very strongly resembles in tooth count and morphology that of the adult *Melampus (D.) floridanus* (Figs. 324–327). This similarity suggests some degree of neoteny in radular development within the genus *Melampus*.

Habitat: *Melampus (D.) morrisoni* lives in association with *Melampus (M.) bidentatus* and *Melampus (D.) bullaoides*. It prefers sheltered inland places in which the mangrove is thin and reached only by very high tides. Individuals aggregate under rocks and in old burrows of fiddler crabs.

Range: South Florida [the St. Augustine record is dubious, according to Morrison (1951a)]; Bahama Islands south to Cuba and Yucatán, Mexico (Fig. 376).

Specimens Examined: FLORIDA: St. Augustine (USNM 492529a); Grant (MCZ 291233); Miami (ANSP 189594, 294333; USNM

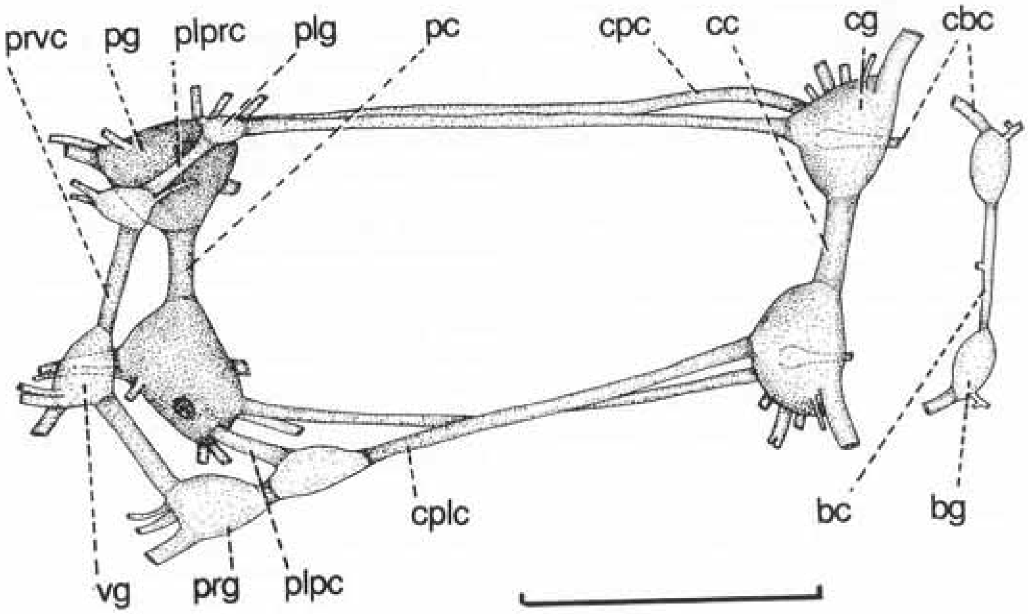


FIG. 375. *Melampus (D.) morrisoni*, central nervous system, Grassy Key, Florida. Scale 1 mm.

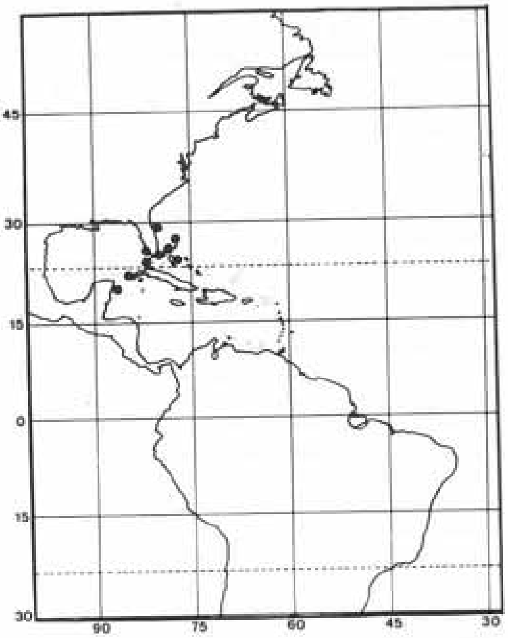


FIG. 376. *Melampus (D.) morrisoni*, geographic distribution.

82844a); Brickell's Hammock, Miami (ANSP 294334); Virginia Key (ANSP 189591; USNM 82859a); Biscayne Bay (MCZ 291230); Florida City (ANSP 294335); Middle Key, Barnes Sound (USNM 338339a); Pumpkin Key, Card Sound (USNM 355114); Key Largo (MCZ 291232; USNM 603120); N of Tavernier Creek, Key Largo (A.M.); 6 km S of Tavernier (MCZ 291234); Tavernier Key (USNM 492552a); S of Ocean Drive, Plantation Key (A.M.); Windley Key (USNM 603105); Indian Key (USNM 462894); Indian Key Fill, N of Indian Key Channel (A.M.); Lower Matecumbe Key (USNM 492554, 700774); Long Key (A.M.); Grassy Key (MCZ 291236; A.M.); Crawl Key (MCZ 291042); Marathon, Key Vaca (ANSP 294336; MCZ 294264); Knight Key (A.M.); Bahia Honda Key (ANSP 189576; USNM 269777, 269980); Spanish Harbor Key (USNM 667407); Newfound Harbor (USNM 272688, 338376); Little Pine Key (USNM 681638); Big Pine Key (ANSP 189583; MCZ 294270; USNM 104092a); end of Kohen Avenue, Big Pine Key (A.M.); Howe Key (USNM 681639); Big Torch Key (ANSP 189579; A.M.); Ramrod Key (MCZ 291043, 294263); Geiger's Key (ANSP 189582); Sugarloaf Key (ANSP 189577; USNM 104094a); Porpoise Point, Big Coppit Key, 5 km N of Key West (MCZ 275573); Boca Chica Key (ANSP 189593; USNM 270329); Stock Island (ANSP 189581; USNM 594589); Key West (ANSP 180089, 189578; MCZ 291235;

USNM 36062, 668245); Chokoloskee Key (ANSP 93430). BAHAMA ISLANDS: GRAND BAHAMA ISLAND (ANSP 374526): North Riding Point (ANSP 371539); GREAT ABACO ISLAND: Witch Point (ANSP 359152; USNM 594592); Angel Fish Point (MCZ 294265); NEW PROVIDENCE ISLAND: Millars Sound by Bacardi Road (A.M). CUBA: Cape Cajón (USNM 492571); Cayo Perro (ANSP 189575; USNM 594590). Cayo Juan Garcia (MCZ 291231); Cayo Maja, near Cayo Santa Maria (MCZ 294217). MEXICO: Isla Mujeres, Quintana Roo, Yucatán (R.B.).

Genus *Tralia* Gray, 1840

Tralia Gray, 1840: 21. Type species by monotypy: *Tralia pusilla* (Gmelin, 1791) [= *Voluta ovula* (Bruguière, 1789)].

Tralica Gray. Reeve, 1877, pl. 1 [in synonymy of *Auricula;* error for *Tralia*].

Description: Shell thick, oval-elongate; aperture moderately long, widest part anterior to columellar tooth; inner lip with three white teeth, first parietal strongest; outer lip thickened, slightly reflected, with distinct anal groove.

Animal white; tentacles flat dorso-ventrally. Internal edge of arms of central radular tooth with prominent medial nodes; first lateral tooth with conspicuous endocone; transition to marginal teeth marked. Salivary glands attached lateroventrally to esophagus; esophagus white. Ovotestis granular; mucous gland very convoluted, not clearly spiral; bursa duct connects at some distance from proximal end of vagina; penis very long, muscular.

Remarks: The genus *Tralia* was created by Gray (1840) for the West Indian *Tralia pusilla* (Gmelin) [= *Tralia ovula* (Bruguière)] on the basis of the peculiar, simple outer lip with its distinct anal groove. H. & A. Adams (1855b: 244) separated *Tralia* Gray from *Melampus* Montfort on the basis of the incorrect observation, "the foot was posteriorly acute, entire." The Adams brothers were confused, however, for they commented, "This group, which appears to have a simple, undivided tail, . . . perhaps, when the animals are better known, will be found to be merely a subgenus of *Melampus.*"

H. & A. Adams recognized four subgenera of *Tralia, Pira, Tifata, Signia* and *Persa.* I have commented on *Pira* and *Tifata* under the remarks for *Detracia* Gray. *Signia,* the third subgenus of *Tralia* introduced by H. & A. Adams (1855b), was later treated as a subgenus of *Melampus* by Thiele (1931) and Zilch (1959). The fourth subgenus, the Pacific *Persa,* was recognized by Thiele and Zilch as belonging to the genus *Tralia;* it is characterized by the very short spire and by the convex, distinctly ribbed whorls. Another subgenus also placed in *Tralia* was introduced by the Adams brothers in 1855 as *Siona,* a genus of *Cassidula,* just prior to the publication of their *Genera of Recent Mollusca.* In this latter publication they changed the name to *Sarnia* without specifying the reason. Thiele (1931) recognized *Siona* as belonging to *Tralia;* Zilch (1959) noted that the name *Siona* was preoccupied and that *Sarnia* should be the correct name. The type of the subgenus, *Tralia (Sarnia) frumentum* (Petit, 1842), from South America, is an Eastern Pacific species conchologically very similar to the eastern North Atlantic *Pseudomelampus exiguus* (Lowe, 1832) [Pedipedinae] and to the genus *Microtralia* (Figs. 174–181). Keen (1971) considered *Pseudomelampus* to be synonymous with *Sarnia* and placed it within the Ellobiinae. According to Marincovich (1973) the radula of *Tralia (Sarnia) frumentum* is similar to that of *Ellobium,* and he considered *Sarnia* to belong in the Ellobiinae. It appears, then, that *Sarnia* cannot be considered a subgenus of *Tralia.* I have considered *Sarnia,* on the basis of the conchological resemblances with *Pseudomelampus,* to belong in the Pedipedinae (see the remarks under the Ellobiidae). A study of the reproductive and nervous systems is needed to ascertain its phylogenetic position, however.

Binney (1865: 16, fig. 16) figured the animal of an alleged *Tralia,* but admitted in a footnote that he did not know which species it represented. Simpson drew from nature a figure of an animal from Charleston, South Carolina, a locality that is not in the range of *Tralia (T.) ovula.* I concur with Dall (1885) that Simpson's drawing probably represents *Myosotella myosotis* (Draparnaud).

