Monograph of the Genus *Cerithium* Bruguière in the Indo-Pacific (Cerithiidae: Prosobranchia)

RICHARD S. HOUBRICK

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ABSTRACT

Houbrick, Richard S. Monograph of the Genus *Cerithium* Bruguière in the Indo-Pacific (Cerithiidae: Prosobrachia). *Smithsonian Contributions to Zoology*, number 510, 211 pages, 145 figures, 45 tables, 1992.—The genus *Cerithium* Bruguière, 1789, comprises a large group of morphologically highly variable species characterized by many-whorled, elongate shells having ovate apertures, slightly reflected anterior canals and sculpture, consisting of axial ribs, spiral cords with beads and nodes, and randomly placed varices. The mantle edge is bilobed in cross-section, and has small papillae arising from the inner lobe. The osphradium is bipectinate and the hypobranchial gland well developed. The radula is taenioglosate, paired salivary glands pass through the nerve ring, an esophageal gland is present, and the large stomach has a style sac, crystalline style, and gastric shield. The nervous system is epiathroid. Pallial gonoducts are open; the pallial oviduct includes a large spermatophore bursa and two seminal receptacles. Males are aphallate and produce dimorphic sperm, which are transferred by spermatophores. Females have a ciliated egg-laying groove on the right side of the foot and the egg mass consists of intertwined, gelatinous strings.

The genus dates from the late Cretaceous, and was species-rich during the Cenozoic: many living species are also known in the Cenozoic fossil record. *Cerithium* species span a broad variety of habitats, but the great majority live intertidally or in shallow water, and are microphagous herbivores. Most species have a planktotrophic larval stage and wide geographic distributions.

The Indo-Pacific Marine Province supports 68 percent of all *Cerithium* species. Forty-two living species, including five new taxa, are recognized: *C. abditum*, new species; *C. africanum*, new species; *C. alexandri* Tomlin; *C. amirantium* E.A. Smith; *C. atromarginatum* Dautzenberg and Bouge; *C. balteatum* Philippi; *C. caeruleum* Sowerby; *C. citrinum* Sowerby; *C. claviforme* Schepman; *C. columna* Sowerby; *C. coralium* Kiener; *C. crassilabrum* Krauss; *C. dialeucum* Philippi; *C. echinatum* Sowerby; *C. egenum* Gould; *C. flemischi* K. Martin; *C. gloriosum*, new species; *C. interstriatum* Sowerby; *C. koperbergi* Schepman; *C. leptocharactum* Rehder; *C. lifuense* Melvill and Standen; *C. lissum* Watson; *C. madreporicolum* Jousseaume; *C. matukense* Watson; *C. munitum* Sowerby; *C. nesioticum* Pilsbry and Vanatta; *C. nodulosum* Bruguière; *C. novaehollandiae* A. Adams; *C. ophioderma* (Habe), new combination; *C. pacificum*, new species; *C. phoxum* Watson; *C. punctatum* Bruguière; *C. rehderi*, new species; *C. rostratum* Sowerby; *C. ruppelli* Philippi; *C. salebrosum* Sowerby; *C. scabridum* Philippi; *C. scobiniforme*, new species; *C. tenellum* Sowerby; *C. torresi* E.A. Smith; C. *traillii* Sowerby; *C. zonatum* (Wood).

Four different types of radular morphology were determined among the above species. The anatomy of twelve species was studied and among these three different types of pallial oviduct arrangements were discerned, suggesting that *Cerithium* may comprise several clades or groups. Monophyly has not been established; thus, formal taxonomic recognition of these morphological groups is withheld until the anatomy of more *Cerithium* species is known.

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Contents

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Introduction

Earth's richest, most varied cerithiid fauna is found in the tropical and subtropical biotopes of the Indo-Pacific Marine Province. Here, well over 70 percent of the estimated 60 valid, recognized species of *Cerithium* Bruguière, 1789, are concentrated. However, the richest of earth's *Cerithium* fauna is also the least known taxonomically, resulting in a largely underutilized or ignored resource for biological studies. Many *Cerithium* species have wide geographic distributions and constitute an important, conspicuous component of the intertidal and subtidal molluscan fauna. *Cerithium* species are style-bearing, microphagous, detrital-algal feeders, and commonly occur in large populations; many species are frequently geographically sympatric or syntopic, have widespread ranges, and are among the most common and numerous of prosobranchs. The paucity of published accounts of their ecology, physiology, reproductive biology, and zoogeography is a direct reflection of our inability to deal with their chaotic systematics.

The concept of the genus *Cerithium* was at first very broad, but subsequently narrowed as many groups were excluded; nevertheless, excessive splitting of taxa has occurred at generic and specific levels, and the number of described *Cerithium* taxa, sensu lato, both fossil and Recent, is now very large. As early as 1865, Sowerby included 149 species in his monograph. The description of many hundreds of obscure, but validly proposed nomina for fossil forms has resulted in numerous homonymous names and synonyms. Rarely do authors agree on the valid name or taxonomic placement of a given taxon, and numerous species have been misidentified or misclassified in other genera or families. This taxonomic instability renders much of the biological literature about living *Cerithium* species useless, and also prevents any meaningful usage of the vast paleontological literature, as one is never sure what species has actually been studied, or if it has been allocated to the correct genus or family. Specific determination of *Cerithium* species has been very difficult and intimidating because the wide range of shell morphology exhibited by most taxa was not appreciated or determined when many of the original descriptions were made.

There is obviously great need for a modern monograph that describes, illustrates, and establishes the range of variation for each species. The types of all valid nominal taxa require careful evaluation, synonymic lists need to be established, geographic ranges of each recognized species determined, and difficult species complexes require identification. It is the objective of this monograph to address these needs and to lay the foundations for further, more detailed studies of Indo-Pacific *Cerithium* species.

MATERIALS AND METHODS.—This paper is a preliminary framework and guide; i.e., the taxonomic decisions presented herein should not be considered as definitive or the "last word" on the subject. There are hundreds (perhaps more than a thousand, including fossil taxa) of validly proposed names for *Cerithium* species, as perusal of the many synonymies presented herein will illustrate; consequently, it is impossible for a work of this scope to treat all species with equal depth and comprehension. Most cerithiids are extremely variable in shell morphology and have widespread geographic ranges; accordingly, an exhaustive examination of thousands of specimens from major museum collections was undertaken to determine the range of variation in each species. All shell characters used in descriptions were those of adult snails, but immature shells also were studied to determine ontogenetic changes in sculpture. Measurements were taken of random samples from throughout the range of each species, and included the largest and smallest specimens observed so that a size range could be established. Morphometric and meristic data included shell length and width, aperture length and width, number of whorls,

Richard S. Houbrick, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

number of spiral cords on the penultimate whorl, number of axial ribs on the penultimate whorl, and number of nodes or beads on the penultimate whorl. In addition, presence or absence of the above last three shell characters was noted and is discussed in each species discussion. Shell characters of the body whorl included the number of axial ribs and spiral cords, number of nodes, and presence or absence of denticles and crenulations in the outer lip of the aperture. Qualitative characters included the relative development of the anal canal, and length and curvature of the anterior siphonal canal. Shell measurements and counts were subjected to standard statistical tests, as outlined in past work (Houbrick, 1985:3), and basic shell measurements (in mm) and meristics of the penultimate whorl are presented in table form with the shell description of each species. However, due to the enormous geographic ranges and the thousands of populations of each species, comprehensive morphometric analyses were not attempted. Protoconch morphology was described following the terminology of Robertson (1974:214) in designating the protoconch as the entire shell formed prior to metamorphosis. Protoconch 1 is the initial embryonic shell secreted by the shell gland, and is normally smooth; protoconch 2 is deposited by the mantle edge during the veliger stage, and is usually sculptured. The type of development, utilizing the classification outlined by Jablonski and Lutz (1980:329–335), was inferred from protoconch morphology. Although *Cerithium* protoconchs are frequently eroded or missing, the protoconchs of many of the species were studied with SEM, and are illustrated in this monograph.

The types of all species recognized herein, as well as the types of their synonymous taxa, were examined and noted in the synonymies. Nearly all types discussed are illustrated. All other specimens examined are listed under the "Materials Examined" section of each species treatment. Throughout the text, the repository of examined specimens is indicated by the following abbreviations.

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences, San Francisco
BPBM	Bernice P. Bishop Museum, Honolulu
DMNH	Delaware Museum of Natural History, Wilmington, Delaware
FU	Florida Museum of Natural History, Gainesville
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MHNG	Museum d'Histoire Naturelle, Geneva
MM	Manchester Museum
MNHNC	Museo National del Historia Natural Chile, Santiago
MNHNP	Muséum National d'Histoire Naturelle, Paris
MPB	Museum of Paleontology, Berkeley
NM	Natal Museum, Pietermaritzburg
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NMNZ	National Museum of New Zealand, Wellington
NMV	National Museum, Victoria
NMW	National Museum of Wales, Cardiff
NSMT	National Science Museum, Tokyo
RMGM	Rijksmuseum van Geologie en Mineralogie, Leiden
RNHL	Rijksmuseum van Natural Historie, Leiden
SAM	South African Museum, Capetown
TAU	Tel Aviv University, Israel
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UGI	University of Guam Marine Laboratory
WAM	Western Australian Museum, Perth
ZMA	Zoologisches Museum, Amsterdam
ZMTA	Zoological Museum, Tel-Aviv University, Israel.

A work of this magnitude precludes an exhaustive study of the biology of each and every species and, of necessity, a morphological species-concept has been utilized. Only incomplete information is available about some species, many of which are known only from shells. A holistic approach was taken toward the better known species, which included all morphological characters and available ancillary information. The anatomy and radulae of live-collected species were examined under SEM, whenever possible. In some cases, radulae were successfully extracted from animals dried in their shells. Animals preserved in formalin or alcohol were also studied; however, anatomical information derived from this kind of material is incomplete or lacking, as the visceral mass, mantle cavity organs, and pallial gonoducts are frequently destroyed or distorted due to poor penetration of the fixation fluid beyond the body whorl. Thus, interspecific anatomical variation among many of the species studied herein is only incompletely understood. Field studies and anatomical dissections of live-collected specimens were undertaken whenever possible. Care was taken to dissect only sexually mature specimens, as the secondary sexual characters of immature or very old *Cerithium* specimens are frequently incomplete or altered; moreover, infections by trematode parasites may cause profound changes in the external anatomical appearance of pallial gonoducts. Methods of dissection and analysis of anatomical characters follow the methodology and procedures of Houbrick (1985:2–3; 1987a:2). Twelve species (*C. atromarginatum, C. columna, C. coralium, C. dialeucum, C. echinatum, C. egenum, C. munitum, C. nesioticum, C. nodulosum, C. punctatum, C. rostratum, C. zonatum*) were well studied and this allowed some comparative anatomical analysis.

Living populations of a number of species were observed in many localities throughout the western Pacific. Ecological zonation and specific ecological activities, such as predator-prey interaction, reproductive behavior, and spawning, were noted whenever possible. These have been incorporated along with observations derived from the literature under the ecological section of each species description. At many of the study sites, records were kept of the activities of live *Cerithium* species under laboratory conditions, and dissections were made on living specimens relaxed in a 7.5 percent $MgCl_2$ solution. A list of sites and the living *Cerithium* species studied at each locale follows. (1) Hong Kong (*C. coralium*); (2) Bagac,

Bataan, Luzon, Philippines (*C. dialeucum*); (3) Pago Bay, Guam (*C. columna, C. echinatum, C. nodulosum, C. rostratum, C. zonatum*); (4) Lizard Island, Queensland, Australia (*C. columna, C. munitum*); (5) Magnetic Island, Queensland, Australia (*C. columna, C. coralium, C. novaehollandiae, C. torresi, C. traillii, C. zonatum*); (6) Enewetak Atoll, Marshall Islands (*C. columna, C. echinatum, C. nesioticum, C. nodulosum, C. punctatum, C. salebrosum, C. tenellum*); (7) Laucala Bay, Viti Levu, Fiji (*C. columna, C. coralium, C. rostratum*); (8) Oahu, Hawaii (*C. atromarginatum, C. columna, C. egenum*); (9) Smithsonian Marine Station at Link Port, Florida (western Atlantic species, for comparison).

Tissues were fixed in Bouin's solution, embedded in paraffin, sectioned at 7–10 μm, and stained with Harris' hematoxylin and eosin or with alcian blue-PAS and counterstained in hematoxylin for histochemical differentiation of mucins (Humason, 1962:269). Protoconchs, radulae, and critical-point dried tissues were examined under SEM using Zeiss Novascan-30 and Hitachi S-570 instruments.

A conservative attitude towards species recognition has been taken throughout this study. Proposal of new taxa has been avoided unless supported by good evidence. Validly proposed names based on poor descriptions or on merely minor phenotypic variants were not seriously considered unless backed up by evidence (statistical, anatomical, reproductive, or ecological). No taxon was recognized as a good species until all available material had been studied and the range of variation was thought to be understood. A number of Indo-Pacific species have wide geographical ranges, exhibit considerable intraspecific variation, and appear to intergrade with other congeners in some areas, forming distinct species complexes that are difficult to resolve. These species complexes appear to be mosaics of numerous, genetically distinct populations separated by narrow zones of hybridization. Such complexes were regarded as a single species if there was any uncertainty about the status or significance of the phenotypic elements comprising them. Taxonomic recognition of subspecies or semispecies was withheld in lieu of significant data justifying such decisions.

Note that on maps of the Pacific area herein, the archaic name Eniwetok is used for the island of Enewetak (Marshall Islands).

ACKNOWLEDGMENTS.—This work resulted from many years accumulation of information, the examination of thousands of specimens, numerous types, and an extensive literature survey. Many people graciously gave of their time and talents in helping to accomplish this task, and a list of everyone who has helped throughout the project would be prohibitive. Nevertheless, I wish to thank all those who have made this study possible. A list of the curators and institutions, whose cooperation, assistance, and loans of specimens, contributed to this monograph follows: Dr. Rüdiger Bieler (DMNH); Dr. Eugene Binder (MHNG); Dr. Kenneth J. Boss (MCZ); Ms. S. Boyd (NMV); Dr. Philippe Bouchet (MNHNP); Dr. Henry Coomans (ZMA); Dr. George M. Davis (ANSP); Dr. Terrance Gosliner (CAS); Dr. William K. Emerson (AMNH); Dr. E. Gittenberger (RNHL); Mr. A. W. Janssen (RGM); Mr. Richard Kilburn (NM) Dr. David Lindberg (MPB); Mr. Ian Loch (AMS); Mr. Bruce Marshall (NMNZ); Dr. James McLean (LACM); Mr. Charles Pettitt (MM); Dr. Winston F. Ponder (AMS); Dr. Robert Robertson (ANSP); Dr. John Taylor (BMNH); Dr. Fred J. Thompson (FU); Ms. Alison Trew (NMW); Ms. Kathy Way (BMNH); Dr. Fred Wells (WAM).

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Systematic Treatment

The species treated below are listed in alphabetical order because the many gaps in morphological data preclude a phylogenetic arrangement at this time. Groups of species that appear closely related on the basis of known radular and anatomical evidence are identified and discussed below. All identified species-complexes (superspecies, sensu Mayr, 1969:52–53), borderline cases of putative subspeciation, and distinctive phenotypes that need more careful study are clearly noted, but are not given formal taxonomic recognition at this time. Recognition of new species within a superspecies is very difficult to support without lengthy, in situ studies employing detailed statistical, anatomical, and biochemical analyses. These kinds of studies are extensive research projects in themselves, and far beyond the scope of this monograph.

