

PHYLOGENETIC RELATIONSHIPS AND GENERIC REVIEW OF THE BITTIINAE
(PROSOBRANCHIA: CERITHIOIDEA)

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ABSTRACT

The anatomy of seven members of the *Bittium* group is described, clarifying the status of the genus-level taxa comprising it. *Bittium reticulatum*, the type species of *Bittium* Gray, is described in depth, thereby establishing criteria for comparisons with other taxa of Bittiinae. The type species of *Stylidium* Dall and *Lirobittium* Bartsch, and representatives of *Bittiolium* Cossmann and *Cacozeliana* Strand are examined and compared with *Bittium*, s.s. Results of anatomical studies and a phylogenetic analysis using the Hennig86 and CLADOS programs, with *Cerithium* as an outgroup, establish monophyly for Bittiinae Cossmann and reveal six different genus-level taxa. A new genus, *Ittibittium*, from the Indo-Pacific, is proposed. Synonymies of each genus-level taxon and representative species examined are presented. Brief accounts of the ecology and zoogeography of each taxon are given. Two taxa formerly attributed to the *Bittium*-group are herein excluded from it and referred to *Cerithium* Bruguière. These are *Cerithium zebrum* Kiener, 1841, and *Cerithium boeticum* Pease, 1861. The subfamily Bittiinae Cossmann, 1906, is thought to comprise nine genera (four of which were not included in phylogenetic analyses): *Bittium* Gray, 1847; *Bittiolium* Cossmann, 1906; *Ittibittium* gen. n., *Stylidium* Dall, 1907; *Lirobittium* Bartsch, 1911; *Cacozeliana* Strand, 1928; *Argyropeza* Melvill & Standen, 1901; *Varicopeza* Gründel, 1976; *Zebittium* Finlay, 1927. The genus *Cassiella* Gofas, 1987, of uncertain placement, is included as a possible member of the group.

Key words: Bittiinae, *Bittium*, Cerithioidea, anatomy, taxonomy, phylogenetic analysis.

INTRODUCTION

Shells of most small-sized cerithiids are notably difficult to classify, even to familial and generic levels. There has been much confusion and disagreement among malacologists as to the limits and subdivisions of genus-level taxa, because most genera have been defined or based upon convergent shell features alone. Reflective of this unstable taxonomy, unreliable curatorial systems exist in most museums, where many lots of small-sized cerithiid taxa are randomly intermixed with each other and with immature specimens of larger-shelled genera, such as *Cerithium*. These mixed lots frequently are assigned to the convenient "trash basket" category *Bittium*.

The genus *Bittium* Gray, 1847, *sensu lato*, comprises many poorly understood species placed in the family Cerithiidae Bruguière, 1789. The concept of *Bittium* has been generally broad, encompassing many other diverse genera, and opinions on the relationships of the genus with other small-shelled cerithiid groups have also been varied. For these reasons and due to the lack of good

anatomical characters, most of the small-sized cerithioideans were left out of my analysis of cerithioidean phylogeny (Houbrick, 1988).

The most recent revision of the *Bittium* group was published by Gründel (1976), who based his taxonomy and phylogeny of the group on sculptural characters of the protoconch (embryonic spiral formation), ontogenetic sculptural development of the teleoconch, and overall shell form. Gründel (1976) included many fossil and extinct taxa in his revision, but did not consider radular, opercular, and anatomical characters of Recent taxa. Although he noted the similarities of *Bittium* and *Cerithium* Bruguière, 1789, he indicated that *Cerithium* differs considerably from *Bittium* in shell form, sculpture, aperture, and especially in ontogenetic sculptural development. On the basis of the ontogeny of early spiral shell sculpture, Gründel (1976: 38) believed that genera in the *Bittium* group (*Bittium*, *Lirobittium*, *Bittiolium*, *Semibittium*) were descendents of the Jurassic genus *Procerithium* Cossmann, 1902, of the family Procerithiidae Cossmann, 1906. Indeed, he remarked that *Bittium* and *Procerithium* shared greater

TABLE 1. *Bittium*-group genera and species used for anatomical studies (asterisk indicates type species).

Genus	Species	Geographic Region
<i>Bittium</i>	* <i>reticulatum</i> (DaCosta, 1778)	São Miguel, Azores
<i>Bittium</i>	<i>impedens</i> (Hedley, 1899)	Honolulu, Hawaii
<i>Bittiolium</i>	<i>varium</i> (Pfeiffer, 1840)	Ft. Pierce, Florida
<i>Bittiolium</i>	<i>alternatum</i> (Say, 1822)	Provincetown, Massachusetts
<i>Ittibittium</i>	<i>parcum</i> (Gould, 1861)	Honolulu, Hawaii
<i>Lirobittium</i>	<i>subplanatum</i> Bartsch, 1911	Palos Verdes, California
<i>Lirobittium</i>	<i>attenuatum</i> (Carpenter, 1864)	Catalina Id., California
<i>Stylidium</i>	* <i>eschrichtii</i> (Middendorf, 1849)	Carmel, California
<i>Cacozeliana</i>	* <i>granaria</i> (Kiener, 1842)	Albany, Western Australia

similarities in ontogenetic sculptural development and overall shell morphology than did *Bittium* and *Cerithium*. Gründel (1976: 40) noted that the genera *Argyropeza* Melvill & Standen, 1901, and *Varicopeza* Gründel, 1976, usually placed near *Bittium*, were strikingly similar in their ontogenetic sculptural development and morphologies to species of the Jurassic genus *Cryptaulax* Tate, 1869 (Procerithiidae), and stated that he considered *Argyropeza* and *Varicopeza* to be recent members of Procerithiidae. Under Procerithiidae, he assigned the *Argyropeza-Cryptaulax* group to the subfamily Cryptaulaxinae Gründel, 1976, which he believed showed many of the "ancient characteristics" of the family, and the *Bittium-Procerithium* group to the subfamily Procerithiinae Cossmann, 1902. Gründel (1976) considered both subfamilies to have developed independently of one another and to have been separate since the Dogger (Middle Jurassic).

Houbrick (1977) discussed the status of *Bittium* Gray, 1847, and included a historical review, extensive synonymy, and a conchological redescription of the genus. This paper noted that most of the supraspecific taxa associated with the *Bittium* group are parochial in conception and scope, based on specific rather than generic characters, and convey little or misleading phylogenetic information about the group. In the interest of pragmatism and taxonomic parsimony, it was suggested that many of the generic and subgeneric names be abandoned or synonymized with *Bittium*, *sensu lato*, until the entire group was properly evaluated on the basis of more than shell characters.

Since Gründel's (1976) work and my paper on *Bittium* (Houbrick, 1977), studies on a number of *Bittium*-like genera and other small-shelled cerithioidean taxa have been

published: *Dahlakia* (Houbrick, 1978), *Argyropeza* (Houbrick, 1980a), *Varicopeza* (Houbrick, 1980b, 1987a), *Glyptozaria* (Houbrick, 1981a), *Alaba* and *Litiopa* (Kosuge, 1964; Houbrick, 1987b; Luque et al., 1988), *Colina* (Houbrick, 1990a), *Plesiotrochus* (Houbrick, 1990b), and *Diala* (Ponder, 1991). Many of these papers include anatomical data that have helped partially to untangle the confusing mixture of cerithiid genera of similar small-shelled morphology.

The relationships of small-shelled species of the family Obtortionidae Thiele, 1925, which are very similar to those of members of the Bittiinae, remain uncertain because anatomical characters are unknown. It is unclear if Obtortionidae constitutes a separate family or should be included under Bittiinae.

MATERIALS AND METHODS

The goals of this study are threefold: first, to examine the anatomy of *Bittium reticulatum* (DaCosta, 1778), the type species of the genus, thus setting the limits of the genus with a description of distinctive anatomical characters; second, to study the anatomy of a number of other "*Bittium*" species, thereby establishing the validity or artificiality of other component groups or closely related higher taxa; and third, to make a phylogenetic analysis of the group based on a morphological data set that includes more than shell characters.

This revision is based primarily on collections of preserved material in the USNM and on living material studied in the field. Fossils representing extinct genera and species were not considered, although a brief survey of extinct forms and their possible relationships to living members of the *Bittium*-group is in-

cluded. The great number of species and higher category groups traditionally included under *Bittium*, *sensu lato*, and the difficulties of obtaining good anatomical material precluded an exhaustive, comprehensive anatomical study of all members the group. Instead, I decided to look at representative taxa of genera assigned to the *Bittium*-group comprising species having diverse shells from widely different geographic regions. A total of seven *Bittium*-group species representing five higher taxa (genera) from different localities were examined by dissecting live-collected material and by studying living populations *in situ*, where possible. These species are listed below in Table 1 and include the type species of *Bittium* Gray, 1847, *Stylidium* Dall, 1907, and *Cacozeliana* Strand, 1928, and representative species of *Bittiolium* Cossmann, 1906, *Lirobittium* Bartsch, 1911, and a new genus, described herein. Two other species, each having a distinctive shell morphology, and considered as putative genera formerly attributed to "*Bittium*," *s.l.*, were also studied in the field: "*Bittium*" *zebrum* (Kiener, 1841) from Pago Bay, Guam, and Enewetak Atoll, Marshall Islands; and "*Bittium*" *boeticum* (Pease, 1861), from Honolulu, Hawaii. When the soft parts of these two species were examined, they were found to lack an epipodial skirt, and the ciliated ridge tract and spermatophore bursa in the lateral lamina of the pallial oviduct, characters distinctive of members of the *Bittium*-group. Therefore, both species were excluded from the *Bittium*-group and assigned to *Cerithium* Bruguière. Due to the current alpha-level taxonomic disarray of the *Bittium*-group, I have attempted to present a comprehensive, annotated synonymy and have illustrated the shells of the species studied in this review. I hope that this will give other workers an unequivocal idea about the species and genera they represent.

All specimens were dissected under water in wax-filled petri dishes using a Wild M-5 dissecting microscope. Methylene blue was used to enhance anatomical features during dissection. Sections were made at 5 μm and stained with Hematoxylin and Eosin. Photomicrography was done using a Zeiss Photomicroscope III.

The emphasis of this study is on the anatomy of *Bittium reticulatum*, the type species of *Bittium*, *s.s.*, which is the criterion against which other *Bittium*-group genera are described and compared in this paper. Descriptions of *Bittiolium*, *Cacozeliana*, *Stylidium*, *Li-*

robittium, and a new genus described herein, are less detailed and emphasize the anatomical differences from *Bittium reticulatum*.

The anatomy of the genera *Argyropeza* and *Varicopeza* is only superficially understood. Anatomical knowledge about *Zebittium* Finlay, 1927, and *Cassiella* remains unknown, because I was unable to obtain preserved material of species representing them; consequently, only the shells are considered in this review.

Phylogenetic Analysis

The guiding principles of this study are those of phylogenetic systematics (Hennig, 1966; Wiley, 1981). The Hennig86 computer package, version 1.5, ie and bb options (copyright James S. Farris, 1988) and CLADOS, version 1.2 program (copyright Kevin C. Nixon, 1988, 1991, 1992) were used to analyse data and construct trees.

Phylogenetic analysis of six genus-group taxa of the Bittiinae (*Bittium*, *Ittibittium*, *Bittiolium*, *Lirobittium*, *Stylidium*, and *Cacozeliana*) was undertaken using 21 morphological characters comprising 51 character states derived from the shell, operculum, radula, and soft anatomy of the taxa listed in Table 1. Initially, there were 30 characters, but these were reduced to 21. Seven of the 21 characters were multi-state characters. Autapomorphies defining terminal branches, which were not part of multistate series, were not included in the analysis, but were retained for the diagnosis of each genus-group taxon. Multi-state characters were unordered.

Genus-Group Taxa Analysed

Six genus-group taxa were included: *Cacozeliana*, *Lirobittium*, *Stylidium*, *Bittium*, *Ittibittium*, and *Bittiolium* (Table 1). The phylogenetic analysis excluded poorly known genera that have been assigned without justification to Bittiinae, such as *Zebittium* and *Cassiella*. Although the shell morphologies, opercular and radular characters of *Argyropeza* and *Varicopeza* have been well studied (Houbrick, 1980a, 1980b), these genera also were left out of the analysis because of lack of anatomical data.

Outgroup Selection

The genus *Cerithium* Bruguière, family Cerithiidae Férussac, 1819, was selected as the

TABLE 2. Comparison of dentition of radular teeth among genera (C = central or main cusp; numbers signify no. of denticles).

Taxon	Rachidian	Lateral	Inner Marginal	Outer Marginal
<i>Bittium</i>	2-3+C+2-3	1+C+3-6	3-4+C+4	3-4+C+0
<i>Bittiolium</i>	3+C+3	2+C+3-4	3-4+C+2-3	6+C+0
<i>Ittibittium</i>	2+C+2	1+C+3-4	2+C+3	5+C+0
<i>Lirobittium</i>	6+C+6	6+C+15-17	15-19+C+5-6	15-19+C+0
<i>Stylidium</i>	2+C+2	1+C+3-4	4-5+C+3	4+C+0
<i>Cacozeliana</i>	2+C+2	1+C+3-4	5-6+C+3-4	4+C+0
<i>Argyropeza</i>	2-3+C+2-3	1+C+5-6	5-6+C+4-5	5-6+C+0
<i>Varicopeza</i>	3-4+C+3-4	1+C+5-6	3-4+C+3	3+C+0

outgroup to root the trees generated by the analyses. The *Bittium*-group traditionally has been considered as a subfamily (Bittiinae) of Cerithiidae by various authors (see below, for history). *Cerithium*, subfamily Cerithiinae, is the most appropriate group to use for outgroup comparison, because it is the closest sister group that is well known anatomically. The anatomy of *Cerithium* species has been described by Houbrick (1971, 1978, 1992) and is very similar to that of Bittiinae members. However, *Cerithium* species have more generalized and less complex external features. Several external anatomical features of members of the *Bittium*-group, such as a metapodial mucus gland, and the epipodial skirt and associated papillae, are lacking in *Cerithium*. The anatomy of such small-sized snails as *Bittium* may be highly derived and/or modified due to their reduction in size. *Cerithium* species are generally much larger animals than "*Bittium*" species, but a number of species are very small and often are confused with "*Bittium*" species.

Among small-shelled cerithioideans, *Litiopa* and *Alaba*, family Litiopidae, were considered as possible outgroup candidates. These small snails have external features, such as an epipodial skirt and epipodial tentacles, similar to those seen among members of the Bittiinae, and are well known anatomically; however, they differ from bittiid species in internal anatomy (Kosuge, 1964; Houbrick, 1987b; Luque et al., 1988). Phylogenetically, Litiopidae is far removed from the family Cerithiidae (Houbrick, 1988: 114), and is therefore rejected as a suitable outgroup.

Another group of small-shelled species, the Dialidae, was also considered as a possible outgroup. However, only one species is known anatomically (Ponder, 1991), and Healy (1986) has shown that the paraspermatzoa of *Diala* are unique and highly derived

among cerithioideans. Ponder's (1991) phylogenetic analysis showed that dialids were closely related to litiopids and far removed from Cerithiidae (Ponder, 1991: 514). *Diala* was therefore rejected as an outgroup.

Characters

The characters listed below comprise three categories: shell characters (1-5), anatomical characters (6-19), reproductive characters (20-21). Radular characters were eliminated from the final analysis because of their autapomorphic condition. Nevertheless, radular characters are important diagnostic characters of genera and are summarized in Table 2.

Because the polarities of multistate characters were largely speculative, all character states were left unordered; i.e., the integer assignment was arbitrary. The coding of these characters and their states are presented in Table 3. An annotated list of the morphological characters and character states used in the phylogenetic analysis is presented below:

Shell Characters: 1. Shell sculpture—0 = spiral; 1 = cancellate. Most members of the subfamily are characterized by a markedly cancellate shell sculpture, in contrast to *Cerithium* species where spiral elements dominate sculptural patterns (Houbrick, 1992). Exceptions are species of the genera *Stylidium* and *Ittibittium*, where spiral sculpture dominates and axial ribs are either lacking or poorly developed.

2. Anal canal—0 = well developed; 1 = weakly developed or missing. A well-developed anal canal is present in *Cerithium* members (the outgroup), but occurs only in two genera of the *Bittium*-group, *Cacozeliana* and *Varicopeza*, and is exceptionally well developed in the latter genus (Houbrick, 1980b).

TABLE 3. Data matrix derived from morphological characters of species representing six genus-group taxa of Bittiinae. *Cerithium* is the outgroup.

Taxon	Character																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bittium</i>	1	1	0	1	0	1	1	0	0	0	2	0	1	2	1	1	1	1	1	0	0
<i>Ittibittium</i>	0	1	0	1	0	0	1	0	0	1	2	1	0	1	1	0	0	0	1	1	1
<i>Stylidium</i>	0	1	1	1	2	0	0	1	1	0	1	0	2	1	1	1	1	1	1	0	1
<i>Cacozeliana</i>	1	0	1	0	2	2	2	0	0	0	1	0	0	0	0	1	1	1	0	0	0
<i>Bittiolium</i>	1	1	0	1	1	0	1	0	0	1	3	0	1	1	1	0	1	1	1	0	0
<i>Lirobittium</i>	1	1	1	1	0	1	0	1	1	0	1	1	2	1	1	0	1	1	1	2	1

3. Varices—0 = present; 1 = absent. Varices, thickened, former growth lines, are a common feature of most cerithiids and occur among members of Bittiinae with the exception of *Lirobittium* and *Stylidium*.

4. Anterior canal—0 = well developed; 1 = weakly developed. The anterior siphonal canal is a strong feature on most cerithiids, but in smaller-shelled taxa frequently is poorly developed (most Bittiinae) or absent (*Cassidella*, *Cerithidium*).

5. Protoconch sculpture—0 = two spiral lirae; 1 = one spiral lira; 2 = entirely smooth. Most outgroup species have strong spiral sculptural elements on their protoconchs (Houbrick, 1992). Bittiinae genera range from species with spiral sculpture to those having only one weak spiral lira or no sculpture, but this is probably reflective of the type of development.

Anatomical Characters: 6. Opercular morphology—0 = ovate shape; 1 = round, circular shape; 2 = round shape with fringed spiral edges. *Cerithium* species have opercula with an ovate shape (Houbrick, 1992), and it is thought herein that the more circular shape observed among several *Bittium*-group taxa are modifications due to size reduction, although this is not always the case (exceptions in *Ittibittium* and *Bittiolium*, both small shelled genera). The spirally fringed condition seen in *Cacozeliana* departs from the norm and is probably derived.

7. Snout shape—0 = wide; 1 = narrow, elongate; 2 = short, narrow. This character is a variable feature among cerithiids. *Cerithium* species usually have large, wide, muscular snouts (Houbrick, 1992), whereas they tend to be narrow and elongate in members of the Bittiinae, especially among taxa of the *Bittium* clade (*Bittium*, s.s., *Ittibittium*, *Bittiolium*).

8. Cephalic tentacle length—0 = elongate; 1 = short. Among cerithiids and the Bittiinae, cephalic tentacles are usually elongate and much longer than the snout, but in the eastern Pacific genera *Lirobittium* and *Stylidium*, the tentacles are much shorter than the length of the snout.

9. Eye size—0 = normal; 1 = small; 2 = large. Most cerithiids have eyes of normal size, but in such deep-water species as *Argyropeza* and *Varicopeza*, the eyes are very large, possibly an adaptation to water depth and poor light. In contrast, the eyes of *Stylidium* and *Lirobittium* species are exceptionally small.

10. Metapodial mucus gland—0 = absent; 1 = present. Although this structure is absent in the outgroup, it does occur among a few other cerithioidean groups (Litiopidae [*Alaba*, *Litiopa*], Cerithiidae [*Colina*]; Houbrick, 1987b, 1990a, respectively). This gland may be an adaptation to an algal and/or high energy habitats. Species having a metapodial gland are known to use the mucus thread secreted by the gland to anchor themselves while they climb about the algal fronds (Houbrick, 1987b, 1990a).

11. Epipodial skirt—0 = rudimentary; 1 = well developed, smooth; 2 = well developed, papillate along edges; 3 = well developed, scalloped. *Cerithium* species have a weak operculigerous lobe on the rear of the foot, which is here interpreted as a rudimentary posterior epipodial skirt. In Bittiinae species, the skirt extends forward along the sides of the foot to form a fully developed epipodial skirt. An epipodial skirt occurs also among small-shelled members of the Litiopidae (Kosuge, 1964; Houbrick, 1987b; Luque et al., 1988) and the Dialidae (Ponder, 1991). Although this character is homoplastic among cerithioideans, an epipodial skirt is characteristic of Bittiinae.

TABLE 4. Comparison of developmental features among Bittiinae genera and species.

Taxon	Max. Shell Length	Protoconch Sculpture	Developmental Type	Egg Size
<i>Bittium</i>				
<i>reticulatum</i>	15 mm	2 spirals	planktonic	0.1 mm
<i>Ittibittium</i>				
<i>parcum</i>	6 mm	2 spirals	direct	0.2 mm
<i>Bittiolum</i>				
<i>varium</i>	7 mm	1 spiral	planktonic	0.1 mm
<i>Lirobittium</i>				
<i>subplanatum</i>	10 mm	2 spirals	direct	0.5 mm
<i>Stylidium</i>				
<i>eschrichtii</i>	17.5 mm	smooth	direct	0.2 mm
<i>Cacozeliana</i>				
<i>granaria</i>	24 mm	smooth	planktonic	0.1 mm
<i>Argyropeza</i>				
<i>divina</i>	7.6 mm	2 spirals	planktonic	?
<i>Varicopeza</i>				
<i>varicopeza</i>	10 mm	1 spiral	planktonic	?

12. Ovipositor—0 = present; 1 = absent. This gland, although common among cerithioideans, is absent in some taxa, such as those having internal brooding (Houbrick, 1987c). The absence of an ovipositor in females may be falsely scored, as it is thought that its presence can be easily ascertained only during breeding season; moreover, this gland is also difficult to detect in some preserved specimens. Among Bittiinae, the ovipositor is absent only in *Ittibittium* and *Lirobittium*.

13. Osphradial morphology—0 = bipectinate; 1 = monopectinate; 2 = vermiform. This character varies greatly among Bittiinae genera. Although the osphradium in *Cerithium* species is bipectinate, it is vermiform among most other cerithioidean families, such as the estuarine Potamididae and freshwater families Thiaridae and Pachychilidae (Houbrick, 1988, 1991).

14. Osphradial length—0 = equal to ctenidial length; 1 = a little less than ctenidial length; 2 = one-half the ctenidial length. This is a highly variable character, but often diagnostic of some taxa. No overlap among character states was detected in the species studied.

15. Zygoneurous nervous system—0 = absent; 1 = present. Bouvier (1887) documented a zygoneurous condition among some cerithiids, and this was summarized by Houbrick (1988). Zygoneury is absent in *Cerithium*, and in all Bittiinae except for *Bittiolum*.

16. Common opening to sperm pouch and seminal receptacle openings—0 = close together; 1 = far apart. In *Stylidium* and *Liro-*

bittium, the openings have a wide separation, whereas in *Bittium* they are not as far apart. In other bittiids and in most other cerithiids, the openings are close together.

17. Spermatophore bursa location—0 = located in medial lamina; 1 = located in lateral lamina. The spermatophore bursa is found in the lateral lamina in most members of the *Bittium*-group, but in *Ittibittium* and in all other known cerithiids, it occurs in the medial lamina (Houbrick, 1988).

18. Ciliated ridge tract—0 = absent; 1 = present. This structure, one of the synapomorphies defining Bittiinae, is lacking in *Ittibittium* members and in most other cerithiids.

19. Seminal receptacle with grape-like morphology—0 = present; 1 = absent. This grape-like configuration may not represent a distinct morphology, but may be due to the highly filled condition of the receptacle. This condition occurs only in *Cacozeliana*.

Reproductive Characters: 20. Spawn morphology—0 = formed into gelatinous string wound into mass; 1 = short gelatinous tube; 2 = balloon-like cluster. A gelatinous string mass is the common spawn morphology seen among cerithioidean taxa and within Bittiinae. The balloon-like cluster of eggs in members of *Lirobittium* is unique, whereas a short gelatinous tube morphology is seen only in *Ittibittium*: both taxa have few, large eggs and undergo direct development (Table 4).