The genus *Tralia* is readily distinguished from *Melampus* by its wide anterior aperture, its strong first parietal tooth and its thickened outer lip with a subposterior internal groove.

The apertural dentition of *Tralia* is unusual for a member of the Melampinae and, after anatomical research is carried out, it is possible that some Indo-Pacific species presently put in this subgenus will be found to belong to other subfamilies.

Habitat: The only information available about the habitat of the genus refers to the West Indian *Tralia (T.) ovula* and, for this reason, comments on habitat will be made under that species.

Range: Tralia is a tropical group, living mostly in the Indo-Pacific. It is represented in the West Indies by one species, *Tralia (T.) ovula*, which seems to have been introduced in West Africa.

Subgenus *Tralia s. s.*

Description: Shell to 16 mm long; spire moderately high, with pitted lines; body whorl smooth or weakly marked with punctate spiral lines.

Remarks: see the remarks under *Tralia s. l.*

Tralia (Tralia) ovula (Bruguière, 1789)
Figs. 377–387, 389–400

Bulimus ovulus Bruguière, 1789: 339 [Guadeloupe, West Indies; location of type unknown]; Cuvier, 1817: 414.

Voluta pusilla Gmelin, 1791: 3436 [locality unknown, herein designated to be Guadeloupe, West Indies; location of type unknown]; Dillwyn, 1817: 507; Wood, 1825: 91, pl. 19, fig. 20; Hanley, 1856: 98, pl. 19, fig. 20.

Voluta triplicata Donovan, 1802, pl. 138 [locality unknown, herein designated to be Guadeloupe, West Indies; location of type unknown]; Montagu, 1808: 99; Dillwyn, 1817: 507; Wood, 1825: 91, pl. 19, fig. 19; Hanley, 1856: 98, pl. 19, fig. 19.

Auricula (Conovulus) ovula (Bruguière). Férussac, 1821: 104; Rang, 1829: 173.

Auricula nitens Lamarck, 1822: 141 [Guadeloupe, West Indies; type in the MHNG (Mermod, 1952)]; Menke, 1830: 36; Gould, 1833: 67; Jay, 1839: 59; Küster, 1844: 18, pl. 2, figs. 11–13.

Melampus ovulum Schweigger. Lowe, 1832: 289.

Pythia triplicata (Donovan). Beck, 1837: 104.

Pythia ovulum (Bruguière). Beck, 1837: 104.

Auricula ovula (Bruguière). Potiez & Michaud, 1838: 204, pl. 20, figs. 13, 14.

Auricula pusilla (Gmelin). Deshayes. 1838: 332.

Auricula (Conovulus) pusillus Deshayes. Anton, 1839: 48.

Tralia pusilla Gray. Gray, 1840: 21.

Auricula ovula Férussac. Orbigny, 1841: 186, pl. 13, figs. 1–3.

Tralia pusilla (Gmelin). Gray, 1847a: 179; H. & A. Adams, 1855b: 244, pl. 82, fig. 8; Binney, 1865: 17, fig. 18; Tryon, 1866: 9, pl. 18, fig. 9; Dohrn, 1866: 133 [first record from Eastern Atlantic]; Dall, 1885: 276, pl. 18, fig. 5; Dall, 1889: 92, pl. 47, fig. 5; Dall *in* Simpson, 1889: 69; Dall & Simpson, 1901: 369, pl. 59, fig. 13; Odhner, 1925: 5, pl. 1, fig. 8B, pl. 2, fig. 18 [radula and reproductive system figured]; Peile, 1926: 88; C. W. Johnson, 1934; 159; Coomans, 1958: 103, pl. 10; Franc, 1968: 525.

Melampus pusillus (Gmelin). C. B. Adams, 1849: 42; C. B. Adams, 1851: 186; Pfeiffer, 1854b: 147: Pfeiffer, 1856a: 46 [erroneously stated as also inhabiting Hawaii]; Binney, 1859: 168, pl. 75, fig. 29; Binney, 1860: 4; Poey, 1866: 394; Jeffreys, 1869: 109; Pease, 1869: 61; Pfeiffer, 1876: 317; Arango y Molina, 1880: 59; Crosse, 1890: 258.

Melampus (Tralia) pusillus (Gmelin). H. & A. Adams, 1854: 10.

Melampus nitens (Lamarck). Shuttleworth, 1854b: 101; Shuttleworth, 1858: 73; Mörch, 1878: 5; Nevill, 1879: 219.

Tralia pusilla Linnaeus. Fischer & Crosse, 1880: 22.

Tralia (Tralia) pusilla (Gmelin). Thiele, 1931: 466.

Tralia ovula (Bruguière). Morrison, 1951b: 9; Nowell-Usticke, 1959: 88; Coomans, 1969: 82; Warmke & Abbott, 1961: 153, pl. 28, fig. m; Morris, 1973: 274, pl. 74, fig. 10; Abbott, 1974: 332, fig. 4095; Emerson & Jacobson, 1976: 193, pl. 26, fig. 29; Gibson-Smith & Gibson-Smith, 1982: 117; Vokes & Vokes, 1983: 60, pl. 22, fig. 17; Mahieu, 1984, 314 pp.

Tralia (Tralia) ovula (Bruguière). Zilch, 1959: 67, fig. 215.

Tralia ovula sculpta Nowell-Usticke, 1959: 88 [St. Croix-by-the-Sea, Cane Bay, St. Croix; lectotype herein selected AMNH 220313 (Fig. 384); listed on page VI as *Tralia ovulata sculpta*].

Tralia cf. *ovula* (Bruguière). Gibson-Smith & Gibson-Smith, 1979: 22 [Cantaure Formation, Venezuela (Miocene)].

Tralia venezuelana Gibson-Smith & Gibson-Smith, 1982, figs. 7–9 [Borburata, Falcón State, Venezuela; holotype USNM 784719 (Fig. 377).

Description: Shell (Figs. 377–387, 389–391) to 16 mm long, oval-elongate, solid, shiny, uniformely chestnut brown to dark purplish brown, sometimes with one or two paler bands on body whorl. Umbilicus present. Spire low to moderately high, with as many as nine flat whorls sculptured with four or five spiral rows of deep pits. Body whorl averaging 85% of shell length, oval-elongate, with striated, uncarinate shoulder; striations visible over entire body whorl of most young, commonly only on anterior region in adults. Aperture averaging 85% length of body whorl, posteriorly angulate, widely rounded anteriorly, white to dark purple inside; inner lip with three evenly spaced, large white teeth; columellar tooth and posterior parietal tooth of same size, reversely oblique, columellar tooth inclined toward base of aperture; first parietal tooth strongest, perpendicular to columellar axis; excavation posterior to second parietal tooth, bordered outside by more or less conspicuous callus, continuing inwards, commonly with small irregularities, sometimes with prominent denticle; outer lip sharp in juveniles, thick and weakly reflected in gerontic individuals, weakly sinuous posteriorly and with thick callous denticle inside, opposite second parietal tooth; outer lip denticle ridge-like, continuing inside aperture, together with second parietal tooth delimiting relatively wide canal. Inner partition of whorls occupying less than half of the body whorl (Fig. 379). Protoconch smooth, yellowish to brown, with nucleus visible (Figs. 389–391).

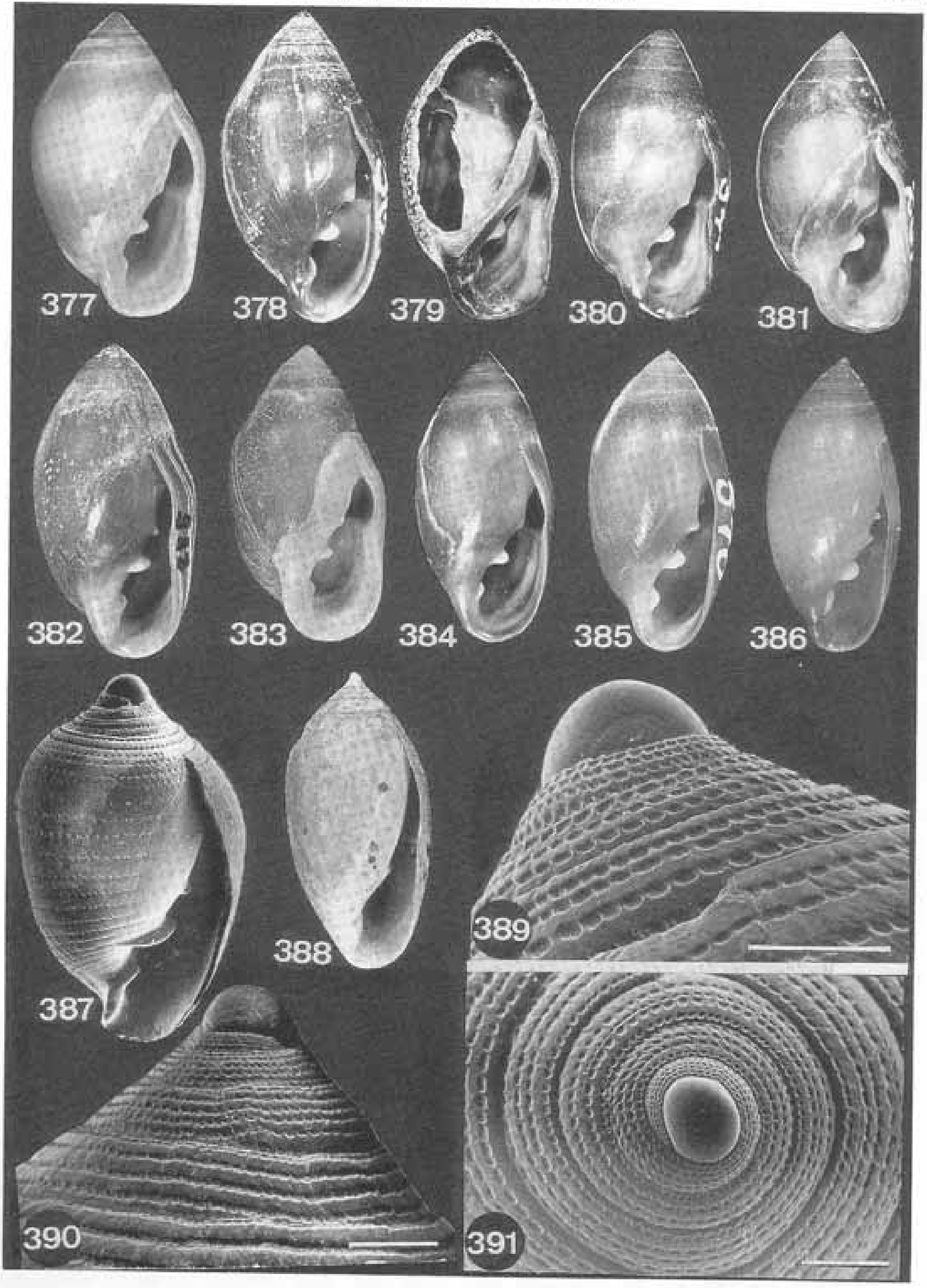
Animal white; foot with transverse groove, whitish, with minute brown spots over bifid posterior end; tentacles dorsoventrally flattened, spatulate, with first quarter bulbous, white, abruptly changing to dark grey or black toward tip; seminal groove unpigmented; mantle skirt with very small brown spots over light brown background. Kidney rectangular, elongate; mantle organ well developed, not pouch-like.