To facilitate quick and easy identification, shells of all but the rarest of *Cerithium* species are shown in Figures 1 and 2. The common, typical phenotype of each species is figured next to other species most closely resembling it. The user may quickly match a specimen(s) with one of the figures and turn to the appropriate section in the monograph describing the figured shell (taxon). The investigator may then examine the range of variation depicted for each species and arrive at a final determination. Users should also consult my monograph on *Clypeomorus* (Houbrick, 1985), as many species of that genus closely resemble *Cerithium* species.

Superfamily CERITHIOIDEA Férussac, 1819

Family CERITHIIDAE Férussac, 1819

Genus *Cerithium* Bruguière, 1789

Cerithium Bruguière, 1789:xv [described, but no species listed; type species: *Cerithium adansonii* Bruguière, 1792:479, by subsequent designation (Melville, ICZN Opinion 1109, 1978:97–98); = *Cerithium erythraeonense* Lamarck, 1822 = *Cerithium nodulosum* Bruguière, 1792:478, herein considered a senior synonym].—1792:467, 479.—Cossmann, 1906:66–67.—MacNeil, 1960:40–41.—Ladd, 1972:38.—Gründel, 1981:5–6.

Contumax Hedley, 1899:436–437, fig. 25. [Type species: *Contumax decollatus* Hedley, 1899 (= *Cerithium nodulosum* Bruguière, 1792), by original designation.]

Ischnocerithium Thiele, 1929:212. [Type species: *Cerithium rostratum* Sowerby, 1855, by original designation].—Wenz, 1940:758, fig. 2199.—Ladd, 1972:32.—Cernohorsky, 1972:66.—Gründel, 1981:15–16.]

Semivertagus Cossmann.—Cernohorsky, 1972:68 [not *Semivertagus* Cossmann, 1889; is *Cerithium* sensu stricto Bruguière].

Conocerithium Sacco.—Cernohorsky, 1972:69; 1978:53–54.—Ladd, 1972:39 [not *Concerithium* Sacco, 1895; is *Cerithium* sensu stricto Bruguière].

Thericium Monterosato.—Ladd, 1972:37 [not *Thericium* Monterosato, 1890; is *Cerithium* sensu stricto].

Tiaracerithium Sacco.—Cernohorsky, 1978:53 [not *Tiaracerithium* Sacco, 1895; is *Cerithium* sensu stricto Bruguière].

DIAGNOSIS.—Shell many whorled, turreted, ranging from ovate to fusiform elongate, and sculptured with variously placed varices, axial ribs, and spiral cords ornamented with beads and nodes. Aperture ovate with crenulated outer lip, distinct anal canal and moderately extended, constricted, slightly reflected anterior siphonal canal. Operculum corneous, ovate, and paucispiral with eccentric nucleus. Mantle edge bilobed with small papillae arising from inner lobe. Propodial mucus gland present; in females, ciliated egg-laying groove on right side of foot. Osphradium elongate, narrow, bipectinate, comprised of tiny leaflets. Hypobranchial gland well developed. Radula taenioglossate. Salivary glands pass through nerve ring; esophageal gland present. Stomach large, with style sac, crystalline style and gastric shield. Nervous system epiathroid. Pallial gonoducts open; pallial oviduct with large spermatophore bursa and small posterior seminal receptacle in medial lamina; anterior seminal receptacle sometimes in lateral lamina. Sperm dimorphic, transferred by spermatophores. Egg mass consisting of gelatinous strings.

SYNONYMIC REMARKS.—Historically, the concept of the genus *Cerithium* Bruguière has been broad, varied, and based solely on shell morphology. The name *Cerithium* has a complex taxonomic history due to the problems of selecting and identifying a proper type species. This has resulted in difficulties of defining and setting limits to the genus. The name *Cerithium* has embraced a heterogenous group of species comprising many higher taxa, and a complete synonymy would have to cite nearly all major malacological works that have included other genera under *Cerithium* "in part." In this monograph, the synonymy of *Cerithium* and its subgenera includes only major revisory works or those treating Indo-Pacific faunas citing cerithiid species.

Comprehensive reviews of the synonymic history of the name *Cerithium* have been made by Cossmann (1906:65–67), Dall (1907:363–369), Wood (1910:6–10), Houbrick (1973a:104–107; 1974b:37–38), and Gründel (1981:5–8). Additional discussions about the taxonomic problems of the name *Cerithium* and its relationships to closely related genera have been published by Houbrick (1975:14–15, 1978b:1–3, 1981:2–3, 1985:1–5). Many of the above papers dealt with the history and nomenclatural problems surrounding the selection of a proper type species. These difficulties were summarized and set forth by Houbrick (1973a), who petitioned the International Commission on Zoological Nomenclature to set aside all previous designations of type species for *Cerithium*, to designate *Cerithium adansonii* Bruguière, 1792, as type species of the genus, and to place the generic name *Cerithium* Bruguière, 1789, on the Official List of generic names in zoology. A positive ruling on this petition was made by the Commission (Melville, 1978:97–98, Opinion 1109, ICZN). The type species, *Cerithium adansonii* Bruguière, 1792, has been shown by Fischer-Piette (1942:250–253) to be the same as *Cerithium erythraeonense* Lamarck, 1822 (herein regarded as conspecific with *Cerithium nodulosum* Bruguière, 1792). Although both *C. nodulosum* and *C. adansonii* were described in the same publication by Bruguière in 1792, the former species is presented a page ahead of the latter and has priority.

Today, the genus *Cerithium* Bruguière, 1789, sensu lato, is

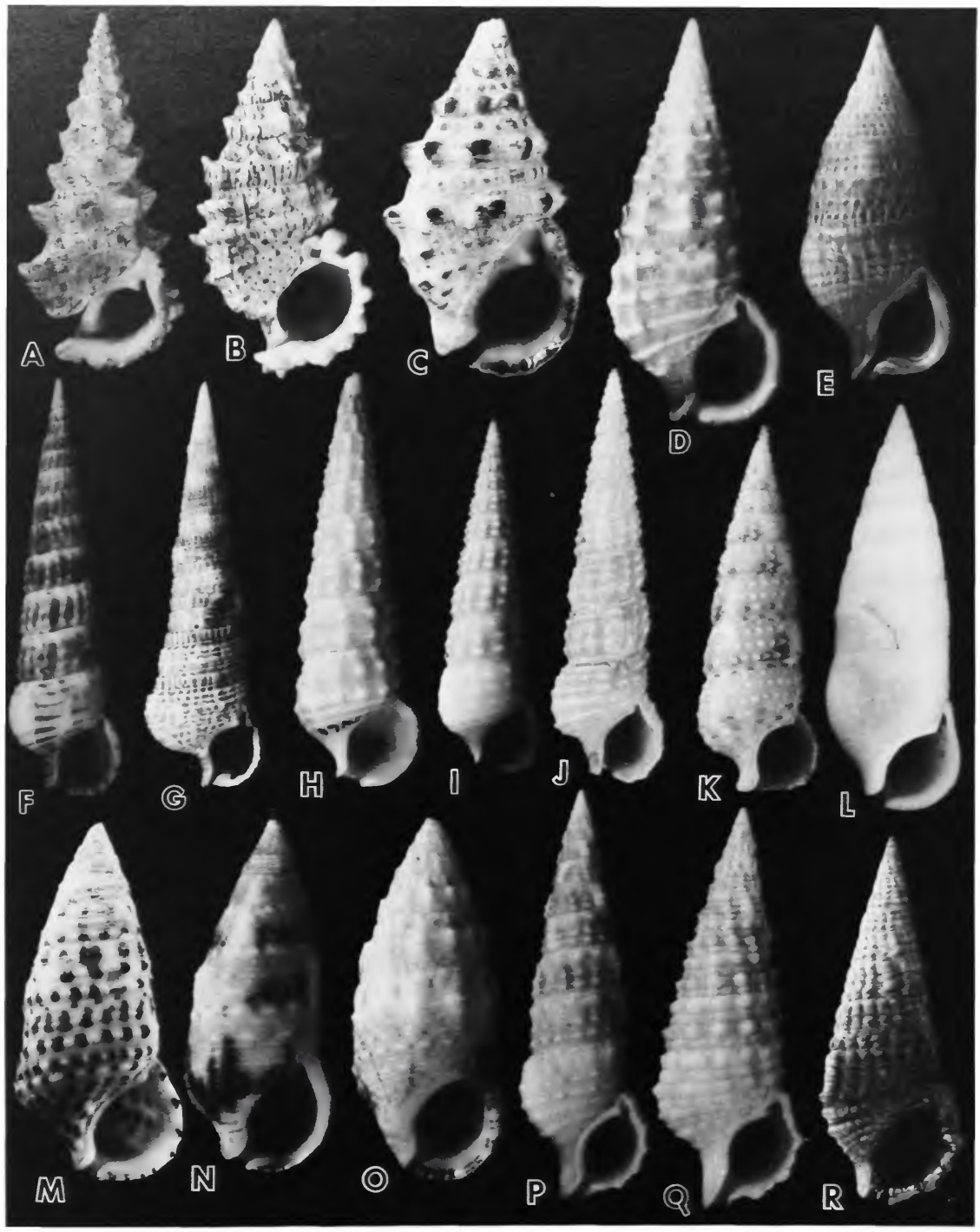


FIGURE 1.—Identification guide to *Cerithium* species arranged according to morphological similarity (specimens not to scale). A, *C. nodulosum* Bruguière, 1792, 101 mm (USNM 582026); B, *C. echinatum* Lamarck, 1811, 54.4 mm (USNM 705661); C, *C. caeruleum* Sowerby, 1855, 34.8 mm (USNM 597267); D, *C. claviforme* Schepman 1906, 31.5 mm (USNM 821796); E, *C. pacificum*, new species, 24 mm (USNM 821845); F, *C. matukense* Watson, 1886, 38 mm (BMNH 18872916602); G, *C. ophioderma* (Habe, 1968), 50.8 mm (USNM 862958); H, *C. flemischi* K. Martin, 1933, 40.5 mm (USNM 238537); I, *C. gloriosum*, new species, 26.4 mm (USNM 862327); J, *C. abditum*, new species, 15 mm (USNM 286404); K, *C. interstriatum* Sowerby, 1855, 16 mm (MNHNP); L, *C. nesioticum* Pilsbry and Vanatta, 1906, 16.5 mm (USNM 770724); M, *C. punctatum* Bruguière, 1792, 9 mm (USNM 579310); N, *C. egenum* Gould, 1849, 8 mm (USNM 72335); O, *C. atromarginatum* Dautzenberg and Bouge, 1933, 12.9 mm (USNM 423323); P, *C. phoxum* Watson, 1879, 26.4 mm (USNM 695390); Q, *C. lissum* Watson, 1879, 22.6 mm (BMNH 1887291665); R, *C. coralium* Kiener, 1841, 48 mm (USNM 661414).

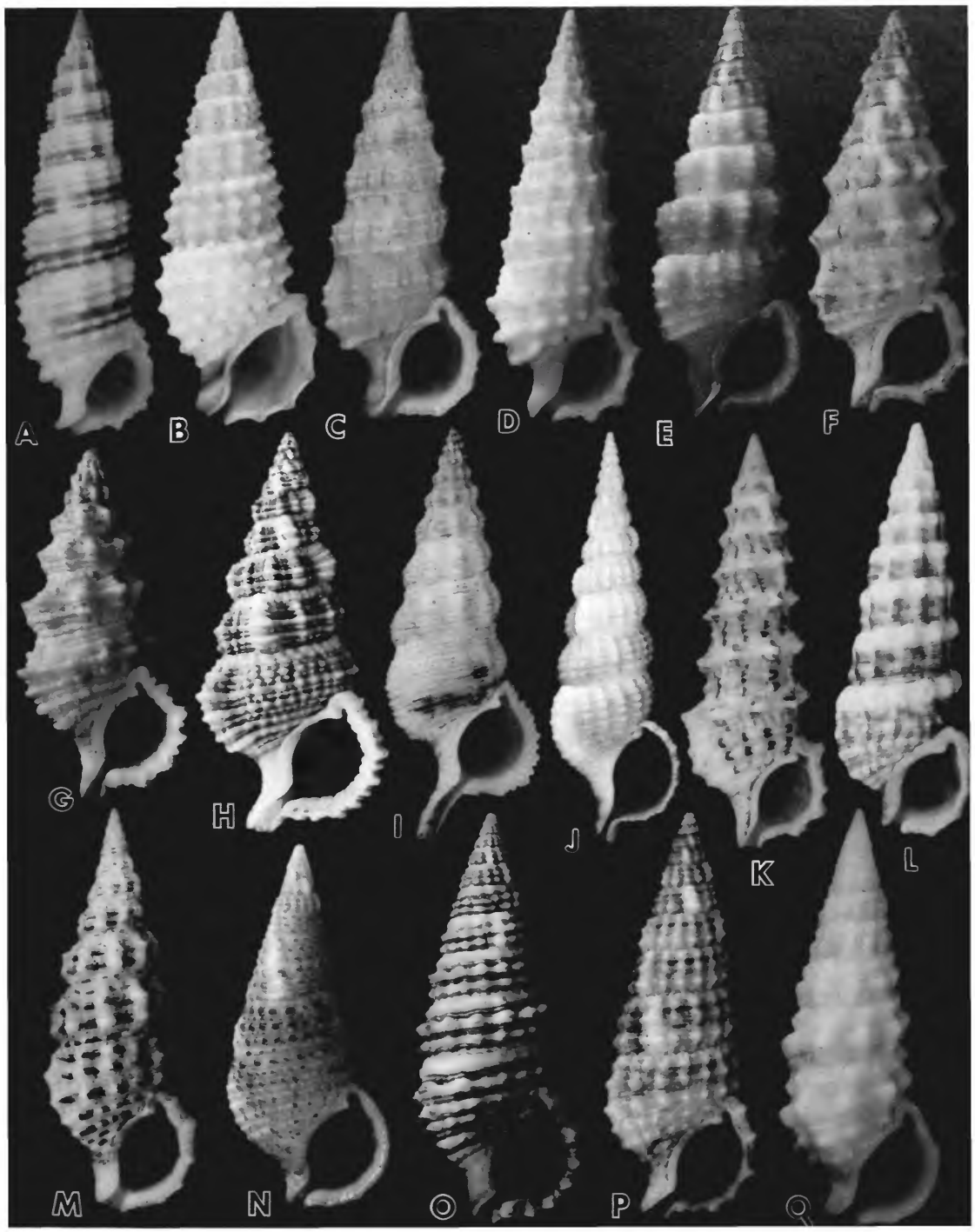


FIGURE 2.—Identification guide to *Cerithium* species arranged according to morphological similarity (specimens not to scale): A, *C. salebrosum* Sowerby, 1855, 24.8 mm (USNM 674900); B, *C. scobiniforme*, new species, 17.2 mm (USNM 837813); C, *C. munitum* Sowerby, 1855, 31.7 mm (USNM 584661); D, *C. ruppelli* Philippi, 1849, 39 mm (USNM 671248); E, *C. balteatum* Philippi, 1848, 16.4 mm (USNM 683971); F, *C. africanum*, new species, 17 mm (ANSP 22548); G, *C. columna* Sowerby, 1834, 40.6 mm (USNM 795123); H, *C. dialeucum* Philippi, 1849, 34.3 mm (USNM 862619); I, *C. citrinum* Sowerby, 1855, 38.9 mm (USNM 766738); J, *C. rostratum* Sowerby, 1855, 21.9 mm (BMNH); K, *C. lifuense* Melvill and Standen, 1895, 25 mm (MCZ 22662); L, *C. novaehollandiae* A. Adams, 1855, 38.7 mm (BMNH 19861741); M, *C. scabridum* Philippi, 1848, 19.3 mm (USNM 862606); N, *C. traillii* Sowerby, 1855, 41.8 mm (USNM 660839); O, *C. zonatum* (Wood, 1828), 31.1 mm (USNM 77068); P, *C. torresi* E.A. Smith, 1884, 18 mm (USNM 660964); Q, *C. tenellum* Sowerby, 1855, 33 mm (USNM 692935).