21. Type of development—0 = planktonic; 1 = lecithotrophic (demersal/direct). Most members of the outgroup have a planktonic

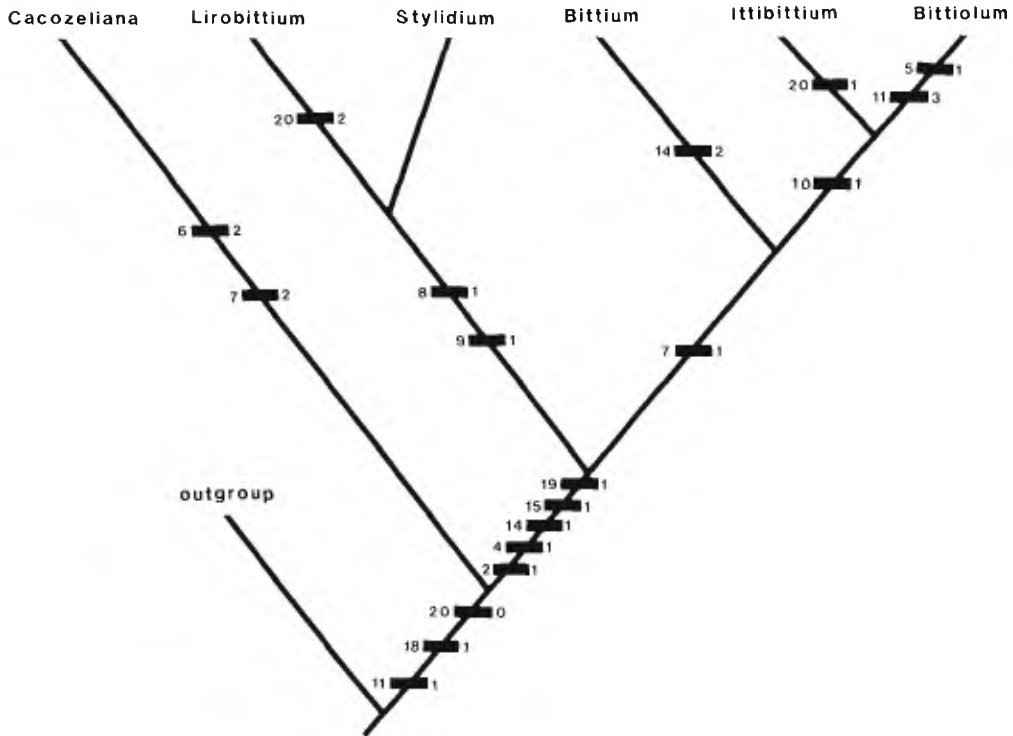


FIG. 1. Cladogram showing relationships among six genera of Bittiinae, using *Cerithium* as the outgroup (L = 41; CI = 70; RI = 53; trees two. Numbers to left of black bars indicate characters: those to right of bars represent character states. Only characters with a CI of 100 are shown).

larval phase in their development. It is thought that planktotrophy can evolve to lecithotrophy but not vice-versa (Strathmann, 1978). Direct developers have larger, fewer eggs per spawn mass (Table 4).

RESULTS

Phylogenetic analysis resulted in two equally parsimonious trees, each with a length of 41 steps, a consistency index of 70, and a retention index of 53 (Fig. 1). The number of steps and the consistency indices of each character used in the construction of the cladogram are shown in Table 5. The supporting branches of both cladograms had identical tree topologies except for the clade supporting *Bittium*, *Ittibittium*, and *Bittiolium*. In the first tree, illustrated herein (Fig. 1), *Ittibittium* and *Bittiolium* are sister groups of *Bittium*, while in the second tree, *Bittium* and *Bittiolium* are sister groups of *Ittibittium*. Both analyses

strongly support the recognition of six genus-level taxa. The monophyly of Bittiinae is established by three synapomorphies (11[1], 18[1], 20[0]) and one homoplastic character (17[1]). The layout of the pallial oviduct, discussed in greater detail below, is the source of two good synapomorphous characters: a ciliated ridge tract and a spermatophore bursa in the medial lamina. An epipodial skirt, while distinctive of the *Bittium*-group, is plesiomorphic, because it occurs also in other cerithioidean groups.

Cacozeliana stands apart at the base of the cladogram from the other taxa and is closest to *Cerithium*, the outgroup. *Cacozeliana* is defined by two autapomorphic characters (6[2], 7[2]) and by two homoplastic characters (5[2], 16[1]). *Cacozeliana* is well separated from all other genera of Bittiinae higher on the tree by five synapomorphies (2[1], 4[1], 14[1], 15[1], 19[1]) and with one homoplastic character (13[1]).

The *Lirobittium*-*Styliidium* clade, which is

TABLE 5. List of steps and consistency indices of characters used in construction of cladogram.

Character	1	2	3	4	5	6	7	8	9	10	11
Steps	3	1	2	1	3	3	2	1	1	1	3
C.I.	33	100	50	100	66	66	100	100	100	100	100
Character	12	13	14	15	16	17	18	19	20	21	
Steps	2	3	2	1	3	2	2	1	2	2	
C.I.	50	66	100	100	33	50	50	100	100	50	

geographically confined to the west coast of North America, is supported by two synapomorphies (8[1], 9[1]), and two homoplastic characters (13[2], 21[1]). In this clade, *Stylidium* is poorly defined by three homoplastic characters (1[0], 5[2], 16[1]), whereas *Lirobittium* is better founded on one autapomorphy (20[2]) and three homoplastic characters (6[1], 12[1], 16[0]).

The *Bittium* clade is supported by one synapomorphy (7[1]) and two homoplastic characters (3[0], 13[1]). *Bittium*, s.s., is defined by one autapomorphy (14[2]) and three homoplastic characters (2[0], 12[1], 18[1]). *Ittibittium* and *Bittiolium*, the sister taxa to *Bittium*, are separated from it by one synapomorphy 10[1]). *Bittiolium* is supported by two autapomorphies (5[1], 11[3]) and two homoplastic characters (11[3], 16[0]). A single autapomorphy (20[1]) and six homoplastic characters (1[0], 12[1], 13[0], 16[0], 17[0], 18[0], 21[1]) define *Ittibittium*. The characters listed above are those derived only from the data matrix (Table 3) used in the construction of the cladogram (Fig. 1). Other autapomorphies defining terminal branches but not part of multistate series were not included in the data matrix. These characters are given under the diagnosis of each genus in the systematic portion of this paper.

DISCUSSION

The phylogenetic analysis of morphological characters of the species in Table 1 resulted in recognition of six different morphological groups (Fig. 1), which are herein interpreted as genus-group taxa under the subfamily Bittiinae Cossmann, 1906. Generic names already exist for five of these groups: *Bittium* Gray, 1847; *Bittiolium* Cossmann, 1906; *Cacozeliana* Strand, 1928; *Stylidium* Dall, 1907; and *Lirobittium* Bartsch, 1911. A new genus, from the Indo-Pacific, is described herein. All of the above genera, with the exception of *Stylidium*, are defined by autapomorphous

characters. If the cladogram shown in Figure 1 is interpreted strictly, *Ittibittium* and *Bittiolium* may be regarded as subgenera of *Bittium*; however, because this is a preliminary revision of the *Bittium*-group, based on only a few representatives of each genus, and not including other poorly known taxa, it is best not to assign differential rank to genus-group taxa at this stage. Therefore, I have decided to treat all terminal nomina as full genera.

As noted in an earlier paper (Houbrick, 1977), other genus-level taxa have been proposed under the *Bittium*-group or are thought to be linked closely to it. Many of these taxa are synonyms of *Bittium*-group genera described herein or have been proposed for fossils. The subfamily Bittiinae, as understood in this paper, is thought herein to comprise nine, possibly ten, Recent genus-group taxa: *Bittium* Gray, 1847; *Bittiolium* Cossmann, 1906; *Ittibittium* gen. n.; *Stylidium* Dall, 1907; *Lirobittium* Bartsch, 1911; *Cacozeliana* Strand, 1928; *Argyropeza* Melvill & Standen, 1901; and *Varicopeza* Gründel, 1976. The genera *Zebittium* Finlay, 1927, and *Cassiella* Gofas, 1987, are provisionally referred to Bittiinae until more information is available.

Argyropeza and *Varicopeza* have been treated previously by Houbrick (1980a, 1980b, 1987a), but their anatomy remains poorly known and they are not described in great detail here. An epipodial skirt has been recorded in *Varicopeza crystallina* (Houbrick, 1987a: 80), but due to poorly preserved anatomical material, this structure could not be ascertained in *Argyropeza* species; however, the radula of *Argyropeza* species (Houbrick, 1980a) is similar to those of members of the *Bittium*-group.

Anatomical knowledge about potential *Bittium*-group species as yet unstudied, such as *Cassiella* from the eastern Atlantic, *Zebittium* from New Zealand, and the many species of small-shelled, *Bittium*-like cerithioideans from the Indo-Pacific, may reveal even more new genus-level taxa to be included under Bittiinae.

SYSTEMATIC TREATMENT OF BITTIINAE

The species studied have been placed into groups (genera) according to the above phylogenetic analysis. The type- or representative species of each genus is described, and notes on reproductive biology and ecology are included, when possible. Shell-length measurements for each species represent the largest specimen observed. Representatives of other genera for which anatomical material was lacking are described from shell morphology and radular morphology, if available.

BITTIINAE COSSMANN, 1906

Bittiinae Cossmann, 1906: 61.
Procerithiinae Cossmann, 1906, *sensu* Gründel, 1976 (in part).

Diagnosis

Shell small, turreted, narrowly elongate to pupate, with moderate spiral and axial sculpture frequently cancellate and/or beaded. Aperture with short but distinct anterior canal. Spiral sculpture usually 4–5 spiral cords per whorl. Animal with epipodial skirt, opercular lobe, and pallial oviducts comprising large sperm bursa and seminal receptacle in posterior part of medial lamina, and spermatophore bursa and ciliated ridge tract in posterior lateral lamina. Ciliated gutter leading from oviduct down right side of foot in females. Glandular ovipositor at base of right side of foot in most species. Nervous system dialyneurous. Spawn consisting of gelatinous, winding strings.

Taxonomic Remarks

The *Bittium*-group (Bittiinae Cossmann, 1906) has been placed under Cerithiidae by nearly all authors (Cossmann, 1906; Thiele, 1929; Wenz, 1938; Golikov & Starabogatov, 1975; Ponder & Warén, 1988), except Gründel (1976), who assigned the group to the Jurassic family Procerithiidae Cossmann, 1906 (erroneously cited by Cossmann as 1905). He allocated 12 genus-group taxa to the subfamily Procerithiinae (= Bittiinae). Of these, *Bittium*, *Bittiolium*, *Semibittium* and *Procerithium* were treated as full genera; *Cerithidium* Monterosato, 1884, *Rasbittium* Gründel, 1976, *Lirobittium* Bartsch, 1911, *Cacozeliana* Strand, 1928, and *Stylidium* Dall, 1907, were considered to be subgenera of *Bittium*. The extinct

taxa *Cosmocerithium* Cossmann, 1906, *Infracerithium* Gründel, 1974, and *Rhabdocolpus* Cossmann, 1906, were treated as subgenera of *Procerithium*. Gründel (1976) also included *Argyropeza* Melvill & Standen, 1901, *Varicopeza* Gründel, 1976, and the extinct genus *Cryptaulax* Gründel, 1976, with subgenera *Pseudocerithium* Cossmann, 1884, and *Xystrella* Cossmann, 1906, in the *Bittium* group under the subfamily Cryptaulaxinae Gründel, 1976. Excluding the Jurassic taxa, the Recent genera *Argyropeza* and *Varicopeza* should probably be included in the Bittiinae, because the few morphological and anatomical characters known about these taxa strongly suggest affinity to this subfamily. The other extinct genus-group taxa and *Procerithium* should be excluded from Bittiinae, because the evidence supporting a relationship of these taxa with the *Bittium*-group is based solely on the ontogenesis of spiral sculpture as seen on the early shell spire, a character which is, at best, tenuous: more characters are needed to lend credence for such a relationship. While Gründel's (1976) hypothesis poses interesting questions, it is founded mostly on shell sculpture, which is taxonomically informative but potentially phylogenetically misleading. Considering the Jurassic age of the *Procerithium* group and the great likelihood of homoplasy in shell morphology, the belief that the *Bittium*- and *Procerithium*-groups are of the same lineage is largely speculative, cannot be falsified, and should not be accepted as evidence for a phylogeny (Houbrick, 1988).

The name *Elassum* Woodring, Bramlette & Kew, 1946, has been traditionally associated with the *Bittium*-group in the literature, and was proposed by Woodring et al. (1946: 68) for Pleistocene and Recent material from southern California previously named *Bittium californicum* Dall & Bartsch, 1901, and originally assigned to the subgenus *Elachista* Dall & Bartsch, 1901. *Bittium californicum* is the type species of *Elachista* by monotypy. However, as *Elachista* is preoccupied, a new name, *Alabina* Dall, 1902, was proposed to replace it. Woodring et al. (1946) did not believe the taxon *californicum* Dall & Bartsch, 1901, was an *Alabina* and thus proposed *Elassum* to accommodate it, noting that the species was more *Bittium*-like than *Alabina*-like. Because *Elachista*, *Elassum*, and *Alabina* have the same type species, *Elassum* becomes a junior synonym of *Alabina*. The shell of the type species somewhat resembles

those of members of the *Bittium*-group, and I concur with Woodring et al. (1946) that it possibly should be included as a component genus of the *Bittium*-group; however, as there is no preserved material of living animals of this taxon to confirm this supposition, *Alabina* [= *Elassium*] is not further treated herein.

Houbrick (1977: 103) initially placed 13 nomina into the synonymy of *Bittium*, *sensu lato*. Subsequent studies on the *Bittium*-group and evidence derived from anatomical characters presented herein now allow exclusion of six genera originally included in that synonymy and a more focused diagnosis of *Bittium*, *s.s.* An annotated list of taxa previously included in the *Bittium*-group, but now excluded, is presented below (Jurassic genera not included):

1. *Bittinella* Dall, 1924 (type species: *Bittium hiloense* Pilsbry & Vanatta, 1908). The type species of this genus is a rissoid of the genus *Isseliella* Weinkauff, 1881, subfamily Rissoiinae (Ponder, 1985: 95; Kay, 1979: 80). *Bittium parcum* Gould, 1861, has been erroneously assigned to *Bittinella* (see below).

2. *Bittiscalia* Finlay & Marwick, 1937 (type species: *Bittium simplex* Marshall, 1917). It is unclear to which group this extinct species should be assigned. Although Finlay & Marwick (1937: 44) placed it under Cerithiidae, they noted its similarity to *Zeacumantus* Finlay, a batillariid (Houbrick, pers. obser.). Their drawing of the type species (Finlay & Marwick, 1937: pl. 5, fig. 20) shows a shell with an anterior canal that is a wide shallow notch, similar to poorly developed anterior canals seen in some *Bittium* and *Alabina* species. Because this is a fossil, we may never know with certainty the correct family assignment. Although the authors placed it under Cerithiidae, they were obviously equivocal about this assignment. It is best to leave *Bittiscalia* under the broader category of Cerithiidae and to exclude it from the more narrow assignment of Bittinae.

3. *Brachybittium* Weisbord, 1962 (type species: *Bittium (Brachybittium) caraboboense* Weisbord, 1962). The type species, a fossil, appears to be an immature or fragmentary *Cerithium* species, judging from its illustration (Weisbord, 1962: pl. 15, figs. 5–6).

4. *Cerithidium* Monterosato, 1884 (type species: *Cerithium submamillatum* Rayneval & Ponzi, in Rayneval et al., 1854). *Cerithidium* was introduced by Monterosato (1884) who noted that it was characterized by a rounded aperture and lack of an anterior canal. Monterosato listed a single species under the ge-

nus, *Cerithium submamillatum* Rayneval & Ponzi, 1854, which he considered a synonym of *Turritella pusilla* Jeffreys, 1860. As Gofas (1987: 110) remarked, the former name was originally given to a Pleistocene fossil which is not conspecific with the Recent species. Gofas (1987) remarked that the designation of *Cerithium submamillatum* as the type species of *Cerithidium* by Cossmann (1906) should prevail over that of *Turritella pusilla* by Wenz (1940). I agree with Gofas (1987: 109–110) that both species are congeneric and have sculpture similar to *Bittium reticulatum*; however, in a *Cerithidium* species examined by Ponder (Ponder, in litt.), the female pallial oviduct was closed, which is very different from the open systems known in all other members of Bittiinae. A closed pallial oviduct has not yet been demonstrated in the type species of *Cerithidium*, but on the basis of the closed system noted by Ponder, *Cerithidium* is excluded provisionally from Bittiinae.

5. *Dahlakia* Biggs, 1971 (type species: *Dahlakia leilae* Biggs, 1971). The type species is a junior synonym of *Cerithium proteum* Jousseume, 1930 (Houbrick, 1978), and I believe both names are probable synonyms of *Cerithium scabridum* Philippi, 1848.

6. *Eubittium* Cotton, 1937 (type species: *Bittium lawleyanum* Crosse, 1863) [not *Eubittium* Cossmann, 1902]. The syntypes of the type species of this genus (MNHN, Paris) are *Batillariella estuarina* (Tate, 1893), which is a batillariid (family Batillariidae), and not closely related to Cerithiidae. In any case, the name *Eubittium* Cotton is a secondary homonym.

7. *Paracerithium* Cotton, 1932 (type species: *Bittium lawleyanum* Crosse, 1863) [not *Paracerithium* Cossmann, 1902]. This taxon is a secondary homonym and has the same type species as the previous taxon, which is a batillariid.

8. *Sundabittium* Shuto, 1978 (type species: *Cerithium fritschi* Boettger, 1883). It is highly unlikely that this fossil genus is related to the *Bittium* group. Shuto himself (1978: 152) was equivocal in assigning it to *Bittium*. The figures of *C. fritschi* depicted by Martin (1914: pl. 5, figs. 132–134) suggest an *Abyssochrysos* species, but this assignment needs confirmation by examination of the type material.

Discussion

The subfamily Bittiinae is characterized by small-shelled species generally having cancellate sculpture and short canals. Monophyly

for Bittiinae is tentatively established by the synapomorphous layout of the pallial oviduct (see description under *Bittium reticulatum*; Fig. 6C); i.e., the presence of three sperm chambers: a large bursa (1), and smaller seminal receptacle (2) in the posterior half of the medial lamina, and a spermatophore bursa (3) in the posterior lateral lamina. The position of the spermatophore bursa in the lateral lamina appears to be a unique synapomorphy defining Bittiinae, but this needs to be confirmed by observation of spermatophores in the bursa in other members of the subfamily. This character does not occur in *Ittibittium*, a new genus described herein; thus, it had a CI of 50 in the analysis. The ciliated ridge tract (Fig. 6B, C, ctr) on the lateral lamina epithelium leading into the spermatophore bursa is also a synapomorphy defining Bittiinae. This is an uncommon feature among cerithioideans, and is unusually long. Some plesiomorphic characters, such as the well-developed epipodial skirt and epipodial tentacles, occur in other cerithioidean groups, but in combination with the above synapomorphous features, are characteristic of the Bittiinae. *Ittibittium*, new genus, deviates from other members of the subfamily in having the albumen gland protrude beyond the posterior mantle cavity into the visceral coil. In other respects, it generally agrees with the remaining genera of the Bittiinae.

The Recent genera treated herein are each characterized by external anatomical characters (Fig. 2), which allow easy classification of living animals. Two genera of the subfamily (*Bittiolium* and *Ittibittium*, *gen. n.*, have a large metapodial mucus gland marked by an elongate slit in the middle of the sole (Fig. 2), leading deep into the center of the foot. While the epipodial skirt and opercular lobe are characteristic of Bittiinae, these characters and the metapodial mucus gland also occur in species of *Alaba* H. Adams & A. Adams, 1854, and *Litiopa* Rang, 1829 (Litiopidae Fischer, 1885), in members of *Colina* H. Adams & A. Adams, 1854 (Cerithiidae Férussac, 1819), and in species of *Plesiotrochus* Fischer, 1878 (Plesiotrochidae Houbriek, 1990b) (Kosuge, 1964; Houbriek, 1987b; Luque et al., 1988; Houbriek, 1990a, 1990b, respectively). I have previously pointed out the anatomical features shared by *Colina* with members of the Bittiinae (Houbriek, 1990a: 50–51). Species of *Plesiotrochus* Fischer, 1878, also have a papillate epipodial skirt and an elongate metapodial slit leading into a large metapodial

mucus gland, but differ considerably from members of the *Bittium*-group in other anatomical characters (Houbriek, 1990b: 247–248), and are an unusual family.

The relationship of the *Bittium*-group to other small-shelled cerithioidean genera such as *Scaliola* A. Adams, 1860, and *Finella* A. Adams, 1860, remains unclear because the anatomy of these taxa is still unknown. Ponder (1991) recently described the anatomy of a species of *Diala* A. Adams, 1861, which resulted in his recognition of a separate family, Dialidae Ludbrook, 1941. According to Ponder (1991: 504–506), *Diala* species have a weak epipodial fold (epipodial skirt), a pair of lateral opercular lobes, and a posterior opercular flap, which appear to be homologous with the epipodial skirt and opercular lobe described in the Bittiinae members above. However, unlike the situation in Bittiinae, *Diala* species lack the metapodial mucus gland and the glandular ovipositor on the right side of the foot in females. Additionally in *Diala* species, the lateral lamina of the pallial oviduct does not have a sperm pouch and the paraspermatozoa are unique among Cerithioidea (Healy, 1986).

The rachidian radular tooth of most members of the *Bittium*-group is characterized by being wider than tall and usually has a basal plate with concave sides. This differs from the hour-glass shape of the rachidian tooth found in small-sized species of *Diala*, *Litiopa*, *Alaba*, and *Varicopeza* (Ponder, 1991: fig. 3F, G; Houbriek, 1987a: figs. 14, 19; 1987b: figs. 9, 10), taxa frequently confused with *Bittium*-group members. For dental cusp patterns among Bittiinae taxa, see Table 2.

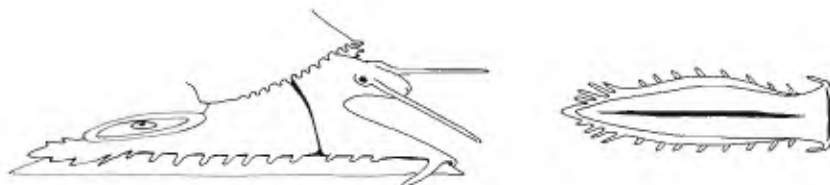
Although members of Bittiinae are primarily grazers of epiphytic microalgae, many species appear to feed on particulate matter gathered by cilia and mucus on the anterior tentidial filaments when the animal is stationary.

The ultrastructure of the sensory epithelium of the osphradia of members of the *Bittium*-group is typical of Cerithioidea, and Haszprunar (1985: 479) has shown that the osphradial cells bear paddle cilia. The osphradial classification of Bittiinae species falls under Haszprunar's (1985) group "Si2." Haszprunar (1985) repeated the Fretter & Graham (1962: 367) statement that the osphradium is a "simple brown ridge," but this is not concordant with my observations of the pectinate condition in many taxa of the group.

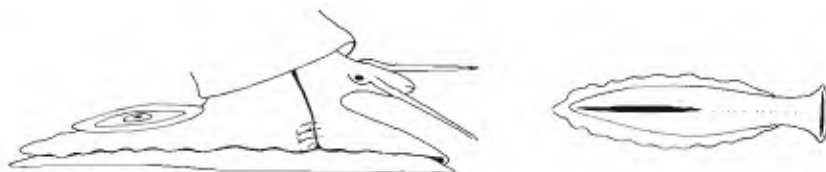
The phylogeny and relationship of members of the *Bittium*-group will remain unclear until the anatomy of other cerithioidean taxa is



BITTIUM



ITTIBITTIUM



BITTIOLUM



STYLIDIUM



LIROBITTIUM



CACOZELIANA

FIG. 2. External anatomical characters of five genera of the *Bittium*-group. Figures to left represent right lateral views of headfoot, showing mantle edge, ciliated gutter, ovipositor and epipodial skirt configuration; figures to left show sole of foot, anterior mucus gland, metapodial mucus gland (when present) and configuration of epipodial skirt.

better understood and a phylogenetic analysis can be accomplished.

BITTIUM GRAY, 1847

- Bittium* Gray, 1847a (Oct.): 270 (Type species by subsequent designation, Gray, 1847b: *Strombiformis reticulatus* DaCosta, 1778). Thiele, 1929: 211; Wenz, 1940: 755; Nordsieck, 1968: 68; Houbriek, 1977: 103.
- Cerithiolum* Tiberi, 1869: 263 (Type species by original designation, *Strombiformis reticulatus* DaCosta, 1778).
- Manobittium* Monterosato, 1917: 20 (Type species by monotypy, *Cerithium latreillei* Payraudeau, 1826, = *S. reticulatus*). Thiele, 1929: 212.
- Inobittium* Monterosato, 1917: 20 (Type species by monotypy, *Cerithium lacteum* Philippi, 1836, = *S. reticulatus*). Thiele, 1929: 212; Wenz, 1940: 757.
- Rasbittium* Gründel, 1976: 53 (Type species by original designation, *Cerithium latreillei* Payraudeau, 1826, = *S. reticulatus*).

Diagnosis

Shell small, elongate, with short anterior canal and sculptured with 4–5 spiral cords with many aligned small beads formed where axial riblets are crossed by spirals. Operculum circular, paucispiral with subcentral nucleus. Epipodial skirt with many small, short papillae. Opercular lobe with small pointed papillae. Well-developed ovipositor comprising parallel glandular ridges and bisected by egg-laying gutter on right side of foot near edge of epipodial skirt. Osphradium ridge-like, weakly monopectinate, one-half the ctenidial length. Openings to sperm bursa well separated from opening to seminal receptacle.

Remarks

Bittium Gray, 1847a, was first proposed in manuscript by Leach in 1818 for a classification of British Mollusca, and it was subsequently made available by Gray (1847a). Leach's list referred *Bittium* and several other diverse genera to Purpuridae and under the 65th entry listed *Murex reticulatum*, *M. tuberculare*, *M. adversum*, *M. elegantissimum*, and *M. spenceri*, consecutively, under *Bittium*. Besides *Bittium reticulatum*, the other species listed by Leach represent two gen-

era, *Triphora* Blainville, 1828, and *Cerithiopsis* Forbes & Hanley, 1851. Neither a description of *Bittium* nor a type species were given. Three months later, Gray (1847b) cited only *Bittium reticulatum* (Da Costa, 1778) under *Bittium*, and this citation is a subsequent designation. (Gray's system is explained in his introduction, pp. 129–130, and the species so listed are to be taken as type designations). The earliest diagnosis of *Bittium* is that of H. Adams & A. Adams (1854) who besides describing shell characters, noted the operculum, epipodial skirt, and opercular lobe.