Radula (Figs. 392–396) having formula $[38 + (1 + 15) + 1 + (15 + 1) + 38] \times 115$. Base of central tooth with conspicuous medial prominences on inner edge of arms; crown length about half of that of lateral teeth, broadly triangular anteriorly, elongate posteriorly; ectocones absent. Lateral teeth 13 to 19; crown broadly triangular; conspicuous endocone on first lateral tooth; posterior medial portion of base of remaining lateral teeth flaring at juncture with crown, simulating endocone; last lateral tooth sometimes with very weak ectocone. Transitional tooth with lateral portion of crown posteriorly elongate, with tricuspid ectocone; base almost straight. Marginal teeth 35 to 43; crown very elongate and irregularly pointed posteriorly; mesocone sharp, long, becoming rounded, spatulate, almost as long as remaining denticles, but much stronger; first marginal tooth with conspicuous endocone and a tricuspid ectocone; as many as nine ectocone cusps on last ten marginal teeth.

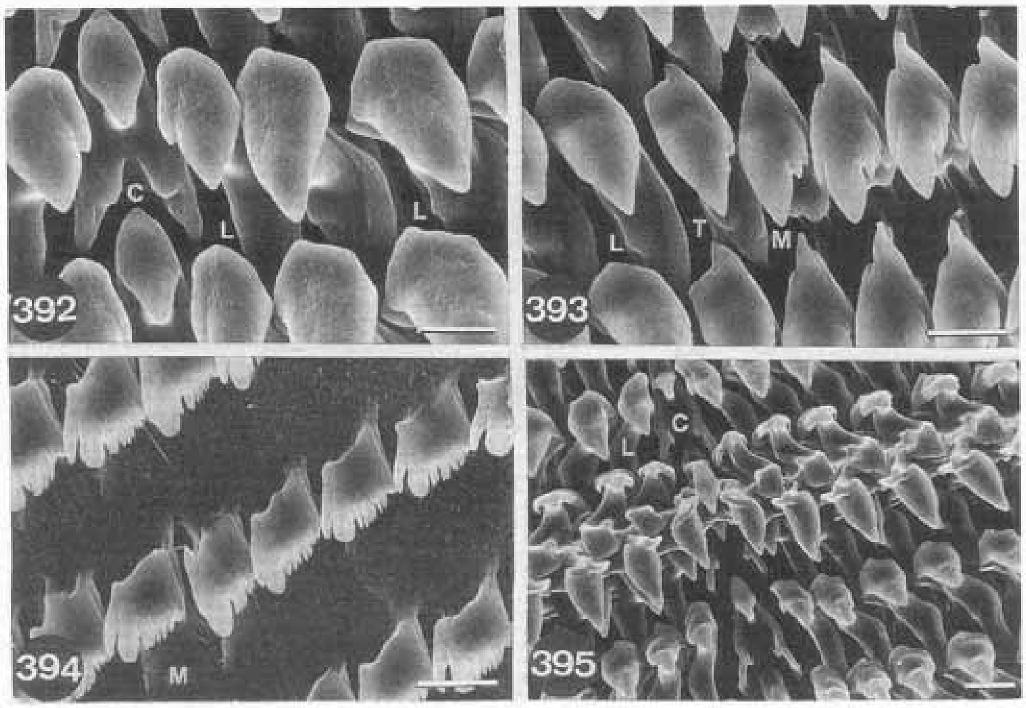
Digestive system with salivary glands attached close together by fine thread on ventral side of white esophagus; posterior crop very dilated, forming pouch before entering stomach; stomach (Fig. 397) as in subfamily; digestive gland pale yellow to bright orange.

Reproductive system (Fig. 398) having ovotestis dark brown with whitish spots, granular; mucous gland and albumen gland interpenetrating at base; spermoviduct cylindrical, very muscular; bursa duct connecting at a point about one-fourth of total length from proximal end of long, muscular vagina; posterior vas deferens about 80% of vagina length; penis long, very muscular, with posterior half sometimes wrapped in membranous sheath; anterior vas deferens of variable length.

FIGS. 377–391. *Tralia.* (377) *T. venezuelana* Gibson-Smith & Gibson-Smith, holotype (USNM 784719), Borburata, Falcón State, Venezuela, sl 12.7 mm. (378) *T. (T.) ovula* (Bruguière), El Palito, Venezuela, sl 13.6 mm. (379) *T. (T.) ovula*, El Palito, Venezuela, sl 13.5 mm. (380) *T. (T.) ovula*, San Juan, Puerto Rico, sl 12.8 mm. (381) *T. (T.) ovula*, Rock Pt., New Providence, Bahamas, sl 14.9 mm. (382) *T. (T.) ovula*, Ilha do Príncipe, Gulf of Guinea (MCZ 73375), sl 9.0 mm. (383) "*Voluta triplicata* Donovan," West Indies (USNM 442093), from Turton's Cabinet, Jeffreys collection, sl 14.8 mm. (384) *T. ovula sculpta* Nowell-Usticke, lectotype (AMNH 220313), St.-Croix-by-the-Sea, Cane Bay, St. Croix, sl 12.0 mm. (385) *T. (T.) ovula*, Haiti (MCZ 18392), sl 10.4 mm. (386) *T. (T.) ovula*, Robin's Bay, Jamaica (USNM 712378), sl 6.4 mm. (387) *T. (T.) ovula*, juvenile, Maravén, Venezuela, sl 2.3 mm. (388) *T. vetula* Woodring, holotype (ANSP 12506), Bowden, Jamaica, sl 5.5 mm. (389) *T. (T.) ovula*, lateral view of spire and protoconch, Tucacas, Venezuela. (390) *T. (T.) ovula*, lateral view of spire and protoconch, Rock Pt., New Providence, Bahamas. (391) *T. (T.) ovula*, top view of spire and protoconch, Haiti (USNM 439659). Scale 1 mm.



FIGS. 377–391.



FIGS. 392–395. *Tralia (T.) ovula*, radular teeth. (392–394) El Palito, Venezuela, sl 14.7 mm. (395) Central tooth and adjacent lateral teeth, with articulation between base of one tooth and crown of next tooth, Bar Pt., New Providence, Bahamas, sl 14.1 mm. Scale 50 µm.

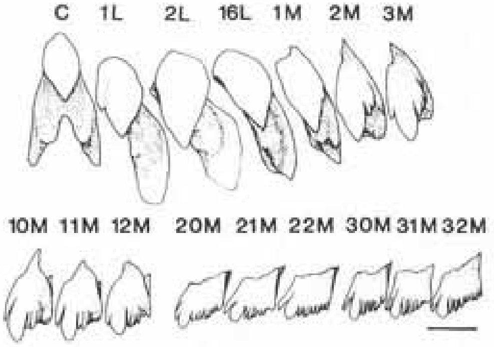


FIG. 396. *Tralia (T.) ovula*, radula, El Palito, Venezuela. Scale 10 µm.

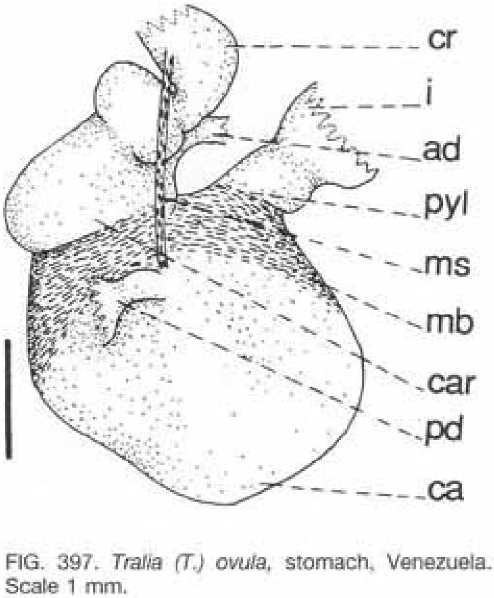


FIG. 397. *Tralia (T.) ovula*, stomach, Venezuela. Scale 1 mm.