TABLE 1.—Generic-level taxa split from *Cerithium*, sensu lato, and used by authors in various combinations with *Cerithium*. Taxa are arranged chronologically; taxa marked with asterisk are those recognized herein.

Taxon	Present Allocation
Clava Martyn, 1784	*Rhinoclavis* Swainson
Vertagus Schumacher, 1817	*Rhinoclavis* Swainson
**Rhinoclavis* Swainson, 1840	*Rhinoclavis* Swainson
**Colina* H. and A. Adams, 1854	*Colina* H. and A. Adams
Aluco Martens, 1880	*Pseudovertagus* Vignal
**Gourmya* Fischer, 1884	*Gourmya* Fischer
**Liocerithium* Tryon, 1887	subgenus of *Cerithium* Bruguière
**Clypeomorus* Jousseaume, 1888	*Clypeomorus* Jousseaume
Semivertagus Cossmann, 1889	*Rhinoclavis* Swainson
Thericium Monterosato, 1890	*Cerithium* Bruguière
Gourmierium Jousseaume, 1894	*Cerithium* Bruguière
Goumierium Jousseaume, 1894	*Cerithium* Bruguière
Pithocerithium Sacco, 1895	*Cerithium* Bruguière
Ptychocerithium Sacco, 1895	*Cerithium* Bruguière
Conocerithium Sacco, 1895	*Cerithium* Bruguière
Tiaracerithium Sacco, 1895	*Cerithium* Bruguière
Tenuicerithium Cossmann, 1896	*Cerithium* Bruguière
Contumax Hedley, 1899	*Cerithium* Bruguière
**Pseudovertagus* Vignal, 1904	*Pseudovertagus* Vignal
Chondrocerithium Monterosato, 1905	*Cerithium* Bruguière
Vulgocerithium Cossmann, 1906	*Cerithium* Bruguière
Pliocerithium Monterosato, 1910	*Cerithium* Bruguière
Gladiocerithium Monterosato, 1910	*Cerithium* Bruguière
Drillocerithium Monterosato, 1910	*Cerithium* Bruguière
Hirtocerithium Monterosato, 1910	*Cerithium* Bruguière
Lithocerithium Monterosato, 1910	*Cerithium* Bruguière
**Ochetoclava* Woodring, 1928	subgenus of *Rhinoclavis* Swainson
Ischnocerithium Thiele, 1929	*Cerithium* Bruguière
**Proclava* Thiele, 1929	subgenus of *Rhinoclavis* Swainson

perceived to comprise a large group of species that are morphologically highly variable. These have been grouped or divided in many different ways by generations of conchologists into numerous genus-group taxa, all used in various combinations. All validly proposed names are summarized in Table 1, the current allocation of each taxon being shown in the right column. Many of the taxa in Table 1 have been regarded as subgenera of *Cerithium*, at one time or another. All of the taxa were based on shell characters alone; indeed, most of the names were proposed by paleontologists to accommodate fossils, usually with equivocal diagnostic shell characters. Under critical scrutiny, many taxa were found to have little or no justification. Some taxa have the same type species; e.g., *Cerithium vulgatum* Bruguière, 1789, is the type species for *Goumierium*, *Gourmierium*, *Thericium*, and *Vulgocerithium*, which are therefore objective synonyms. Other taxa, such as *Drillocerithium*, *Gladiocerithium*, *Hirtocerithium*, and *Pliocerithium*, have type species that I consider synonymous with *C. vulgatum*, and are therefore subjective synonyms. *Rhinoclavis*, *Pseudovertagus*, and their respective subgenera should be excluded from *Cerithium* (see Houbrick, 1978b). A broad concept of the genus *Cerithium* has been employed by most workers, a practice similar to that adopted for the complex and speciose genera *Cypraea* and *Conus*. This approach is adopted herein, and although the concept of *Cerithium* is narrowed by more precise definition and exclusion of some taxa, the monophyly of the genus must remain uncertain until the anatomy of many more species is studied.

The type species of *Contumax*, *C. decollatus* Hedley, as later noted by Thiele (1931:738), is merely an immature specimen of *Cerithium nodulosum*, as may be seen in Figure 89B,E,H. Hedley (1899:437) acknowledged the close resemblance of *C. decollatus* to *Mathilda eurytima* Melvill and Standen, which is also an immature *C. nodulosum* (see Figure 89E).

Ischnocerithium Thiele, 1929, based on the type species *C. rostratum* Sowerby, should be regarded as a synonym of *Cerithium*, sensu stricto. The radula and pallial oviduct anatomy of *C. rostratum* (see Figure 116) are typical of *Cerithium* species. Thiele (1929:212) considered *Cerithium rostratum* to be a subgenus of *Colina* H. and A. Adams, 1854, a genus that differs substantially in shell and radular morphology from *Cerithium* (Houbrick, pers. obs.). *Colina* is herein considered a full genus.

Clypeomorus Jousseaume 1888, has been treated thoroughly elsewhere (Houbrick, 1985:5-7), and is accorded full generic status.

Liocerithium Tryon, 1887, although its pallial oviduct is similar to that of *Cerithium* (Houston, 1985:186), needs further

anatomical work, and is herein provisionally recognized as a full genus because of its unique shell morphology.

Cernohorsky (1978:53) considered *Gourmya* Fischer, 1884, to be a subgenus of *Cerithium*, but *Gourmya* has been shown to be part of a Tethyan lineage separate from *Cerithium*, and is today represented only by the relict *Gourmya gourmyi* (Crosse, 1861), which is anatomically distinct from *Cerithium* (Houbrick, 1981).

Cerithium (sensu lato for earlier works) has been monographed by Bruguière (1792), Kiener (1841–1842), Sowerby (1855, 1865), Tryon (1887), Kobelt (1888–1898), Keen (1971, eastern Pacific species), Nordsieck (1974, eastern Atlantic and Mediterranean species), and Houbrick (1974b, western Atlantic species).

DISCUSSION.—The shell of the type species, *C. nodulosum*, is in many ways atypical of the the genus. It is many times larger than those of all other *Cerithium* species and the sculpture on early post-nuclear whorls differs considerably from that of the adult whorls. Moreover, the nodes are unusually large and the great hook-like extension of the outer lip over the siphonal canal is also atypical (Figure 86). Internal anatomy is, however, similar to that of all other *Cerithium* species, except for differences in pallial oviduct configurations that are described below.

Given the extensive variability seen in *Cerithium* shell morphology, and the interspecific similarity among the many radular and anatomical features, it is difficult to discern real groups representing phyletic lineages. Unfortunately, the general anatomy and especially the pallial oviducts of many species remain unknown, precluding a comprehensive phylogenetic analysis. Despite this, present knowledge of the radula and pallial oviducts of a number of species described below supply some characters that may be instructive in suggesting a taxonomy based on phylogeny.

Radula: *Cerithium* species all share a similar, taenioglossate radular morphology. Bandel (1984:56) has commented on the close resemblance among radulae of the western Atlantic species. Although a notable similarity in radular morphology also exists among most Indo-Pacific species, there are some differences. Rachidian tooth morphology has been divided into four types, which are summarized in Table 2, illustrated in Figure 3, and discussed below:

Type-1: In this most common rachidian morphology, the tooth is roughly square with slightly rounded edges and has a basal plate with a short, median, basal projection and a pair of crescentic ridges, and a cutting edge with a large, central, main cusp flanked by two smaller denticles on each side (Figure 3A). Twenty-four species have Type-1 morphology (see Table 2), including *C. nodulosum*, the type species of *Cerithium*.

Type-2: This kind of rachidian tooth is triangular, with a constricted basal plate having a long median, basal projection (Figure 3B), and occurs in *C. balteatum*, *C. lissum*, *C. salebrosum*, and *C. scobiniforme*. It is noteworthy that all these species have similar, rugosely sculptured, slender shells with

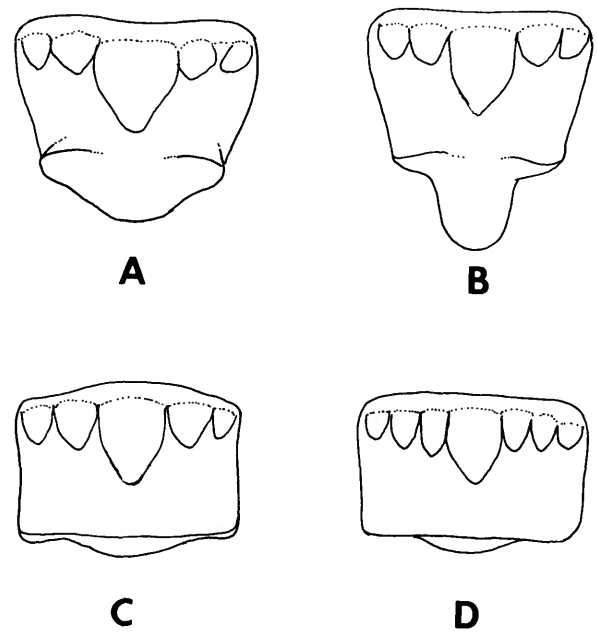


FIGURE 3.—Rachidian tooth morphology types as found among *Cerithium*, sensu lato, species: A, Type-1 rachidian; B, Type-2 rachidian; C, Type-3 rachidian; D, Type-4 rachidian.

TABLE 2.—Indo-Pacific *Cerithium* species grouped according to the four types of rachidian tooth morphology.

Type-1	Type-2	Type-3	Type-4
africanum	*balteatum*	*flemischi*	*abditum*
atromarginatum	*lissum*	*gloriosum*	*interstriatum*
caeruleum	*salebrosum*	*matukense*	
citrinum	*scobiniforme*	*ophioderma*	
claviforme			
columna			
coralium			
crassilabrum			
dialeucum			
echinatum			
egenum			
munitum			
nesioticum			
nodulosum			
novaehollandiae			
phoxum			
punctatum			
rostratum			
ruppelli			
scabridum			
tenellum			
torresi			
traillii			
zonatum			

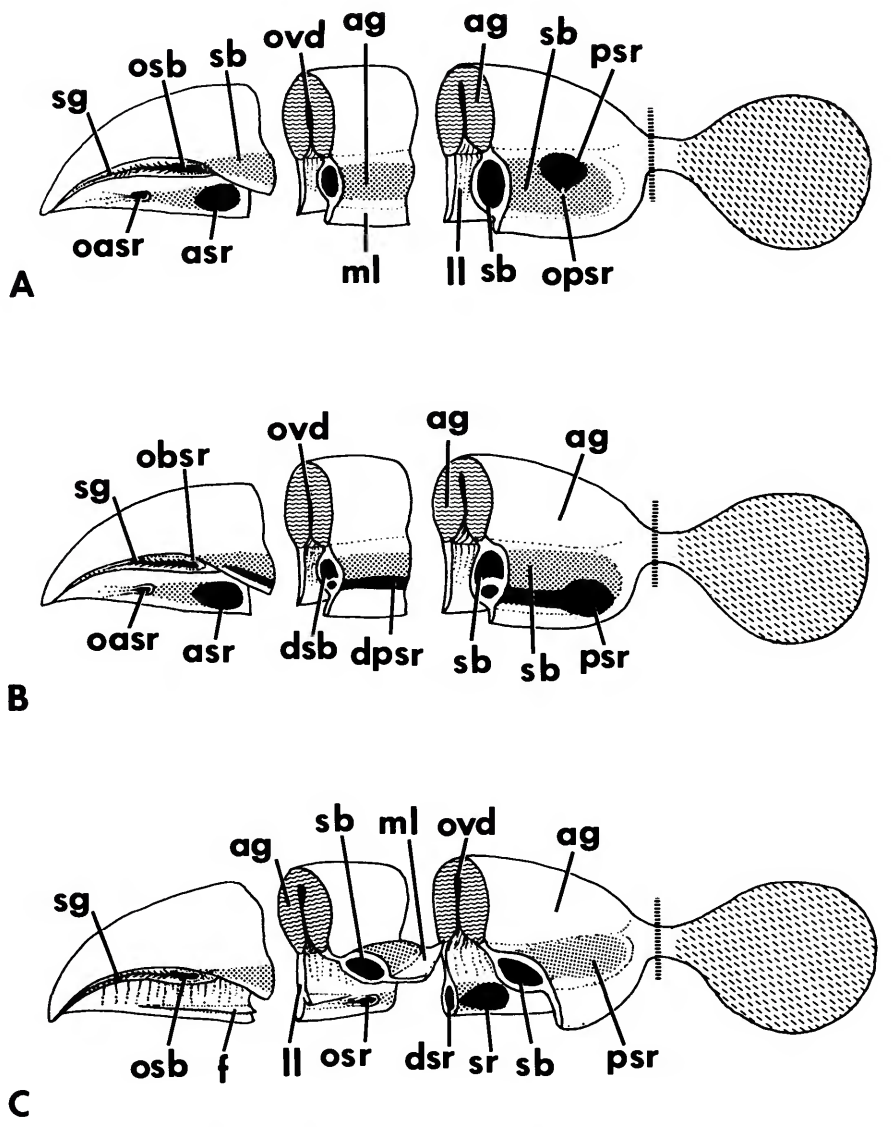


FIGURE 4.—Diagrammatic representation of three types of pallial oviducts found among species of *Cerithium*, sensu lato. (broken line represents division between pallial oviduct and coelomic oviduct): A, Type A oviduct, *Cerithium* sensu stricto; B, Type B oviduct; C, Type C oviduct. (Abbreviations: *ag* = albumin gland; *asr* = anterior seminal receptacle; *dsb* = duct of spermatophore bursa; *dsr* = duct of seminal receptacle; *dpsr* = duct of posterior seminal receptacle; *f* = flange; *ll* = lateral lamina; *ml* = medial lamina; *oasr* = opening to anterior seminal receptacle; *obsr* = opening to spermatophore bursa and seminal receptacle; *osb* = opening to spermatophore bursa; *osr* = opening to seminal receptacle; *ovd* = oviduct; *psr* = posterior seminal receptacle; *sb* = spermatophore bursa; *sg* = sperm gutter.

deeply excavated bases, and well-defined, tubular siphonal canals.

Type-3: This type of rachidian tooth is square with a cutting edge having two small denticles flanking each side of the rounded main cusp, and a broad basal plate with a shallow basal projection (Figure 3C). The three taxa having a Type-3 rachidian tooth, *C. flemischi*, *C. gloriosum*, and *C. matukense*, are deep-water shelf species, having a common sandy habitat. They have similar, long, slender shells with ratchet sculpture and identical protoconchs, and an operculum with a subcentral nucleus. Although their anatomy is not well known, the conchological and radular characters, and a common deep-sea habitat suggest that they belong to a separate lineage.

Type-4: In this morphology, seen in *C. abditum* and *C.*

interstriatum, the rachidian tooth is rectangular with a narrow basal plate having a very shallow median posterior projection and a cutting edge with three denticles flanking each side of the main central cusp (Figure 3D). Both species with this rachidian type have small shells with dominant spiral sculpture, small apertures, and multispiral opercula with central nuclei.