My original paper on *Bittium* (Houbriek, 1977) reviewed the nomenclatural history of the genus, and should be consulted for detailed information about the confusion and taxonomic problems between *Bittium* and other taxa of small-shelled cerithioideans. Subsequent to that review, there have been many changes and the synonymy of *Bittium* originally published (Houbriek (1977: 103) has been modified herein: some taxa have been excluded, and genera not originally included have been added. A commentary on the present synonymy follows: *Cerithiolum* is an objective junior synonym of *Bittium*: both genera share the same type species, *Bittium reticulatum*. Gründel (1976) regarded *Cerithidium* and *Rasbittium* Gründel, 1976, as subgenera under *Bittium*, s.s., but as shown before, *Cerithidium* is excluded from Bittiinae. *Rasbittium* is a primary objective synonym of *Manobittium* as seen in the synonymy above. *Manobittium* and *Rasbittium* are considered subjective junior synonyms of *Bittium* because both share the same type species, *Cerithium latreillei*, which is considered by me and a number of authors to be conspecific or subspecific with *Bittium reticulatum* (see Verduin, 1976). The eastern Atlantic species, *Cerithium lacteum*, which is the type species of *Inobittium*, also is considered herein to be conspecific with *Bittium reticulatum*. Wenz (1940: 757) regarded *Inobittium* as a synonym of *Lirobittium*, but I see no close resemblance between the shells of the two. Should *Cerithium lacteum* be a distinct species, as thought by Verduin (1976), the differences are certainly not of generic weight; consequently, *Inobittium* is regarded as a subjective junior synonym.

Discussion

The genus *Bittium* is characterized by a cancellate, beaded shell sculpture formed by 4–5 dominant spiral cords and numerous axial rib-

lets (Fig. 3A-E), a circular operculum with subcentric nucleus (Fig. 3F), and by the small papillae along the edge of the epipodial skirt and opercular lobe (Fig. 2). The ovipositor in females is a highly developed, raised glandular lump at the base of the foot near the sole edge, forming a series of parallel, glandular ridges bisected by the deep ciliated egg-laying groove (Fig. 4B, ovp). The ridge-like monopectinate osphradium is unusual in having the pectins on its right side. It is half the length of the ctenidium. The openings to the sperm bursa and seminal receptacle in the lateral lamina of the pallial oviduct (Fig. 6B, C, osr, osp) are well separated from each other in contrast to most other members of the *Bittium*-group.

The shells of small-sized *Cerithium* species frequently are erroneously misclassified as *Bittium* species. Gründel (1976) presented several conchological features that he believed separated the two genera. He stated that *Cerithium* differs from *Bittium* in having a more complex aperture, but this is only true for larger *Cerithium* species: some small species, such as *Cerithium atomarginatum*, *Cerithium egenum*, and *Cerithium zebrum*, have apertures like those of *Bittium* (Houbrick, 1978). Gründel (1976) further indicated that ontogenetic sculptural development in *Cerithium* begins with a single primary spiral cord that becomes stronger and more prominent, forming a keel that is not integrated with the weaker axial riblets; moreover, there are many fine spiral threads of varying strength. In *Bittium*, whorl sculpture begins with two spirals that quickly become four primary spiral cords forming a network with sharply defined axial riblets. The so called "definitive" shell characters proposed by Gründel (1976) are unreliable, because the more species that are examined, the more exceptions and ambiguities one encounters.

Marcus & Marcus (1963) cited the presence of a metapodial mucus gland in *Bittium reticulatum*, crediting this information to Fretter (1948). However, no such gland was observed in living or preserved, sectioned specimens from the Azores; furthermore, Ponder (in litt.) did not note this structure on specimens of *Bittium reticulatum* from the western coast of Sweden. Fretter's (1948: 628) paper merely cites the presence of this gland in such small gastropods as *Bittium*, *Cerithiopsis*, and *Triphora*, but as she mentioned only generic names, it is unclear what "*Bittium*" species she actually observed.

All living, observed members of the *Bittium*-nae appear to be feeders of epiphytic microalgae, such as diatoms, which occur commonly on sea grasses. Most species occur in large populations and are highly gregarious.

Species of the genus *Bittium* appear to be primarily concentrated in the eastern Atlantic: the *Bittium reticulatum* complex and species closely related to it are commonly found throughout the Mediterranean, north African, and western European regions, and appear to be adapted to temperate and cold waters. *Bittium impendens* from the Indo-Pacific, which differs from the Atlantic *Bittium* species only in lacking a monopectinate osphradium, is herein included under the genus *Bittium*. If this species truly belongs in *Bittium* s.s., and if other anatomically unknown Indo-Pacific species are examined, the geographic distribution of the genus *Bittium* may be far wider than is now thought.

Bittium reticulatum (Da Costa, 1778)
(Figs. 3–6)

Strombiformis reticulatus Da Costa, 1778: 117, pl. 8, fig. 13.

Murex reticulatus (Da Costa). Montagu, 1803: 272.

Cerithium latreillei Payraudeau, 1826: 143.

Cerithium lacteum Philippi, 1836: 195.

Cerithium reticulatum, Risso, 1826: 157; G. B. Sowerby, 1855: pl. 15, fig. 8; Jeffreys, 1867: 258; 1869: pl. 80, fig. 4; 1885: 57.

Bittium reticulatum, Watson, 1886: 540; Bucquoy et al., 1884: 212–215, pl. 25, figs. 3–9; Tryon, 1887: 150–151, pl. 29, figs. 78–83; Dautzenberg, 1889: 40–41.

Description

Shell (Fig. 3A–H): Shell elongate, reaching 15 mm in length, comprising 9–10 moderately inflated whorls. Protoconch (Fig. 3G) comprising two weakly sculptured whorls. Early whorls beginning with two spiral cords and broad subsutural ramp (Fig. 3H). Adult whorls sculptured with 4–5 spiral cords beaded where many small axial riblets cross over them, creating cancellate sculpture. Suture deeply impressed. Body whorl a little under one-third shell length, having weak basal constriction and small anterior canal weakly reflexed to left. Body whorl sculptured with five major spiral cords and 5–6 weaker cords on its base. Aperture ovate, a little over one-third shell length, with concave columella having

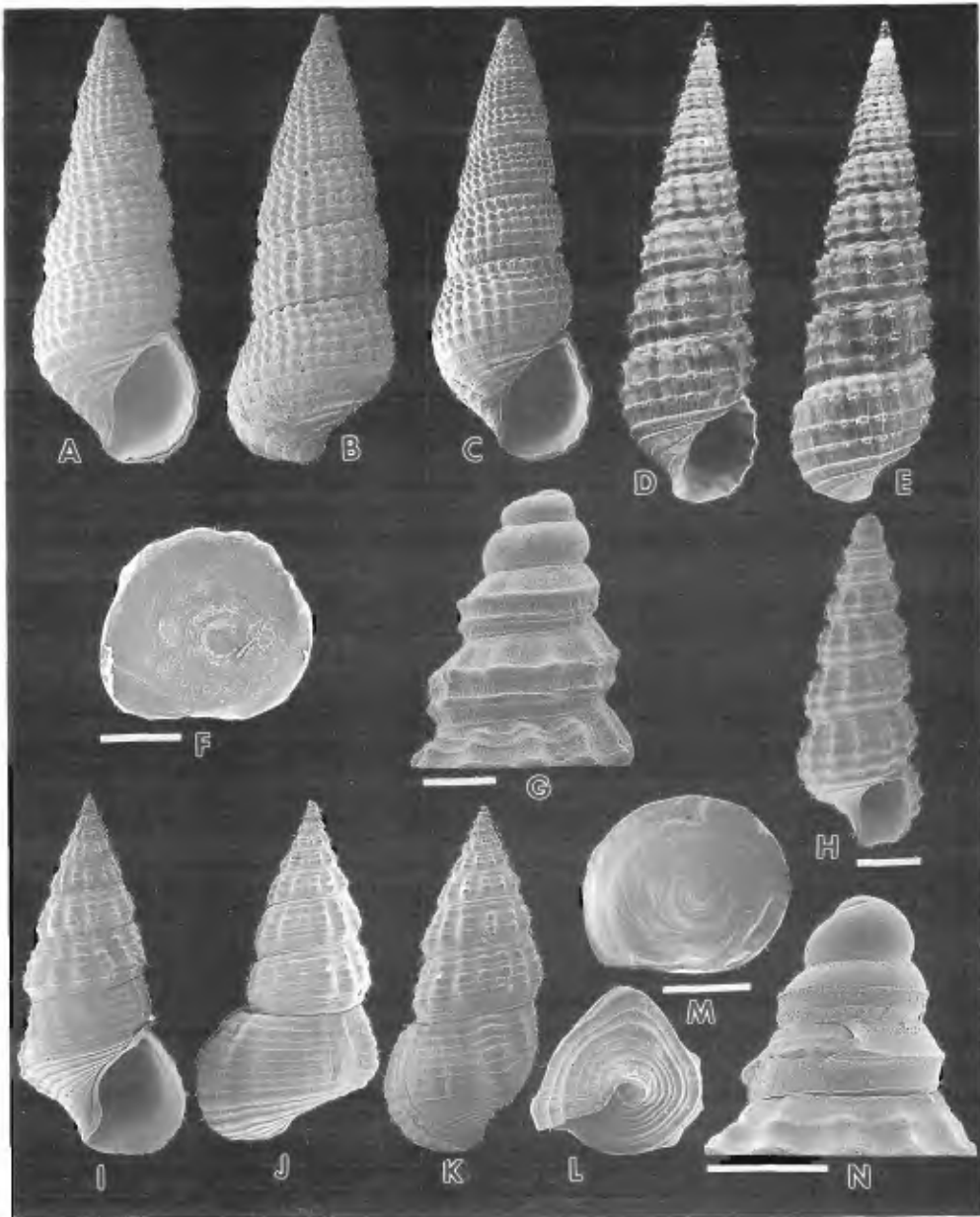


FIG. 3. Representatives of genus *Bittium*: A–H, *B. reticulatum*; I–N, *B. impendens*. A–C, SEM micrographs of *B. reticulatum* from São Miguel, Azores (USNM 878030), 6 mm length; D, E, *B. reticulatum* from Tunisia (USNM 754051), 11 mm length; F, SEM micrograph of operculum of *B. reticulatum*, bar = 0.5 mm; H, SEM micrograph of immature shell of *B. reticulatum*, bar = 0.5 mm; I–L, SEM micrographs of shell of *B. impendens* from Honolulu, Hawaii (USNM 857098), 5 mm length; M, SEM micrograph of operculum of *B. impendens*, bar = 0.5 mm; N, SEM micrograph of protoconch of *B. impendens*, bar = 150 μ m.

slight columellar callus; anterior canal short, shallow; anal canal very small; outer lip rounded, weakly crenulate. Periostracum thin, light tan.

Animal (Figs. 4–6): Head-foot of animal pigmented light yellowish-brown overlain by large dark brown blotches and small white spots. Visceral mass with 8 visceral whorls, comprising mostly digestive gland and overlying gonads. Ovary white; testis dirty yellow. Stomach about one whorl in length. Kidney large, light tan, about two-thirds whorl in length. Columellar muscle white, broad, short, about one-half length of pallial cavity. Head (Fig. 4A) with elongate, narrow snout (Fig. 4B, sn), flattened dorso-ventrally, expanded at bilobed tip, with bright yellow, oval-shaped oral pad at antero-ventral end (Fig. 4A, C, 1). Cephalic tentacles (Fig. 4A, t) elongate, narrow, with broad peduncular bases each with large dark eye. Foot narrow, elongate, crescent shaped anteriorly. Deep transverse slit (Fig. 4C, amg) between epipodial lips marks entrance to large ovate anterior mucus gland extending via central duct deep into anterior foot. Epipodium separated from lower foot and densely ciliated sole by deep, laterally placed groove (Fig. 4B, egg) forming broad epipodial skirt (Fig. 4B, C, eps) extending posteriorly on each side of foot from corners of anterior epipodial lips of anterior mucus gland around entire foot base, joining behind and below opercular lobe. Lateral epipodial skirt scalloped along edges of each side of median and posterior parts of epipodium, having small papillae (Fig. 4B, C, ep); epipodial skirt forming long opercular lobe (Fig. 4B, C, opl). Sole of foot (Fig. 4C, s) indistinctly divided into two parallel axial parts, forming anterior longitudinal fold. No metapodial mucus gland. Operculum (Fig. 3F) corneous, tan, circular, paucispiral with subcentral nucleus and with thin, transparent border. Ciliated gutter (Fig. 4B, C, cg) emerging from right side of mantle cavity (Fig. 4C, ex) and running down right side of foot; ciliated gutter leads to large glandular ovipositor (Fig. 4B, C, ovp) and egg-laying pit at base of epipodium in females. Ovipositor oval-shaped, comprised of glandular, transparent white tissue formed into many parallel pleats divided transversely by deep central slit. Mantle bilobed at edge, having smooth outer lobe and inner lobe with many small papillae, becoming smooth ventrally. Mantle papillae (Fig. 4B, C, mp) slender, darkly pigmented, each with

white spot. Mantle edge thickened at inhalant (Fig. 4C, inh) and exhalant siphons.

Pallial Cavity: Pallial cavity deep, comprising about two whorls. Osphradium olive colored, ridge-like, pectinate on right side only, bordered on each side by narrow ciliated strip. Osphradium wide, about one-half ctenidial length, beginning close behind inhalant siphon and extending length of ctenidium. Ctenidium bluish-gray, comprising numerous finger-like, triangular filaments with narrow bases. Hypobranchial gland narrow, glandular comprising several kinds of large gland cells that stain dark blue. Rectal tube distended, filled with elongate, ovoid-shaped fecal pellets. Pallial gonoducts open, beginning behind mantle edge and extending posteriorly as far as kidney.

Reno-pericardial System: Kidney large, about two-thirds whorl in length, beginning at anterior end of style sac, extending anteriorly well into mantle cavity roof, lying over one-third of posterior pallial gonoduct. Kidney with simple kidney opening, but no renopericardial duct. Pericardium typically monotocardian, lying adjacent to posterior wall of mantle cavity.

Alimentary System: Mouth (Fig. 4A, m) lying antero-ventrally on snout, opening into oral cavity between two semicircular lips (Fig. 4A, C, 1). Buccal mass (Fig. 4D, bm) relatively small, about one-third snout length, loosely attached to snout wall by numerous thin muscle strands. Jaw tan, semicircular, comprised of cuticular cones and lying on either side of entrance to anterior buccal cavity. Radular ribbon (Fig. 5A; Table 2) folded beneath buccal mass and radula sac emerging behind it. Rachidian tooth (Fig. 5C) with dorso-ventrally compressed basal plate with concave sides rounded base and with V-shaped base buttressed on each side with a basal lateral extension; rachidian broader above than below, having cutting edge with slightly concave top, and comprising large, spade-shaped central cusp flanked on each side by 2–3 small, pointed denticles. Lateral tooth (Fig. 5B) with broad basal plate comprising long, ventrally extending, central pillar having small pustule on its face, and with moderately long lateral extension; cutting edge comprising very large spade-shaped cusp with one inner denticle and 3–6 outer denticles. Marginal teeth (Fig. 5A) curved, elongate, with broad, swollen shafts, narrowing and becoming spatulate at tips; inner marginal tooth with tip having long

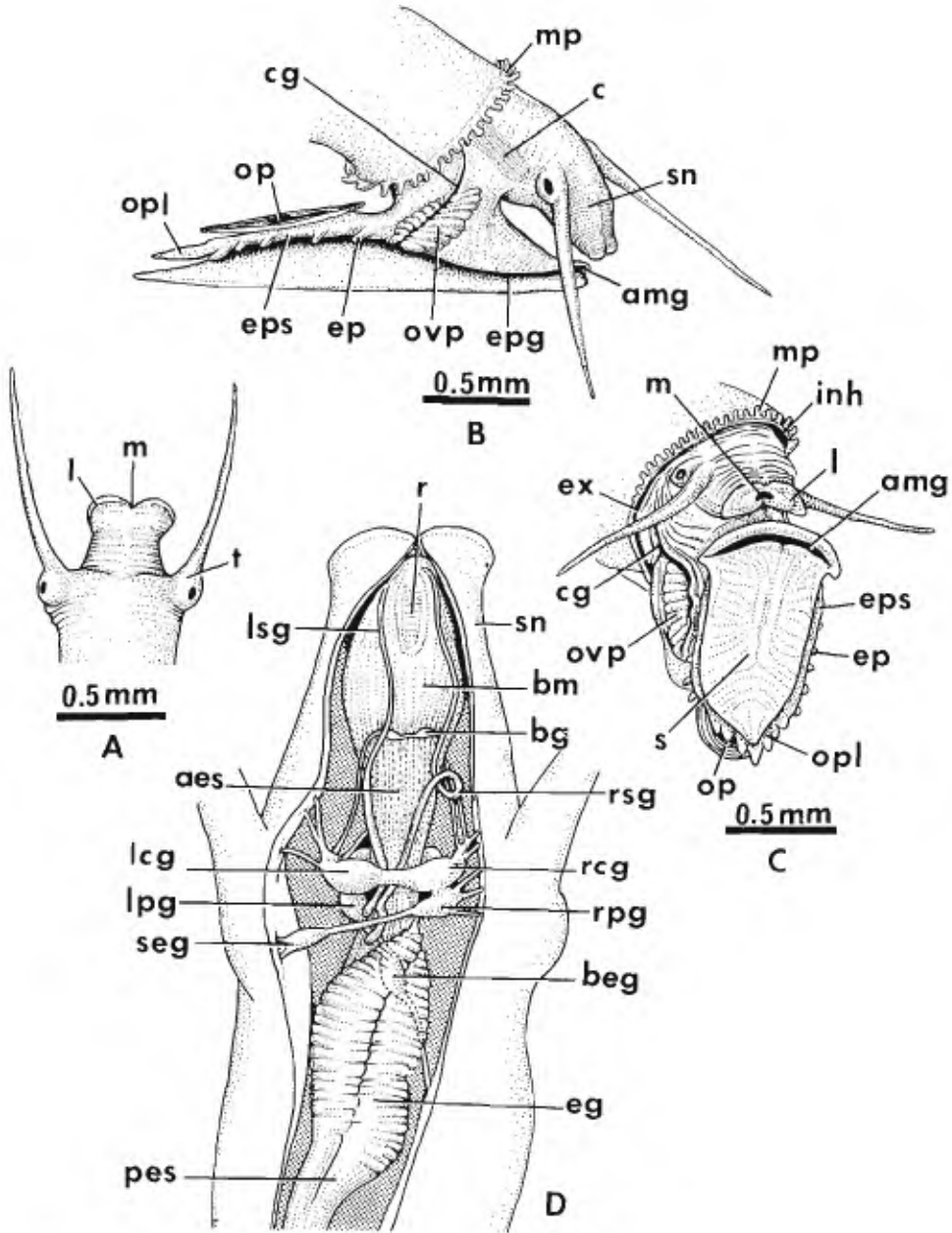


FIG. 4. Anatomical representations of *Bittium reticulatum*. A, head and snout; B, lateral view of headfoot; C, head and sole of foot; D, anterior alimentary system exposed by dorsal longitudinal cut through wall of buccal cavity. aes = anterior esophagus; amg = anterior mucus gland; beg = subesophageal gland; bg = buccal ganglion; bm = buccal mass; c = ciliated strip; cg = ciliated gutter; eg = esophageal gland; ep = epipodial papilla; epg = epipodial groove; eps = epipodial skirt; ex = exhalant siphon; inh = inhalant siphon; l = lip; lcg = left cerebral ganglion; lpg = left pleural ganglion; lsg = left salivary gland; m = mouth; mp = mantle papilla; op = operculum; opl = opercular lobe; ovp = ovipositor; pes = posterior esophagus; rcg = right cerebral ganglion; rpg = right pleural ganglion; rsg = right salivary gland; s = sole; seg = supraesophageal ganglion; sn = snout; t = tentacle.

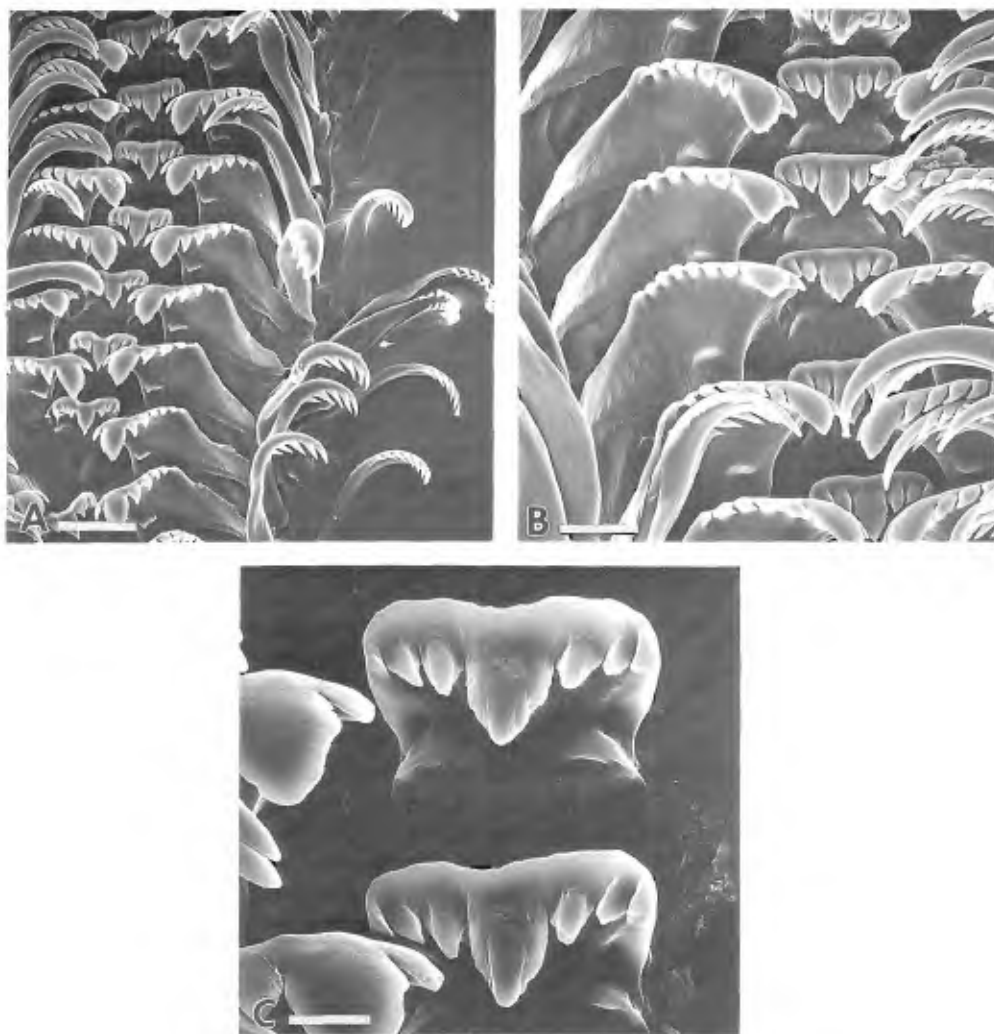


FIG. 5. Scanning electron micrographs of radula of *Bittium reticulatum* from São Miguel, Azores (USNM 878030). A, half row with marginal teeth folded back, bar = 19 μm ; B, rachidian and lateral teeth, bar = 15 μm ; C, detail of rachidian teeth, bar = 4 μm .

central cusp, 3–4 inner denticles, 4 outer denticles; outer marginal tooth same, but lacking outer denticles. Salivary glands (Fig. 4D, rsg, lsg) comprising pair of narrow, uncoiled, shiny tubes, beginning behind nerve ring, extending through it anteriorly, opening into far anterior portion of buccal cavity. Buccal cavity opening and enlarging immediately behind nerve ring, having pair of prominent dorsal folds and smaller pair of smaller ventral folds. Interior mid-esophageal walls highly

folded, forming large, olive-brown esophageal gland (Fig. 4D, eg). Internal epithelium of esophageal gland (Fig. 7A, B, eg) forming numerous transverse folds or lamellae, staining dark blue with Methylene blue. Posterior esophagus (Fig. 4D, pes) narrow and straight, running on top of columellar muscle, entering into left side of stomach. Stomach large, comprising about one whorl of visceral mass, including style sac. Esophageal opening into median ventral part of stomach floor. Large

sorting field with many fine folds adjacent to right side of esophageal opening. Minor typhlosole bordering right side of esophageal opening. Large central elevated pad in center of stomach adjacent to single duct to digestive gland lying short distance below esophageal opening. Digestive gland comprising single brown lobe consisting of digestive cells and secretory cells with dark brown granules. Gastric shield on right side of stomach having cuticular lining with protruding, toothed edge. Depressed epithelial pocket on floor of stomach adjacent to posterior part of gastric shield. Style sac short, about one-third the stomach length, nearly spherical, and containing crystalline style. Style sac adjacent to but separate from intestine opening, except for limited connection where both enter stomach. Anterior part of stomach with many parallel ciliated folds and closed off from style sac by major typhlosole. Internal intestinal walls with many fine folds where exiting stomach. Intestine curves around style sac, turns to right, and runs straight forward. Rectum with thin muscular wall, terminating in anal-bearing papilla.