Nervous system (Fig. 399) with cerebral commissure as long as width of cerebral ganglion; left parietovisceral connective two to three times longer than right one; left parietal ganglion half size of right one; vis-

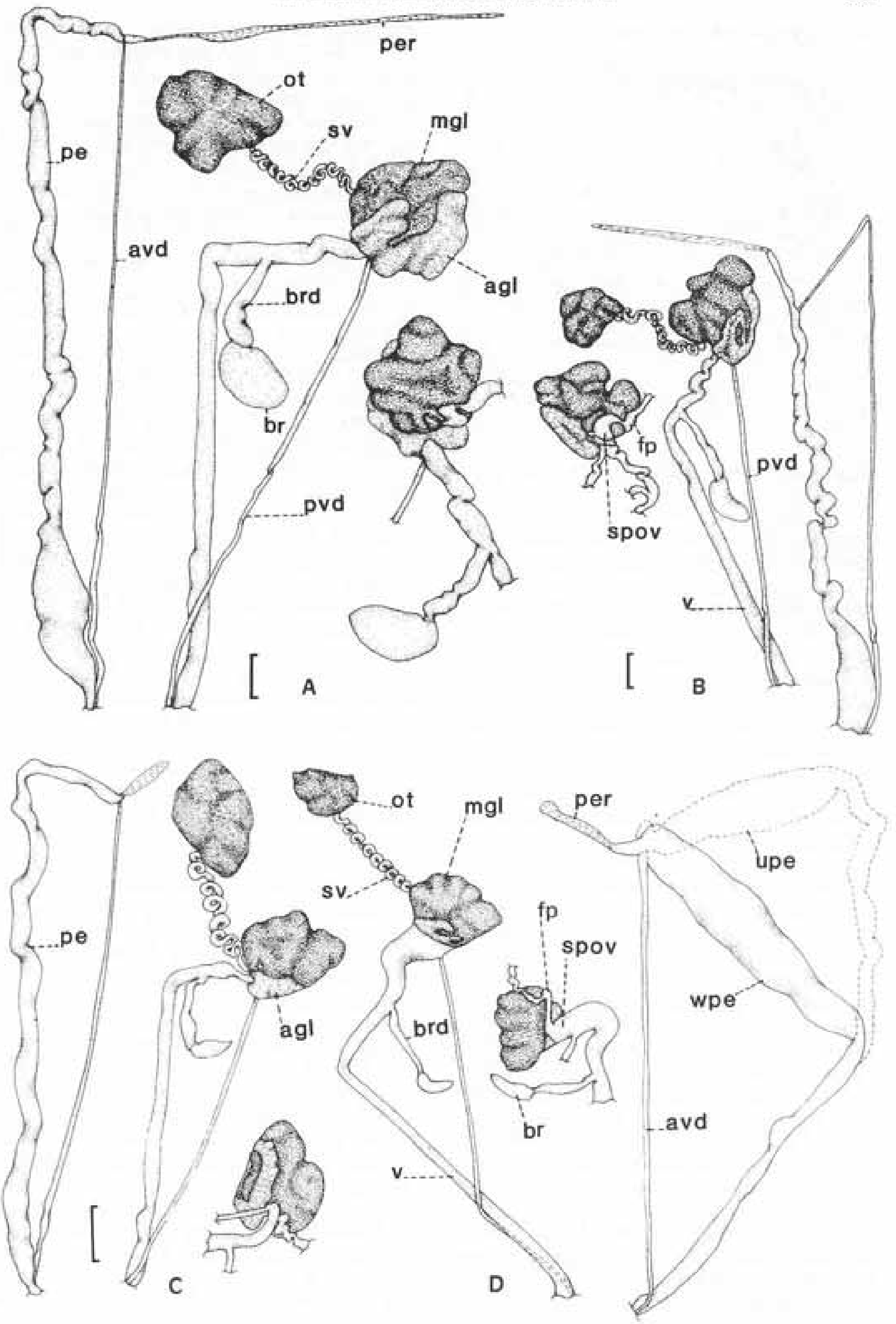


FIG. 398. *Tralia (T.) ovula,* reproductive system. A, Clifton Pt., New Providence, Bahamas; B, Puerto Rico, sl 13.8 mm; C, Tucacas, Venezuela, sl 10.9 mm; D, El Palito, Venezuela, sl 13.8 mm. Scale 1 mm.

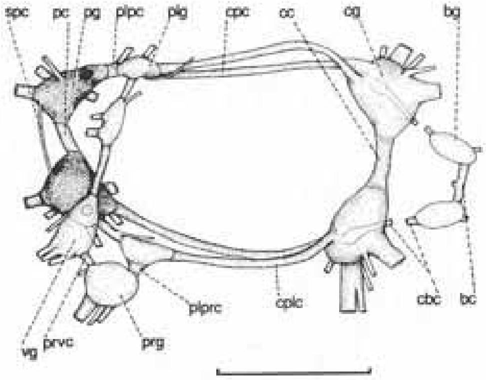


FIG. 399. *Tralia (T.) ovula*, central nervous system, San Juan, Puerto Rico, sl 13.8 mm. Scale 1 mm.

ceral ganglion as large as right parietal ganglion.

Remarks: The names *Bulimus ovulus* Bruguière, 1789, and *Voluta pusilla* Gmelin, 1791, were thought to have appeared in the same year (Dall, 1885) and early authors were more inclined to use the latter. In fact Bruguière's name antedates Gmelin's and it has now been accepted as the correct name by most authors.

Gmelin's description, although mentioning the tridentate columella, is brief and omits the geographic origin of the specimen. The fact that both Gmelin and Bruguière referred to Martini (1773, fig. 446) indicates that these authors were describing the same species.

Donovan (1802) introduced *Voluta triplicata* (Fig. 383) based on material of unknown origin, although Montagu later stated (1808) that the specimens were from Guernsey, England. As in the case of *Melampus (D.) bullaoides* (Montagu) and of its junior synonym *Auricula multivolvis* Jeffreys, Donovan's material might have reached England in the ballast of ships coming from the West Indies. *Auricula (Conovulus) triplicatus* Anton (1839) should not be confused with Donovan's species. Anton referred to the highest (posterior) parietal tooth as the strongest, a characteristic of most Pedipedinae. Connolly (1915) considered Anton's species a junior synonym of *Marinula pepita* King, 1832.

Bruguière (1789) and Dillwyn (1817) both mentioned Martini's (1773) reference to fine, axial striations on the shell; this can refer only to the very fine growth lines that are sometimes visible. The shell can be sculptured with well-marked spiral striae, however (Figs. 387, 389–391). It was on the basis of the spiral striations that Nowell-Usticke (1959: 88) described *Tralia ovula sculpta* in two words, "spire lined" (Fig. 384). Shuttleworth (1858) was the first to mention the five deeply pitted spiral lines on the early whorls, erroneously adding that they were "ciliated" in juveniles. Juveniles and some adults of *Melampus (D.) monile,* which at a first glance can be confused with *Tralia (T.) ovula,* have a crown of hairs on the spire (Fig. 341), but neither the adults nor the young of *Tralia (T.) ovula* have hairs.

Gibson-Smith & Gibson-Smith (1982) described *Tralia venezuelana* from Borburata, Venezuela (Fig. 377), which they distinguished from *Tralia (T.) ovula* on the basis of its pitted spire and the presence of a fourth denticle in the aperture. I have observed a pitted spire, more or less pronounced, on all well-preserved specimens and on all young shells of *Tralia (T.) ovula.* It is particularly marked in some thin-shelled, elongate, dwarf morphs from Cuba, Jamaica, Haiti and St. Croix. The fourth denticle, in the shallow posterior parietal excavation, also occurs in specimens from Cuba, Jamaica, Haiti, Puerto Rico and St. Croix. Specimens from the Bahamas have an irregular surface on the posterior portion of the inner lip, but no distinct denticle. The fourth denticle seems to be a variable character, not associated with differences in radula, anatomy, or shell. Presence of extra parietal teeth has been reported in the Pacific *Melampus fasciatus, Melampus luteus* and *Melampus nucleolus* and it is not considered a reliable taxonomic character for those species (Jickeli, 1872). Extra denticles also occur in *Melampus (M.) coffeus* and *Melampus (M.) bidentatus* (Martins, personal observation). I therefore have placed *Tralia venezuelana* Gibson-Smith & Gibson-Smith in the synonymy of *Tralia (T.) ovula.*

In some Venezuelan specimens the posterior half of the very muscular penis was folded and wrapped in a membranous sheath (Fig. 398D). Such specimens also had an unusually muscular spermoviduct and a shorter anterior vas deferens. Except for larger size (average 14 vs. 12 mm) no other shell and radular characters were associated with the phenomena. They were not associated with the presence of a fourth denticle on the aperture. It is possible that such phenomena are anomalies of gerontic specimens of that population.

There are two reports of fossil West Indian *Tralia*. Woodring (1928) described *Tralia (T.) vetula* from the Pliocene Bowden Formation of Jamaica (Fig. 388). After examining several lots of Recent material from Jamaica, I compared Woodring's example with the thinner-shelled, slender, dwarf specimens of *Tralia* referred to above; I found that these recent specimens show all gradations of thickness. *Tralia (T.) vetula* is considered a distinct species on the basis of the less pronounced dentition of the inner lip, however. Gibson-Smith & Gibson-Smith (1979) reported a *Tralia ? ovula* from the Early Miocene Cantaure Formation of Paraguaná, Venezuela, and also from the Late Pliocene Mare Formation of Cabo Blanco, Venezuela (Gibson-Smith & Gibson-Smith, 1982). In the latter publication the Gibson-Smiths identified those specimens with their *Tralia venezuelana*, which I consider synonymous with *Tralia (T.) ovula*.

Habitat: Tralia (T.) ovula lives along the high-tide mark. The animals prefer piles of boulders on open rocky shores, but they also live in the less-protected mangroves.

Range: Bermuda; Florida Keys; West Indies to Trinidad; Central America to Venezuela; Ilha do Príncipe, Gulf of Guinea, Africa (Fig. 400).