The rachidian tooth of both *C. atromarginatum* and *C. caeruleum* differs slightly from those of other Type-1 species, but not enough to qualify it as a separate type. These four basic types of rachidian morphology are somewhat incongruent with the three kinds of pallial oviduct morphology described below.

Pallial Oviducts: In addition to radular patterns, pallial oviduct configurations appear to supply the most reliable and useful anatomical character set upon which to base potential supraspecific determinations. However, pallial oviduct anatomy is difficult to ascertain without study of living, ripe, adult females. The pallial oviducts of 12 of 42 Indo-Pacific *Cerithium* species have been determined, and of these, only five species (*C. atromarginatum, C. columna, C. echinatum, C. nodulosum, C. rostratum*) are well understood. Three different pallial oviduct layouts have been discerned among these 12 known Indo-Pacific species, and are listed in Table 3 and represented, in cartoon fashion, in Figure 4. Descriptions of these follow.

Type-A (Figure 4A). This pallial oviduct configuration occurs in *Cerithium nodulosum*, the type species of *Cerithium* sensu stricto, and in *C. atromarginatum, C. columna, C. echinatum, C. nesioticum, C. punctatum, C. rostratum*, and *C. traillii*. There are two seminal receptacles, an anterior one in the non-glandular part of the anterior lateral lamina (Figure 4A, asr), and a posterior one (Figure 4A, psr) on the dorsal side of the spermatophore bursa (Figure 4A, sb) in the non-glandular, posterior medial lamina (Figure 4A, ml). The opening to the bursa (Figure 4A, osb) in the sperm gutter (Figure 4A, sg) is adjacent to the opening of the anterior seminal receptacle (Figure 4A, oasr) in the lateral lamina (Figure 4A, ll). A more detailed description and many figures of this type of oviduct morphology are found in the section on *Cerithium nodulosum*, page 126.

Type-B (Figure 4B). This morphology occurs in *C. dialeucum, C. egenum*, and *C. zonatum*, and appears to be intermediate, between the Type-A layout seen in *Cerithium* sensu stricto, and that of *Clypeomorus* Jousseaume, 1888, as defined by Houbrick (1985:6, 29, fig. 13F). Indeed, *Clypeomorus nympha* Houbrick, 1985, was only tentatively included in *Clypeomorus* by Houbrick (1985:118), who noted that the pallial oviduct layout was more like those seen in some *Cerithium* species. As in the Type-A layout, Type-B has two seminal receptacles, one anterior (Figure 4B asr) and another posterior (Figure 4B, psr), but the posterior one is located at the inner (ventral) side of the bursa (Figure 4B, sb) in the medial lamina. A detailed description of this type of layout is found in the section under *Cerithium egenum*, page 86.

The pallial oviduct of *Cerithium dialeucum*, differs somewhat from other Type-B layouts in having two openings in the sperm gutter, one to the bursa and the other to the seminal receptacle, via long, ciliated ducts (see Figure 46).

TABLE 3.—Indo-Pacific *Cerithium* species grouped according to three types of pallial oviduct configurations.

Type-A	Type-B	Type-C
atromarginatum	*dialeucum*	*coralium*
columna	*egenum*	
echinatum	*zonatum*	
nesioticum		
nodulosum		
punctatum		
rostratum		
traillii		

Type-C (Figure 4C). This is perhaps the most unusual pallial oviduct in relation to the other three, and was seen only in *C. coralium*. There is only a single posterior seminal receptacle (Figure 4C, sr) in the mid-posterior, non-glandular part of the lateral lamina (Figure 4C, ll), and there is a long, wide ciliated tract on the lateral lamina (Figure 4C, ll), partially covered with a longitudinal flange (Figure 4C, f). See the section under *C. coralium*, page 61, for a detailed description of this kind of pallial oviduct.

These three configurations are not the only kinds observed among *Cerithium* species, on a global basis. Eastern Atlantic species, as exemplified by *Cerithium vulgatum* Bruguière, 1789, the type species of *Thericium* Monterosato, 1890, have a gonoduct layout similar to that of *Cerithium*, sensu stricto (Type-A), but differ in lacking the posterior seminal receptacle (Johansson, 1953:2–4, figs. 1–4). Eastern Atlantic species have traditionally been assigned to the subgenus *Thericium*, recently accorded generic rank by Gründel (1981:8). However, Johansson (1953) may not have seen the posterior seminal receptacle, which is very small in Type-A species, and discernible only in fully ripe females. Should this receptacle be present in eastern Atlantic species, they too would fall into the Type-A group, leaving only unreliable shell characters to define and justify the validity of *Thericium*. I previously assigned western Atlantic species to *Thericium* (Houbrick, 1974b:38), but have since determined that they have a posterior seminal receptacle; thus, western Atlantic taxa should also be referred to *Cerithium*, sensu stricto.

If the gonoduct layouts seen in species of *Clypeomorus* Jousseaume, 1888, and *Rhinoclavis* Swainson, 1840, are included (Houbrick, 1985, fig. 13F), there are five, possibly six, morphlogical types known for species originally considered as *Cerithium*, sensu lato. I originally accorded *Clypeomorus* full generic status (Houbrick, 1985:6–7), but in light of emerging patterns, the rank of *Clypeomorus* may change; however, it is premature to make a final decision on this until more anatomical evidence is at hand. The oviducts of *Rhinoclavis* species need reexamination, but preliminary investigations

indicate that several patterns also exist in that group (Houbrick, pers. obs.). The pallial oviduct layouts in species of *Pseudovertagus* Vignal, 1904, and *Cerithioclava* Olsson and Harbison, 1953, remain unknown.

Limited available data suggest absence of congruence between pallial oviduct types and radular types: *Cerithium* species sharing Type-1 radular morphology have differing pallial oviduct configurations, and comprise members of all four pallial oviduct groups. Pallial oviducts of species having Type-2 and Type-3 rachidian morphologies are unknown. Bearing in mind the caveats about ascertaining adult pallial oviduct layouts mentioned previously (pages 2, 10), premature decisions regarding the taxonomic significance of the pallial oviduct types relative to each other and to other cerithiid higher taxa such as *Clypeomorus* Jousseaume, *Rhinoclavis* Swainson, *Cerithioclava* Olsson and Harbison, and *Pseudovertagus* Vignal, are not warranted. Until the full range of pallial oviduct variation of all component species of *Cerithium*, sensu lato, is known, it is unwise to add to the existing generic inflation by creating new supraspecific names for the partially understood species groups described above. When more information is available, a more reliable comparison may be made among genera and with radular types.

PALEOHISTORY.—*Cerithium*, sensu lato, has an extensive fossil record, but this is obfuscated by broad or discordant interpretations of the limits of the genus by past workers. Thus, many taxa referred to *Cerithium* in the paleontological literature are frequently members of other genera, families, and even superfamilies. There are hundreds of nominal, fossil *Cerithium* species described from Indo-Pacific strata (many from fragments), and their description, evaluation, identity, and integration into a systematic account of Recent species would be a daunting task, far beyond the scope of this project.

Of the Recent Indo-Pacific *Cerithium* species, 23 (55 percent) are known as fossils (7 Miocene, 7 Pliocene, 13 Pleistocene, 12 Holocene). The three species with the widest fossil distributions and most commonly cited in the literature are *C. coralium*, *C. munitum*, and *C. nodulosum*, all of which may be traced back to the Miocene. The survival and stability of many *Cerithium* species through the Cenozoic to the present has been documented elsewhere: nearly all western Atlantic Recent *Cerithium* species were represented in the Pliocene and Pleistocene epochs (Houbrick, 1974b:35) and six extant *Clypeomorus* species are recorded with records as far back as the Miocene (Houbrick, 1985:10). The Caribbean Recent genus *Cerithioclava* Olsson and Harbison, 1953, can be traced back to the Pliocene (Houbrick, 1986). In addition, 12 living, Indo-Pacific rhinoclavid species, of the genera *Rhinoclavis* Swainson, 1840, *Pseudovertagus* Vignal, 1904, and *Clavocerithium* Cossmann, 1920, have fossil records in the Cenozoic (Houbrick, 1978b). It should be pointed out that fossils thought to be conspecific with living species are judged so only on the basis of conchological similarity.

A number of living *Cerithium* species (*C. claviforme*, *C. flemischi*, *C. koperbergi*, *C. madreporicolum*) were described from fossils before they were known to be extant. Common, widespread, Recent species for which no fossil records exist are *C. nesioticum* and *C. novaehollandiae*. The most common, widespread, Recent species, *C. columna*, surprisingly has only a few fossil records. Species that live in muddy estuarine habitats, in quiet lagoons associated with reefs, or in subtidal, silty, sand bottoms appear to have better chances of fossil preservation than those from intertidal, rocky, high-energy habitats. A summary of Recent species having fossil records is presented in Table 4.

CONCHOLOGICAL VARIATION.—A hallmark of many cerithioideans is intraspecific variation in shell morphology. This phenomenon occurs markedly in some groups; perhaps one of the most striking examples of variability is the diversity of phenotypes seen in *Tympanotonus fuscatus* (Linné, 1758), of the estuarine family Potamididae H. and A. Adams, 1854. These phenotypes have been described and illustrated by Pilsbry and Bequaert (1927:245–247, pl. 20: figs. 1–6). Variability in shell morphology is also exceptional among many members of the freshwater families Thiaridae Troschel, 1857, and Pleuroceridae Fischer, 1885. Some species in these two families represent classic examples of this phenomenon; e.g., see Pilsbry and Bequaert (1927:267–272, pls. 23, 24) for an account of the astonishing polymorphism of species of *Pachymelania* E.A. Smith (Thiaridae), and C.C. Adams (1900, 1915) for similar, wide, phenotypic variation in members of *Io* Lea, 1831 (Pleuroceridae).

It is among members of the marine family Cerithiidae that variability is exceptionally notable (Houbrick, 1974b:33, 1977:102, 1978b:14, 1985:1). Broad intraspecific variability is a common phenomenon among many *Cerithium* species, as I have previously shown for western Atlantic species (Houbrick, 1974b:60, pl. 28; 64–65, pls. 31, 32). Among Indo-Pacific *Cerithium* species, one need only peruse the species accounts and figures herein to appreciate the wide and bewildering variation among specific taxa of this genus. Indeed, shell characters within a particular *Cerithium* species may show more diversity and variability than those used to define and distinguish genera of other prosobranch families. For example, the extreme phenotypic variation seen in species such as *C. balteatum*, *C. columna*, *C. echinatum*, *C. lifuense* *C. munitum*, *C. ruppelli*, *C. tenellum*, and *C. zonatum*, equals that documented for the potamidid, thiarid, and pleurocerid taxa mentioned above.

The possible functional significance of this variability in *Cerithium* and other cerithiids has been discussed elsewhere (Houbrick, 1978a, b:15; 1980a; 1985:8–9). In general, it appears that basic shell form and sculpture of each *Cerithium* species reflects substrate preference and microhabitat, and three basic morphological patterns may be discerned:

1. Burrowers of sandy habitats are elongate with small apertures relative to shell length, and have long, curving,

TABLE 4.—Fossil records of Recent Indo-Pacific *Cerithium* species.

Species	Epoch	Locality	Source
atromarginatum	Late Miocene	Marshall Ids	Ladd, 1972:40 (as *C.* aff. *egenum*)
balteatum	Miocene	Saipan	Ladd, 1972:38 (as *C. schmidti*)
caeruleum	Pleistocene	Somalia	Abrard, 1942:60
claviforme	Holocene	Celebes	Schepman, 1907:187
columna	Pliocene-Holocene	Marshall Ids	Ladd, 1972:37
	Pliocene-Pleistocene	Guam	Ladd, 1972:39
coralium	Pliocene-Pleistocene	Indonesia	Altena, 1941:23
	Pleistocene-Holocene	Taiwan	Wissema, 1947:62
	Pliocene	Philippines	Popenoe and Kleinpell, 1978 (as *C. rubus*)
	Pleistocene	Philippines	this study
	Pliocene	Timor	Tesch, 1920:55 (as *C. rubus*)
	Pleistocene	New Hebrides	Ladd, 1972:38 (as *C. ruppelli*)
dialeucum	Pleistocene	Japan	McNeil, 1960:41
	Holocene	Borneo	this study
echinatum	Pleistocene	Zanzibar	Cox, 1927:85
	Cenozoic	Timor	Tesch, 1920:52
	Holocene	Marshall Ids	Ladd, 1972:37 (as *C. mutatum*)
egenum	Holocene	Marshall Ids	Ladd, 1972:39
flemischi	Miocene	Indonesia	Martin, 1933:29
	Pleistocene	Fiji	this study
koperbergi	Quaternary	Celebes	Schepman, 1907:188
lifuense	Pleistocene-Holocene	Loyalty Ids	this study
madreporicolum	Holocene	Somalia	Jousseaume, 1930:276
	Pleistocene	Somalia	Abrard, 1942:59
munitum	Pleistocene-Holocene	W. Australia	this study
	Miocene-Pliocene	Celebes	this study
	Pliocene	Java	Martin, 1899:197 (as *C. sucaradjanum*)
	Pliocene	Java	Martin, 1899:201 (as *C. talahabense*)
	Pliocene	Nias	Icke and Martin, 1907:241 (as *C. boettgeri*)
nodulosum	Miocene	Marshall Ids	Ladd, 1972:39
	Pliocene-Pleistocene	Guam	Ladd, 1972:39
	Miocene	Fiji	Ladd, 1972:39
	Neogene	Palau	Ladd, 1972:39
pacificum	Holocene	Loyalty Ids	this study
punctatum	Pleistocene	Saipan	Ladd, 1972:37 (as *C. alveolus*)
	Holocene	Marshall Ids	Ladd, 1972:37 (as *C. alveolus*)
	Holocene	W. Australia	this study
rostratum	Pleistocene	Somalia	Abrard, 1942:60
	Miocene-Pleistocene	Marshall Ids	Ladd, 1972:32
	Holocene	Marshall Ids	Ladd, 1972:32
salebrosum	Pleistocene	Kenya	this study
	Pliocene-Holocene	Loyalty Ids	this study
scabridum	Pleistocene	Somalia	Abrard, 1942:60
	Pleistocene	South Africa	Kilburn and Tankard, 1975:197 (as *C. rufonodulosum*)
tenellum	Pliocene	Okinawa	McNeil, 1960:41 (as *C. kobelti*)
traillii	Pliocene	Borneo	Beets, 1950:307
	Pliocene	Nias	Wissema, 1947:63 (as *C. niasensis*)
zonatum	Miocene	Marshall Ids	Ladd, 1972:34 (as *Rhinoclavis marshallensis*)

siphonal canals. Their sculpture tends to consist of dominant axial elements, with ridges, beads, and tubercles asymmetrically aligned to form what Signor (1983) termed "ratchet sculpture." This presumably prevents backwards slippage when burrowing in sand (but see p. 93, this paper). Examples are *C. abditum*, new species, C. flemischi, C. gloriosum C. matukense, C. salebrosum, and *C. tenellum* .

2. Subtidal species living on hard substrate or on the rubble of reef flats are moderately elongate with larger apertures and moderately developed siphonal canals, and tend to have a sculpture of strong spiral elements that have large, sometimes spinose, nodes. Examples are *C. echinatum* and *C. nodulosum.*

3. Species from high energy environments or rocky, intertidal habitats are short, stocky, have large apertures in relation to shell length, short siphonal canals, and an overall beaded sculpture comprising axial and spiral elements. Exam-

ples are *C. atromarginatum, C. egenum,* and nearly all *Clypeomorus* species.