Nervous System: Nervous system epiathroid, dialyneurous. Nerve ring comprised of large ganglia. Pleural ganglia (Fig. 4D, rpg, lpg) close to cerebral ganglia (Fig. 4D, rcg, lcg). Cerebral connective equalling length of cerebral ganglion. Buccal ganglia (Fig. 4D, bg) small, lying at posterior edge of buccal mass. Subesophageal ganglion (Fig. 4D, beg) very close to left pleural ganglion (Fig. 4D, lpg). Supraesophageal connective moderately long, about twice length of right pleural ganglion; dialyneury between left pallial nerve and nerve emerging from supraesophageal ganglion (Fig. 4D, seg). Visceral ganglion located in floor of posterior mantle cavity.

Reproductive System: Testis creamy yellow, overlying dark brown digestive gland, extending anteriorly about five whorls, ending one-half whorl before stomach. Testicular ducts on inner side of visceral coil, joining to form spermatic duct, enlarging anteriorly, becoming seminal vesicle and containing two kinds of spermatozoa: euspermatozoan with single long flagellum and paraspermatozoan with [four ?] flagellae. Males aphallate. Male pallial gonoduct (Fig. 6A) open, comprising two thin walled laminae (Fig. 6A, 11, ml) with thicker transverse glandular folds at their attached bases bordering gonoductal groove (Fig. 6A, gd). Posterior half of male gonoduct thick,

glandular, comprising prostate gland (Fig. 6A, pg). Anterior half of male gonoduct glandular, not as thick, putative spermatophore-forming organ (Fig. 6A, so).

Ovary opaque white, thin-walled, overlying digestive gland, extending anteriorly, ending about one-half whorl before stomach. Coelomic oviduct (Fig. 6B, C, cod) short tube, highly ciliated within, beginning anterior to stomach with duct wall lying against pericardium (no connection), ending at posterior mantle cavity where circular sphincter muscle separates it from pallial oviduct. Female pallial oviduct (Fig. 6B, C) large, comprising two laminae, enlarged and glandular at their bases, attached basally to each other and to mantle floor, forming ciliated oviductal groove (Fig. 6B, C, ovg). Posterior end of pallial oviduct closed. Medial, free lamina with wide anterior ciliated sperm gutter (Fig. 6B, C, sg) along its edge leading to two, well-separated, pocket-like openings. First opening (Fig. 6B, C, osp) leading into large, deep bursa having smooth inner epithelium and containing large numbers of non-directed spermatozoa (Fig. 7C, D, sp); ciliated gutter continuing posteriorly to open (Fig. 7C, osr) into pouch-like, muscular seminal receptacle (Fig. 6C, B sr; 8C, D, sr) containing oriented euspermatozoa with heads embedded in receptacle walls. Lateral lamina attached to pallial wall, having anterior ciliated tract comprising many parallel elongate, fine ciliated folds (Fig. 6B, C, ctr; 7A, B, ctr) running posterior to open into thin-walled tube leading into posterior pouch-like bursa having highly vacuolated epithelium and functioning as spermatophore bursa (Fig. 6B, C, sb). Ciliated tract and folds opening to seminal receptacle on lateral lamina located opposite sperm gutter and opening to seminal receptacle of medial lamina, both edges interdigitating to form closed system. Posterior half of glandular portion of both laminae opaque white color, comprising albumen gland (Fig. 6B, C, ag; 7C, D, ag); anterior half dirty white, comprising capsule gland (Fig. 6B, C, cg; 7A, B, cg).

Spawn comprising thin gelatinous string (about 25 mm length, uncoiled) tightly coiled clockwise or irregularly folded on itself and attached to substrate. Jelly string containing many small opaque eggs (0.65 μm diameter) each within thin, transparent hyaline capsule (110 μm diameter). Entire spawn mass contains about 800 eggs. Free swimming bilobed planktotrophic veliger larval stage present. Larval shell ranging from 170–330 μm , de-

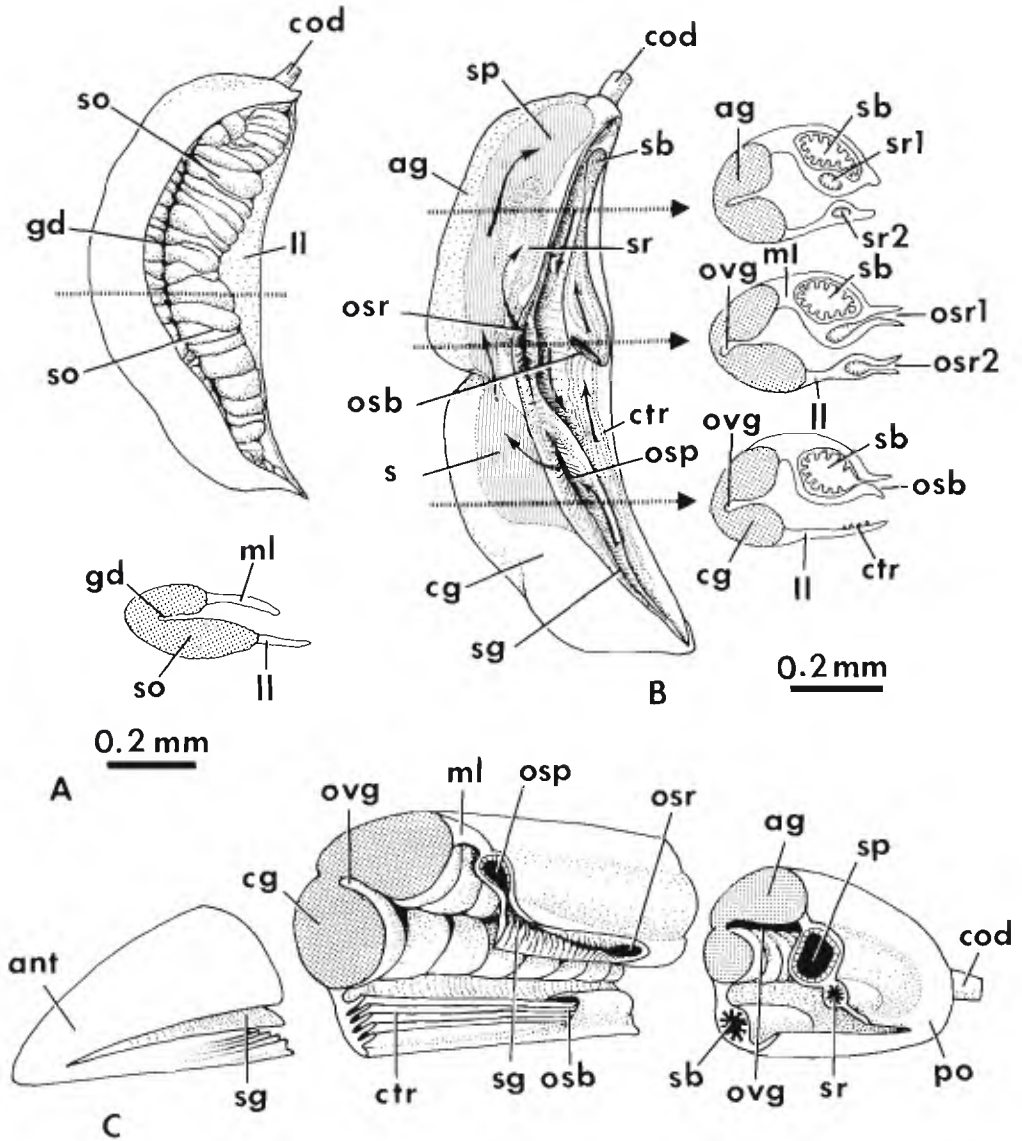


FIG. 6. Representation of pallial gonoducts of *Bittium reticulatum*. A, male pallial gonoduct, showing section through mid-duct beneath, represented by dotted line; B, pallial oviduct showing three cross sections of duct represented by dotted arrows and sections to right; C, reconstruction of pallial oviduct showing configuration of ducts and glands (anterior to right). ag = albumen gland; ant = anterior; cg = capsule gland; cod = coelomic oviduct; ctr = ciliated ridge tract; gd = gonaductal groove; ll = lateral lamina; ml = medial lamina; osp = opening to sperm bursa; osb = opening to spermatophore bursa; osr = opening to seminal receptacle; ovg = oviductal groove; po = closed portion of pallial oviduct; sb = spermatophore bursa; sg = spermatophore-forming organ; s = sperm gutter; sp = sperm bursa; sr = seminal receptacle; so = spermatophore-forming organ.

pending upon age. Larval shell with rounded, nearly smooth whorls having thin spiral thread forming weak keel and with deep sinusigeral notch (Thorson, 1946: 192, fig. 109).

Discussion

The status of the many specific and sub-specific names comprising the *Bittium reticu-*

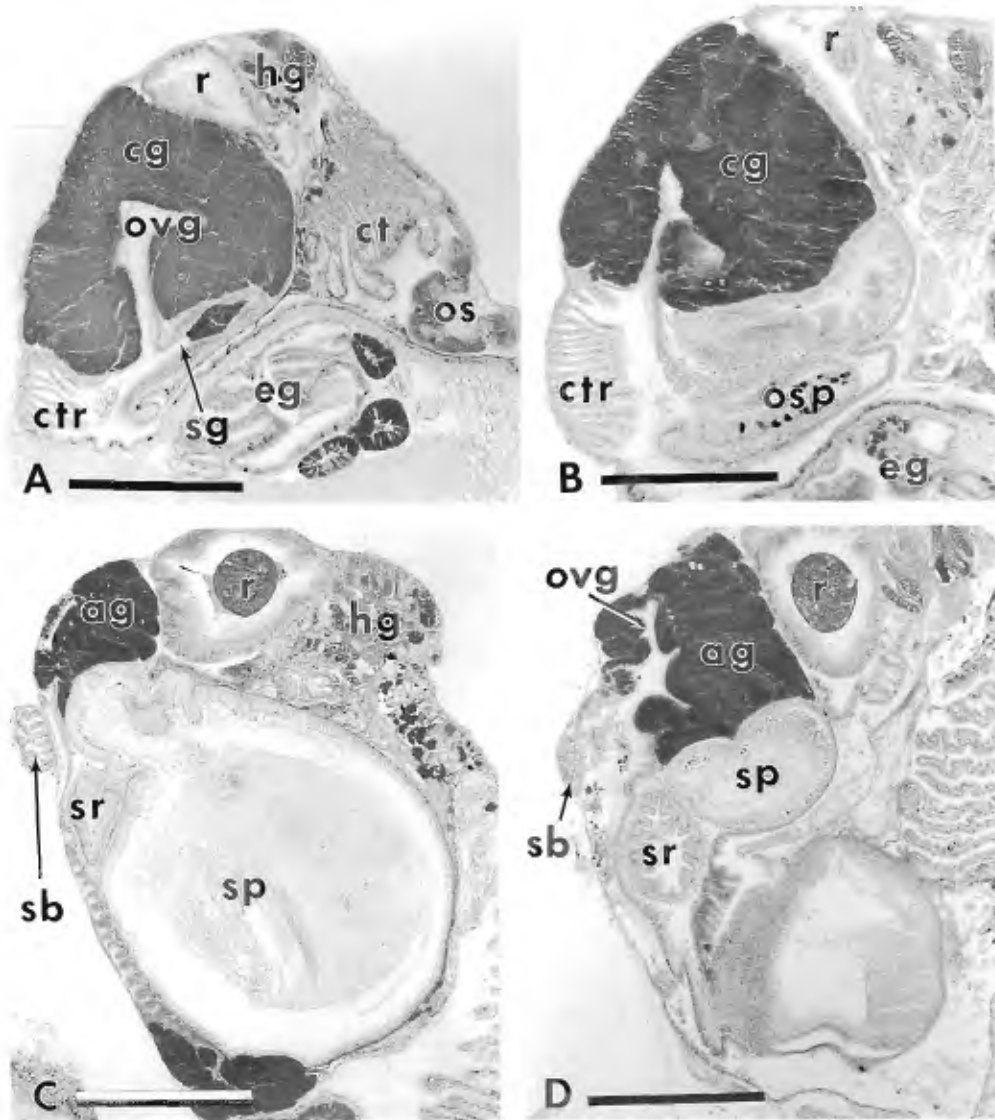


FIG. 7. Successive sections, anterior to posterior, through pallial oviduct of *Bittium reticulatum*. A, anterior of pallial oviduct showing relationship of mantle cavity organs to oviduct, bar = 0.25 mm; B, mid-section showing ciliated ridge tract and opening to sperm bursa, bar = 0.25 mm; C, section through enlarged sperm bursa in posterior pallial oviduct, bar = 0.25 mm; D, section through closed posterior of pallial oviduct, bar = 0.25 mm. ag = albumin gland; cg = capsule gland; ct = ctenidium; ctr = ciliated ridge tract; eg = esophageal gland; hg = hypobranchial gland; os = osphradium; osp = opening to sperm bursa; ovg = oviductal groove; r = rectum; sb = spermatophore bursa; sg = sperm gutter; sp = sperm bursa; sr = seminal receptacle.

latum complex is controversial (Verduin, 1976). It is not my intention to address alpha-level problems in this generic review, but the Azorean population used for the anatomical study herein is considered by some as a sub-

species or a closely related species of the *Bittium reticulatum* complex. *Bittium reticulatum* is exceedingly variable in shell sculpture throughout its range (compare Figs. 2A, C, D), but this is not unusual among cerithioide-

ans. The pallial oviduct described by Johansson (1947) and notes and sketches made by Ponder (Ponder, in litt.) on the anatomy of specimens from western Sweden agree substantially with my observations of Azorian specimens. For the purposes of this study, the *Bittium reticulatum* complex is regarded in the broad sense (*sensu lato*), as a single species.

The epipodial skirt, characteristic of members of the *Bittium*-group, forms a highly ciliated lateral groove where it overhangs the foot, and carries detrital particles posteriorly to the back of the foot where they are discarded.

The posterior roof of the pallial cavity is covered by the anterior extension of the renal organ, which overlays the posterior pallial gonoduct. The renal organ opens via a muscular sphincter, the renal opening, into the posterior pallial cavity.

The ridge-like osphradium of *Bittium reticulatum* is unusual in being pectinate on its right side. Although these pectins are small, they are clearly visible and very unlike simple nonpectinate osphradia of closely related taxa.

The rachidian tooth of the radula of *Bittium reticulatum* is similar to those of members of other genera in the group, but unlike that of *Cacozeliana* (see below). Table 2 gives the comparative dentition of the radular teeth.

Bittium reticulatum has three sperm storage spaces, two connected to the ciliated groove of the non-glandular portion of the medial free lamina, and one in the posterior part of the non-glandular attached lateral lamina (Fig. 6B, 11). It is not entirely clear how these three bursae function. Of the two bursae in the medial lamina, the smaller one is clearly the seminal receptacle, because oriented euspermatozoa are found in it, exclusively (Fig. 7C, D, sr). The larger bursa (Fig. 6B, sp) contains considerable numbers of unoriented sperm, and much nondescript material (presumably disintegrating paraspermatozoa and degenerating spermatophores), although some euspermatozoa occur with heads oriented on the inner wall epithelium, especially near the opening to the sperm gutter (Fig. 7D). Although this large bursa in the medial lamina contains spermatophores in most cerithiids, this is not the case in members of the *Bittium*-group, where it appears to function as a sperm storage and ingesting area. It is inferred that the pouch in the posterior of the lateral lamina (Fig. 6C, sb, Fig. 7C, D, sb)

functions as a spermatophore bursa in *Bittium reticulatum* and probably in most other members of the *Bittium*-group, because Marcus & Marcus (1963) found spermatophores in this structure in the western Atlantic *Bittium varium*. I was unsuccessful in finding spermatophores in either structure in specimens of *Bittium varium* from Florida. A new genus from the Indo-Pacific, *Ittibittium*, described herein, deviates from the typical pallial oviduct layout in lacking the spermatophore bursa in the lateral lamina and in having the albumen gland protrude posteriorly beyond the back of the pallial cavity into the visceral coil.

The spawn of *Bittium reticulatum* was first described and figured by Meyer & Möbius (1872), and the spawn and larvae described by Lebour (1937) and Graham (1988). Spawn, larvae, veliger, protoconchs, and juvenile shells of this species were described and well illustrated by Thorson (1946: 192, fig. 109). Other depictions of the larval shell of this species are those of Fretter & Pilkington (1970: 10–11, fig. 6) and Richter & Thorson (1975: pl. 3, figs. 16–17). According to Graham (1988), British *Bittium reticulatum* is a summer breeder and attaches its spawn to shells, stones or weeds. Spawn comprises a cylindrical ribbon about 3 mm in diameter, having a total length of 25 mm, and coiled in tight spirals. A spawn mass contains about 1000 eggs, which develop to veliger larvae.

The geographic range of the *Bittium reticulatum* complex is broad, comprising western Europe, the Azores, North Africa, and the Mediterranean.

Bittium impendens (Hedley, 1899)
(Fig. 3, I–N)

Cerithium impendens Hedley, 1899: 434–435, fig. 23 (Holotype: AMS C5944; type locality: Funafuti Atoll, Ellice Islands); Kay, 1979: 118, 120, fig. 45A.

Description

Shell: (Fig. 3I–N). Shell short, stout, with wide base, reaching 7 mm length and comprising 8–9 convex whorls. Protoconch (Fig. 3N) comprising 2.5 whorls; protoconch 1 smooth; protoconch 2 sculptured with thin central, spiral keel and weak presutural spiral thread; lower part of each whorl with microscopic pustules. Whorls slightly pendant abapically, constricted at suture. Adult shell sculptured with 3–4 major spiral cords inter-

spersed with spiral threads. Spiral cords weakly beaded and beads aligned to form axial riblets. Suture well defined. Weak varices randomly distributed. Body whorl very broad, about one-half the shell length, with prominent wide, dorsal varix (Fig. 3J, L); body whorl sculptured with about 14 spiral cords and strongly constricted at base. Aperture a little over twice shell length, broadly ovate, with short, wide, shallow anterior canal and smooth outer lip extending widely at shell base (Fig. 3I).

Animal: Headfoot pinkish white, blotched with brown, covered with white spots and with chestnut stripes. Kidney bright pink. Right side of foot in females with ciliated gutter ending in small ovipositor at edge of lateral groove. Epipodial skirt having very small pustules or protuberances along lateral edges on each side of foot; opercular lobe scalloped and pointed at end. Sole of foot pink, without metapodial mucus gland. Mantle edge fringed dorsally with papillae; underside of inhalant siphon with three large papillae. Marginal teeth of radula having three inner denticles. Osphradium a thin brown ridge, non-pectinate. Openings to sperm pouch and seminal receptacle in medial lamina close to each other, situated within common aperture at end of sperm gutter in edge of anterior third of medial lamina adjacent to opening of spermatophore bursa of lateral lamina. No ciliated tract leading to spermatophore bursa.

Discussion

Examination of the type lot (holotype and 7 paratypes) of *Cerithium impendens* confirms that the Hawaiian specimens studied herein are conspecific with this taxon. This species has not been cited frequently in the literature.

The assignment herein of *Bittium impendens* to the genus *Bittium* is made with some doubt. The shell morphology of this widespread Indo-Pacific species is quite different from that of the type species of *Bittium*, *Bittium reticulatum* (compare Fig. 3A–E and 3I–L), and unlike the shells of other eastern Atlantic *Bittium* species. In addition, the osphradium is ridge-like rather than monopectinate, and there does not appear to be a ciliated tract associated with the spermatophore bursa on the lateral lamina. Instead, the opening to the spermatophore bursa is adjacent to the two openings of the bursae in the medial lamina. The radula of *Bittium impen-*

dens is very similar to that of *Bittium reticulatum* except that the marginal teeth have fewer outer and inner denticles. Aside from these differences, the animal shares most of the anatomical features of *Bittium reticulatum*. Although an argument could be made that this species represents yet another new genus, I have conservatively placed *Bittium impendens* under *Bittium*, s.s., with a query, because it does have many characters in common with the type species of *Bittium*.

The shell of *Bittium impendens* differs from other *Bittium*-group genera by its fir-tree outline and wide body whorl with prominent dorsal varix (Fig. 3I–L). The protoconch (Fig. 3N) is smooth except for a thin spiral thread and a deep sinusigeral notch, indicative of a planktonic larval phase. Judging from specimens from other regions that appear to be conchologically conspecific, this species has a wide Indo-Pacific distribution, occurring from central Pacific islands throughout the Indo-West-Pacific to east Africa.

ITTIBITTIUM, New Genus

Diagnosis

Shell small, reaching 6 mm length, with inflated whorls and dominant spiral sculpture of 4–5 cords. Protoconch with depressed, concave apex, broad sutural ramp, sculptured with minute axial striae and two strong spiral cords. Operculum ovate, paucispiral with eccentric nucleus. Each side of propodium with elongate papilla. Epipodial skirt laterally fringed with slender papillae. Large opercular lobe having elongate papillae. No ovipositor in females. Sole of foot with long, central longitudinal slit marking entrance into large metapodial mucus gland. Osphradium weakly bipectinate. Albumen gland extending past posterior of pallial cavity into visceral coil. No spermatophore bursa in lateral lamina of pallial oviduct. Spawn comprising short gelatinous tube.

Type Species: *Bittium parcum* Gould, 1861.

Etymology: A compound of "itti," American vernacular prefix for very small, and *Bittium*.

Remarks

This genus is perhaps one of the most distinctive of the *Bittium* group, in terms of its unusual protoconch and anatomical features.

The protoconch with depressed apex and broad sutural ramp (Fig. 8I) is unique among the *Bittium*-group. The distinctive propodial and epipodial papillae, well-developed epipodial skirt, and long metapodial mucus gland are conspicuous autapomorphic characters in living specimens (Fig. 2). The lack of a spermatophore bursa in the lateral lamina of the pallial oviduct and the protrusion of the albumen gland through the posterior pallial cavity into the visceral coil are highly unusual autapomorphies, and set *Ittibittium*, gen. n., apart from the rest of the Bittiinae. The placement of the spermatophore bursa in the lateral lamina is one of the synapomorphic character used in this review to define the subfamily Bittiinae; therefore, it is noteworthy that *Ittibittium*, gen. n., has lost this feature. The spawn mass of *Ittibittium*, gen. n., is also unusual in being a simple, short tube.

In some museum collections, *Bittium parcum* and species similar to it are incorrectly assigned to *Bittinella* Dall, 1924, a genus based on *Bittium hiloense* Pilsbry & Vanatta, 1908, which has been shown to be a rissoid of the genus *Isselia* (Ponder, 1985: 95; Kay, 1979: 80).

Ittibittium parcum (Gould, 1861)
(Figs. 8–11)

Bittium parcum Gould, 1861: 387 (Lectotype, R. Johnson, 1964, USNM 2040; type locality Okinawa, Ryukyu Islands); G. B. Sowerby, 1866: pl. 18, fig. 125; Tryon, 1887: 155, pl. 30, fig. 20; R. Johnson, 1964: 122, pl. 12, fig 14; Kay, 1979: 120, figs. 22D, 45D, E.

Cerithium hawaiiensis Pilsbry & Vanatta, 1905: 576 (Holotype ANSP; type locality: Hilo, Hawaii).

Description

Shell (Fig. 8): Shell small, pupate-elongate, comprising about 8 inflated, angulate whorls and reaching 5.8 mm length. Protoconch (Fig. 8F-I) comprising two concave whorls, concavely flattened apex, very broad sutural ramp sculptured with minute axial striae (Fig. 8F); protoconch whorls sculptured with two strong, keel-like spiral cords, with central spiral cord becoming dominant one. Early whorls sharply angulate (Fig. 8I); first post-larval whorl with keel-like median spiral cord; second whorl with another spiral cord above keel and third whorl having 3 spiral cords above

keel. Adult whorls angulate, sculptured with keel-like median cord, 7–8 minor spiral cords, each cord abapically overlapped by successive one. Eight to nine weak to strong axial ribs occasionally on whorls, especially on upper ones (Fig. 8J). Varices randomly placed. Suture moderately impressed. Body whorl (Fig. 8L) slightly constricted at base, comprising a little less than half shell length, sculptured with 15–19 weak flattened spiral cords, occasional weak axial ribs and with broad varix. Aperture about one-third shell length, ovate with smooth outer lip and short broad anterior canal. Slight columellar callus present. Periostracum thin, nearly transparent.

Animal: Animal pigmentation highly variable, ranging from greenish-yellow to pink and brown and covered with white blotches. Cephalic tentacles wide at bases, elongate, twice snout length. Snout elongate, narrow, bilobed at tip. Operculum (Fig. 8K) thin, corneous, tan, circular-ovate, paucispiral with subcentral nucleus. Anterior part of foot crescent-shaped, cowl-like, having single long papilla on each side (Fig. 2). Narrow transverse slit at edge of propodium leading into large, spherical anterior mucus gland, staining deep purple in toluidine blue. Lateral epipodial skirt with about 10 small, slender papillae along edges (Fig. 2) on each side of foot, extending posteriorly to large opercular lobe having long papillae along its edges; papillae show through edges of opercular border. Sole of elongate, narrow foot having deep, centrally placed, narrow longitudinal slit (Fig. 2) beginning behind anterior mucus gland slit (Fig. 2) and extending posteriorly to back of foot; slit leading by way of ciliated duct into deep, massive, metapodial mucus gland, staining deep purple in toluidine blue. Males with ciliated strip on right side of foot, emerging from right side of mantle cavity and extending down to edge of sole. Ciliated gutter on right side of foot in females deep, running down side of foot and extending through lateral epipodial groove (Fig. 2). No ovipositor present. Mantle edge dorsally fringed with many small papillae.