Specimens Examined: FLORIDA (USNM 37597, 39873): Tavernier Key (USNM 492519); Lower Matecumbe Key (USNM 492595); Long Key (A.M.). BERMUDA (MCZ 304151; USNM 6531, 94434). BAHAMA ISLANDS (USNM 492465): GRAND BAHAMA ISLAND (ANSP 173482, 375528): Eight Mile Rock (MCZ 294268); GREAT ABACO ISLAND: Little Harbor (USNM 180486); ANDROS ISLAND (MCZ 58507, 66744, 66756); NEW PROVIDENCE ISLAND: Nassau (USNM 534924); Rock Point (A.M.); Clifton Point (A.M.); RUM CAY (MCZ 304157); LONG ISLAND (ANSP 173483): 3 km NE of O'Neill's (MCZ 304152); GREAT INAGUA ISLAND: Matthewstown (MCZ 304153). TURK'S & CAICOS: TURK'S ISLAND (MCZ 304150; USNM 492469, 509960a). CUBA (ANSP 56807; USNM 10965, 492472): Habana (MCZ 294794); Cayo Birricu (ANSP 362825); Jaimanitas (MCZ 294199); Matanzas (ANSP 167243; MCZ 304168); La Playa (MCZ 304159, 304165); Versalles (MCZ 304154); Varadero (MCZ 304164); Caibarién (MCZ 304163, 304175); Cayo Francés (MCZ 294200); Siboney (USNM 533913); Punta de Piedras (MCZ 304166); Bahia de Santiago (MCZ 304161); Cabo Cruz (MCZ 304156). JAMAICA (ANSP 66964; MCZ 294269, 304158, 304167, 304169, 304174; USNM 49744a, 94745, 492467, 492471, 492593): Montego Bay (ANSP 359145); Robin's Bay (USNM 442092a, 442093); Jack's Bay (USNM 441834); Port Maria (USNM 711209); Buff Bay (USNM 441195); Stoney Cove (USNM 440762); Port Antonio (ANSP 62022; USNM 712147); Priestman's River (USNM 492468); Manchioneal Bay (ANSP 61883; MCZ 9950; USNM 127359; R.B.); Port Royal (USNM 395452a, 442419a); Runaway Bay (USNM 202657); Little River (USNM 128047, 492463). HAITI: Yuma River (ANSP 60950); St. Louis (USNM 439390); St. Marc (USNM 492470); Port Salut (ANSP 226694; MCZ 183922; USNM 440024); Île-à-Vache (USNM 401874, 401875, 439169); Les Cayes (USNM 439746); Torbeck (USNM 402261, 439659); Aquin (USNM 403256a, 440170a); Baïe Anglaise, near Aquin (USNM 439548); between Vieux Bourg and Baïe des Flamands (USNM 403425); N of Metesignix (USNM 404149); Saltrou (ANSP 387078; USNM 439342a, 442813); Bizoton (USNM 439828a). DOMIN-

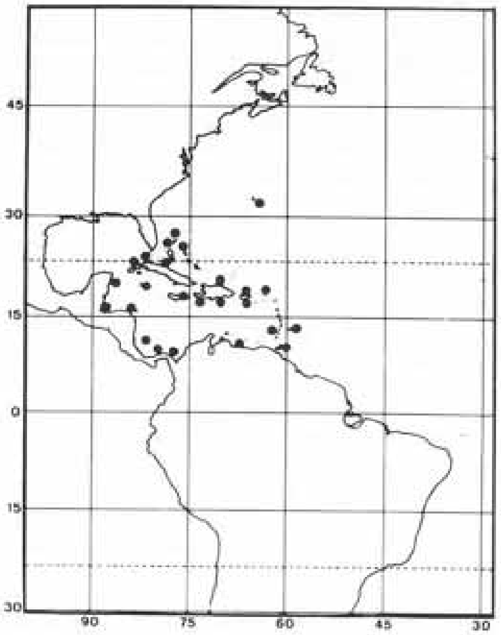


FIG. 400. *Tralia (T.) ovula*, geographic distribution.

ICAN REPUBLIC (MCZ 304172; USNM 151297): Santo Domingo (ANSP 62910); Monte Cristi (MCZ 304162); Samaná (MCZ 281639). PUERTO RICO: Puerta de Tierra, San Juan (A.M.); Rifle Range Beach, Punta Agurejeada (MCZ 233299); Arecibo (MCZ 304160); Cabo Rojo Lighthouse (MCZ 294202); Ensenada Honda, Culebra Island (USNM 169886). VIRGIN ISLANDS: ST. CROIX (ANSP 56806; MCZ 200448, 304155; USNM 621395): Prosperity Beach (MCZ 304173); St. Croix-by-the-Sea, Cane Bay (AMNH 192356, 220313; ANSP 231952); ST. THOMAS (ANSP 56805, 359147; USNM 250034, 530175): Sapphire Beach (ANSP 306673); Water Bay (ANSP 56808); ST. JOHN'S (MCZ 304171); GUANA ISLAND (MCZ 294203): North Bay (ANSP 351790). LESSER ANTILLES: ANGUILLA BANKS (MCZ 294201); ANTIGUA (ANSP 109155; USNM 215048): off Falmouth (USNM 502098); GUADELOUPE (USNM 492466, 492518): Anse-Dumont, Gosier (USNM 758066); BARBADOS: (MCZ 304170, 304177, 304178; USNM 502104, 502105); Bridgetown (USNM 502102); Needham Point (USNM 502101); Maxwell's Coast (USNM 603783); Pelican Island (USNM 502100); GRENADA: Prickly Bay (ANSP 297184); TRINIDAD: South Coast (ANSP 363992). CARIBBEAN ISLANDS: SWAN ISLAND (MCZ 36612, 294267); CAYMAN ISLANDS: Little Cayman (MCZ 294204); ST. ANDREWS ISLAND (ANSP 159360); CURAÇAO: Port Marie and Daaibooi Baai (R.B.). MEXICO: Ascension Bay, Quintana Roo (USNM 736380). BELIZE: Belize (USNM 151050). HONDURAS: Roatan Island (USNM 364701a). COSTA RICA: Portete, Limón (USNM 702826, 706404). PANAMA: Fort Sherman, Devil's Beach (USNM 620530); Toro Point, Fort Sherman (USNM 732868, 734071). COLOMBIA: Sabanilla (USNM 193612). VENEZUELA: Cayo Punta Brava, Parque Nacional de Morrocoy, Tucacas (A.M.); El Palito (A.M.); Borburata (USNM 784719, 784772); Maravén, Borburata (A.M.). EASTERN ATLANTIC: Ilha do Príncipe, Gulf of Guinea (MCZ 73375).

CONCLUSIONS

Phylogeny and Classification

Gastropods have long been divided into prosobranchs, opisthobranchs and pulmonates. Ihering's (1876, 1877) anatomical research led him to conclude that the Gastropoda were polyphyletic. He derived the prosobranchs from the annelids, and the opisthobranchs and the pulmonates from the platyhelminths. Ihering's view has not been accepted and there is consensus that the gastropods are in fact monophyletic. A difference of opinion arises, however, about the way in which the generally more advanced euthyneurans (opisthobranchs and pulmonates) are related to the more primitive streptoneurans (prosobranchs). Pelseneer (1894a) and Hubendick (1945) thought that the euthyneurans arose from the archaeogastropods. Pelseneer based his decision upon the similarities of the rhipidoglossan radula of the trochids with that of the cephalaspideans and basommatophorans. Morton (1955c) slightly modified this view by proposing a pre-archaeogastropod as the ancestor of the archaeogastropods and euthyneurans. A different view was held by Fretter (1946, 1975), Boettger (1954) and Gosliner (1981), who considered the mesogastropod stock as the ancestor of the euthyneurans. For the first two authors this origin would be located near the Rissoacea, on the basis of the size and habitat of the Recent species of that superfamily, which live in marine, estuarine, freshwater and terrestrial habitats. Their small size could explain the loss of the ctenidium, and the invasion of the terrestrial habitat would favor the secondary development of an air-breathing pallial cavity. In addition, the mesogastropod lineage explains the absence of the right kidney throughout the Euthyneura and the similarity of the reproductive tract with that of a female mesogastropod (Fretter, 1975). Gosliner (1981), however, on the basis of the reproductive system, together with the fossil record, considered the Littorinacea as the stock that produced the euthyneurans.

More recently emphasis has been put on the Pyramidelloidea Gray, 1840, a superfamily of mostly small streptoneurans assembled within the suborder Allogastropoda Haszprunar, 1985. Separation of this superfamily from the Opisthobranchia has favored the hypothesis of a common ancestry for the Pyramidelloidea and euthyneurans (Haszprunar, 1985, 1988; Salvini-Plawén & Haszprunar, 1987).

Traditionally the ellobiids have been considered the living representatives of the primitive pulmonates and simultaneously they have been associated with the primitive opisthobranchs. Mörch (1865: 11) was the first to recognize the affinities of pulmonates and opisthobranchs when, on the basis of their hermaphroditism, he included both groups within his subclass Androgyna. Pelseneer (1894a) broadened that relationship by also calling attention to their detorted (euthyneurous) nervous system. This euthyneurous condition led some authors to consider both groups members of the subclass Euthyneura Spengler, 1881 (Boettger, 1954; Taylor & Sohl, 1962; Burch, 1962; Haszprunar, 1985). Others, while recognizing the close similarities between the two groups, still prefer the traditional terminology, considering the Pulmonata and the Opisthobranchia as separate subclasses (Morton, 1955c; Fretter & Graham, 1962; Robertson, 1973; Fretter, 1975; Hubendick, 1978; Salvini-Plawén, 1980).

Pelseneer (1893, 1894a), Thiele (1935) and Boettger (1954) derived the pulmonates from the cephalaspidean *Acteon* and considered the ellobiids to be the link between the two groups. Pelseneer found support for his decision in the earlier fossil record of the acteonids and on the similarities of the shell apertures of the acteonids and ellobiids. Morton (1955c) suggested that these conchological characters might be adaptive only and, as such, their taxonomic value is not significant. As Harry (1951) pointed out, the heterostrophy common to the ellobiids and the opisthobranchs constitutes a much stronger taxonomic character. More common is the opinion that the opisthobranchs and pulmonates arose from the same prosobranch stock, not one from the other (Morton, 1955c; Fretter, 1975; Gosliner, 1981).

Within the pulmonates, the relationship between the basommatophorans and the stylommatophorans also has been the object of several hypotheses. Apart from the direct line "opisthobranch-ellobiid (basommatophoran)-stylommatophoran" scheme advocated by Pelseneer (1893, 1894a), Hedley (1917) and Boettger (1954), the more commonly held opinion is that the basommatophorans are too diverse to be considered collectively as ancestors to the stylommatophorans. Burch (1962), based on the number of chromosomes, proposed that a hypothetical prebasommatophoran (called Ur-Basommatophora) with opisthobranchiate ancestry might have given rise to Morton's (1955c) Archaeopulmonata and Branchiopulmonata. The first group includes the Ellobiidae, Amphibolidae and Siphonariidae, commonly considered the "lower basommatophorans." The second group includes the freshwater pulmonates, or "higher limnic basommatophorans." According to this view the Stylommatophora are polyphyletic, although having all originated from the Archaeopulmonata. Harry (1964) slightly modified Burch's phyletic tree by adding a "pre-pulmonate" ancestor to the Urbasommatophora [*sic*]. A similar framework of classification, also followed here, was adopted by Van Mol (1967), Hubendick (1978), Salvini-Plawén (1980), Boss (1982) and Tillier (1984), who restricted the term Basommatophora to Burch's "higher limnic basommatophorans."