Intermediates and exceptions to the above morphological patterns are not uncommon. Although each *Cerithium* species has a preferred microhabitat to which it is generally restricted, some species have the ability to colonize adjacent, differing microhabitats. *Cerithium columna* and *C. zonatum* are very plastic in respect to habitat, and this may be reflected in the high degree of phenotypic variability observed in their shells. Phenotypic variation is frequently observed within a single *Cerithium* species population from a given site. However, the phenotypes of the individuals comprising a population appear to be closely correlated with differences in local microhabitat. For example, apparent ecoclinal variation in shell morphology was noted in a population of *C. columna* from Enewetak Id, Enewetak Atoll, Marshall Islands (see the section on *C. columna,* p. 56, this paper, for more detailed description).

ECOLOGY.—Few ecological studies have been published about Indo-Pacific *Cerithium* species, although there are numerous, short, anecdotal reports that often cite taxa whose identity is not clear. These observations are discussed in each species treatment herein. Perhaps the most comprehensive ecological publication is that of Ayal and Safriel (1982), who studied the ecology of *Cerithium* species around the Sinai peninsula in the Red Sea. The only other thorough ecological account is the study of *Cerithium nodulosum* by Yamaguchi (1977).

Cerithium species span a broad variety of habitats, both in regard to substrate and vertical depth distribution. The generalized habitats of all *Cerithium* species are summarized in Table 5. The great majority of species occur intertidally or in shallow water on sand-rubble substrates, where they crawl on the surface or partially burrow around rocks. Many species tend to burrow partially during the day. but are active crawlers on the surface during the night. *Cerithium* species are only occasionally infaunal; indeed, of all shallow-water species, only *Cerithium salebrosum* is a true infaunal sand dweller, although *Cerithium tenellum* is sometimes found in this habitat also. All five deep-water species, *Cerithium abditum,* new species, *C. flemischi, C. gloriosum, C. matukense,* and *C. ophioderma,* new combination, are partial burrowers, but not truly infaunal. Most other cerithiid infaunal sand dwellers are *Rhinoclavis* species. Among Indo-Pacific *Cerithium* species, *Cerithium rostratum* is unique in being frequently found living on blades of marine angiosperm grasses. *Cerithium columna* and *C. zonatum* also occur in sea-grass beds but are usually confined to the substratum. A number of species prefer solid rocky substrates such as large boulders, or rocky coralline platforms and benches. Species commonly found in this kind of habitat are *Cerithium caeruleum, C. echinatum, C. nodulosum* and *C. scabridum.* Among smaller species, *Cerithium atromarginatum, C. egenum,* and *C. punctatum* are confined to intertidal algal mats. *Cerithium dialeucum, C. interstriatum,* and *C. torresi* prefer silty sand environments, while *C. coralium* is unique in occurring on muddy sand in estuarine substrates around mangroves.

All examined *Cerithium* species are algal-detritus feeders, but most appear to graze on diatoms and microalgae rather than on larger pieces of algae. The alimentary systems of all known species comprise paired salivary glands, an esophageal gland, a stomach with large sorting areas, a short style sac and crystalline style, and a gastric shield. Gut contents normally comprise detritus, microalgae, sand grains, and foraminifera that are engulfed during grazing.

Most *Cerithium* species occur in large populations and are prey to many different marine animals, including birds. Fish, other mollusks, and crustaceans are primary predators, particularly of juveniles. Drilled shells are commonly found, suggesting heavy predation by naticid and muricid snails. Empty *Cerithium* shells are an abundant resource utilized by many hermit crabs. Many intertidal *Cerithium* species are intermediate hosts for trematode parasites of birds, and some populations may be nearly 100 percent infected at certain times of the year. The visceral masses of parasitized snails become filled with sporocysts, rediae, and cercaria larvae that frequently alter the secondary sexual characters of their hosts.

Species with broad geographic ranges, exposed to many different kinds of habitats, are under differing ecological constraints, and adjust accordingly to their local biotope. Although each species appears to have a generalized, "preferred" habitat, local populations may sometimes undergo ecological release and occur on atypical substrates or at unusual depths.

REPRODUCTIVE BIOLOGY.—Although the egg masses of all eastern and western Atlantic *Cerithium* species have been described (Houbrick, 1973b, 1974b), only those of four species from the Indo-Pacific are known. These include descriptions of the spawn of *C. caeruleum* (see Hulings, 1986:323), *C. scabridum* (see Barash and Zenziper, 1980:301, fig. 1), *C. nodulosum* (see Houbrick, 1971:563–564, fig. 2), and *C. tenellum* (this paper, p. 179), all of which are similar in overall morphology to each other and to western Atlantic species. Eggs are each enclosed within a hyaline capsule, embedded in a thick gelatinous matrix, and deposited within a long, filamentous string surrounded by an external limiting membrane. The egg string is wound back and forth and irregularly coiled to form a ribbon-like mass. Nurse eggs have never been noted. Egg masses of *Cerithium* species having planktonic development have many small eggs (<300 μm diameter) within tightly wound egg strings, while species having direct development have larger, fewer eggs (>300 μm diameter) and a thicker gelatinous matrix comprising their egg strings.

The life histories of a number of *Cerithium* species are relatively well known, and there have been two detailed studies of the type species, *Cerithium nodulosum,* one on spawn, larvae, and development (Houbrick, 1971), and the other on growth (Yamaguchi, 1977). Houbrick (1973b; 1974b) demonstrated that both planktotrophy (4 species) and lecithotrophy (2

TABLE 5.—Ecological distribution of Indo-Pacific *Cerithium* species (common habitats and percentages of species in each zone given).

Species n = 42	Intertidal	Subtidal		
	low to mid 35.7%	low 16.6%	shallow 59.5%	deep 14.3%
abditum	–	–	–	sand
africanum	–	rubble, sand	–	
alexandri	–	–	–	?
amirantium	–	rubble, sand	–	
atromarginatum	algal turf	–	–	–
balteatum	–	rubble, sand	–	
caeruleum	tide pools, rocks	–	–	–
citrinum	–	–	rubble–sand	–
claviforme	–	–	coral, rubble	–
columna	sand, rubble	sand, rubble	–	
coralium	muddy sand	–	–	–
crassilabrum	algae, tide pools	–	–	
dialeucum	–	–	silty sand	–
echinatum	–	–	rocks, rubble	–
egenum	algae, tide pools	–	–	–
flemischi	–	–	–	sand
gloriosum	–	–	–	sand
interstriatum	–	–	silty sand	–
koperbergi	–	–	sandy gravel	–
leptocharactum	sandy tide pools	–	–	–
lifuense	–	–	sand, rubble	–
lissum	–	–	sand, rubble	–
madreporicolum	–	–	?	–
matukense	–	–	–	sand
munitum	–	–	coral, rubble	–
nesioticum	sandy tide pools	–	sand, rubble	–
nodulosum	rocky platforms	–	–	–
novaehollandiae	sand, rubble	sand, rubble	–	
ophioderma	–	–	–	sand
pacificum	–	–	coral, rubble	–
phoxum	–	–	sand, rubble	–
punctatum	algal mats, benches	–	–	
rehderi	–	–	sand, rubble	–
rostratum	–	–	grass beds	–
ruppelli	–	–	coral, rubble	–
salebrosum	–	–	sand	–
scabridum	hard substrates	–	–	–
scobiniforme	–	–	sand, rubble	–
tenellum	–	–	sand, rubble	–
torresi	–	silty sand	sand, rubble	–
traillii	rubble	rubble	–	–
zonatum	–	algae, rubble	algae, rubble	–

species) occur in western Atlantic *Cerithium* species. The two common Mediterranean *Cerithium* species also have different types of developmental strategies (Bandel, 1975:91; Richter and Thorson, 1975:129–130, pl. 4: figs. 22, 23). Western Atlantic *Cerithium* species all reach reproductive maturity within a year and appear to have a life span of slightly over one year (Houbrick, 1974a). This is probably true of most Indo-Pacific species, but Yamaguchi (1977) showed that *C. nodulosum*, the largest of *Cerithium* species, reaches adulthood within three years of settlement, suggesting that some other large species, e.g., *C. echinatum*, *C. matukense*, may be equally long-lived. Ayal and Safriel (1982) found that *Cerithium caeruleum* has a seven-year life history.

The life histories of Indo-Pacific *Cerithium* species, summarized in Table 6, are derived from developmental studies, direct field observations, protoconch morphology, or have been inferred from geographic distributions. Study of larval shell morphology permits inferences to be made concerning developmental types of living and extinct species (Shuto, 1974; Jablonski and Lutz, 1980:329–335). In general, species with planktotrophic larvae have many-whorled, highly sculptured protoconchs with a deep sinusigeral notch at the aperture;

TABLE 6.—Life history strategies of Indo-Pacific *Cerithium* species (x = data derived from protoconchs or developmental studies; * = data suggested by geographic range; dash = no data).

Species	Life History		Source
	Pelagic	Direct	
C. abditum	x	–	this study
C. africanum	–	–	–
C. alexandri	–	*	this study
C. amirantium	–	–	–
C. atromarginatum	x	–	Taylor, 1975; this study
C. balteatum	–	x	this study
C. caeruleum	x	–	this study
C. citrinum	*	–	this study
C. claviforme	*	–	this study
C. columna	x	–	this study
C. coralium	*	–	this study
C. crassilabrum	–	*	this study
C. dialeucum	*	–	this study
C. echinatum	x	–	Taylor, 1975; this study
C. egenum	x	–	Kay, 1979; this study
C. flemischi	x	–	this study
C. gloriosum	x	–	this study
C. interstriatum	x	–	Taylor, 1975, this study
C. koperbergi	–	*	this study
C. leptocharactum	–	*	this study
C. lifuense	*	–	this study
C. lissum	*	–	this study
C. madreporicolum	*	–	this study
C. matukense	x	–	this study
C. munitum	*	–	this study
C. nesioticum	x	–	this study
C. nodulosum	x	–	Houbrick, 1971
C. novaehollandiae	–	*	this study
C. ophioderma	–	–	–
C. pacificum	*	–	this study
C. phoxum	–	–	–
C. punctatum	x	–	this study
C. rehderi	–	*	this study
C. rostratum	x	–	this study
C. ruppelli	*	–	this study
C. salebrosum	*	–	this study
C. scabridum	x	–	Ayal and Safriel, 1977; Barash and Zenziper, 1980
C. scobiniforme	–	–	–
C. tenellum	*	–	this study
C. torresi	*	–	this study
C. traillii	*	–	this study
C. zonatum	x	–	this study

species having lecithotrophic larvae or direct development have fewer-whorled, weakly sculptured protoconchs that lack the deep sinusigeral notch. With the exception of Yamaguchi's (1977) study of *C. nodulosum*, which is the largest and possibly the most atypical of *Cerithium* species, nothing is known of post-settlement growth of other Indo-Pacific species.

Larval shell morphology also gives an indication of dispersal capability (Shuto, 1974:253; Jablonski and Lutz, 1980:355–356). Planktotrophic species with a relatively long pelagic stage have greater dispersal abilities over wide geographic areas and can maintain gene flow among disjunct populations.

TABLE 7.—Species numbers of cerithiid genera (excluding *Bittium*) within geographic provinces (IP = Indo-Pacific; EP = Eastern Pacific; WA = Western Atlantic; EA = Eastern Atlantic and Mediterranean).

Genus	Total taxa	IP	EP	WA	EA
Cerithium	60	42	9	6	3
Clypeomorus	15	15	0	0	0
Rhinoclavis	8	8	0	0	0
Pseudovertagus	5	5	0	0	0
Argyropeza	5	5	0	0	0
Colina	5	5	0	0	0
Plesiotrochus	3	3	0	0	0
Proclava	2	2	0	0	0
Glyptozaria	2	2	0	0	0
Varicopeza	2	1	0	1	0
Cerithioclava	1	0	0	1	0
Indocerithium	1	1	0	0	0
Ochetoclava	1	0	1	0	0
Longicerithium	1	1	0	0	0
Fastigiella	1	0	0	1	0
Royella	1	1	0	0	0
Gourmya	1	1	0	0	0

These species are more likely to be immune to local catastrophes and extinctions. In contrast, species with non-planktonic larvae tend to have smaller, more continuous ranges. If evidence for the type of development of Indo-Pacific *Cerithium* species is limited to actual developmental studies and protoconch morphology (indicated by "x," Table 6), the developmental modes of only 17 species (40.5 percent) are known, and of these, 16 species (38.1 percent) are planktotrophic, while only one species (2.4 percent) is lecithotrophic. If the data are expanded by inference from geographic distributions (indicated by "*," Table 6), the developmental modes of 37 (88.1 percent) species can be categorized, of which 30 (71.4 percent) are planktotrophic, and seven (16.6 percent) lecithotrophic. Positive correlations exist between *Cerithium* species having planktotrophic larvae and wide geographic ranges, and those with direct development and restricted ranges, as examination of the distribution maps in this monograph will confirm.

DIVERSITY AND GEOGRAPHIC DISTRIBUTION.—*Cerithium* is the most specious genus in the Cerithiidae Férussac, 1819 (with the possible exception of *Bittium* Gray, 1847, for which there is no reliable data, as this group has never undergone a taxonomic revision). Table 7 summarizes the numbers of cerithiid taxa within geographical provinces. There are about 60 Recent *Cerithium* species in the world oceans. Not all geographic regions have been carefully studied, but as the two major biogeographic provinces are now well known (Houbrick 1974b, western Atlantic; Houbrick, this study, Indo-Pacific), and the eastern Pacific and Mediterranean *Cerithium* faunas reasonably understood, this estimate is fairly accurate. Of the total number of *Cerithium* species, 70 percent are Indo-Pacific species. Of the remainder, 15 percent comprise eastern Pacific species, 10 percent western Atlantic species, and 5 percent

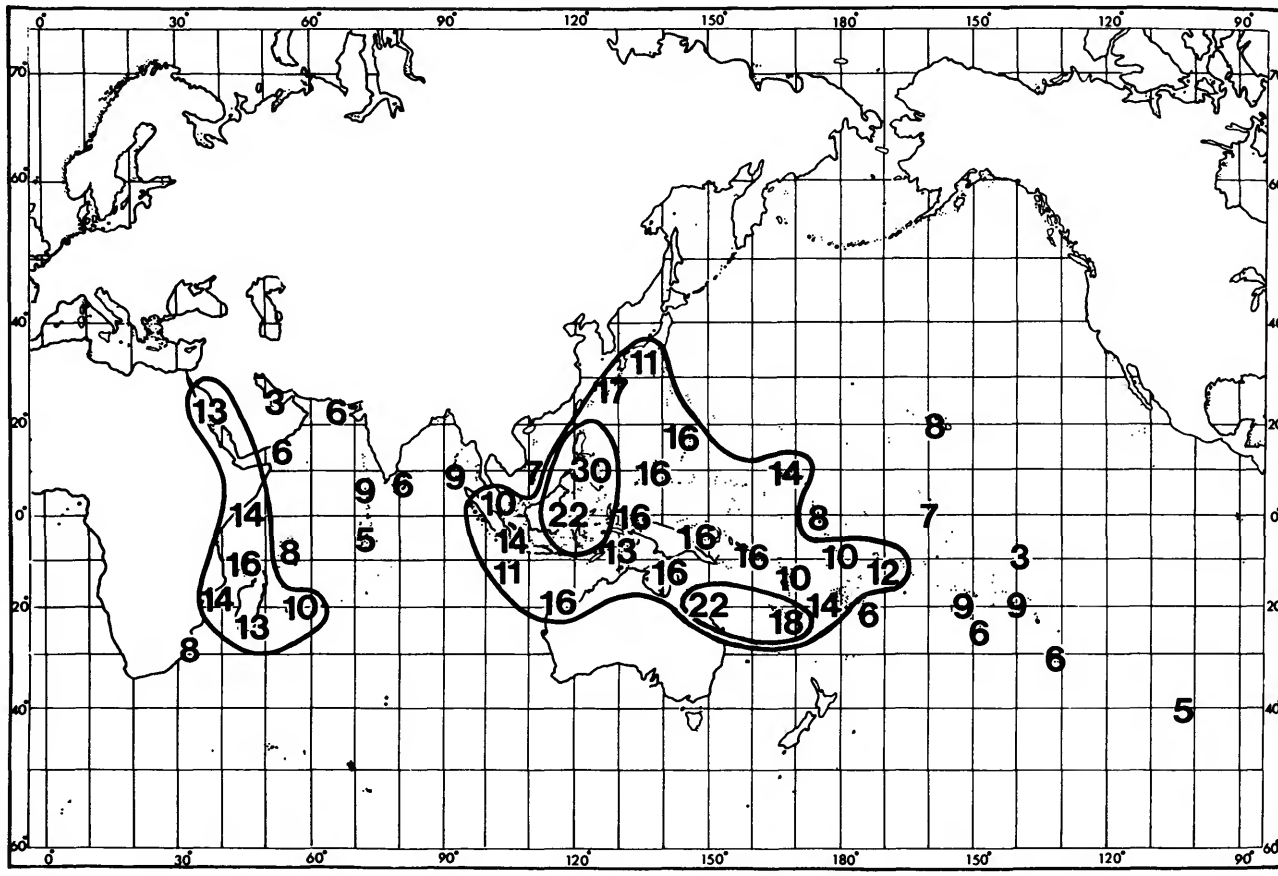


FIGURE 5.—*Cerithium* species-richness throughout the Indo-Pacific region, based on collection data (areas of highest species numbers encircled).

eastern Atlantic and Mediterranean species; thus, in comparison to other zoogeographic provinces, there is no question that *Cerithium* has undergone extensive speciation in the Indo-Pacific.