Pallial Cavity: Osphradium a little less long than ctenidium, broad, about one-third ctenidial width, dark brown, weakly bipectinate with small pectins on each side but unconnected dorsally; osphradium becoming monopectinate at inhalant siphon. Ctenidium narrow, extending length of pallial cavity, comprising

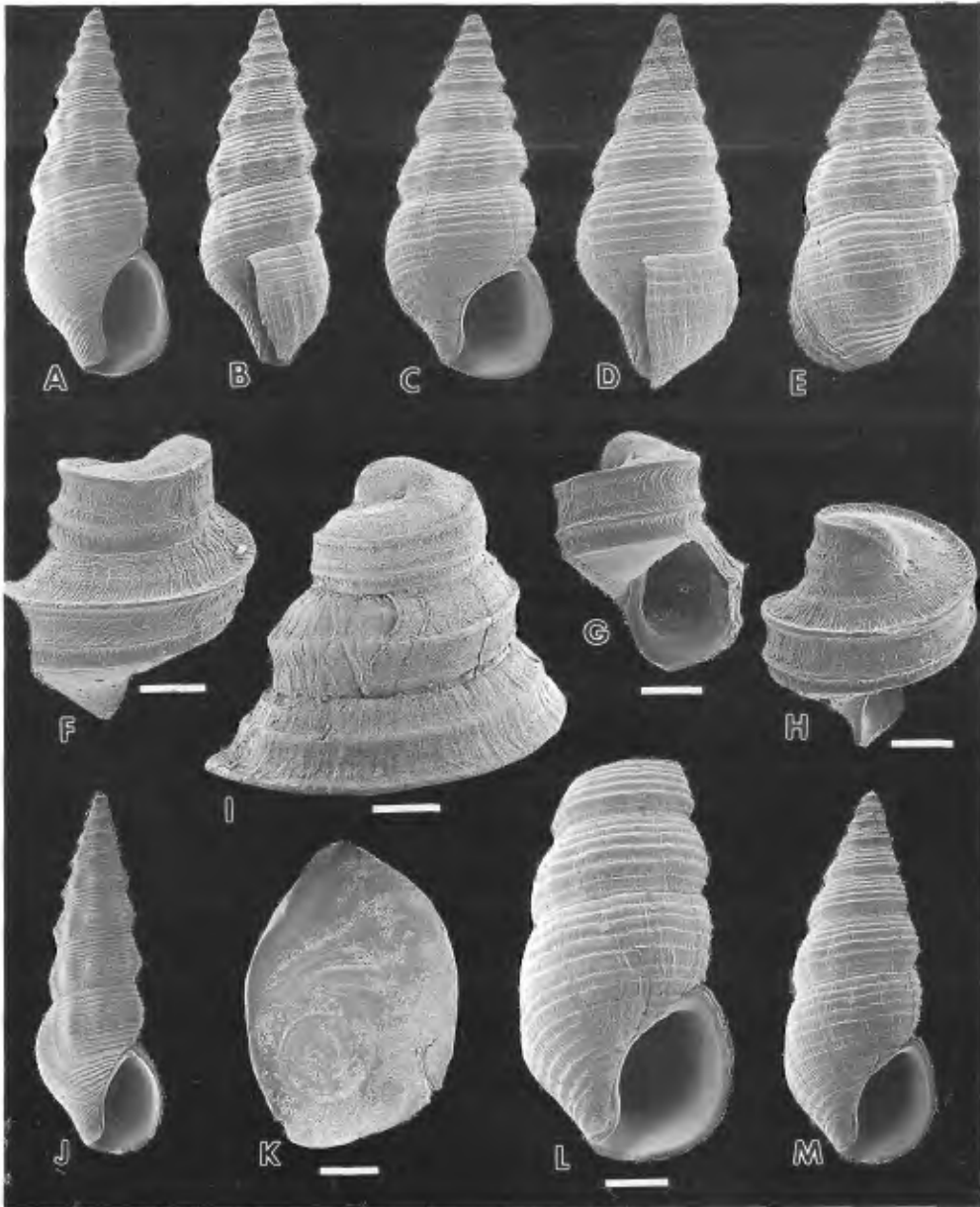


FIG. 8. SEM micrographs of *Ittibittium parcum* from Honolulu, Hawaii (USNM 857100). A, B, apertural and lateral views of shell, 3.6 mm length; C–E, apertural, lateral and dorsal views of shell, 3.6 mm length; F, newly hatched larval shell showing protoconch and details of whorl sculpture, bar = 63 μ m; G, H, embryonic shells removed from egg capsule, bar = 23 μ m; I, larval and early whorls of shell, bar = 0.4 mm; J, shell with strong axial ribs, 5.3 mm length; K, operculum, bar = 0.2 mm; L, detail of penultimate and body whorl, showing details of sculpture and aperture, bar = 0.6 mm; M, apertural view of shell, 3.6 mm length.

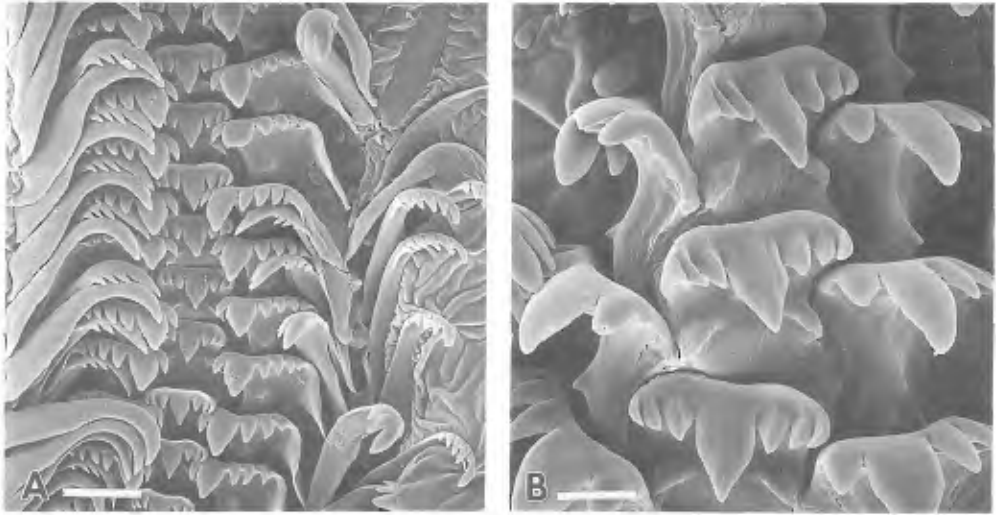


FIG. 9. SEM micrographs of radula of *Ittibittium parcum* from Honolulu, Hawaii (USNM 857100). A, middle of radular ribbon with right marginal teeth folded back, bar = 30 μm ; B, detail of rachidian and lateral teeth, bar = 8 μm .

long, finger-like, triangular filaments. Hypobranchial gland partially overlaying rectum, well developed, composed of several large, dark-staining glandular cells.

Reno-pericardial System: Pericardium lying adjacent to posterior pallial wall. Kidney large, extending from anterior of style sac forward, into roof of posterior pallial cavity.

Alimentary System: Snout tip and lips of mouth yellow. Buccal mass large, about two-thirds snout length. Radula (Fig. 9A) short, about one-tenth shell length. Rachidian tooth having weak hour-glass shape and cutting edge with large central cusp flanked by 2 denticles on each side. Lateral tooth (Fig. 9B) having cutting edge with large pointed cusp, one inner denticle, 3–4 outer denticles. Inner marginal tooth with 2 inner denticles, large elongate major cusp and 3 outer denticles; outer marginal tooth with 5 inner denticles. Salivary glands paired, comprising tangled mass behind nerve ring, extending through it anteriorly as slender tubes. Esophagus becoming wide behind nerve ring, developing lateral glandular pouches with many small transverse internal folds, comprising short esophageal gland. Stomach large, about one whorl in length, having single opening to digestive gland, central raised pad, gastric shield, short crystalline style and style sac,

about two-thirds the stomach length. Intestine leaving stomach looping dorsally and across anterior style sac, turning sharply, running anteriorly, adjacent to right side of kidney and albumen gland. Rectum slightly wavy, wide, containing large ovoid fecal pellets.

Nervous System: Cerebral ganglia very large, twice size of pleural ganglia. Subesophageal ganglion very close to left pleural ganglion. Supraesophageal ganglion separated from right pleural ganglion by connective two-thirds ganglion length.

Reproductive System: Testis white, overlaying brown digestive gland. Males aphyllate with open pallial gonoducts. Pallial oviduct open, with large albumen gland extending through posterior of mantle cavity mantle cavity, protruding into visceral coil. Albumen gland staining cream-green in toluidine blue. Capsule gland very large, swollen, staining dark blue in toluidine blue. Large spermatophore bursa in posterior medial lamina. No ciliated ridge tract or seminal receptacle in lateral lamina. Spawn mass comprising wide gelatinous tube covered with thin membrane forming compact, short tube about 2 mm long, and 1.2 mm wide, containing large opaque, compacted eggs each 0.2 mm in diameter. Eggs arranged in short jelly tube about 3–4

deep. Development direct with young snails hatching from eggs.

Discussion

"*Bittium*" *parcum* has not been cited commonly in the literature, and due to great inter-specific variability in shell sculpture and color, is frequently misclassified or unidentified in museum collections. Shell shape can vary from slender, elongate (Fig. 8J) to shorter, more inflated (Fig. 8C-E), and shell sculpture is highly variable: the axial ribs seen in some specimens may be entirely lacking in others. The protoconch with its flattened apex, broad sutural ramp and concave whorls is highly distinctive and unusual (Fig. 8F-H). However, *Ittibittium parcum* is readily distinguished from by several external anatomical features: (1) the epipodial skirt and opercular lobe are fringed with well-developed papillae; (2) a pair of long epithelial extensions (papillae) of the front of the foot (propodium); (3) the longitudinal slit marking the entrance to the metapodial mucus gland is very long. *Ittibittium parcum* has an unusual pallial oviduct in that the albumen gland projects posteriorly past the posterior end of the mantle cavity into the visceral coil, and there is no seminal receptacle in the lateral lamina of the pallial oviduct.

Living snails are quick, active crawlers, and even when removed from their shells showed a great deal of movement.

The operculum in this species tends to be more ovate than circular: in most other species of the *Bittium*-group, the operculum is circular. The opercular lobe papillae show through the transparent edges of the operculum.

This species undergoes direct development. The embryos pass through a veliger stage and hatch out as juvenile snails after losing the velar lobes. Direct development, while also occurring in *Stylidium*, is not the common mode of development among members of the *Bittium*-group. The comparatively large eggs of *Ittibittium parcum* are each enclosed within individual hyaline capsules about 0.2 mm diameter, and the egg capsules are stacked within a short, wide gelatinous tube and deposited on the substrate in an irregular mass. Here they undergo development, passing through a modified veliger stage and producing a well-developed embryonic shell (Fig. 8F-H), after which they emerge as small snails.

Ittibittium parcum is common in shallow wa-

ter throughout the Hawaiian chain, and also occurs in French Polynesia (Naim, 1982) where it is very abundant in some localities. Naim (1982) found that this species represented 89% of the molluscan fauna associated with algae in Tiahura Lagoon in French Polynesia.

A species from Western Australia, very similar to the type species, recently has been described in great detail (Ponder, in press), and appears to be closely related to *Ittibittium parcum*.

BITTIOLUM COSSMANN, 1906

Bittiolium Cossmann, 1906: 139. (Type species by original designation: *Bittium podagrinum* Dall, 1892). Wenz, 1940: 755; Olsson & Harbison, 1953: 289-290.

Diagnosis

Shell small, turreted, stout, sculptured with 4 spiral cords and many axial ribs, and occasional weak varices. Protoconch with one spiral lira. Whorls presuturally constricted, body whorl elongate, narrow at aperture and constricted at base, having less width than penultimate whorl. Operculum ovoid-circular, paucispiral and with subcentral nucleus. Anterior canal weakly defined, short. Mantle edge smooth, epipodial skirt scalloped. Foot elongated anteriorly and having median longitudinal slit in posterior part of sole, leading into large metapodial mucus gland. Ovipositor small. Osphradium bipectinate, wide, one-third ctenidial length. Nervous system with right zygoneury and with short supraesophageal connective.

Remarks

Bittiolium species have small shells (Table 3) and are distinctive in having the body whorl elongated and constricted basally so that the aperture width is less than that of the penultimate whorl. The smooth mantle edge, narrow elongate anterior foot, right zygoneury and short supraesophageal connective are autoapomorphic characters of this genus.

The type species of this genus is a Neogene fossil from Florida that has a shell morphology very similar to that of living *Bittiolium varium* and *Bittiolium alternatum*. As the fossil species occurs in mid- to late-Neogene strata, and in the same geographic area as Recent

Bittium varium, it is not unreasonable to infer that the two species belong to the same clade, and the living species is considered to be congeneric with *Bittium podagrinum*. Cossmann (1906: 140) pointed out that *Bittium varium* (Pfeiffer) (cited as *Cerithium*) occurred from the Pleistocene of Florida and extended into the Recent. He further noted the superficial resemblance of *Bittium varium* to some fossils of *Aneurychilus* Cossmann, 1889, which he placed in the Diastomatidae (as Diastomidae, Cossmann, 1906: 174).

Dall (1889) was the first author to confuse American members of *Bittium* with the genus *Diastoma* Deshayes, 1850, when he referred *Bittium varium* to that genus. Abbott (1974), probably following this cue, later referred western Atlantic species of *Bittium*, s.l., to *Diastoma* Deshayes, 1850, but this subsequently has been shown to be incorrect (Houbrick, 1977: 102, 1981b), as the latter genus belongs to the Diastomatidae Cossmann, 1894, a totally different lineage represented by individuals of much larger size and different anatomy that are not closely related to the *Bittium*-group (Houbrick, 1981b).

The anatomy of "*Bittium*" *alternatum*, from the northeastern coast of North America, is identical to that of its southeastern, Caribbean Province congener, *Bittium varium*. Thus, these two species and probably all other American western Atlantic species belong in the genus *Bittium*, which is also represented by several eastern Pacific species, such as *Bittium fastigiatum* (Carpenter, 1864).

Because the two *Bittium* representatives studied, *B. varium* and *B. alternatum*, are so alike, they are treated jointly in the section below.

Bittium varium (Pfeiffer, 1840)
(Figs. 10–11)

Cerithium varium Pfeiffer, 1840: 256.

Cerithium columellare Orbigny, 1842: pl. 23, figs. 13–15; 1845: 244 (in part; syntypes BMNH).

Cerithium gibberulum C. B. Adams, 1845: 5 (Lectotype MCZ 186078, type locality Jamaica).

Bittium varium (Pfeiffer). Tryon, 1887: 152, pl. 29, fig. 86; Perry, 1940: 134, pl. 28, fig. 202.

Cerithium (*Bittium*) *gibberulum* (C. B. Adams). Kobelt, 1898: 245–246, pl. 43, fig. 1.

Diastoma varium (Pfeiffer). Abbott, 1974: 107, fig. 1037.

Description

Shell (Fig. 10): Shell turreted, pendent-shaped, comprising about 10 flat-sided whorls and reaching 7 mm length. Protoconch (Fig. 10I) comprising 2.5 whorls; protoconch 1 smooth, protoconch 2 with central keel-like spiral lira and microscopic pustules on apical part of whorl. Early whorls (Fig. 10H) with two weak spiral lirae, and sculptured with dominant suprasutural spiral cord and two weaker spiral cords above it, and with weak axial ribs. Adult whorls sculptured with 4 spiral cords and 14 strong axial ribs forming small beads at crossover points and producing cancellate pattern. Body whorl elongate, more than one-third shell length, constricted at aperture and more at siphon; body whorl sculptured with about 10 flattened spiral cords and 14 weak axial ribs. Aperture ovate, constricted, not as wide as width of body whorl, narrowing posteriorly and having short, distinct siphonal canal. Columella concave with slight callus. Outer lip of aperture smooth, rounded, thin and pendant, extending beyond siphonal canal. Periostracum thin, tan.

Animal: Snout, cephalic tentacles, and neck slender, extremely long and extensible. Snout bilobed at tip. Foot narrow, extremely elongate anteriorly, three times snout length, and with crescent-shaped propodium (Fig. 2). Deep crescentic transverse slit formed by two lips in anterior foot and leading via a central duct into large anterior mucus gland (Fig. 11A, amg). Corners of anterior pedal lips extending laterally and posteriorly forming unciliated undulating epipodial skirt (Fig. 11A–B, es) delineating lateral groove between epipodium and sole; epipodial skirt weakly scalloped posteriorly (Fig. 2), forming lanceolate opercular lobe, scalloped around edges. Ciliated gutter (Fig. 11B, cg) in both sexes emerging from floor of right side of pallial cavity, running down right side of foot leading into epipodial groove. Ciliated gutter terminating in small glandular ovipositor (Fig. 11B, ovp) at edge of foot in females. Posterior third of sole with median longitudinal slit leading into massive mesopodial mucus gland (Fig. 11A, mmg), extending deeply into head foot up to nerve ring and cephalic hemocoel. Operculum (Fig. 10F, G) corneous, light tan, circular-ovate, paucispiral with subcentric nucleus. Mantle edge (Fig. 11B, me) bilobed, smooth,

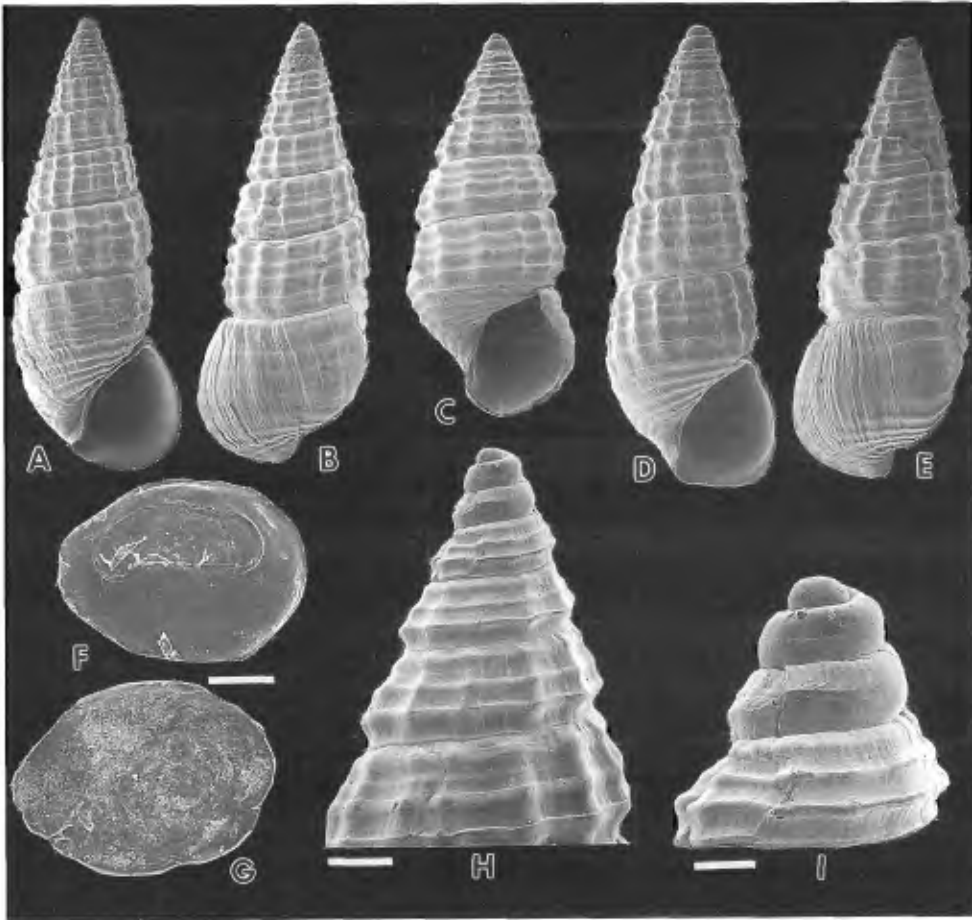


FIG. 10. SEM micrographs of *Bittium varium* from Ft. Pierce, Florida (USNM 77639). A, B, D, E, two shells showing sculptural variation and shell shape; length 3.2 mm; C, immature shell, length 2.8 mm; F, G, operculum, bar = 0.2 mm; H, sculpture of early whorls, bar = 0.3 mm; I, protoconch, bar = 88 μ m.

without papillae, slightly scalloped, iridescent at edges.

Pallial Cavity: Osphradium wide, one-third ctenidial length, weakly monopectinate, comprising small, dorsally placed pectins, flanked on each side by weak ciliated strip. Ctenidium comprising long, triangular filaments with soft rods and mucus glands.

Alimentary System: Radula (Fig. 11C) short. Rachidian tooth (Fig. 11D) with cutting edge of 3 small denticles on each side of central cusp. Lateral tooth (Fig. 11D) with two outer and 3–4 inner denticles. Inner marginal tooth with 3–4 inner and 2–3 outer denticles. Outer

marginal tooth with 6 small inner denticles. Midesophagus with wide ciliated dorsal food groove; posterior esophagus narrow.

Nervous System: Cerebral ganglia slightly larger than pedal ganglia and with short connective (about one-third cerebral ganglion length). Pedal ganglia nearly fused at connective, each with posterior statocyst; two pairs of accessory pedal ganglia present: pair of small propodial ganglia, and larger pair of metapodial ganglia. Subesophageal connective between subesophageal ganglion and left pleural ganglion equal in length to left pleural ganglion; supraesophageal connective about equal in length to subesophageal connective.

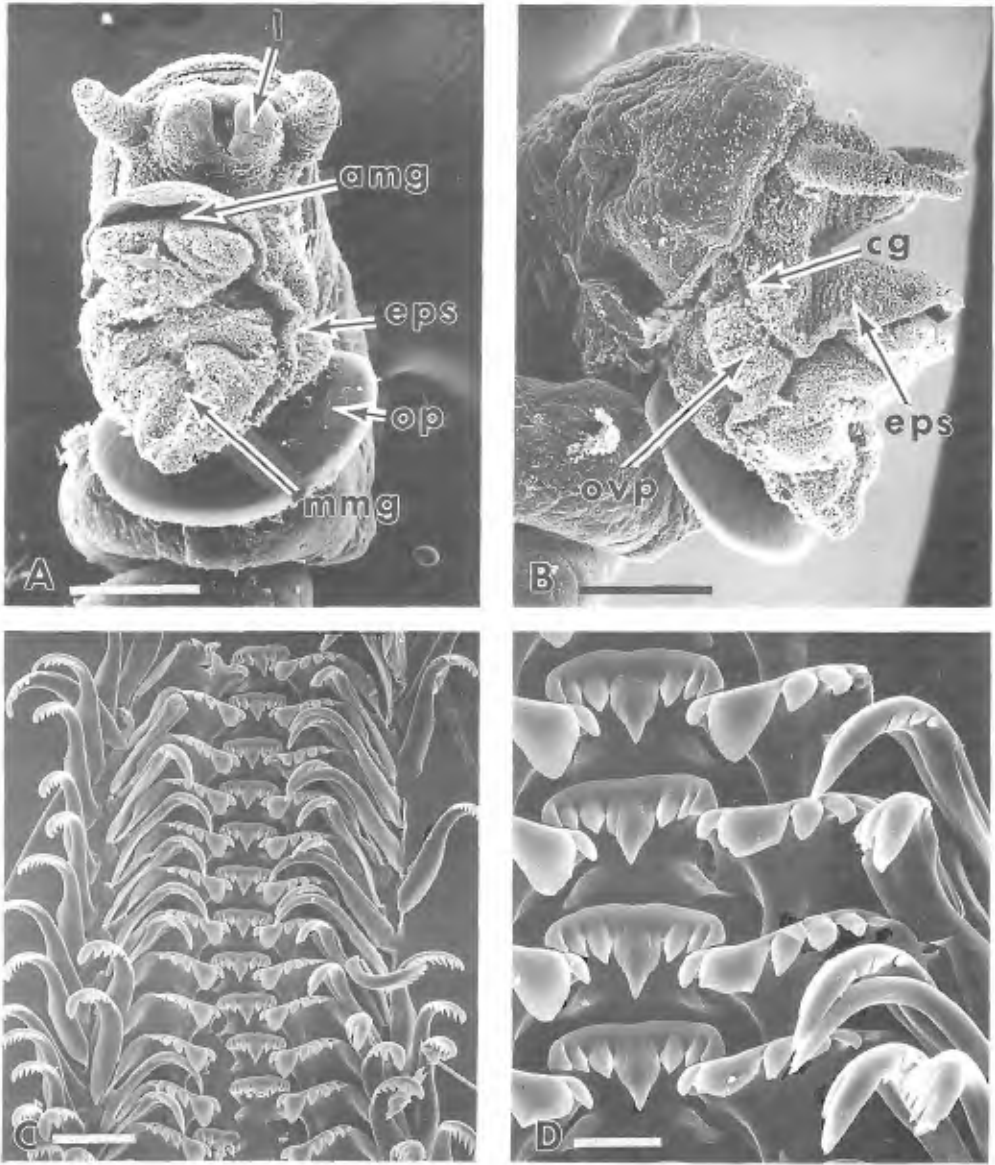


FIG. 11. SEM micrographs of *Bittium varium* from Ft. Pierce, Florida (USNM 776639). A, B, critical point dried specimens showing external anatomical features of headfoot, bar = 0.2 mm; C, mid-section of radula, bar = 21 μ m; D, detail of rachidian and lateral teeth, bar = 7 μ m. amg = anterior mucus gland; cg = ciliated groove; eps = epipodial skirt; l = lip of mouth; mmg = metapodial mucus gland; op = operculum; ovp = ovipositor.