Quite a different view was proposed by Starobogatov (1976), mostly on the basis of the reproductive system. He reversed the direction of the evolutionary relationships within the pulmonates and considered the basommatophorans as derived from the stylommatophoran stock. Starobogatov did not consider the widespread fusion of the ganglia in the stylommatophorans, a condition that is considered derived. Reversal to a more dispersed condition of the ganglia is very unlikely and has not been reported for other groups.

Phylogenetic relationships within the Ellobiidae, although obscured by the presence in each subfamily of primitive and derived characters, can be elucidated by comparing the reproductive and nervous systems. Diauly, nonglandular condition of the pallial gonoducts and ganglionic concentration on the nervous system are derived conditions (Gosliner, 1981; Haszprunar, 1985, 1988; Salvini-Plawén & Haszprunar, 1987); I consider these features decisive in the interpretation of the degree of departure from the ancestral plan. A tentative phylogenetic tree elaborated on that basis is presented in Figure 401 and Tables 5 and 6 (Appendix).

Consistent patterns of organization allowed a clear delimitation of subfamilial boundaries. Five types of organization of the reproductive system were identified, corresponding to Morton's (1955c) subfamilial divisions, for which they are named. First is the Pythiinian type, monaulic, with the anterior mucous gland and prostate gland running parallel to each other and covering the pallial gonoduct as far as the vaginal atrium. Second is the Ellobiinian type, diaulic, with the anterior mucous gland and prostate gland covering the pallial gonoducts for all their length. Third is the Carychiinian type, monau-

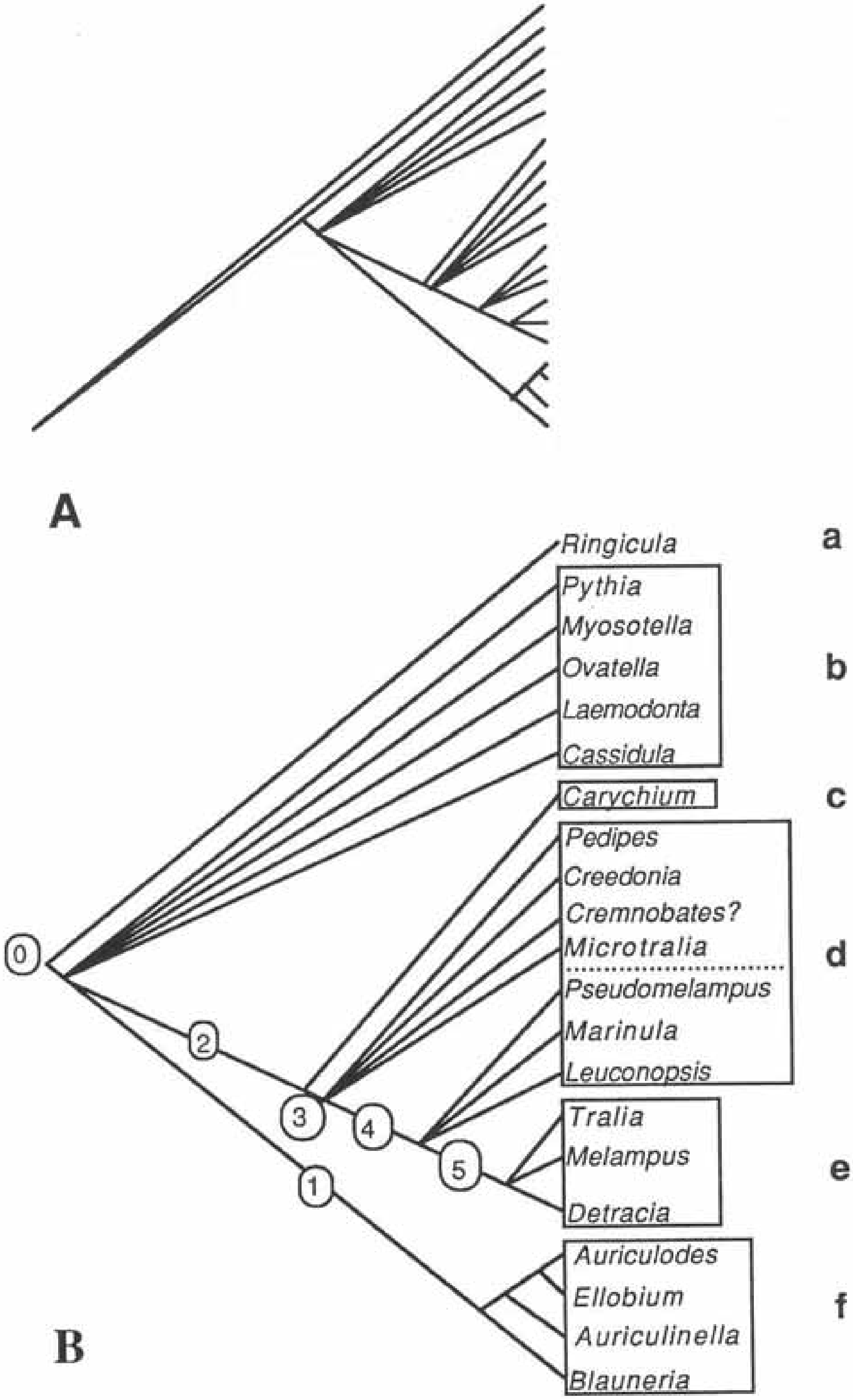

A
Ringicula
a
Pythia
Myosotella
Ovatella
b
Laemodonta
Cassidula
Carychium
c
Pedipes
Creedonia
Cremnobates?
Microtralia
d
Pseudomelampus
Marinula
Leuconopsis
Tralia
Melampus
e
Detracia
Auriculodes
Ellobium
f
Auriculinella
Blauneria
0
2
3
4
5
1
B

FIG. 401.

lic, with the pallial gonoduct glandular and the prostate gland concentrated distally in the gonoduct. Giusti (1975), in a sketchy representation of the reproductive system of *Zospeum*, left doubt whether the system is monaulic or diaulic, but the glandular appearance resembles the pythiinian or ellobiinian types; however, dissections of *Carychium* cf. *tridentatum* from the Azores using superficial staining with methylene blue (Martins, personal observation) indicated an agglomeration of what appeared to be a prostate gland near the distal portion of the pallial gonoduct, thus substantiating Morton's (1955c) interpretation. Fourth is the Pedipedinian type, monaulic or incipient semidiaulic, with the anterior mucous gland and the prostate gland covering only the proximal half of the pallial gonoduct. Fifth is the Melampinian type, advanced semidiaulic, with a very short, nonglandular spermoviduct and separated, nonglandular, long vagina and posterior vas deferens.

Although not so discrete as in the reproductive system, patterns were found in the organization of the central nervous system, concerning the relative lengths of the various connectives. Three types were identified. The Pythiinian type has a wide visceral nerve ring and a long right parietovisceral connective. The Ellobiinian-Carychiinian type has a wide visceral nerve ring, sometimes with marked chiastoneury, and a very short right parietovisceral connective. The Pedipedinian-Melampinian type has a short visceral nerve ring; the connectives between the cerebral ganglia and the visceral nerve ring are longer and symmetrical in the Melampinae, whereas they are generally shorter in the Pedipedinae, with the right ones longer than the left ones.

The phylogenetic relationships within the different subfamilies of halophilic Ellobiidae are better explained if one considers the Pythiinae as the representatives of the primitive core from which the Ellobiinae, the Carychiinae and the remaining taxa as a third group independently radiated. First, the Pythiinae have a monaulic, glandular pallial gonoduct and a wide visceral nerve ring. *Pythia* still has a very weak remnant of chiastoneury and retains a functional open spermatic duct. The presence of a pallial gland in species of *Pythia, Cassidula, Ovatella* and *Laemodonta* suggests a relationship of that group of the Pythiinae with the terrestrial Carychiinae. Secondly, the Ellobiinae must have separated from the primitive stock very early, for they retain the most primitive nervous system. The reproductive system is diaulic; the pallial gonoducts, although glandular in their entirety, separate immediately anterior to the seminal vesicle, eliminating the spermoviduct. Thirdly, the Pedipedinae and the Melampinae might have arisen from the same stock. In both subfamilies the visceral nerve ring is very short, concentrating the ganglia in the cephalopedal region. In the Pedipedinae there is some proximal concentration of the anterior mucous gland and prostate gland, giving rise to a partly nonglandular pallial duct that is monaulic in most genera. In *Leuconopsis* and *Pseudomelampus* the vas deferens separates some distance before the female genital opening, giving rise to what is called here an **incipient** semidiaulic reproductive system [Visser's semidiaulic system], vaguely resembling a rudimentary step toward the condition in the Melampinae. In this subfamily the reproductive system is here called **advanced** semidiaulic. There is a very short spermoviduct, on which the inconspicuous prostate gland is located, and the anterior mucous gland has completely disappeared. In *Tralia* the bursa duct inserts more distally in the vagina, a fact that suggests that there might have been a proximal migration of that structure and of the spermoviduct. The combination of ganglionic concentration and nonglandular, advanced semidiaulic pallial gonoduct indicates that the Melampinae are the least primitive ellobiids.

The subfamilies, listed in order of increasingly derived characters, are Pythiinae, Ellobiinae, Pedipedinae and Melampinae. As stated above, however, primitive and derived characters occur in each subfamily. The Pythiinae, for example, live farther inland than any other halophilic ellobiid (Morton, 1955c); this habit is seen as a derived condition. Some Pedipedinae (*Pedipes, Creedonia*) do

FIG. 401. Cladograms for Ellobiidae generated by PAUP from data in Tables 5, 6 (Appendix). A, Consensus of 703 trees, all characters included; B, Consensus of 1396 trees, excluding character G, status of sperm groove. a, Outgroup; b, Pythiinae; c, Carychiinae; d, Pedipedinae; e, Melampinae; f, Ellobiinae. O, Plesiomorphies (monauly, pallial ducts entirely glandular, wide visceral nerve ring); 1, Apomorphy diauly; 2, Apomorphy concentration of visceral nerve ring; 3, Apomorphy pallial ducts partly glandular; 4, Apomorphy incipient semidiauly; 5, Apomorphies advanced semidiauly and pallial ducts nonglandular.

not resorb their inner whorls and are considered primitive in this respect. The Melampinae retain a free-swimming veliger larva and, consequently, have a highly heterostrophic protoconch, which is a primitive feature. The occurrence of such a variety in the expression of the different characters within the Ellobiidae obscures the tracing of a linear phylogenetic relationship for the family. I conclude with Morton (1955c) that the evolution among the Ellobiidae is better understood as following a mosaic pattern, in which the organs and the mode of life evolve at different rates in the various taxa.