In the Indo-Pacific Province, the most widely distributed, shallow-water *Cerithium* species are *C. atromarginatum* (Figure 1O), *C. columna* (Figure 2G), *C. echinatum* (Figure 1B), *C. egenum* (Figure 1N), *C. nesioticum* (Figure 1L), *C. punctatum* (Figure 1M) and *C. rostratum* (Figure 2J). All of these species have many-whorled, highly sculptured protoconchs. *Cerithium interstriatum* (Figure 1K) also has a very wide, but disjunct, Indo-Pacific distribution. Shallow-water species with disjunct, moderately wide geographic ranges are *C. dialeucum* (Figure 2H), *C. lissum* (Figure 1Q), *C. munitum* (Figure 2C), and *C. salebrosum* (Figure 2A). *Cerithium madreporicolum* has a disjunct range within the Indian Ocean. Deeper water *Cerithium* species, such as *C. flemeschi* (Figure 1H) and *C. matukense* (Figure 1F), have wide, disjunct distributions between the Indian and Pacific Oceans, but as they are obtained only by dredging, the Indian Ocean distribution gap may be explained by poor sampling. The same is true for *C. gloriosum*, new species (Figure 1I), which also has a disjunct range in the Indian Ocean, and *C. abditum*, new species (Figure 1J), with a western Pacific disjunct range. *Cerithium ophioderma* (Figure 1G) is known only from a restricted range in deeper waters of the western Pacific. A number of species appear to be restricted to the shores of high islands and archipelagos of the Indo-West-Pacific. These include *Cerithium balteatum* (Figure 2E), *C. coralium* (Figure 1R), *C. lifuense* (Figure 2K), *C. phoxum* (Figure 1P), *C. scobiniforme* (Figure 2B) *C. tenellum* (Figure 2Q), *C. torresi* (Figure 2P), and *C. traillii* (Figure 2N). Two species, *C. claviforme* (Figure 1D) and *C. pacificum*, new species (Figure 1E), have narrow range extensions from the western Pacific archipelagos onto the Pacific plate. *Cerithium novaehollandiae* (Figure 2L) appears to be nearly endemic to Australasia. Two species endemic to the eastern South Pacific are *C. leptocharactum*, at Easter Id, and *C. rehderi* new species, in the Marquesas. Snails with the

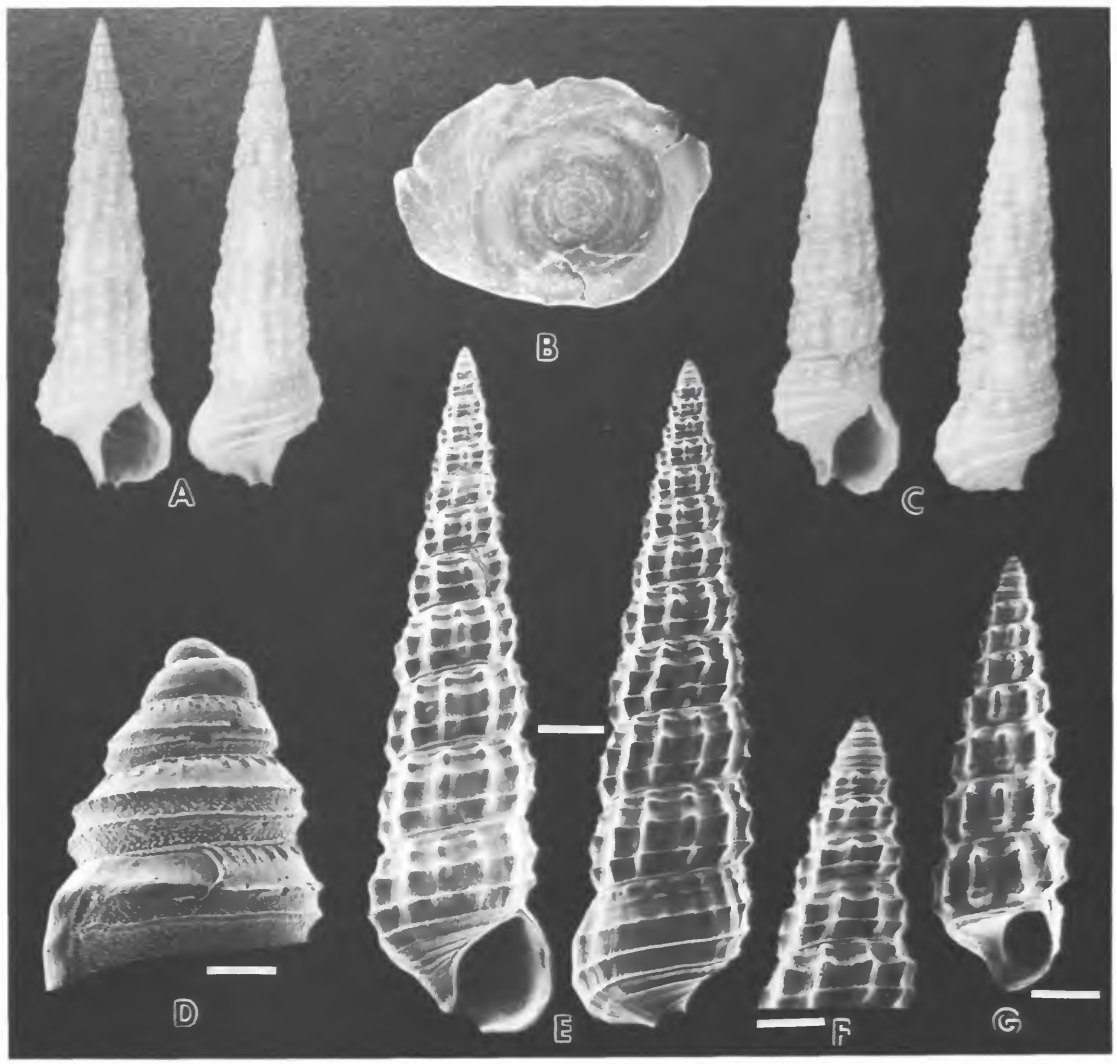


FIGURE 6.—*Cerithium abditum*, new species A, Holotype, 554 m, off Simaluc Id, Tawitawi, Philippines, 15 mm (USNM 286404); B, operculum, same data as A, 1.25 mm; C, same data as A, 14.1 mm; D, SEM of protoconch, SE Chanter Islets, Raoul Id, Kermadecs (bar = 0.68 mm; NMNZ MF25608); E, SEM, 208 m off Gigantangan Id, NW Leyte, Philippines (bar = 0.88 mm; USNM 287547); F, SEM of early whorls, same data as E (bar = 0.6 mm); G, 160 m off Arena Pt, Ragay Gulf, Leyte, Philippines (bar = 0.65 mm; USNM 284115).

most restricted ranges are *C. koperbergi*, which is endemic to a limited area in eastern Indonesia, and *C. crassilabrum*, endemic to southeastern Africa. Species with limited, eastern African ranges include *Cerithium africanum*, new species (Figure 2F), *C. ruppelli* (Figure 2D), *C. caeruleum* (Figure 1C), and *C. scabridum* (Figure 2M), the last two of which have planktonic larvae. *Cerithium scabridum* has passed through the Suez Canal, and is rapidly establishing itself in the Mediterranean Sea. No Indo-Pacific *Cerithium* species has been found in the Panamic (eastern Pacific) Province.

Species richness in various areas of the Indo-Pacific region is shown in Figure 5. The center of diversity is the Philippines followed by the Indonesian Archipelago, northeastern Australia, and the large, mountainous islands of Melanesia, such as New Guinea, the Solomons, New Caledonia, and Fiji. Other Pacific areas rich in species numbers are the Ryukyu Islands and the Marshall Islands. Some outlying, isolated island groups in the central and southern Pacific, such as Hawaii, the Pitcairn Islands, and Easter Island, have relatively high numbers of species. The western Indian Ocean is rich in species numbers,

especially around Madagascar, and even in the Red Sea, but unsuitable habitats and/or the discharge of fresh water from large rivers probably account for the poorer fauna of the northern shores of the Indian Ocean (Pakistan and India), and the depauperate Persian Gulf.

Species Treatment

Cerithium abditum, new species

FIGURES 6–8

DESCRIPTION.—*Shell* (Figure 6A,C–G): Shell small, thin, porcelanous, turreted, reaching nearly 15.4 mm length and 4.5 mm width, comprising 14 or 15 moderately inflated whorls. Protoconch (Figure 6D) brown, comprising 4.5–5 whorls and with deep sinusigeral notch. Protoconch I smooth; protoconch II sculptured with spiral, subsutural plications and two spiral bands, first of which slightly beaded. Minute pustules on base of last protoconch whorl (Figure 6D). Teleoconch sculptured with 3 beaded spiral cords; weakest cord subsutural; remaining 2 spiral cords becoming progressively stronger anteriorly. Spiral cords crossed by 12–14 axial ribs on penultimate whorl (Figure 6E,G). Axial sculpture dominant, with opisthocline ribs; beads aligned with ribs where crossing spiral cords. Beads sometimes slightly pointed and facing shell apex (Figure 6E,F). Early whorls (Figure 6F) with fewer ribs and spiral cords. Suture impressed, slightly wavy. Body whorl broad with large varix. Body whorl sculpture same as penultimate whorl, but with two smooth spiral cords and several thin, weak spiral cords on siphonal constriction. Varices randomly distributed; largest varix opposite outer lip of aperture. Aperture ovate, a little less than one-fourth the shell length. Columella concave and with very weak callus. Anterior canal moderately long, slightly reflected upwards and left of shell axis. Anal canal weak. Outer lip rounded, slightly crenulated or wavy. Measurements (Table 8). Periostracum thin. Operculum (Figure 6B) corneous, circular-ovate, paucispiral and with subcentral nucleus. Free surface of operculum covered with minute scales.

Radula (Figure 7): Type-4 radular ribbon (Figure 3D) very small, about one-tenth the shell length, comprising about 20 rows of teeth. Rachidian tooth (Figure 7B,D) rectangular having flat basal plate with slight ventral extension; cutting edge with pointed central cusp flanked on each side by two small denticles. Lateral tooth (Figure 7B) rhomboidal having short basal-lateral extension, weak inner buttress, and weak median, transverse peg on broad basal plate; cutting edge with single, pointed, inner denticle, large, pointed cusp, and 5 or 6 pointed, outer denticles. Marginal teeth (Figure 7C) long, spatulate, curved at distal ends, and with long, pointed tips flanked by thin, needle-like denticles. Tips of inner marginal tooth serrated with four, sharp, inner denticles and five, sharp, outer denticles. Outer marginal tooth same, but lacking outer denticles.

Anatomy: Soft parts unknown except for pair of tiny, thin, semilunar-shaped jaws with scale-like surface.

TABLE 8.—Shell morphometrics of *Cerithium abditum*.

Character	$\bar{x}$ (n = 10)	sd	v	Range
Shell length	12.5	2.0	4.2	9.3–15.4
Shell width	3.5	0.5	0.2	3–4.5
Aperture length	2.3	0.3	0.1	2–2.8
Number whorls	14.8	0.4	0.2	14–15
Number spiral cords	3	–	–	3
Number axial ribs	13.5	1.1	1.2	12–14

HOLOTYPE.—USNM 286404, 15 × 4.2 mm (Figure 101A).

PARATYPES (5).—USNM 860482.

TYPE-LOCALITY.—Off Simaluc Id, Tawitawi, Philippines, 554 m.

ETYMOLOGY.—From the Latin *abditus* (hidden, concealed).

ECOLOGY.—This species lives in deep water, to a depth of 987 m, on sand and rubble bottoms. The many whorled, sculptured protoconch (Figure 6D) indicates a planktotrophic larval stage in life history. It appears to be a common species, and has been dredged in large numbers at some stations.

DISCUSSION.—This species is characterized by small size, a porcelaineous, white shell with brown protoconch, and sculpture of dominant opisthocline axial ribs that form beads where they cross over 3 or 4 spiral cords. Shell sculpture varies in degree of bead size, cuestae definition, and number of spiral cords per whorl. In some specimens, spiral sculpture is nearly lost (Figure 6G). Larger, older specimens have four spiral cords on the adult whorls (Figure 6A,B). Older specimens also have a large varix opposite the outer lip of the aperture, and a wide body whorl, characteristic of other deep water cerithiids, such as *Cerithium gloriosum*, new species, *C. matukense*, and *C. ophioderma*.