Right zygoneury between subesophageal and right pleural ganglion.

Reproductive System: Ducts of testicular follicles joining to form spermatic duct, moving

anterior as seminal vesicle, containing dimorphic sperm. Males producing crescent-shaped spermatophore with flared bifurcate end and pointed, filamentous tip. Spermatophores containing both eu- and parasperma-

tozoa. Ovary cream colored, overlying brown digestive gland, extending forward to stomach. Pallial oviduct open, but closed in far posterior portion. Common aperture to opening of spermatophore bursa in lateral lamina anterior to opening of sperm pouch and opening of seminal receptacle located on edge of medial lamina one-third from posterior of lamina. Opening to spermatophore bursa not adjacent to opening on medial lamina, but located one-third back from anterior of lateral lamina. Spermatophore bursa comprising ciliated and high vacuolated epithelial cells. Spawn mass composed of spirally wound thin jelly string containing many small eggs 100–120 μm in diameter, hatching as veliger larvae, becoming planktotrophic.

Bittiolium alternatum (Say, 1822)

Turritella alternata Say, 1822: 243.

Pasithea nigra Totten, 1834: 369, figs. 7a, b.
Bittium nigrum (Totten), Gould, 1870: 321, fig. 590.

Bittium alternatum (Say), C. W. Johnson, 1915: 127.

Diastoma alternata (Say), Abbott, 1974: 107, fig. 1037.

Description

This species is essentially the same as *Bittiolium varium*, described above, although the shell differs slightly in being more pupoid and less narrowly elongate.

Remarks

Marcus & Marcus (1963) thoroughly described the anatomy of *Bittiolium varium* in Brazil. My work on populations of this species from Florida basically confirms their detailed observations. In addition, the basic anatomy of the Brazilian and Florida specimens is very similar to that of *Bittiolium alternatum* from the American northeastern coast, suggesting that the latter is probably a sister taxon of *Bittiolium varium*.

Bittiolium is the only genus studied in which the mantle edge is smooth, with no trace of papillae, a character noted by Marcus & Marcus (1963). A wavy epipodial skirt and narrowly elongate anterior foot are also distinctive external features (Fig. 2) of both examined *Bittiolium* species. The ovipositor

(Fig. 11B, ovp) is barely visible only during the breeding season, but is basically the same as that observed in *Bittium*. The massive metapodial mucus gland located in the posterior part of the sole differs from that seen in *Ittibittium* species, in which the slit is much longer. This gland secretes a string of mucus by which the animal can suspend itself in the algae, but the thread does not have the tensile strength of the mucous threads produced by members of the Litiopidae (Houbrick, 1987b). Except for major differences in external features, the radula and internal anatomy of *Bittiolium varium* is quite similar to that of *Bittium reticulatum*. The radula differs only minor details (Table 2). Although *Bittiolium varium* primarily is a grazer of epiphytic microalgae, Marcus & Marcus (1963: 79) have shown that the snail can use its anterior tentidial filaments for particle feeding while stationary.

Marcus & Marcus (1963: 88–89) found four spindle-shaped spermatophores, each 1 mm long and 0.06 mm wide, in the bursa of the lateral lamina in *Bittiolium varium*, and noted that the spermatophores dissolve in this bursa. The location of the spermatophore bursa in the lateral lamina is a unique feature among cerithioidean taxa, and this layout is probably the same among other members of the *Bittium*-group, in which the bursa in the lateral lamina has been confirmed. However, spermatophores have not been observed in this bursa in any other species.

Bittiolium varium lays its eggs mostly on seagrasses. In the Indian River, Florida, I observed numerous irregular egg masses comprising strands of eggs embedded in a loose jelly matrix deposited on *Halodule* grass blades and on ramose algae. In the spring, nearly all adults were ripe and egg laying continued through the summer months tapering off in September.

Bittiolium varium has been the subject of a number of ecological investigations. Virnstein & Curran (1986) measured the colonization time of this species in seagrasses in the Indian River, Florida. Hardison & Kitting (1985) found that *Bittiolium varium* fed primarily on diatoms and coralline algae in seagrass meadows of the northwest Gulf of Mexico. Despite the high population densities of this snail (3,000/m²), little impact on its food could be detected. In Chesapeake Bay, Van Montfrans et al. (1982) found that the grazing activities of *Bittiolium varium*, which selectively eats diatoms from blades of marine grasses,

could have important implications for the abundance and distribution of *Zostera*.

Bittium varium has a wide range in the western Atlantic, occurring from Chesapeake Bay south to Florida and the Gulf of Mexico, throughout the Caribbean, and south to Brazil.

STYLIDIUM DALL, 1907

Stylidium Dall, 1907: 178 (Type species by original designation: *Bittium eschrichtii* Middendorf, 1849). Thiele, 1929: 211; Wenz, 1940: 757; Abbott, 1974: 106.

Diagnosis

Shell relatively large, dirty chalky white, smooth, weakly sculptured with four broad spiral cords defined by incised lines. Protoconch unsculptured. Snout twice length of cephalic tentacles. Epipodial skirt poorly developed, smooth along edges, but opercular lobe with small, pointed papillae. No metapodial mucus gland. Osphradium non-pectinate. Common aperture to sperm bursa and seminal receptacle in edge of anterior third of medial lamina of pallial oviduct. Openings to sperm bursa and seminal receptacle well-separated. Long ciliated ridge tract in lateral lamina of pallial oviduct. Development direct.

Remarks

This genus is represented by species living in cold-water habitats from California north to Alaska. The shell is dull and chalky under the periostracum. Shell length can be quite large (Table 3) for a member of the Bittiinae, and the large smooth protoconch, without sinusigeral notch, is indicative of direct development.

At first glance, the shell of *Stylidium* does not appear to fit the *Bittium*-group mold. However, anatomical features, such as the epipodial skirt, large opercular lobe (Fig. 2) and pallial gonoduct configuration unmistakably place it into the Bittiinae. The common aperture to sperm pouch and seminal receptacle is unusual in being located in the far anterior edge of the medial lamina of the pallial oviduct, and not adjacent to the opening of the spermatophore bursa of the lateral lamina. The length of the ciliated ridge tract of the lateral lamina is also atypical.

Stylidium eschrichtii (Middendorf, 1849)
(Figs. 12–14)

Turritella eschrichtii Middendorf, 1849: 396–397, pl. 11, fig. 1 (Holotype, Zoological

Institute, St. Petersburg; type locality, Sitka, Alaska).

Bittium (Stylidium) eschrichtii icelum Bartsch, 1907: 178 (Holotype USNM 15209a; type locality, Neah Bay, Washington); 1911: 388, pl. 57, fig. 3; Ruhoff, 1973: 81.

Bittium eschrichtii (Middendorf). Oldroyd, 1927: 18–19, pl. 79, fig. 4.

Bittium (Stylidium) eschrichtii (Middendorf). Abbott, 1974: 106, fig. 1010.

Description

Shell (Fig. 12): Shell large, turreted, reaching 17.5 mm in length, comprising 9–11 convex whorls. Protoconch (Fig. 12G) has two smooth whorls. Early whorls (Fig. 12E–G) sculptured with three spiral bands. Adult whorls sculptured with 4 weak, widely flattened spiral bands separated from one another by deep incised spiral grooves. Penultimate whorls with 5 wide, spiral, weak bands. Suture well defined, slightly counter-sunk into each abapical whorl. Body whorl a little less than one-third shell length, sculptured with about 8 broad spiral cords and incised lines. Shell base weakly constricted at base; anterior siphon broad and shallow. Aperture ovate having concave columella with weak callus; outer lip of aperture circular, crimped where spiral grooves end. Shell color chalky white-gray, covered by thin tan periostracum.

Animal: Base color dirty white with transverse black stripes on snout, head, and epipodium (Fig. 14A). Ciliated epithelial strip running from mantle cavity floor on each side of headfoot and ending beneath peduncle of each cephalic tentacle. Ciliated gutter on right side of foot in females ending in small pink, glandular ovipositor at foot edge. Snout very long, twice length of cephalic tentacles, wide, bilobed at tip. Eyes very small. Lateral epipodial skirt with minute pointed papillae along edge of posterior third of foot; opercular lobe long, pointed posteriorly, darkly pigmented and with small pointed papillae along edge (Fig. 2). Anterior foot crescent-shaped with long slit along edge leading into centrally placed, ovate mucus gland deep within propodium. No metapodial mucus gland. Operculum (Fig. 12H, I) thick, ovate, paucispiral, with eccentric nucleus. Mantle edge bilobed, with small papillae, and with slightly elongate exhalant siphon. Mantle roof folded longitudinally over exhalant siphon forming dorsal, posteriorly extending ridge.

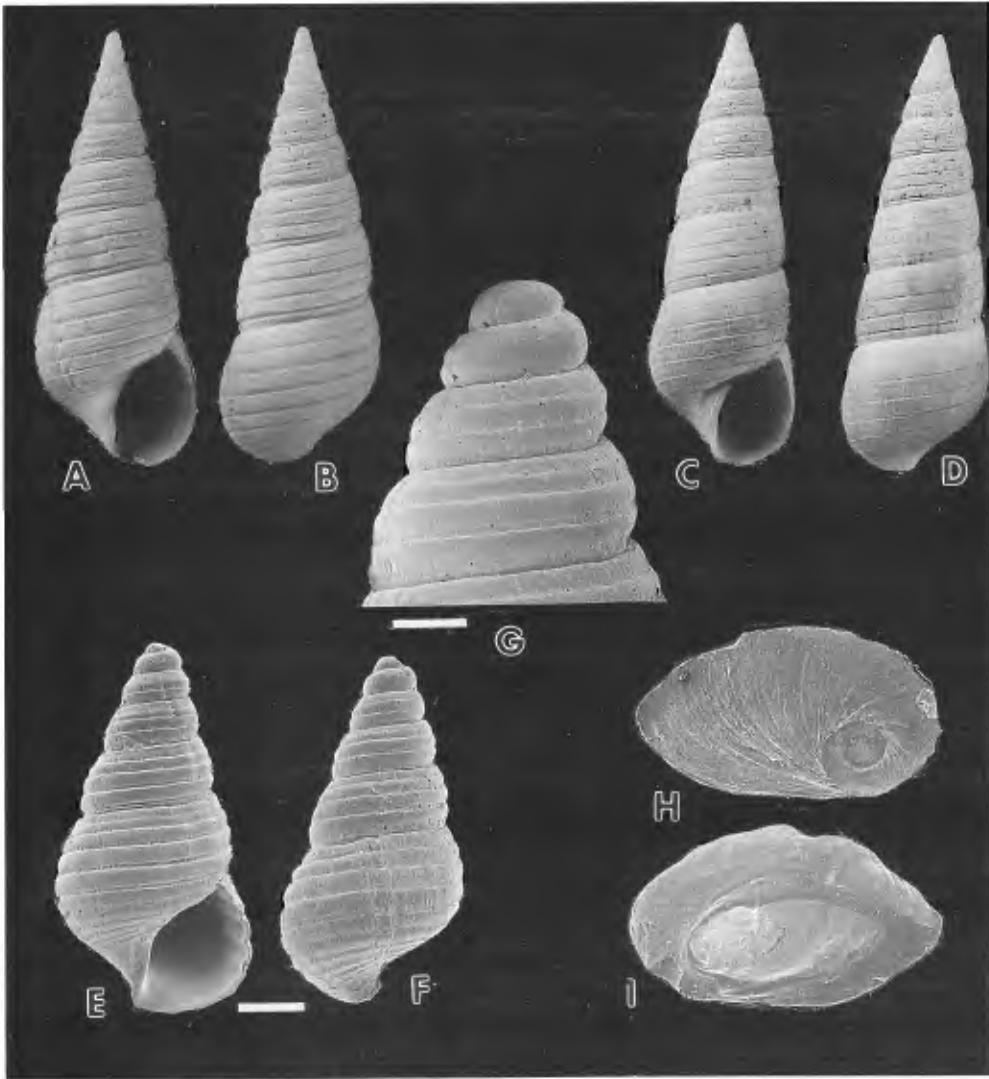


FIG. 12. *Styliidium eschrichtii* from Carmel, California. A–D, two shells showing sculptural variation (USNM 804376), 22.4 and 20.2 mm length, respectively; E, F, SEM micrographs of immature shells showing early sculptural patterns, bar = 0.5 mm; G, SEM micrograph of protoconch and early whorls, bar = 0.3 mm; H, I, SEM micrographs of operculum, showing eccentric nucleus and attachment scar, 2.4 mm length.

Pallial Cavity: Osphradium tan, vermiform, non-pectinate, extending length of pallial cavity, but slightly shorter than ctenidium. Ctenidium pink, comprising long, finger-like filaments twice length of their attached bases.

Alimentary System: Radular ribbon (Fig. 13A) short. Lateral tooth (Fig. 13B) with long lateral basal extension and cutting edge with

3 inner denticles, and 3–5 outer denticles; inner marginal tooth with 4–5 inner and 3 outer denticles. Paired salivary glands vermiform, loosely compacted, lying mostly anterior to nerve ring, but beginning behind it as thick swellings, and passing through as thin tubes. Stomach large, about one whorl in length; internally with large sorting area and roundish central pad; single opening to digestive gland on right side of pad; 6–7 large transverse ribs

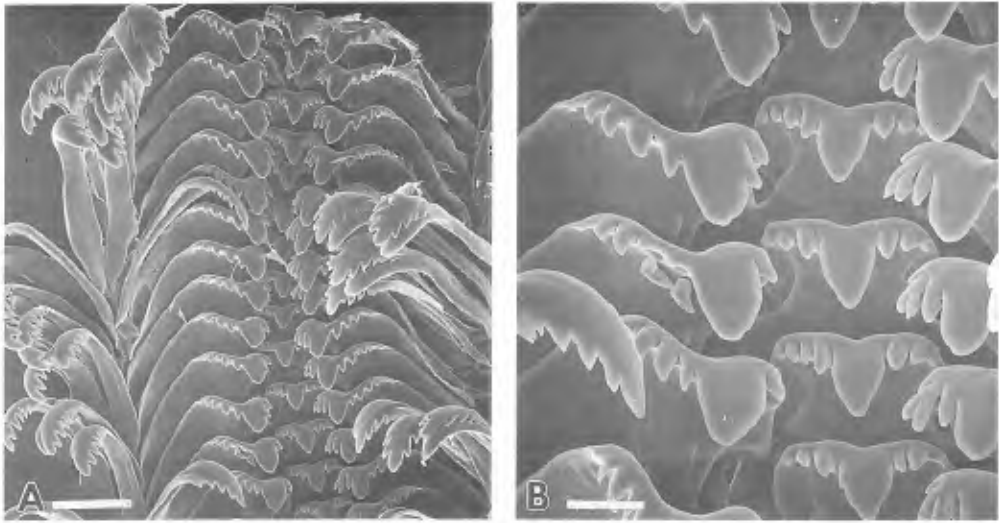


FIG. 13. SEM micrographs of radula of *Styliidium eschrichtii* (USNM 804376); A, section of mid-radular ribbon with marginal teeth folded back, bar = 38 μm ; B, detail of rachidian and lateral teeth, bar = 12 μm .

on left side of pad, posterior to cuticular gastric shield; short, wide style sac one-half stomach length, separate from intestinal opening. Intestine opening separated from lumen of style sac by typhlosole ridge.

Nervous System (Fig. 14): Nerve ring large with thick commissure connecting cerebral ganglia. Dialyneury (Fig. 14B, d) between left pallial nerve and nerve arising from supraesophageal ganglion. Supraesophageal connective (Fig. 14A, sec) twice length of right pleural ganglion. Subesophageal ganglion (Fig. 14A, sbe) closely adjacent to left pleural ganglion.

Reproductive System Posterior half of pallial oviduct with thick, white, opaque albumen gland comprising flocculant transverse glandular ridges; mid-section of pallial oviduct with thin, weak glandular transparent walls; very thick, opaque transverse glandular ridges present in anterior third of pallial oviduct, comprising capsule gland. Sperm gutter in anterior edge of medial lamina having elongate common aperture to spermatophore bursa and seminal receptacle. Openings to sperm pouch and seminal receptacle within common aperture well separated. Long tube within edge of medial lamina leading to posteriorly placed pouch-like seminal receptacle. Large sperm pouch with internal transverse epithelial folds, occupying posterior third of

medial lamina. Very long ciliated ridge tract beginning in anterior part of lateral lamina, leading into posterior spermatophore bursa. Spawn comprising thin gelatinous string wound into irregular mass. Eggs 0.2 mm in diameter. Development direct.

Remarks

Several subspecific taxa have been described, but it is debatable if all of these nominal taxa are good subspecies or merely clinal/ecophenotypic varieties of *Styliidium eschrichtii*. Abbott (1974) synonymized the subspecies *icelum* Bartsch with *S. eschrichtii*.

Styliidium eschrichtii is characterized by its chalky gray, smooth shell sculptured with broad flattened spiral cords. The protoconch is large, unsculptured, and lacks a sinusigeral notch (Fig. 12G). The ovate operculum (Fig. 12H, I) with eccentric nucleus is a departure from a more circular operculum with subcentral nucleus, as seen in other bittiid species. Shell length seems to vary greatly among populations, but some individuals can be very large, approaching 18 mm length (Table 3). Large shell size appears to be more common in northern populations.

This species lives on intertidal to subtidal rubble in cool waters of the northeastern Pacific. I observed a large intertidal population living among the intertices of gravel and algae

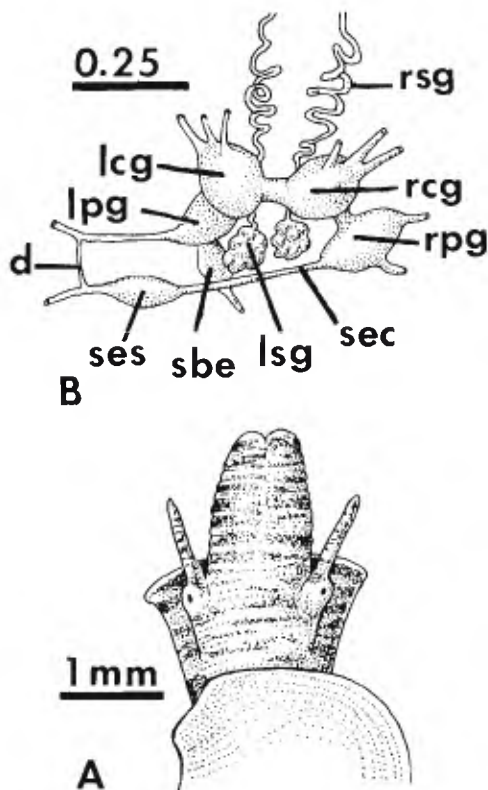


FIG. 14. Anatomical features of *Styliidium eschrichtii*. A, head and anterior foot, showing pigment pattern; B, position of salivary glands relative to nerve ring. d = left dialaneury; lcg = left cerebral ganglion; lpg = left pleural ganglion; lsg = left salivary gland; rcg = right cerebral ganglion; rsg = right salivary gland; rpg = right pleural ganglion; sbe = subesophageal ganglion; sec = supraesophageal ganglion; seg = supraesophageal ganglion.

at Carmel, California. According to Strathmann (1987), *Styliidium eschrichtii* has direct development. Spawn is deposited on the substrate in gelatinous masses (presumably comprising coiled strings) containing egg capsules measuring 0.2 μ m diameter in which the embryos undergo direct development, passing through the veliger stage and hatching as small snails.

LIROBITTIUM BARTSCH, 1911

Lirobittium Bartsch, 1911: 384 (Type species by original designation, *Bittium catalinensis* Bartsch, 1907). Thiele, 1929: 211; Wenz, 1940: 757; Abbott, 1974: 106; Gründel, 1976: 54.

Diagnosis

Shell turreted, elongate, sculptured with axial riblets and spiral beaded cords. Protoconch with two spiral lirae. Varices not present on adult whorls. Operculum circular. Radular ribbon very small; radular teeth with many small denticles. Snout long; head with small cephalic tentacles and small eyes. Ovipositor and ciliated groove on right side of foot absent. Mantle edge with long papillae. Epipodial skirt very weakly developed. Osphradium vermiform, wide. Spawn comprising large egg capsules, each attached to long stalk and anchored together. Development direct.

Remarks

Bartsch (1911) divided *Bittium*-group species from the American west coast into four genera: *Bittium*, *Lirobittium*, *Semibittium*, and *Styliidium*. His groups were defined only on superficial shell characters, such as the presence or absence of varices, protoconch sculpture, and axial and spiral sculpture. Many of the species Bartsch (1911) included under his generic scheme have been ignored or referred by subsequent authors to different generic taxa.

The genus *Lirobittium* Bartsch, from the temperate eastern Pacific, was based on minor shell sculptural characters: Bartsch (1911: 384) noted that the defining characters of *Lirobittium* were a protoconch with two spiral lirae and the absence of varices from the adult whorls. These features were also mentioned by Gründel (1976: 54), who additionally noted that of the two primary spiral cords, the abapical one was inserted a little later. Gründel (1976: 54–56) assigned *Cacozeliana* and *Styliidium* (with a query) as subgenera of *Lirobittium*. He indicated that *Cacozeliana* differed from *Lirobittium* by the formation of varices, and *Styliidium* by the suppression or complete absence of axial ribs. It has been shown herein that the *Cacozeliana* is separated from *Lirobittium* by many significant characters.

The above history of *Lirobittium* shows that much of the confusion regarding the placement of the numerous California species stems from the original superficial generic descriptions based solely on shell morphology. It is obvious that the characters derived by these authors from minor sculptural details hardly seem to be of generic weight and have

resulted in poorly defined, ambiguous genera with broad or discordant limits, and that have been used in varying combinations. Although shell sculpture may have some value at the specific level, it is generally not useful at the generic level, especially in cerithiids. Not a single author has included radular or opercular characters and no mention is made of anatomical features in the definition of genera.

Abbott (1974: 106) considered both *Bittium catalinense* and *B. subplanatum* to be synonyms of *Lirobittium attenuatum* Bartsch, 1911, but gave no reasons for this decision. Hertz (1981: 40) showed that *Lirobittium subplanatum* (cited as *Bittium*) was a valid species. I have examined two species of *Lirobittium*: *L. catalinense* (one dried specimen) and well-preserved material of *L. subplanatum*. Observations on the poorly preserved, dried animal of *L. catalinense* are included because it is the type species of the genus, but the bulk of the descriptive anatomical characters of *Lirobittium* are derived from study of *L. subplanatum*. The two species are anatomically very similar, have similar radulae, and are undoubtedly congeneric. The above diagnosis and following specific descriptions represent an integrated analysis of generic characters, based on these two species.

Lirobittium catalinense Bartsch, 1907

Bittium catalinensis Bartsch, 1907: 28, pl. 57, fig. 13 (Holotype: USNM 165232, type locality: Santa Barbara, California [Pleistocene]); Abbott, 1974: 106, fig. 1013.

Bittium (Lirobittium) catalinense Bartsch, 1911: 402–403, pl. 51, fig. 1.

Remarks

The type species of this genus is a Pleistocene fossil, but Bartsch (1911) described many subspecies, some of which are Recent. *Bittium catalinense* is now regarded as a synonym of "*Bittium*" *attenuatum* Carpenter, 1864 (Abbott, 1974: 106).

Examination of a reconstituted, dried specimen of the type species of *Lirobittium*, *Bittium catalinense* (= *Bittium attenuatum*), showed that the animal is basically the same as *Lirobittium subplanatum*. It is relatively unpigmented, has a large, broad snout, bilobed at the anterior end and short cephalic tentacles, about half the snout length. The mantle edge has many long papillae along its dorsal and lateral sides, while the mantle edge forming

the inhalant siphon has large paddle-shaped papillae. The buccal mass is small, and the radula minute, about one-thirteenth the shell length. The rachidian tooth has a triangular basal plate with a long glabella and is as wide as tall; there is a deep concave indentation and a cutting edge with a long pointed central cusp flanked on each side by 4–5 small denticles. The lateral teeth are deeply concave on the top, have a wide basal plate with a large central buttress, and have numerous small denticles. The marginal teeth are slender, and serrated along their tips with many small pointed denticles (Fig. 15).

Lirobittium subplanatum (Bartsch, 1911)
(Figs. 15–17)

Bittium (Semibittium) subplanatum Bartsch, 1911: 395–396, pl. 57, fig. 5 (Holotype, USNM 160076; type locality, Catalina Id., California); Oldroyd, 1927: 23; Ruhoff, 1973: 130.

Bittium subplanatum Bartsch. Dall, 1921: 146; Hertz, 1981: 40, figs. 23–27.

Bittium subplanatum Bartsch. Oldroyd, 1927: 23.

Bittium (Lirobittium) subplanatum (Bartsch). Abbott, 1974: 106.