Zoogeography of the Ellobiidae

The Recent Ellobiidae are a primarily tropical family, distributed in three centers.

The first is the Indo-Pacific center, extending from the East African coast to Polynesia. This center is characterized by large ellobiids, such as *Ellobium, Cassidula* and *Pythia.* Only four of the 21 genera of halophilic ellobiids are not represented in this center, the Mediterranean *Ovatella* and *Auriculinella,* the Eastern Atlantic *Pseudomelampus* and the newly created West Indian *Creedonia.* Besides *Ellobium s.s.* and the other two genera that characterize this center, four others are endemic in the Indo-Pacific, *Cylindrotis,* known from the Philippines and Thailand (Brandt, 1974), *Ophicardelus,* from the Australian region, *Allochroa,* recorded from the Pacific Islands and from the Red Sea, and the widely distributed *Auriculastra.*

The second is the West Indian center, which includes the Neartic and Neotropic regions and Ascension Island. The genus *Melampus* characterizes this center. Ten genera are present in the Western Atlantic, of which only the new genus *Creedonia* is endemic. Of the 18 western Atlantic species seven belong to the genus *Melampus.*

Wallace (1876) assigned with difficulty another mid-South Atlantic island, St. Helena, to his Ethiopian region, but he did not even mention Ascension Island. Rosewater (1975) noted that Ascension Island is very poor in endemic marine mollusks (only one subspecies and the new ellobiid species *Leuconopsis manningi*) and that the malacofauna of the island contains even numbers of species from both sides of the Atlantic. The inclusion of Ascension Island in the West Indian center is justified by the presence of the Western Atlantic *Pedipes mirabilis* and of the new species *Leuconopsis manningi.* These are the only ellobiids reported from that South Atlantic island.

The third is the Mediterranean center, which includes the Macaronesian Islands (Azores, Madeira, Canary Islands and Cape Verde Islands), is characterized by the endemic *Auriculinella* and *Ovatella,* and also by the more widely distributed *Pseudomelampus* and *Myosotella. Pseudomelampus* is reported from South Africa [*Melampus acinoides* (Morelet, 1889)] and *Myosotella,* represented by the extremely variable and equally overnamed *Myosotella myosotis,* has become cosmopolitan.

The tropical character of the ellobiids is well exemplified in their Western Atlantic distribution. Of the 18 recorded species only three are reported from the American coast north of southern Florida, *Melampus (M.) bidentatus, Melampus (D.) floridanus* and the introduced European *Myosotella myosotis.*

Bermuda was included by Wallace (1876) in his Alleghenian subregion of the Neartic, but it appears that the island should belong rather in the Antillean subregion of the Neotropical. Eight (67%) of the ellobiid species not represented on continental shores north of southern Florida were recorded from Bermuda.

Another interesting note is the record of *Tralia (T.) ovula* from the African coast. It appears to be an isolated report, for the genus has not been reported from elsewhere in Africa; however, the 49 specimens collected by Dohrn in 1866 and deposited in the Museum of Comparative Zoology indicate that the species was not rare at Ilha do Príncipe, in the Gulf of Guinea. This West Indian species might have been transported to Africa in the ballast of ships, which I think was important in the dispersal of *Myosotella myosotis* as well.

It is worth noting that both species of *Pedipes,* although broadly overlapping in the West Indies and Bermuda, overlap very little in Florida; I could not substantiate in any museum collection or in my extensive collections any record of *Pedipes mirabilis* from the Florida Keys.

As noted in the remarks under the family, the fossil record of the Ellobiidae is relatively poor. It is interesting that the oldest known fossil ellobiids are the European *Carychiopsis* from the Paleozoic of France. This genus resembles the Recent terrestrial *Carychium,* which is known from the Jurassic of Asia, Europe, America and West Indies (Zilch, 1959). The Paleozoic of Europe contains fossils of the heavily dentate *Traliopsis* and the high-spired *Stolidoma*, which resemble some Recent examples of the Pedipedinae or the Pythiinae. They were most probably halophilic, as were *Rhytophorus* and *Melampoides* [Melampinae] from the Cretaceous of North America. It appears, then, that the ellobiids had already invaded the terrestrial habitat through the Carychiinae during the Paleozoic, which implies that the group had separated very early from the prosobranch stem.

Another interesting note on the paleogeography of the Ellobiidae is the presence of the Recent Indo-Pacific genera *Ellobium* and *Cassidula* in the Eocene of Europe, which suggests a Tethyan distribution.

The Tertiary and Quaternary ellobiid genera of the West Indies are representatives of the Recent fauna both in their taxonomy and geographic boundaries. *Marinula* from the Pacific coast of Costa Rica (Dall, 1912), *Pedipes* from Venezuela (Gibson-Smith & Gibson-Smith, 1979, 1985), *Tralia* from Venezuela (Gibson-Smith & Gibson-Smith, 1982) and Jamaica (Woodring, 1928), and *Melampus (Detracia)* from Virginia (Conrad, 1862) reflect the modern distribution of the respective genera.

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APPENDIX

TABLE 1. Number of specimens used for various morphometric comparisons. G, reproductive organs; R, radula; S, shell.

Species	S	R	G	LOCALITY
M. coffeus	9	5	5	Hungry Bay, Bermuda
M. coffeus	16	9	—	Grassy Key, Florida, U.S.A.
M. coffeus	5	5	5	Knight Key, Florida, U.S.A.
M. coffeus	42	—	—	Big Pine Key, Florida, U.S.A.
M. coffeus	14	5	5	Mullet Key, Florida, U.S.A.
M. coffeus	17	—	—	Hawksbill Creek, Eight Mile Rock, Grand Bahama Island, Bahamas
M. coffeus	5	5	5	South Mastic Pt., Andros Island, Bahamas
M. coffeus	2	—	—	Shore of Millars Road, New Providence Island, Bahamas
M. coffeus	17	—	—	Anegada, Virgin Islands
M. coffeus	5	5	5	Piñones, Boca de Cangrejos, San Juan, Puerto Rico
M. coffeus	5	5	5	Punta Arenas, Puerto Rico
M. coffeus	5	5	5	Laguna Rincón, Bahía de Boquerón, Puerto Rico
M. coffeus	25	5	5	Tucacas, Venezuela
M. bidentatus	10	10	10	Jamestown, Rhode Island, U.S.A.
M. bidentatus	5	5	5	Narrow River, Wakefield, Rhode Island, U.S.A.
M. bidentatus	50	—	—	Stonington, Connecticut, U.S.A.
M. bidentatus	5	5	5	Bivalve, New Jersey, U.S.A.
M. bidentatus	38	23	15	Cedar Island, North Carolina, U.S.A.
M. bidentatus	5	5	5	Woodville, North Carolina, U.S.A.
M. bidentatus	5	5	5	Yemassee, South Carolina, U.S.A.
M. bidentatus	5	5	5	Crescent, Georgia, U.S.A.
M. bidentatus	5	5	5	Valona, Georgia, U.S.A.
M. bidentatus	5	5	5	New Smyrna Beach, Florida, U.S.A.
M. bidentatus	5	5	5	Grassy Key, Florida, U.S.A.
M. bidentatus	18	12	12	Knight Key, Florida, U.S.A.
M. bidentatus	38	—	5	Big Pine Key, Florida, U.S.A.
M. bidentatus	20	20	20	Big Torch Key, Florida, U.S.A.
M. bidentatus	5	5	5	Big Bend Road (Rt. 672), Hillsborough Co., Florida, U.S.A.
M. bidentatus	5	5	5	Hudson, Florida, U.S.A.
M. bidentatus	39	21	21	Hungry Bay, Bermuda

(*continued*)

TABLE 1. Number of specimens used for various morphometric comparisons. G, reproductive organs; R, radula; S, shell (*Continued*).