I was originally puzzled by this species (Houbrick, 1980b:15–16), which has a protoconch (Figure 6D) similar to species of *Argyropeza* Melvill and Standen, 1901. The same kind of protoconch sculpture also occurs in some *Bittium* and *Cerithium* species (pers. obsr.); thus, as similar protoconch sculpture crosses major generic groups, it does not seem to be a good indicator of generic phylogeny, except in a very broad sense. A small, deep-water species, *Bittium porcellanum* Watson, 1886, hardly mentioned since its description, closely resembles *C. abditum*, new species. Watson (1886:559) remarked in the original description, "This is a very aberrant form of *Bittium*, both in color and in sculpture, but the form of the mouth unmistakably connects it with this genus." Examination of the lectotype and two paralectotypes (BMNH 1887291750-2) has shown that they are juveniles, lacking adult whorls, and the outer lip of the adult aperture. The juvenile shell and protoconch illustrated by Watson (1886, pl. 38: fig. 8) closely resemble the earlier whorls of *Cerithium abditum*, new species. Although the shell size of *"Bittium" porcellanum* is small, it is larger than the upper limits of length attained by most *Bittium* species, and the adult axial sculpture, moderately elongate, reflected, anterior canal, and crenulate outer lip are

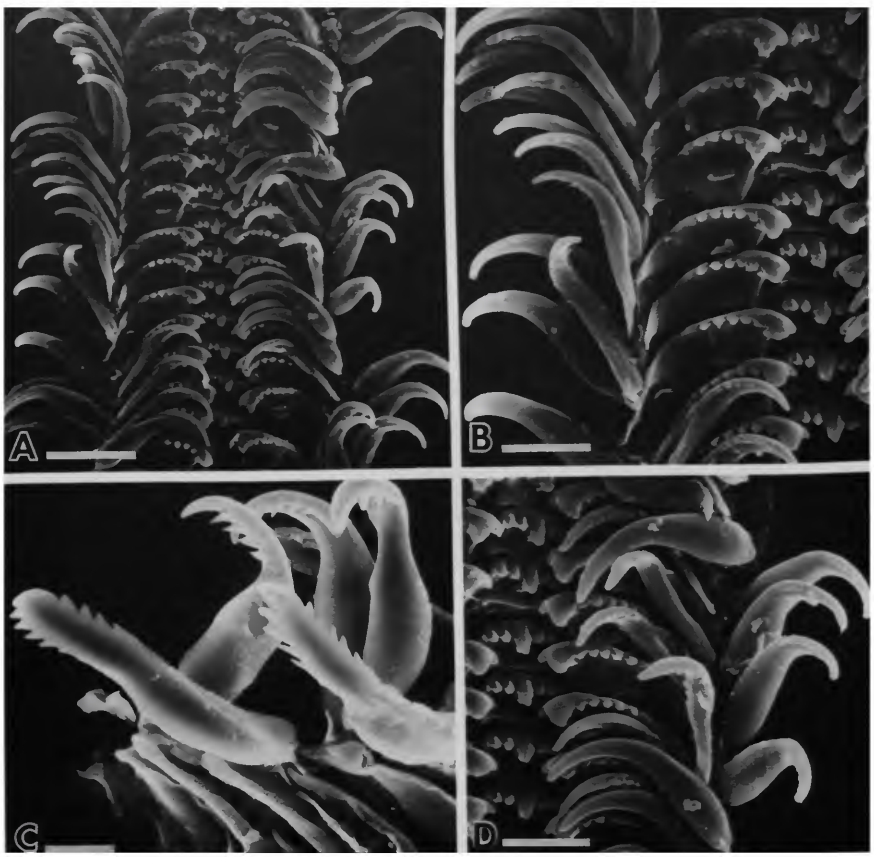


FIGURE 7.—Radula of *Cerithium abditum*, new species A, radula with marginals spread open, Gigantangan Id, NW Leyte, Philippines (bar = 70 μm; USNM 287547); B, half row, same data as A (bar = 30 μm); C, inner marginal teeth, Simaluc Id, Tawitawi, Philippines (bar = 12 μm; USNM 286404); D, half row showing marginal teeth (same data as C; bar = 30 μm).

characters not frequently seen in *Bittium* (Houbrick, 1977:103); consequently, it seems appropriate to assign this species to *Cerithium* Bruguière. When more comparative material is available, the two species may prove to be closely related or conspecific.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 8).—*Cerithium abditum*, new species, appears to be confined to the Indo-West Pacific, ranging from the Philippines south through New Caledonia to the Kermadec Islands. It occurs on fine grained sediments at an average depth of 384 m (n = 30; range = 88–987 m).

SPECIMENS EXAMINED.—CHINA: 255.9 m, USBF sta 5312, off Pratas Id, China (USNM 304102); 274.2 m, USBF sta 5313, off Pratas Id, China (USNM 787971). PHILIPPINES: 246.7 m, USBF sta 5110, SW of Corregidor, Luzon (USNM 294307); 192 m, Musortom, *Coriolis* sta DR102, 14°01′N, 120°18′E, off Luzon (MNHNP); 170–187 m, Musorstom, *Coriolis* sta CP51, 14°00′N, 120°17′E, off Luzon (MNHNP); 186.5 m, USBF sta 5278, off Malavatuan Id, W Luzon (USNM 258305, 775112); 191.9 m, USBF sta 5217, off N Burias, Ragay Group, Luzon (USNM 775055); 597.8 m, USBF sta 5385, off Arena Pt, Ragay Group, Luzon (USNM 285378); 233.9 m, USBF sta 5382, off Arena Pt, Ragay Group, Luzon (USNM 285327); 160.6 m, USBF sta 5381, off Arena Pt, Ragay Group, Luzon (USNM 284115); 197.4 m, USBF sta 5312, off Sibugay Id, E of Masbate (USNM 775124); 246.7 m, USBF sta 5392, off Adyagan Id, E Masbate (USNM 775117); 296.1 m, USBF sta 5412, off Lauis Pt, E Cebu (USNM 775121, 775122, 775125); 215.7 m, USBF sta 5391, off Destacado Id (USNM 774764); 208.4 m, USBF sta 5398, off Gigantangan Id, NW Leyte (USNM 287547); 522 m, *Siboga* sta 95, 50°43′5″N, 119°40′E, Sulu Sea (ZMA); 553.9 m, USBF sta 5569, off Simaluc Id, Tawitawi (USNM 286404, 787135); 444.2 m, USBF sta 5565, off Dammi Id, Sulu Archipelago (USNM 286538).

INDONESIA: 475.3 m, USBF sta 5589, off Mabul Id,

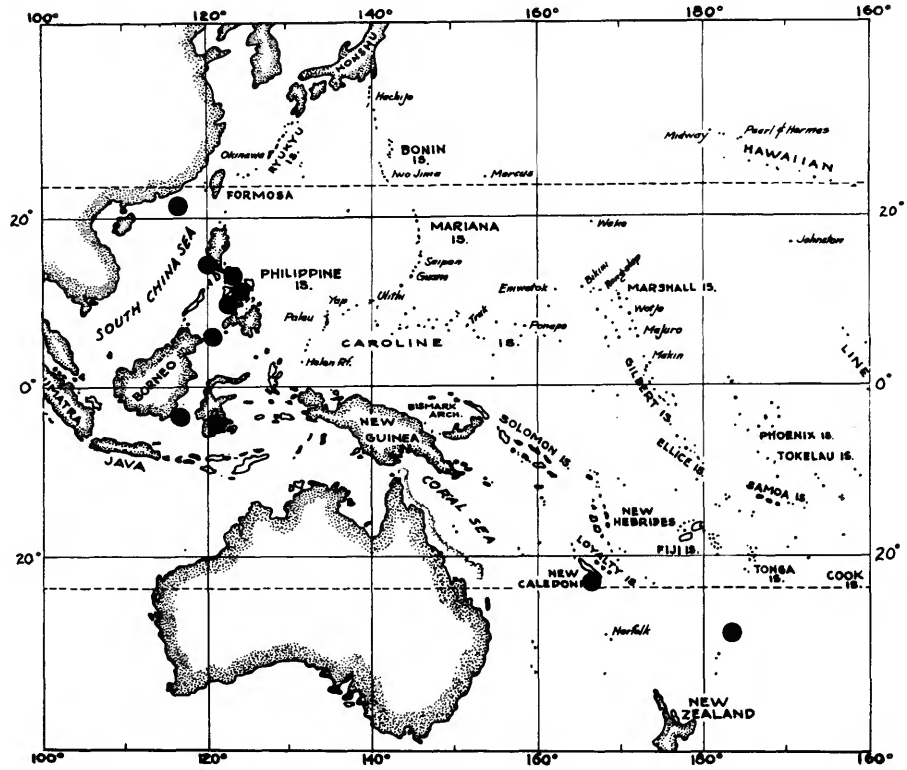


FIGURE 8.—Geographic distribution of *Cerithium abditum*, new species.

Sebuko Bay, Borneo (USNM 278808); 987 m, USBF sta 5650, off Lamulu Pt, Gulf of Boni, Celebes (USNM 280070). NEW CALEDONIA: 505–515 m, N.O. *Jean-Charcot*, sta DW66, 24°55′S, 168°22′E (MNHNP); 570–610 m, N.O. *Jean-Charcot*, sta DW46, 22°53′S, 167°17′E (MNHNP); 250 m, N.O. *Jean-Charcot*, sta DW64, 24°48′S, 168°09′E (MNHNP); 435 m, N.O. *Jean-Charcot*, sta DW08, 20°34′S, 166°54′E (MNHNP); 360 m, N.O. *Jean-Charcot*, sta DW38, 23°00′S, 167°15′E (MNHNP); 775 m, N.O. *Jean-Charcot*, sta DW18, 23°00′S, 167°29′E (MNHNP); 520 m, N.O. *Vauban*, sta DW1, 24°56′S, 168°22′E (MNHNP); 530–537 m, N.O. *Vauban*, sta DW2, 24°53′S, 168°22′E (MNHNP); 505 m, N.O. *Vauban*, sta DW6, 24°56′S, 168°21′E (MNHNP). KERMADEC ISLANDS: 512–549 m, RV *Archeron* sta BS442, 29°16.5′S, 177°49.5′W, SE of Chanter Islets, Raoul Id (NMNZ MF25608).

Cerithium africanum, new species

FIGURES 9–11

DESCRIPTION.—*Shell* (Figure 9): Shell turreted, reaching 22.9 mm in length, 10.1 mm in width, and comprising 11–13 straight-sided, anteriorly angulate, solid whorls sharply impressed beneath suture. Protoconch unknown. Early whorls cancellate with fine spiral cords and strong axial ribs. Adult whorls sculptured with 4 spiral cords, numerous fine spiral striae, and 10–15 axial ribs. Largest spiral cord abapical, spinose, with 11–14 pointed nodes; three, narrow, beaded, spiral cords above spinose cord. Sutural cords usually with more beads. Interspaces of main spiral cords with fine spiral striae. Spiny nodes on main spiral cord sometimes elongated into axial folds forming discontinuous ribs, weaker anteriorly. Suture deeply impressed, slightly wavy. Varices randomly distributed; largest varix opposite outer lip of aperture. Body whorl sculpture as in adult whorls, but with two large, closely spaced, smooth, occasionally beaded, spiral cords above siphonal constriction. Numerous fine spiral threads on siphonal constriction. Base of body whorl concave. Siphonal canal slightly reflexed, 45° to left of shell axis. Aperture ovate, about one-fourth shell length. Columella concave with narrow, distinct columellar callus and lip. Anterior canal elongate, tightly closed, reflexed to left of shell axis. Anal canal distinct, marked with parietal plate extending well into shell aperture. Outer lip thickened, convex, crenulate, with 7 paired, tiny, inner denticles, stronger in older specimens. Shell color white or dark brown, flecked with brown and tan, or with white spiral stripes of varying width. Shell measurements (Table 9). Operculum unknown.

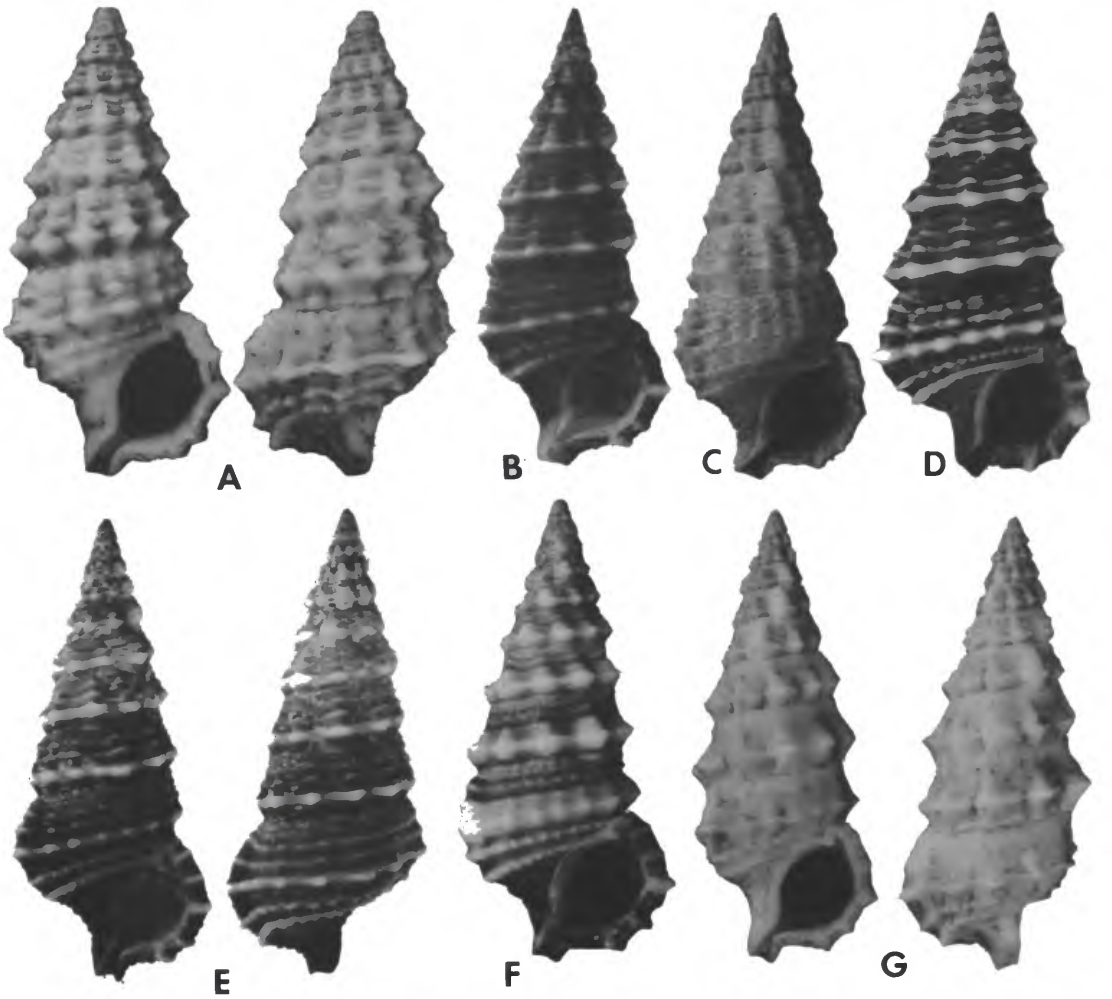


FIGURE 9.—*Cerithium africanum*, new species, showing morphological diversity: A, lightly pigmented specimen, apertural and abapertural views, Zanzibar, 17.3 mm (USNM 598452); B, S Nossi Bé, Madagascar, 16.7 mm (USNM 46039); C, Pte du Cratère, SW Nossi Bé, Madagascar, 16.4 mm (ANSP 258922); D, holotype, SW Conducia Bay, NW of Choca, Mozambique, 22.9 mm (NM H1861); E, paratype, apertural and abapertural views, Mozambique, 20 mm (USNM 629034); F, Nyange Id, W Zanzibar, 21.4 mm (ANSP 225485); G, lightly pigmented specimen, apertural and abapertural views, Nyange Id, W Zanzibar, 17 mm (ANSP 22548).

TABLE 9.—Shell morphometrics of *Cerithium africanum*.