Description

Shell (Fig. 15): Shell elongate, turreted, comprising 8–9 moderately inflated whorls. Protoconch (Fig. 15) about 1.5 whorls, well rounded, smooth. Early whorls sculptured with two major spiral lirae, soon crossing over axial riblets (Fig. 15). Adult whorls sculptured with three major spiral cords crossed over by numerous thin axial ribs (24–26), forming cancellate appearance; small beads occurring at crossover points. Body whorl (Fig. 15) sculptured with four major spiral cords and numerous axial ribs; moderately constricted at base. Shell base with about 7 spiral cords. Aperture ovate with oblique columella and curved, thin outer lip. Anterior canal moderately developed; anal canal weak. Shell color white, covered with brown periostracum.

Animal (Fig. 16A, B): Animal pure white with pink buccal mass showing through snout. Head large with very large, wide, extensible snout, dorso-ventrally flattened, bilobed at tip; cephalic tentacles small, a little less than one-third snout length, each with small black eye adjacent to opaque white spot at tentacular peduncular base. Snout ringed with many

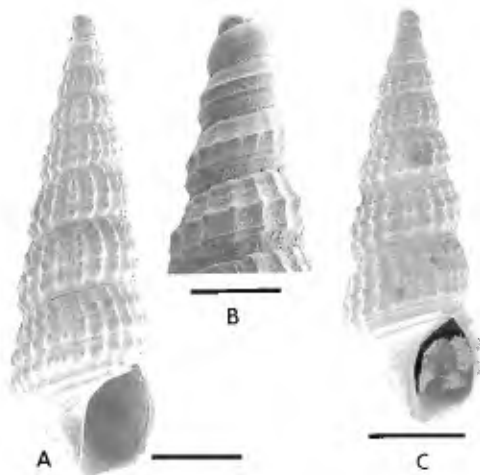


FIG. 15. SEM micrographs of shells of *Lirobittium subplanatum* from Palos Verdes, California (USNM 881021). A, bar = 1.8 mm; B, detail of protoconch and early teleoconch sculpture, bar = 0.6 mm; C, bar = 1.8 mm.

deep, transverse epithelial folds (Fig. 16B). Foot with very weak epipodial skirt and without papillae or distinctive operculiferous lobe. No ciliated groove on right side of foot; no ovipositor. Anterior of sole crescent shaped with deep transverse slit marking entrance to anterior mucus gland. No metapodial mucus gland. Mantle edge bilobed, fringed with many papillae emerging from ventral side of mantle edge.

Pallial Cavity: Osphradium brown, vermiform, without pectens, wide, about one-third the ctenidial width, nearly equaling ctenidial length. Ctenidium extending length of pallial cavity. Hypobranchial gland thick, comprising transversely ridged glandular tissue.

Alimentary System: Mouth at tip of snout, defined by pair of fleshy pads. Buccal mass (Fig. 16B, bm) pink, small, about one-third snout length.

Radular ribbon (Fig. 17) small, about one-ninth shell length. Rachidian tooth (Fig. 17C) with large glabrella, long serrated central cusp and 6 small denticles on each side. Lateral tooth (Fig. 17 B,C) with broad basal plate; cutting edge has large denticle with 6 inner denticles and 15–17 outer denticles. Marginal teeth (Fig. 17D) long, curving; inner marginal tooth with 15–19 inner denticles, large central cusp and 5–6 outer denticles; outer marginal tooth same, but lacking outer denticles.

Stomach with central pad, gastric shield, short style sac and crystalline style; one opening to digestive gland.

Nervous System: Cerebral ganglia joined by short connective. Pleural ganglia close to cerebral ganglia; left pleural ganglion connected to subesophageal by very short connective. Supraesophageal connective about two-thirds length of right pleural ganglion.

Reproductive System (Fig. 16A): Testis white, producing dimorphic sperm; ovary cream-yellow containing large ova, 0.5 mm in diameter. Glandular portion of female pallial oviduct comprising many transverse folds, posterior opaque white portion comprising albumen gland (Fig. 16A, ag), and anterior, transparent greyish-white portion comprising capsule gland (Fig. 16A, cg). Anterior two-thirds of edge of medial lamina with large sperm gutter (Fig. 16A, sg) leading into deep slit containing two openings: anterior opening (Fig. 16A, osp) into large sperm bursa and posterior opening (Fig. 16A, osr) into small tubular sac-like seminal receptacle (Fig. 16A, sr). Lateral lamina less glandular than medial lamina and with short ciliated ridge tract (Fig. 16A, crt) leading into opening of spermatophore bursa (Fig. 16A, osb), adjacent to openings on medial lamina. Spermatophore bursa (Fig. 16A, sb) small, elongate, sac-like.

Discussion

Bartsch (1911) assigned this species to the subgenus *Semibittium*, and his assignment was followed by Dall (1921), Oldroyd (1927), and Hertz (1981). *Semibittium* is shown herein to comprise a group of Eocene fossils probably related to the extant Australian monotypic genus *Cacozeliana*, which differs considerably in anatomy from the California species. Abbott (1974) transferred this species, which he considered a synonym of *Bittium attenuatum* Carpenter, 1864, to *Lirobittium*, but gave no reasons for doing so.

The shell is of moderate size (Table 3) and has a large protoconch sculptured with two spiral lirae and lacking a sinusigeral notch. Although the shell of *Lirobittium subplanatum* does not resemble that of *Stylidium eschrichtii*, the anatomical features of the two species are quite similar. As far as can be seen in preserved material, *Lirobittium subplanatum* appears to have a very weak epipodial skirt, but closer examination of living animals may show that this character is com-

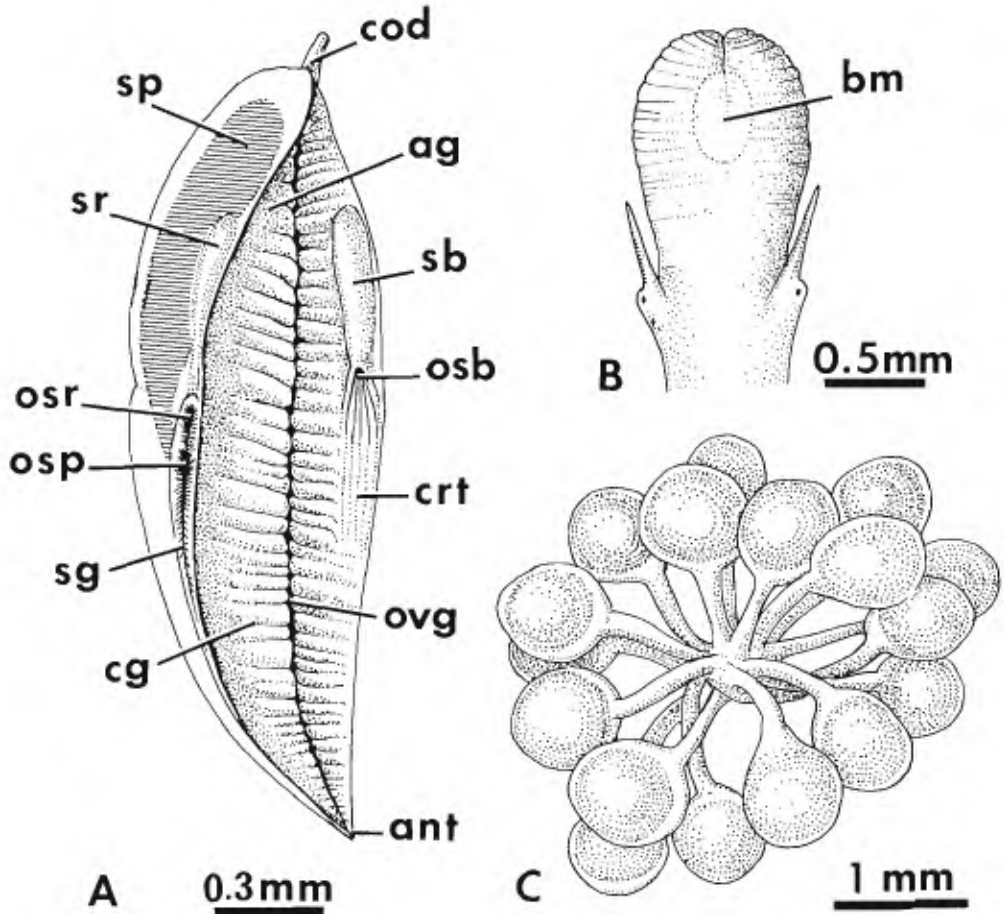


FIG. 16. *Lirobittium subplanatum*. A, pallial oviduct, spread open to reveal details; B, head, showing broad snout, short cephalic tentacles and small buccal mass; C, dorsal view of attached spawn mass, showing individual capsules with enclosed embryos and attachment strands. ag = albumen gland; ant = anterior of pallial oviduct; bm = buccal mass; cg = capsule gland; cod = coelomic oviduct; crt = ciliated ridge tract; osp = opening to sperm pouch; osb = opening to spermatophore bursa; ovg = oviductal groove; sb = spermatophore bursa; sg = sperm groove; sp = sperm pouch; sr = seminal receptacle.

pletely absent. The operculum also differs in being more typically rounded than that of *Stylidium*.

The radula of *Lirobittium subplanatum* (Fig. 16) is very similar to that of *Lirobittium attenuatum*, but differs in having many more denticles on the teeth. The exact dentition formula is given in Table 2.

There has apparently been some difficulty in identifying this species, as it has been considered synonymous with a number of other sympatric species, but Hertz (1981) has shown that it is a distinct, valid species. As mentioned above, the radula is distinct.

Lirobittium subplanatum lives offshore on sandy-rubble bottoms. The shell is frequently severely eroded and abraided.

Spawn morphology of *Lirobittium* is unique among Bittiinae (Fig. 17C) and is deposited on pieces of rubble or empty shells. It comprises clusters of large egg capsules, each about 0.5 mm in diameter and containing one embryo. Each egg capsule is connected by a strand to a central attachment point so that the spawn mass looks like a group of small balloons with their strings attached together. Embryos revolve slowly with their capsules, where they pass through the veliger stage,

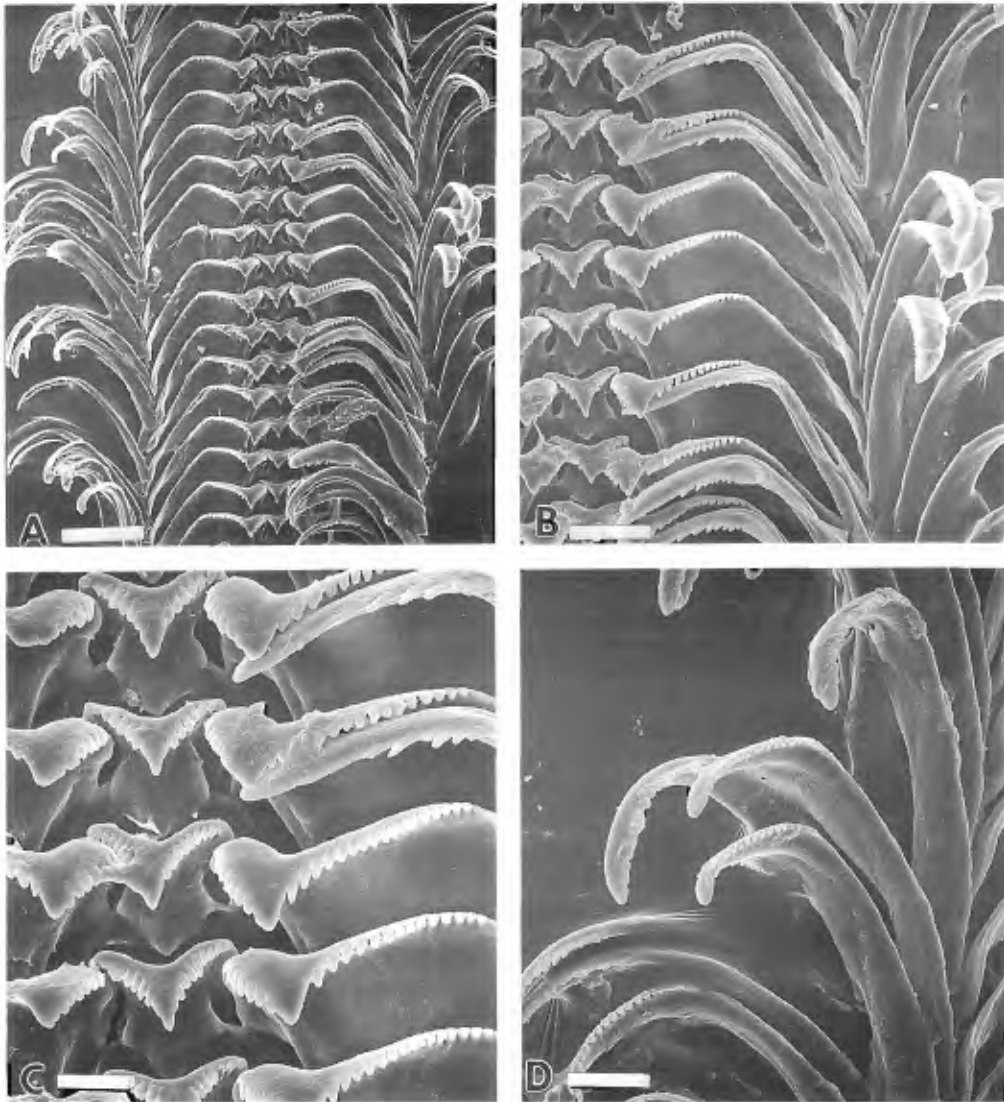


FIG. 17. SEM micrographs of radula of *Lirobittium subplanatum* (USNM 881021). A, radular ribbon with marginal teeth spread open, bar = 35 μm ; B, half row showing rachidian and lateral teeth, bar = 19 μm ; C, detail of dentition of rachidian and lateral teeth, bar = 10 μm ; D, detail of dentition of marginal teeth, bar = 12 μm .

finally hatching out as small snails. Development is direct (pers. obs.).

CACOZELIANA STRAND, 1928

? *Semibittium* Cossmann, 1896: 29 (Type species by original designation: *Cerithium cancellatum* Lamarck, 1804; not *Semibittium* Bronn, 1831; nor Lea, 1842;

nor Tuomey, 1848; nor J. de C. Sowerby, in Dixon, 1850). Thiele, 1929: 211; Wenz, 1940: 756; Gründel, 1976: 56–57. *Cacozelia* Iredale, 1924: 246 (Type species by monotype: *Cerithium lacertinum* Gould, 1861); not *Cacozelia* Grote, 1878 [Lepidoptera]. Thiele, 1929: 211; Murray, 1969: 111.

Cacozeliana Strand, 1928: 66 (new name for *Cacozelia* Iredale, 1924). Wenz, 1940: 756.

Lirobittium (*Cacozeliana*) Strand. Gründel, 1976: 54–55.

Diagnosis

Shell large, elongate with many weakly inflated whorls, sculptured with four beaded spiral cords per whorl and having overall pustulose appearance. Protoconch unsculptured except for microscopic subsutural pustules, but large sinusigeral notch present (Fig. 18F). Operculum circular-ovate, paucispiral with subcentric nucleus and fringed edges. Epipodial skirt with smooth edges. Snout short, narrow. Opercular lobe lanceolate and with longitudinal median groove. Large ovipositor gland on right side of foot. Osphradium bipectinate. Salivary glands anterior to nerve ring. Rachidian tooth without glabella. Openings to sperm bursa and seminal receptacle well separated. Seminal receptacle comprising several grape-like lobes.

Remarks

The genus *Cacozelia* was proposed by Iredale for *Cerithium lacertinum* Gould, a subjective synonym of *Cerithium granarium* Kiener. The living Australian species is thought to be congeneric with the Paris Basin Eocene species *Cerithium cancellatum* Lamarck, which is the type species of *Semibittium* Cossmann; however, as *Cacozelia* is a junior homonym, the name *Cacozeliana* was subsequently proposed by Strand (1928) as a replacement. The allocation of *Cacozeliana* as a subgenus of *Liocerithium* by Gründel (1976) was made on the observation that in *Cacozeliana*, the fourth primary spiral cord is initially weaker than the three formed earlier, whereas in *Liocerithium* all four are equally strong. Gründel (1976) also pointed out that varices are present in the subgenus, whereas they are absent in *Lirobittium*. These minor sculptural differences hardly seem appropriate as generic-level characters; furthermore, radular and anatomical characters of *Cacozeliana* show that it is far-removed from *Lirobittium*.

The type species of *Semibittium*, which is placed into synonymy with *Cacozeliana* with a query, is an Eocene fossil from the Paris Basin, *Cerithium cancellatum* Lamarck. This fossil species is conchologically very close to

Cerithium granarium Kiener, the living type species of *Cacozeliana* from southern Australia redescribed herein; however, because the anatomy of the fossil is unknown, it is impossible to declare with confidence that the two species are congeneric. Gründel (1976: 56) considered the Eocene genus *Semibittium* to be separate from *Cacozeliana*. He noted that the shell of *Semibittium* species has a slight varix on the lip of the protoconch followed by an almost simultaneous insertion of the three primary spiral cords. The name *Cerithium cancellatum* Lamarck is preoccupied, and needs a replacement name. Moreover, the name *Semibittium* cannot be used because it is thrice preoccupied. The possibility that *Cacozeliana granaria* is a living survivor of the Eocene genus *Semibittium* represented by *Cerithium cancellatum* should be considered, because several other Tethyan Eocene cerithioidean genera survive among the living Australian molluscan fauna; e.g., *Diastoma* Deshayes, 1850; *Gourmya* Fischer, 1884; *Campanile* Fischer, 1884; and *Plesiotrochus* Fischer, 1878 (Houbrick, 1981b, 1981c, 1981d, 1990b, respectively). It is also notable that *Cacozeliana* falls out at the base of the cladogram (Fig. 1) as the closest taxon to the outgroup. Moreover, *Cacozeliana* is separated from all other *Bittium*-group genera by five non-homoplastic synapomorphies (Fig. 1), further demonstrating its distinctiveness. Gründel's (1976: 56–57) separation of *Semibittium* from *Cacozeliana* was based on the order of the insertion of spiral lirae on the early whorls, but this character has not been shown to be of generic weight, and therefore is not seriously considered herein. If *Cacozeliana* is truly congeneric with *Semibittium*, the genus would date from the Eocene, when the latter was common in the Paris Basin fauna (Cossmann, 1906: 138). *Cacozeliana* is today monotypic and confined to the temperate waters of southern Australia. The type species, *Cacozeliana granaria* (Kiener), undoubtedly has the largest shell of any representative of the subfamily Bittiinae and differs from other species of the group in several ways:

1. The short narrow snout (Fig. 20A) is distinctive, as is the fringed operculum (Fig. 18G).

2. The rachidian tooth of *Cacozeliana granaria* is unique, differing from other Bittiinae members in lacking a glabella on the basal plate. Additionally, the rachidian tooth lacks concave sides and a strong pair of basal buttresses (Fig. 19B). Moreover, the lateral basal

extensions of the basal plate are nearly absent.

3. The pallial oviduct of *Cacozeliana granaria* (Fig. 20C), while having a typical layout, is unique among known pallial oviducts in the *Bittium*-group in having the seminal receptacle divided into several grape-like lobes (Fig. 20C, sr) and in having a highly developed, swollen anterior capsule gland (Fig. 20C, cg). As pointed out earlier, a grape-like seminal receptacle also occurs in some species of *Cerithium* Bruguière, 1789, *Rhinoclavis* Swainson, 1840, and in *Diala* A. Adams, 1861 (Houbrick, 1971, 1978, 1992, pers. obser.; Ponder, 1991), although this structure in *Diala* is not proven to be a seminal receptacle. This kind of seminal receptacle does not necessarily indicate relatedness among these groups: the bulging, grape-like morphology may be due to the swollen state of the filled seminal receptacle and may represent sexual "ripeness" rather than a distinct morphological character state of the seminal receptacle.

Cacozeliana granaria (Kiener, 1842)
(Figs. 18–20)

Cerithium granarium Kiener, 1842: 72–73, pl. 19, fig. 3 (Holotype MNHNP; type locality, "les côtes de Timor," in error, here corrected and restricted to Albany, Western Australia); G. B. Sowerby, 1855: 879, pl. 184, figs. 225–227; 1865: pl. 19, fig. 135; Kobelt, 1898: 249, pl. 23, fig. 9.

Cerithium lacertinum Gould, 1861: 368 (Holotype USNM 16571; type locality Sydney Harbor, New South Wales, Australia); 1862: 141; G. B. Sowerby, 1866: pl. 18, fig. 128; Tryon, 1884: 155, pl. 30, fig. 100; R. Johnson, 1964: 96, pl. 11, fig. 4.

Bittium granarium (Kiener). Tryon, 1887: 155, pl. 30, fig. 98; Wells, 1984: 30–31.

Synonymic Remarks

Kiener's (1842) name, *granarium*, predates Gould's (1861) *lacertinum*. Examination of the holotypes of both taxa leaves no doubt that the two are conspecific.

Description

Shell (Fig. 18): Shell large, elongate, turreted, reaching 24 mm in length comprising 12–13 nearly flat-sided whorls sculptured with four beaded spiral cords. Protoconch (Fig. 18F) comprising two smooth whorls with

weak, microscopic subsutural pustules, no spiral lirae, and with deep sinusigeral notch. Early whorls (Fig. 18H) sculptured with 3 spinosely beaded spiral cords aligned to form about 12–13 axial riblets. Adult whorls slightly beveled abapically, defining weak suture. Body whorl one-third shell length, having 6 spiral beaded cords and weakly constricted base. Aperture ovate, small, about one-fifth shell length. Columella concave with weak columellar callus and smooth, rounded outer lip. Anterior canal short, narrow, well defined. Shell color white to tan, blotched with pink to reddish brown and having brown spiral bands with white flecks (Fig. 18C, D). Beads sometimes white (Fig. 18A B). Periostracum light tan, thin.

Animal (Fig. 20): Head, snout and epipodium pigmented tan with chocolate blotches, tiny white spots, and iridescent green. Cephalic tentacles darkly pigmented, having many black spots, slender, elongate, about twice snout length. Snout narrow, short (Fig. 20A, sn) with flared bilobed tip. Mantle edge fringed with very small papillae each bearing white spot. Pair of ciliated strips emerging from mantle floor and running to base of cephalic tentacles on each side of headfoot. Deep ciliated groove running down right side of foot to edge, ending in small flap in males. Ciliated groove in females having thick glandular strips on each side of groove, comprising ovipositor. Epipodial skirt poorly developed, smooth along edge, forming short lanceolate opercular lobe with dorsal longitudinal furrow and without papillae along edge. Crescent-shaped propodial slit at edge of anterior foot leading into deep oval anterior mucus gland (Fig. 20A, amg). Longitudinal fold in middle of sole, but no metapodial mucus gland present. Operculum (Fig. 18G) circular-ovate, paucispiral, with subcentral nucleus. Opercular spiral fringed with thin lamella (Fig. 18G).

Pallial cavity: Osphradium bipectinate, with weak pectens. Osphradium equaling ctenidial length. Ctenidium comprising light tan elongate, triangular filaments. Hypobranchial gland thick, comprising irregular transverse glandular folds, secreting large amounts of mucus.

Alimentary system (Fig. 19B): Buccal mass large, filling snout cavity, having small jaws and short radula (Fig. 19A). Rachidian tooth (Fig. 19B) with rectangular basal plate lacking

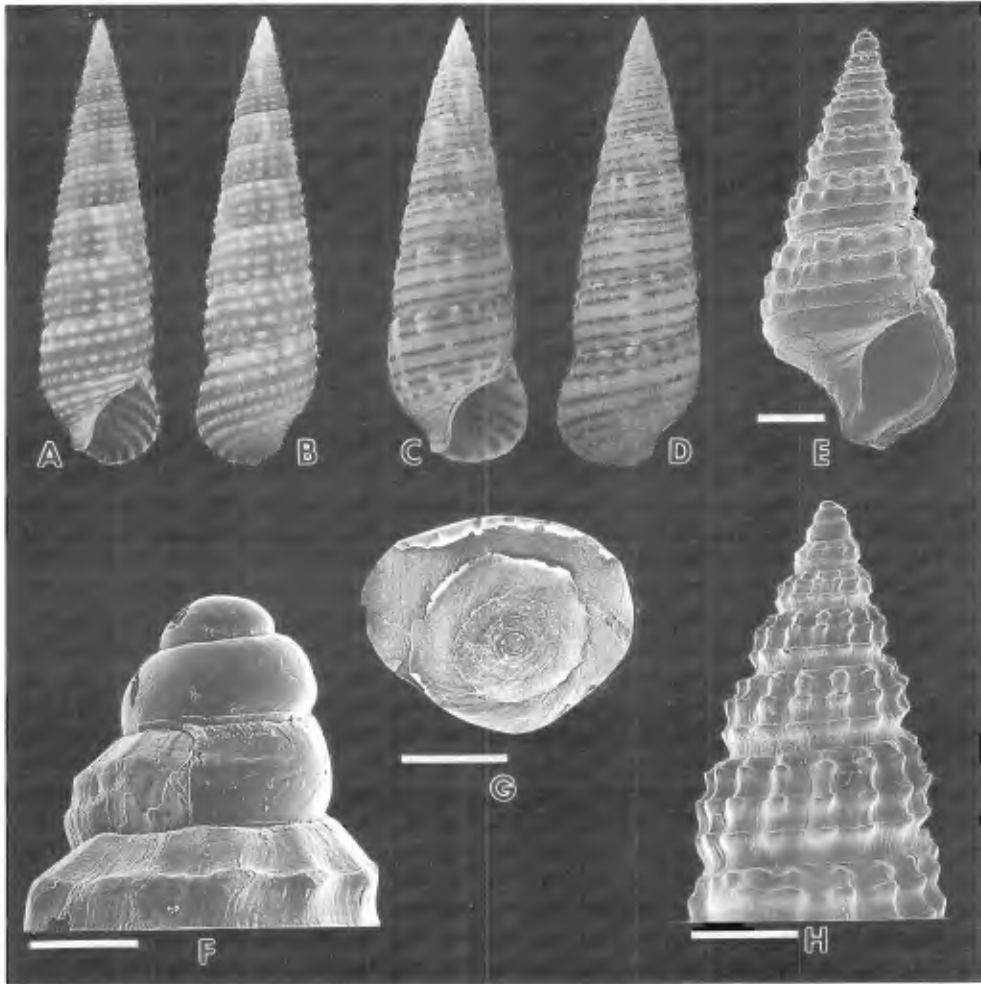


FIG. 18. *Cacozeleliana granaria* from King George Sound, Western Australia (USNM 858551). A–D, two shells showing variation in color pattern and sculpture, length 22.4 mm and 20.2 mm, respectively; E, SEM micrograph of immature shell, bar = 0.6 mm; F, SEM micrograph of protoconch, bar = 16 μ m; G, SEM micrograph of operculum, bar = 0.8 mm; H, SEM micrograph showing early sculpture, bar = 0.8 mm.

strong basal lateral buttresses, with straight base and equal in length to top of tooth; cutting edge with small central cusp flanked by two denticles on each side. Lateral tooth (Fig. 19B) with one inner denticle and 3–4 outer denticles. Inner marginal tooth with 5–6 inner denticles and 3–4 outer denticles. Outer marginal tooth (Fig. 19A) with 4 inner denticles. Salivary glands (Fig. 20B, lsg, rsg) paired, vermiform, coiled, lying anterior to nerve ring. Midesophagus expanded laterally having

many transverse internal epithelial folds comprising esophageal gland. Stomach with one digestive gland opening to left of large central pad dividing left sorting area from right gastric shield complex. Style sac separated from intestinal opening by large typhlosole fold.