Species	S	R	G	LOCALITY
M. bidentatus	51	—	—	Mangrove Cay, Andros Island, Bahamas
M. bidentatus	6	6	6	Bonefish Pond, New Providence Island, Bahamas
M. bidentatus	9	9	9	Millars Sound, New Providence Island, Bahamas
M. bullaoides	35	11	—	Hungry Bay, Bermuda
M. bullaoides	5	2	—	Somerset Bridge, Bermuda
M. bullaoides	10	8	—	Big Pine Key, Florida, U.S.A.
M. floridanus	3	—	—	Dividing Creek, New Jersey, U.S.A.
M. floridanus	5	—	—	Woodville, North Carolina, U.S.A.
M. floridanus	15	4	—	Myakka River at Rt. 41, Sarasota Co., Florida, U.S.A.
M. paranus	4	—	—	Pará [Belém], Amazon, Brazil
M. morrisoni	5	—	—	Key Largo, Florida, U.S.A.
M. morrisoni	3	—	—	Long Key, Florida, U.S.A.
M. morrisoni	10	10	10	S of Ocean Dr., Plantation Key, Florida, U.S.A.
M. morrisoni	81	15	—	Grassy Key, Florida, U.S.A.
M. morrisoni	3	3	3	Knight Key, Florida, U.S.A.
M. monile	6	—	—	Long Bird Bridge, Bermuda
M. monile	26	23	—	Shelly Bay, Bermuda
M. monile	4	—	—	Hungry Bay, Bermuda
T. ovula	18	—	—	Rock Pt., New Providence Island, Bahamas
T. ovula	13	10	13	Clifton Pt., New Providence Island, Bahamas
T. ovula	10	—	—	Havana, Cuba
T. ovula	4	—	—	Jamaica
T. ovula	20	—	—	Port Salut, Haiti
T. ovula	81	10	11	San Juan, Puerto Rico
T. ovula	8	—	—	Maravén, Borburata, Venezuela
T. ovula	50	20	20	El Palito, Venezuela
T. ovula	20	—	—	Ilha do Príncipe, Gulf of Guinea
P. mirabilis	40	1	—	Shelly Bay, Bermuda
P. mirabilis	15	—	—	Morgan's Bluff, Andros Island, Bahamas
P. mirabilis	4	—	—	Paradise Island, Bahamas
P. mirabilis	15	1	—	Clifton Pt., New Providence Island, Bahamas
P. mirabilis	20	—	—	San Juan, Puerto Rico
P. mirabilis	18	—	—	Punta Arenas, Puerto Rico
P. mirabilis	19	2	—	El Palito, Venezuela
P. mirabilis	13	1	—	Puerto Cabello, Venezuela
P. ovalis	10	2	—	Ely's Harbour, Bermuda
P. ovalis	40	1	—	Big Pine Key, Florida, U.S.A.
P. ovalis	10	—	—	Mullet Key, Florida, U.S.A.
P. ovalis	10	1	—	Morgan's Bluff, Andros Island, Bahamas
P. ovalis	5	—	—	Clifton Pt., New Providence Island, Bahamas
P. ovalis	2	—	—	Punta Arenas, Puerto Rico
P. ovalis	2	1	—	Puerto Cabello, Venezuela
C. succinea	5	4	—	Long Key, Florida, U.S.A.
M. occidentalis	5	—	—	Hungry Bay, Bermuda
M. occidentalis	4	3	—	Crawl Key, Florida, U.S.A.
L. novimundi	1	—	—	Indian Key, Florida, U.S.A.
L. novimundi	2	—	—	Pigeon Cay, Bimini Islands, Bahamas
L. novimundi	2	—	—	Mintie Bar, South Bight, Andros Island, Bahamas
L. novimundi	1	—	—	Morgan's Bluff, Andros Island, Bahamas
L. novimundi	1	—	—	Mangrove Cay, Andros Island, Bahamas
L. novimundi	8	1	—	Clifton Pt., New Providence Island, Bahamas
L. novimundi	2	—	—	Jack's Bay, Jamaica
L. manningi	13	1	—	English Bay, Ascension Island
M. myosotis	7	7	—	Jamestown, Rhode Island, U.S.A.
M. myosotis	13	7	—	Newport River, Beaufort, North Carolina, U.S.A.
M. myosotis	10	10	—	Hungry Bay, Bermuda
L. cubensis	6	6	—	Grassy Key, Florida, U.S.A.
E. dominicense	14	14	—	Big Torch Key, Florida, U.S.A.
B. heteroclita	10	7	—	Hungry Bay, Bermuda.

TABLE 2. Shell morphometry of several species of *Marinula* and of *Creedonia succinea*. Measurements of *Creedonia succinea* from specimens in my collection; all others from Connolly (1915). AL/BWL, ratio aperture length/body whorl length; BWL/SL, ratio body whorl length/shell length; SL, shell length (mm); W, number of whorls.

SPECIES	SL	W	BWL/SL	AL/BWL
M. pepita	10.4	4.00	0.89	0.76
M. pepita	10.3	4.00	0.91	0.64
M. pepita	9.3	4.00	0.86	0.75
M. xanthostoma	9.9	5.00	0.88	0.71
M. tristanensis	10.4	3.75	0.92	0.92
M. velaini	9.0	3.50	0.93	0.79
M. parva	9.2	4.00	0.91	0.71
M. filholi	7.4	3.50	0.85	0.71
M. mandroni	4.0	—	—	—
C. succinea	3.3	4.50	0.80	0.72
C. succinea	3.3	4.25	0.79	0.69
C. succinea	3.0	4.25	0.79	0.76
C. succinea	3.0	4.20	0.81	0.72
C. succinea	2.8	4.00	0.80	0.70

TABLE 3. Radular formulae of species of *Marinula* and of *Creedonia succinea*. Transitional teeth were counted as lateral teeth; in some cases lateral teeth and marginal teeth were pooled.

SPECIES	RADULAR FORMULA	SOURCE
M. xanthostoma	(112 + 1 + 112) × 180	Odhner (1925)
M. parva	(135 + 1 + 135) × 180	Odhner (1925)
M. juanensis	(45 + 110 + 1 + 110 + 45) × 180	Odhner (1925)
M. tristanensis	(75 + 35 + 1 + 35 + 75)	Connolly (1915)
M. filholi	(121 + 1 + 121)	Powell (1933)
C. succinea	(14 + 10 + 1 + 10 + 14) × 65	Martins, this paper
C. succinea	(12 + 14 + 1 + 14 + 12) × 82	Martins, this paper
C. succinea	(13 + 12 + 1 + 12 + 13) × 62	Martins, this paper
C. succinea	(12 + 12 + 1 + 12 + 12) × 72	Martins, this paper

TABLE 4. Shell measurements and radular counts of young *Melampus coffeus*. LOC, localities: BAH, Millars Road, New Providence, Bahamas; PR, Bahía de Boquerón, Puerto Rico. L_1, L_2, L_3, number of lateral tooth first appearing unicuspid, bicuspid and tricuspid; M, number of marginal teeth; R, number of horizontal rows; SL, shell length (mm); T, number of transitional teeth; W, number of teleoconch whorls; 2–7, number of denticles first appearing on second through fourteenth marginal tooth.

LOC	SL	W	R	L_3	L_2	L_1	T	M	2	3	4	5	6	7
PR	2.33	4.55	—	1	—	7	1	10	2	3	4	5	8	9
PR	3.48	5.85	75	1	3	7	1	14	2	4	6	7	10	12
BAH	4.63	7.10	79	—	7	5	1	19	2	6	8	11	14	—
BAH	4.76	7.50	70	—	6	5	1	16	2	6	8	12	14	—

TABLE 5. Characters used to generate the cladogram presented in Fig. 401. Characters (A-I) as explained in the table; character states (0–3), the condition of each character, from primitive to advanced when polarized; type, polarized (ordered) or nonpolarized (unordered) character; weight (1–4), ascending assigned importance of the character.

CHARACTERS		TYPE	WEIGHT	CHARACTER STATES
A.	Auly (separation of pallial gonoducts)	Ordered	4	0.- Monauly 1.- Incipient semidiauly 2.- Advanced semidiauly 3.- Diauly
B.	Glandular cover of pallial gonoducts	Ordered	4	0.- Entirely covered 1.- Partly covered 2.- Naked
C.	Position of insertion of bursa duct	Ordered	3	0.- Near female genital opening 1.- On anterior third of oviduct 2.- On posterior third of oviduct
D.	Origin of posterior vas deferens (as a nonglandular duct)	Ordered	2	0.- Opposite insertion of bursa duct 1.- Posterior insertion of bursa duct
E.	Pallial gland	Ordered	1	0.- Present 1.- Absent
F.	Status of sperm groove	Ordered	4	0.- Open 1.- Closed
G.	Chiastoneury	Ordered	4	0.- Present 1.- Absent
H.	Oesophageal/Visceral rings (ratio of total length of connectives, excluding ganglia)	Ordered	4	0.- <0.80 1.- 0.80–1.20 2.- 1.21–1.99 3.- >2.00
I.	Parietovisceral connectives (ratio left/right)	Unordered	1	0.- <0.90 1.- 0.90–1.9 2.- 2.0–4.0 3.- >4.0

TABLE 6. Taxa and data matrix used to generate the cladogram presented in Fig. 401. Names in boldface are the taxon and rank represented in the cladogram. Explanation of characters in Table 5. Data on the outgroup *Ringicula* sp. from Fretter (1960) and Gosliner (1981); all others are original. ? no information; * character reversed, owing to sinistrality of the taxon.

		CHARACTERS								
TAXON	LOCALITY	A	B	C	D	E	F	G	H	I
Ringicula sp. [**outgroup**]	North Atlantic	0	0	0	0	0	0	0	0	?
Pythia *plicata* (Férussac)	Thailand	0	0	0	0	1	0	0	1	0
Myosotella *myosotis* (Draparnaud)	Bermuda	0	0	0	0	0	1	1	1	1
Ovatella *aequalis* (Lowe)	Azores	0	0	0	0	1	1	1	0	0
Laemodonta *cubensis* (Pfeiffer)	Bermuda	0	0	0	0	1	1	1	1	0
Cassidula *mustelina* (Deshayes)	Hong Kong	0	0	1	0	0	1	1	1	0
Carychium cf. *tridentatum* (Risso)	Azores	0	0	0	0	1	1	1	2	3
Ellobium (***Auriculodes***) *dominicense* (Draparnaud)	Florida, U.S.A.	3	0	0	0	0	1	0	0	1
Ellobium (***Ellobium***) *aurismidae* (Linnaeus)	Thailand	3	0	1	0	0	1	0	0	3
Auriculinella *bidentata* (Montagu)	Azores	3	0	0	0	0	1	1	0	2
Blauneria *heteroclita* (Montagu)	Bermuda	3	0	0	0	0	1	1	1	1*
Pedipes *mirabilis* (Mühlfeld)	Bahamas	0	1	0	0	0	1	1	3	2
Creedonia *succinea* (Pfeiffer)	Florida, U.S.A.	0	1	0	0	0	1	1	2	1
Marinula (*Cremnobates*) *xanthostoma* (H.& A. Adams)	Oman	0	1	0	0	0	1	1	2	0
Microtralia *occidentalis* (Pfeiffer)	Bermuda	0	1	0	0	0	1	1	3	3
Pseudomelampus *exiguus* (Lowe)	Azores	1	1	0	1	0	1	1	3	2
Marinula (***Marinula***) *tristanensis* Connolly	Gough Id., S Atlantic	1	1	0	1	0	1	1	2	2
Leuconopsis *novimundi* Pilsbry & McGinty	Bahamas	1	1	0	1	0	1	1	2	1
Tralia *ovula* (Bruguière)	Puerto Rico	2	2	2	1	0	1	1	3	3
Melampus (***Melampus***) *coffeus* (Linnaeus)	Florida, U.S.A.	2	2	2	0	0	1	1	3	0
Melampus (***Detracia***) *bullaoides* (Montagu)	Florida, U.S.A.	2	2	2	0	0	1	1	3	2