Nervous System (Fig. 20, B): Cerebral ganglia joined by short connective, one-third the ganglion length. Subesophageal ganglion very close to left pleural ganglion.

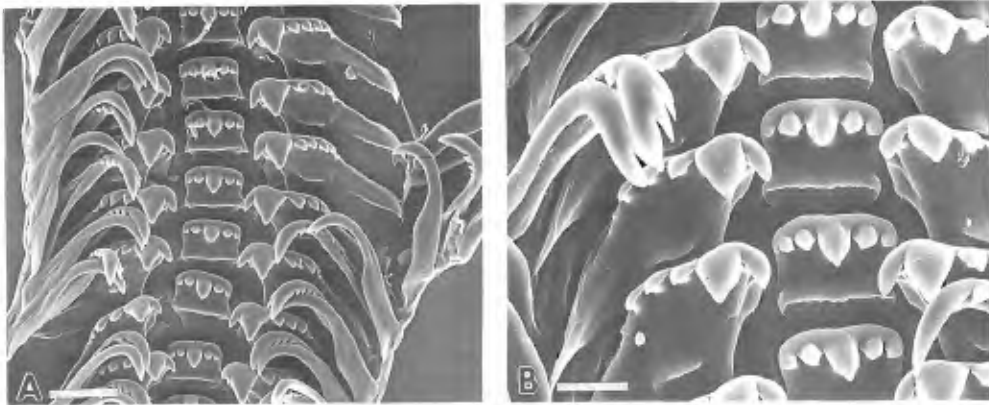


FIG. 19. Radula of *Cacozeliana granaria* from King George Sound, Western Australia (USNM 858551). A, mid-section of radula, bar = 60 µm; B, details of rachidian and lateral teeth, bar = 15 µm.

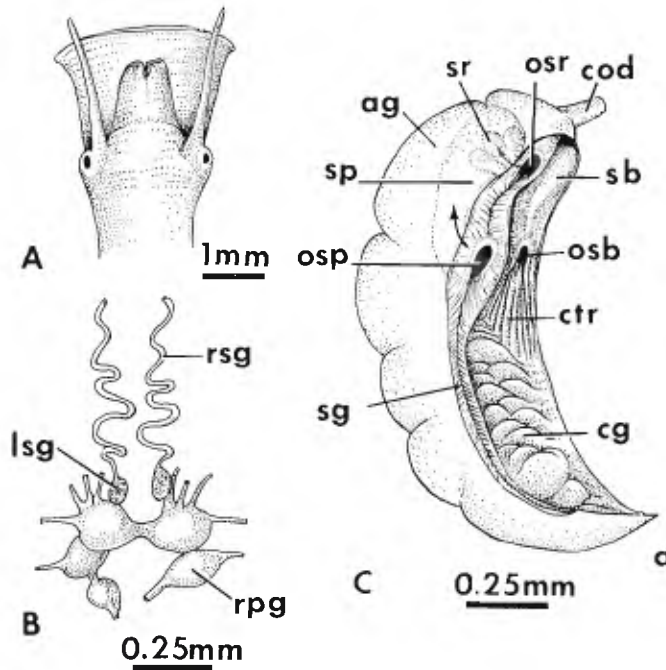


FIG. 20. Anatomical features of *Cacozeliana granaria*. A, head and foot anterior, showing narrow snout; B, position of salivary glands anterior to nerve ring; C, pallial oviduct, spread open to reveal interior details. a = anterior end of pallial oviduct; ag = albumen gland; cg = capsule gland; cod = coelomic oviduct; ctr = ciliated ridge tract; lsg = left salivary gland; osb = opening to spermatophore bursa; osp = opening to sperm pouch; osr = opening to seminal receptacle; rpg = right pleural ganglion; rsg = right salivary gland; sb = spermatophore bursa; sg = sperm groove; sp = sperm pouch; sr = seminal receptacle.

Reproductive System: Male pallial gonoduct thick, glandular, having wide transverse folds forming spermatophore organ in posterior

half; anterior half of male pallial gonoduct less glandular, white but not opaque. Female pallial oviduct (Fig. 20C) having seminal recep-

tacle comprising several grape-like lobes in medial lamina (Fig. 20C, sr). Openings to the sperm pouch (Fig. 20C, osp) and seminal receptacle (Fig. 20C, osr) separated by long ciliated groove. Ciliated ridge tract (Fig. 20C, ctr) beginning behind anterior capsule gland (Fig. 20C, cg) comprising many swollen transverse elements. Opening to spermatophore bursa (Fig. 20C, osb) in lateral lamina adjacent to opening of sperm pouch in medial lamina. Spawn mass comprising a jelly string containing many encapsulated eggs, 0.1–0.13 mm diameter, wound into flattened coil about 20 mm wide. Eggs opaque, white, each within hyaline capsule. Development indirect with free swimming veliger stage.

Discussion

Although the shell of *Cacozeliana granaria* (Fig. 18) looks very much like those of some *Cerithium* species, the weak epipodial skirt, pallial oviduct, and other anatomical features are very typical of members of the Bittinae. The protoconch, as indicated by Gründel (1976), differs from those of most other genera in being nearly smooth, and in lacking any spiral threads (Fig. 18F; Table 3), but it does have a deep sinusigeral notch, indicative of planktotrophy. *Stylidium* species also have a smooth protoconch. The operculum of *Cacozeliana* is unusual in having a thin lamellar-like fringe along its spiral (Fig. 18G). The shell of this species is undoubtedly the largest of any member of the *Bittium*-group (Table 3), but the aperture is very small in relation to the shell length. There is much color variation within populations.

The early life history of this species has been described by Murray (1969), who illustrated the spawn (1969: pl. 17). The spawn comprises a coiled gelatinous thread containing encapsulated eggs that hatch as planktotrophic veligers. Murray (1969) stated that 8–9 days after deposition, veliger-stage embryos hatched out and were maintained in sea water containers for up to 10 weeks.

Cacozeliana granaria is found in the shallow subtidal, temperate waters of southern Australia where it is common among *Posidonia*, *Zostera*, and other sea grasses. It also occurs on moderately exposed and sheltered shores, on sandy-muddy bottoms, under stones, and on rocky areas. I observed large populations of this species living on algal mats and on *Posidonia* grass blades in King George Sound, Western Australia, and in

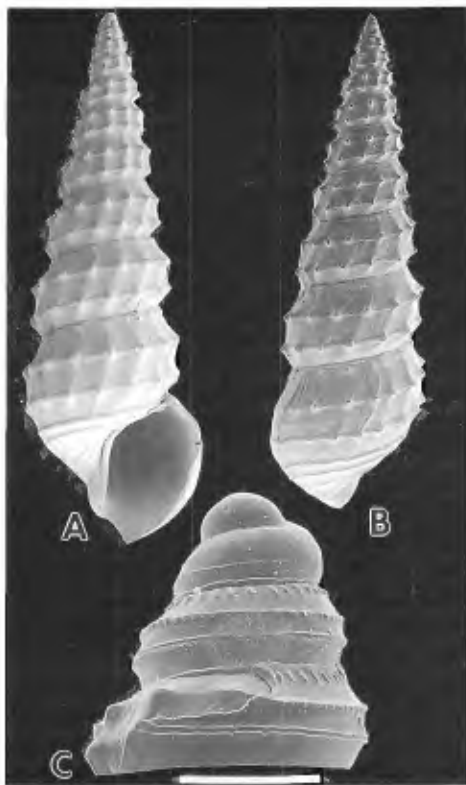


FIG. 21. SEM micrographs of shell of *Argyropeza divina* Melvill & Standen, from Refugio Id., Tanon Str., Philippines (USNM 302513); A, B, apertural and dorsal views of adult shell, 6.3 mm length; C, protoconch showing sculpture and sinusigeral notch, bar = 1 mm.

similar habitats in Sydney Harbor and Botany Bay, New South Wales.

ARGYROPEZA MELVILL & STANDEN, 1901

Argyropeza Melvill & Standen, 1901: 371–372 (Type species by original designation, *Argyropeza divina* Melvill & Standen, 1901). Thiele, 1929: 212; Wenz, 1940: 757; Gründel, 1976: 44; Houbrick, 1980a: 2.

Diagnosis

Shell small, turreted, thin and vitreous, sculptured with axial and spiral elements, varices, and with many small nodules. Protoconch comprising three and a half whorls with deep sinusigeral notch; sculptured with two

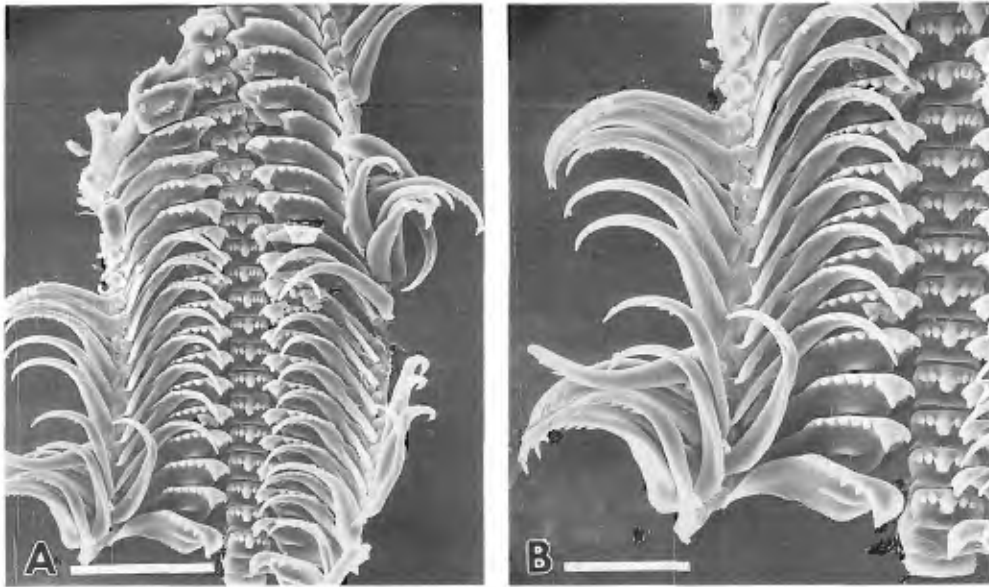


FIG. 22. SEM micrographs of radula of *Argyropeza divina* (USNM 302513), A, radular ribbon with marginal teeth spread open, bar = 100 µm; B, half row, bar = 50 µm.

spiral cords and many minute subsutural folds. Aperture ovate with well-developed, short anterior canal. Operculum corneous, subcircular, paucispiral, with subcentral nucleus. Snout broad with large cephalic tentacles and large eyes. Foot with anterior mucus gland. Mantle edge papillate. Pallial gonoducts open. Radula taenioglossate; rachidian tooth wider than tall; lateral tooth with transverse ridge on basal plate; marginal teeth slender, scythe-shaped.

Remarks

An alpha-level review of *Argyropeza* has been published by Houbriek (1980a), which should be consulted for details about taxonomy, morphology and geographic distribution. The genus comprises five described species and several undescribed ones (pers. obser.). Members of this genus live on fine-grained substrates of deep water shelves and slopes, and not much is known about their biology. All examined species have small shells and protoconchs sculptured with two spiral lirae, subsutural pleats, and a deep sinusigeral notch (Fig. 21C; Table 3) indicative of a planktotrophic larval stage. The anatomy of *Argyropeza* species is virtually unknown except for superficial observations made from reconsti-

tuted, dried specimens. The shell and radula of the type species, *Argyropeza divina* Melvill & Standen, 1901, are shown in Figures 21 and 22. I do not agree with Powell's (1979) suggestion that *Tasmalira* Dell, 1956, may be closely related to *Argyropeza*, because the shell morphology does not appear to fit the limits of the genus. *Argyropeza* is tentatively assigned to the Bittiinae until more complete anatomical information is available.

VARICOPEZA GRÜNDEL, 1976

Varicopeza Gründel, 1976: 46 (Type species by tautonymy, *Varicopeza varicopeza* Gründel, 1976). Houbriek, 1980b: 525; 1987: 85.

Diagnosis

Shell small, slender, turreted, vitreous, having impressed suture, and sculptured with strong spiral cords, weaker axial elements, and many nodules. Protoconch having three and one-half smooth whorls, with weak, median spiral cord, minute subsutural pustules, and sinusigeral notch. Aperture ovate with short, well-developed anal and anterior canals. Operculum corneous, ovate, paucispiral, with subcentral nucleus. Radula taenio-

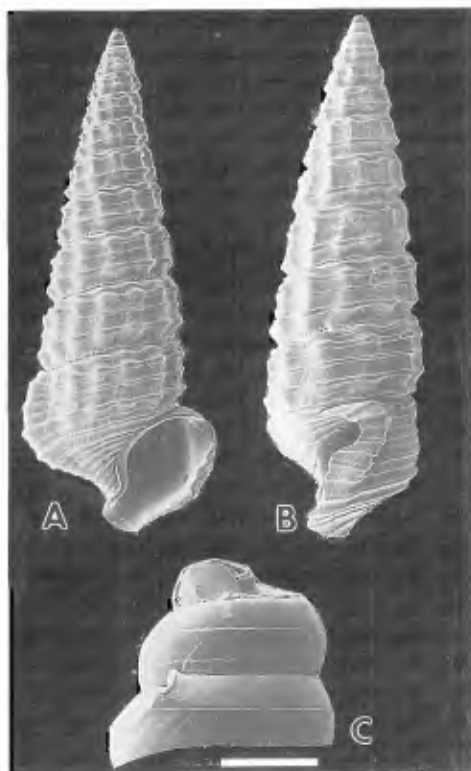


FIG. 23. SEM micrographs of shell of *Varicopeza pauxilla* (A. Adams, 1854) from Nagubat Id., E. Mindanao, Philippines (USNM 276898). A, B, apertural and side views of adult shell, 8.1 mm length; C, protoconch, bar = 100 μ m.

glossate with hourglass-shaped rachidian tooth; lateral tooth with transverse ridge on basal plate; marginal teeth elongate, slender with denticulate sickle-shaped tips. Animal with large headfoot, elongate, wide snout, long cephalic tentacles and very large eyes. Deep ciliated groove on right side of foot. Mantle edge having short, thick papillae.

Remarks

The two known species of *Varicopeza* have been thoroughly described by Houbrick (1980b, 1987a). These publications should be consulted for specific information about taxonomy and a detailed description of the type species. The shell is of moderate length (Table 3) and has a protoconch sculptured with one spiral lira and a shallow sinusigeral notch (Fig. 23C). Although the shell and radula (Fig.

24) are well described, only a few external anatomical features are known. *Varicopeza* species occur at moderate subtidal depths on fine-grained substrates in the tropical Atlantic and Pacific. The shell sculpture of *Varicopeza* (Fig. 23A, B) is similar to that of *Argyropeza* species, differing chiefly in protoconch morphology. The aperture (Fig. 23A, B) is distinctive in having a large, flaring anal sinus. The radula (Fig. 24) has more denticles on the marginal teeth than in *Argyropeza* (Table 2).

Gründel (1976) suggested that *Varicopeza* was closely related to the extinct Jurassic genus *Cryptaulax* and considered it to be a Recent representative of the of the extinct family Procerithiidae Cossmann, 1905. The shell and radula of *Varicopeza pauxilla* (A. Adams, 1854) is shown in Figures 23 and 24. This genus is tentatively assigned to the *Bittium*-group until more complete anatomical information is available.

ZEBITTIIUM FINLAY, 1927

Zebittium Finlay, 1927: 381 (Type species by original designation, *Cerithium exilis* Hutton, 1873); Wenz, 1940: 756; fig. 2191; Powell, 1979: 132, fig. 32:1.

Diagnosis

Shell very small, turreted, sculptured with beaded spiral cords, and weak axial riblets, having impressed suture. Aperture ovate with weak notch-like anterior canal. Protoconch two and a half whorls, bluntly rounded, unsculptured.

Remarks

This genus was proposed without any defining characters, and was apparently introduced only to accommodate the New Zealand species, *Bittium exile* Hutton and *Bittium vitreum* Suter. The shell of *Zebittium exile* (Hutton, 1873) is shown in Figure 25. *Zebittium* was assigned as a subgenus of *Bittium* by Wenz (1940), who noted that the genus occurred from the Miocene to the Recent of New Zealand. The shell of the type species closely resembles those of *Bittium* and *Bittiolium* species and does not appear to have any distinguishing features of generic significance. The unsculptured protoconch (Fig. 25D) appears to indicate lecithotrophic development. No preserved material of this species was avail-

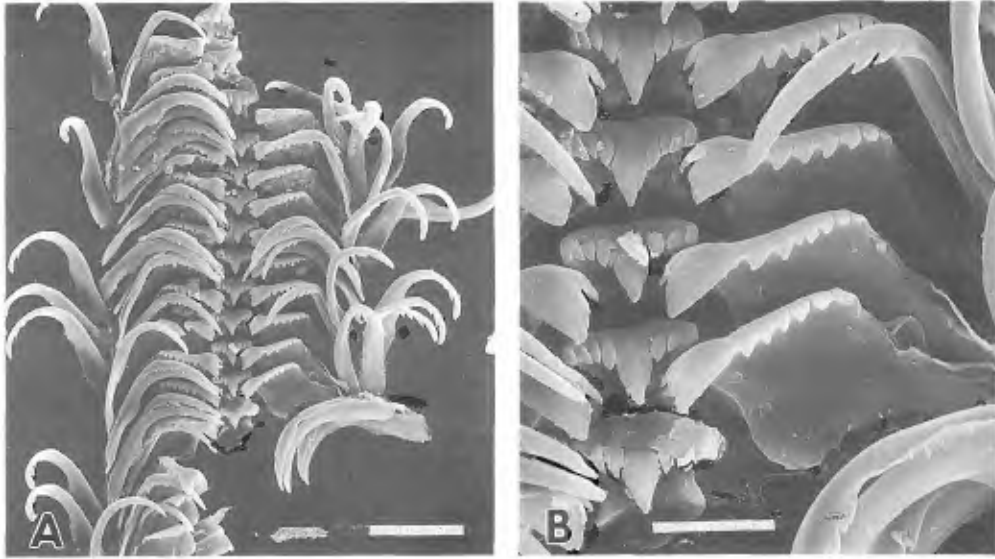


FIG. 24. SEM micrographs of radula of *Varicopeza pauxilla*. A, section of ribbon with some marginal teeth spread open, bar = 50 µm; B, detail of rachidian and lateral teeth, bar = 25 µm.

able for study; therefore, the genus *Zebittium* is included in this review only tentatively.

CASSIELLA GOFAS, 1976

Cassiella Gofas, 1987: 109 (Type species by original designation, *Cassiella abylenensis* Gofas, 1987).

Diagnosis

Shell small, slender, turritid, sculptured with spiral cords, without varices and with impressed suture. Aperture ovate, without anterior canal and simple outer lip. Operculum corneous, ovate, paucispiral, with subcentral nucleus. Animal with bilobed snout and two elongate cephalic tentacles. Foot short and broad without ovipositor or ciliated groove on right side, and with large opercular lobe. Radula taenioglossate; rachidian tooth with squarish basal plate, moderately concave on each side with small median glabella, and having cutting edge with large central cusp flanked by 3 smaller denticles on each side. Lateral tooth with large triangular cusp with one small inner denticle and 7–8 outer denticles. Marginal teeth elongate, spatulate with curved tips; inner marginal teeth denticulate on both sides; outer marginal teeth lacking outer denticles.

Remarks

This monotypic genus was recently proposed and described by Gofas (1987), and his publication should be consulted for descriptive details of the genus and figures of the type species. *Cassiella abylenensis* does not fit easily into the *Bittium*-group, although there are some resemblances. The shell of *Cassiella abylenensis* (Fig. 26) varies highly in color pattern and in spiral sculpture (Gofas, 1987: 111). The shell morphology is unlike those of other members of the *Bittium*-group. No vestige of an anterior canal is present, and the shell morphology strongly resembles those of some rissoids. The absence of an anterior canal is also a feature of *Cerithidium Monerosato*, a taxon I have excluded from Bittiinae.

The external anatomy of *Cassiella abylenensis* was depicted by Gofas (1987: figs. 10, 14, 15). The animal does not have epipodial tentacles, although there is an inconspicuous groove around the foot, just above the edge of the sole, which may be homologous with the epipodial skirt found in members of Bittiinae. The opercular lobes are said to be "massive" (Gofas, 1987: 111), but they are not depicted or labeled in the figures of the external anatomy. The headfoot, operculum, and radula are not unlike those observed in other species

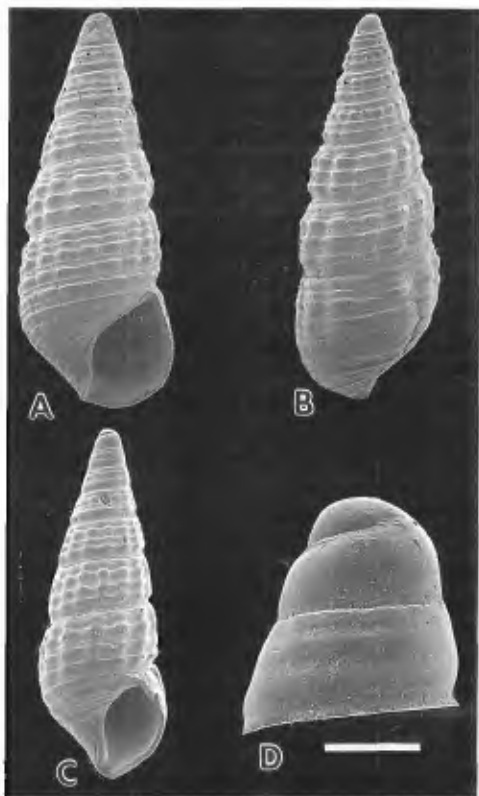


FIG. 25. SEM micrographs of shell of *Zebittium exile* (Hutton, 1873) from Long Bay, Auckland, New Zealand (USNM 681043); A, apertural view of adult shell, 4.7 mm length; B, dorsal view, 4.6 mm length; C, immature shell, 4.4 mm length; D, protoconch, bar = 0.25 mm.

of Bittinae. There is no metapodial mucus gland, no ovipositor is indicated, and males are aphallate (Gofas, 1987: 111).

Pending further anatomical studies, the eastern Atlantic taxon *Cassiella* is tentatively assigned to Bittinae with doubt.

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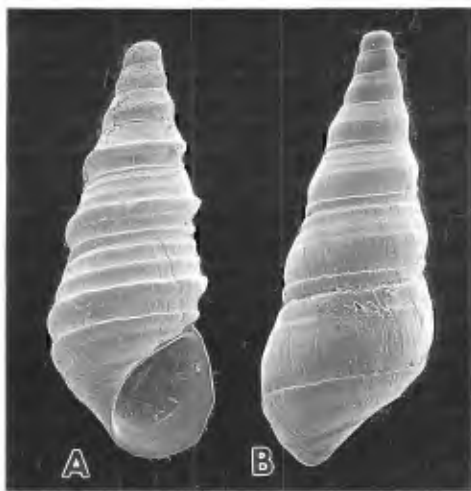


FIG. 26. SEM micrographs of shell of *Cassiella abylenis* Gofas, 1976, from Ceuta, Spain (USNM 869532); A, apertural view of shell, 2.3 mm length; B, dorsal view of shell, 2.5 mm length.

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