Character	$\bar{x}$ (n = 18)	sd	v	Range
Shell length	18.3	3.5	12.5	7.9-22.9
Shell width	7.7	1.5	2.1	3.8-10.1
Aperture length	4.5	1.1	0.9	2-5.8
Aperture width	3.5	0.7	0.5	1.7-4.6
Number whorls	11.8	0.6	0.4	11-13
Number spiral cords	4	-	-	4
Number axial ribs	12.2	1.3	1.8	10-15

Radula (Figure 10): Type-1 radular ribbon a little more than one-eighth the shell length, comprising about 66 rows of teeth. Rachidian tooth (Figure 10B) rectangular, with slightly concave anterior front. Basal plate with slight median, posterior extension and pair of crescentic ridges. Cutting edge with large, central, pointed cusp flanked on each side by two small denticles. Rhomboidal lateral tooth (Figure 10B) with broad basal plate, long lateral-posterior projection, and large central ridge projecting posteriorly and bearing blunt denticle. Cutting

FIGURE 10.—Radula of *Cerithium africanum*, new species, from Mazizini, W Zanzibar (ANSP 214726): A, radular ribbon with marginal teeth spread open (bar = 83 μm); B, detail of rachidian and lateral teeth (bar = 40 μm).

edge with large, broad, pointed main cusp, one inner flanking denticle, and three outer flanking denticles. Small flange on anterior outer margin of lateral tooth. Marginal teeth (Figure 10A,B) with long stalks, rounded bases, and curved tips with spoon-shaped main cusps flanked with sharp denticles. Inner marginal tooth with two inner flanking denticles and one outer flanking denticle (Figure 10B). Outer marginal tooth same but without outer flanking denticles.

Anatomy: Unknown.

HOLOTYPE.—NM H1861, 22.9 × 10 mm (Figure 9D).

PARATYPES (5).—USNM 629034 (Figure 9E).

TYPE LOCALITY.—SW Conducia Bay, NW of Choca, Mozambique; in muddy sand near rocks, intertidal.

ETYMOLOGY.—This species, endemic to eastern Africa, is named after that continent.

REMARKS.—Despite the plethora of available names for *Cerithium* species, none of them appear to apply to this species. I therefore propose the name *africanum*, in reference to its restricted distribution to the eastern Africa coasts of the Indian

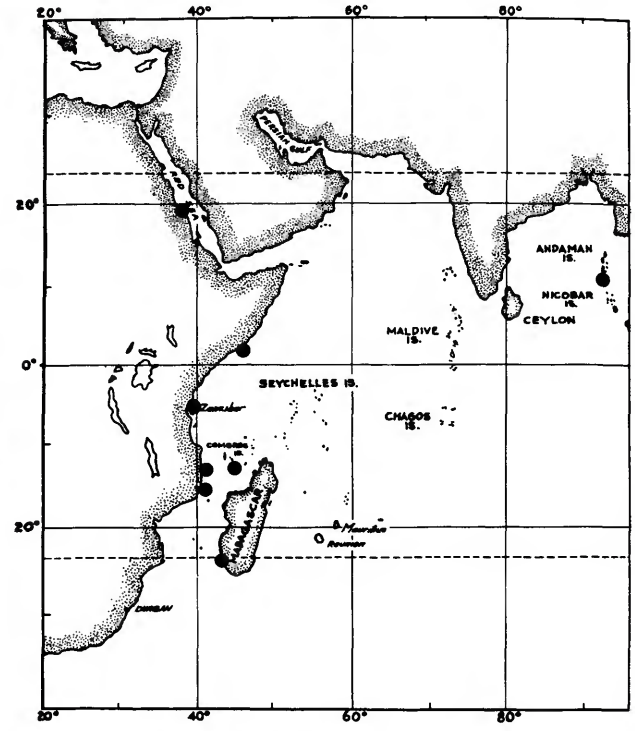


FIGURE 11.—Geographical distribution of *Cerithium africanum*, new species.

Ocean. *Cerithium africanum*, new species, has been incorrectly labeled *C. dialeucum* Philippi, 1849 (a synonym of *C. suturale* Philippi, 1849) in some museums.

ECOLOGY.—Museum records indicate that this species occurs at depths of 1–16 m on sandy, shelly, rubble bottoms associated with sea grasses or marine algae.

DISCUSSION.—The shell of *Cerithium africanum*, new species, is distinguished by its fir tree outline, and by a prominent presutural, spiny, spiral cord and a broad subsutural, nearly convex, ramp on each whorl. *Cerithium africanum* displays considerable sculptural variation, such as the absence or presence of spiral cords on the whorls, and in the relative development of axial ribs. Strong cancellate sculpture is present on the penultimate and body whorls of some specimens (Figure 9A–D), whereas in others it is very weak or lacking (Figure 9F,G). Shell color may vary from nearly white individuals (Figure 9A,G) to darkly pigmented, striped specimens (Figure 9B,D–F). *Cerithium africanum*, does not appear to be a common species or to occur in large populations, as it is not well represented in museum collections.

FOSSIL RECORDS.—None known.

GEOGRAPHIC DISTRIBUTION (Figure 11).—*Cerithium africanum*, new species, appears to be endemic to eastern Africa, Madagascar, and a few offshore island groups associated with the continent.

SPECIMENS EXAMINED.—EAST AFRICA: Mozambique

City, Mozambique (ANSP); NW of Choca, SW Conducia Bay, Mozambique (NM H1861); Port Amelia, Mozambique (NM G3415, USNM 598452, 629034, 629035); Zanzibar (USNM 598452); 3.2 km W of Nyange Id, W Zanzibar (ANSP 226485); N side, Pwakuu Id, W Zanzibar (ANSP 226473); 1.6 km WNW Ras Mbweni, W Zanzibar (ANSP 141230, 226418); Mazizini, W Zanzibar (ANSP 214726, 214740); Mogadiscio, Somalia (ANSP); Port Sudan (ZMA). MADAGASCAR: Nossi Bé (USNM 719579, 719704); 3 m, N of Nossi Iranja, SW Nossi Bé (ANSP); Pt Fièvre, Nossi Bé (USNM 719781); E of Pt Mahatsingo, S Nossi Bé (DMNH 46039); inside crater, Pte du Cratère, SW Nossi Bé (ANSP 258922); 3.2 km WNW of Ankifi, 11.2 km S of Nossi Bé (ANSP 261202); between Ambatalooka and Madirokely, SW Nossi Bé (MCZ 264743); Befotoka, NW Nossi Bé (ANSP); Andilana and Nossi Autsaibory, NW Nossi Bé (ANSP); E Bay, between Nossi Ambariotelo and SE Nossi Bé (ANSP); 18 m, Grand Récif, Tulear (MNHNP); Grand Récif, lagoon Grande Vasque, Tulear (MNHNP); stations 255t, 256t, 761t, 1346t, Beloza Reef, Tulear (MNHNP); station 264, Sangoritelo Reef, Tulear (MNHNP). INDIAN OCEAN ISLANDS: 15 m, Benthedi S18, S Îlot Gome Doume, Mayotte, Comoro Islands (MNHNP); Port Blair, Andaman Islands (BMNH).

Cerithium alexandri Tomlin, 1923

FIGURE 12

Cerithium alexandri Tomlin, 1923:48, 52, fig. 1 [lectotype herein selected: BMNH 192310263; type locality: Scottburgh, Natal, 32.3 mm × 10.4 mm].—Barnard, 1963:133–134, fig. 26a.—Kensley, 1973:79, fig. 264.

DESCRIPTION.—*Shell* (Figure 12): Shell tall, large, reaching 37.5 mm length, 11.6 mm width, and comprising 14 or 15 moderately inflated, occasionally medially concave, solid whorls. Protoconch unknown. Early whorls with strong spiral striae and axial ribs. Teleoconch whorls sculptured with fine spiral striae crossed by broad, rounded, sinuous, colabral, pre-and postsuturally strongly plicate axial ribs. Suture lightly impressed, distinct, markedly wavy. Body whorl wide, with thick, varix-like axial rib opposite outer lip of aperture. Body whorl weakly sculptured except for postsutural axial plicae and many fine spiral striae; base of body whorl somewhat flattened, sculptured with many fine spiral striae. Aperture ovate-circular, a little over one-fourth the shell length. Columella concave, without callus. Anterior canal moderately short, tightly closed, reflected to left of shell axis. Anal canal deep, well developed, defined by prominent parietal plait extending well within aperture. Outer lip convex, smooth, slightly pendant anteriorly, somewhat thickened posteriorly, with internal thickening opposite parietal plait. Shell color white with numerous, orange-brown, narrow, continuous, spiral bands or spiral rows of squarish dots. Bands and dots sometimes lacking or replaced by brownish axial flammules. Periostracum, operculum unknown.

FIGURE 12.—*Cerithium alexandri* Tomlin, apertural and abapertural views of lectotype from Scottburgh, Natal, South Africa, 32.3 mm (BMNH 192310263).

Radula: Unknown.

Anatomy: Unknown.

REMARKS.—This is one of the rarest *Cerithium* species, and has been virtually ignored in the literature. Few museums have examples, and most extant specimens have been taken from fish stomachs and are badly eroded or damaged. The paratype and paralectotypes are badly worn specimens. The available, limited material indicates high interspecific variation in shell form and sculpture. The figure of *C. alexandri* given by Barnard (1963, fig. 26a) differs somewhat from the lectotype (Figure 9). Barnard (1963:133) pointed out that the type material differed greatly from specimens dredged by the *Pieter Faure* off Cape Morgan and called attention to a "pseudosuture," caused by a slight concavity in the center of each whorl. I find no difficulty in separating the so-called "pseudosuture" from the true suture, which is clearly visible in all specimens examined.

Despite the variability of this rare species, it is not likely to be confused with any other congener. Its limited restriction to South Africa, the large shell size, flattened base, and unique color pattern clearly distinguish it. *Cerithium alexandri* resembles some *Rhinoclavis* species in outward configuration, but lacks the median columellar plait distinctive to that genus. The ontogeny of the early whorls is unknown due to severe erosion of all examined specimens, but when fresh, live-collected material is available, this species may prove to be a

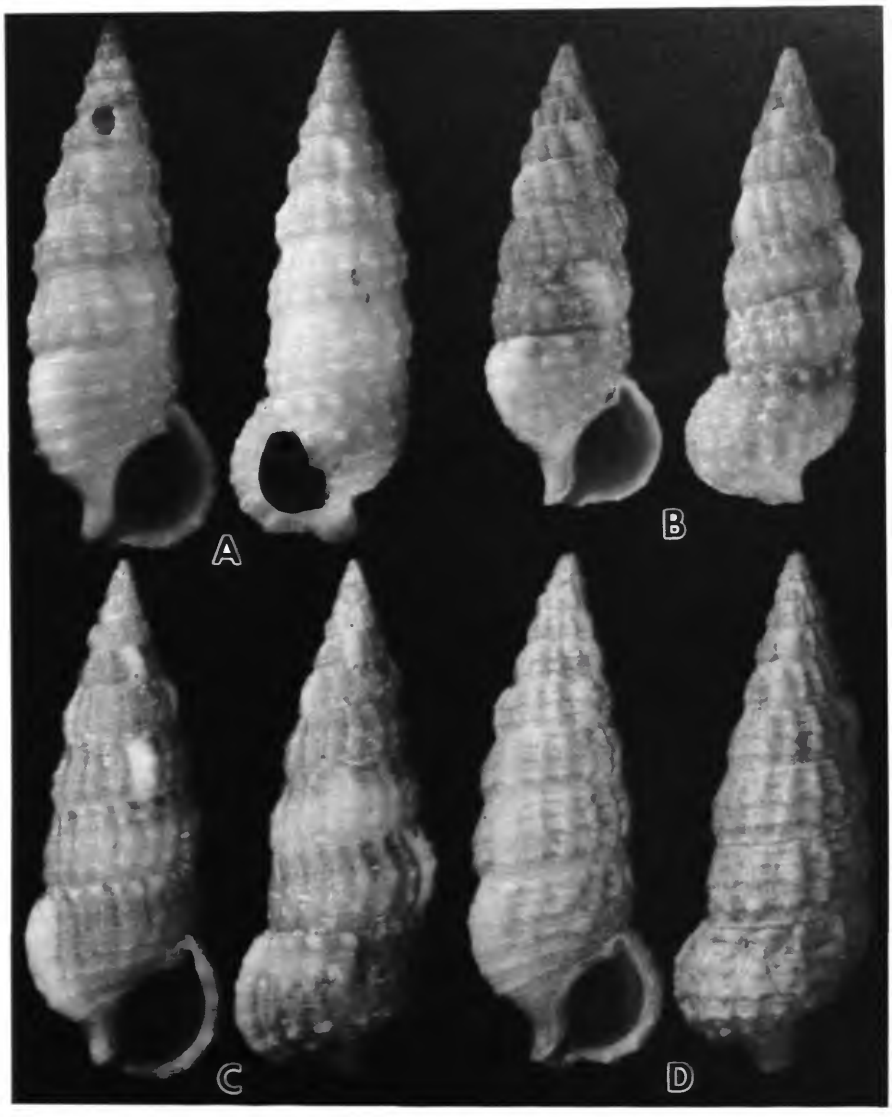


FIGURE 13.—*Cerithium amirantium* A. Smith, showing apertual and abapertural views: A, lectotype, Amirantes Ids, 14 mm (BMNH 1882126221); B, Amirantes Ids, 14.4 mm (BMNH 1910831206); C, Seychelles, 13.6 mm (MNHNP); D, Seychelles, 12.2 mm (MNHNP).

member of the genus *Pseudovertagus* Vignal.

Little is known of the habitat of this species. Both the examined material and literature indicate a subtidal, deep-water habitat. All known specimens have come from fish stomachs or have been dredged at depths of 62–82 m.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION.—Endemic to the eastern coast of South Africa.

SPECIMENS EXAMINED.—EAST AFRICA: Palm Beach, S coast of Natal, South Africa (NM 6669); Scottburgh, Natal, South Africa (BMNH 1923102263, lectotype); *ex pisce*, off Durban, Natal, South Africa (NM B502).

LITERATURE CITATIONS.—RV *Pieter Faure*, 81 m, off Cape Morgan; RV *Pieter Faure*, 77.4 m, off Rame Head, S of Port St Johns (both SAM, Barnard, 1963:133).

Cerithium amirantium E.A. Smith, 1884

FIGURE 13

Cerithium amirantium E.A. Smith, 1884:501, pl. 44: fig. R [lectotype, herein selected: BMNH 1882126221; type locality: Darros Id, Amirantes, Seychelles, 4 m; 14 × 4.4 mm].

DESCRIPTION.—*Shell* (Figure 13): Shell small, turreted,

TABLE 10.—Shell morphometrics of *Cerithium amirantium*.

Character	$\bar{x}$ (n = 3)	sd	v	Range
Shell length	12.7	0.9	0.8	12.2–13.7
Shell width	4.6	0.3	0.1	4.3–4.9
Aperture length	3.3	0.3	0.1	3–3.5
Aperture width	2.5	0.5	0.2	2.1–3
Number whorls	11.66	0.6	0.3	11–12
Number cords	4.0	–	–	4.0
Number ribs	17	2.6	7.0	15–20

reaching 13.7 mm in length, and comprising about 12 inflated, somewhat angulate whorls. Protoconch unknown. Early whorls with 3 spiral cords and strong axial ribs. Teleoconch whorls each with strong varix; largest varix on body whorl opposite outer lip of aperture. Posterior of each whorl broadly beveled at suture, especially on early whorls. Teleoconch whorls sculptured with 4 major beaded, spiral cords and 5 thin spiral lirae. Anterior 2 spiral cords dominant, but subsutural cord sometimes well developed. Fifteen to 20 axial ribs present on each whorl, most prominent on middle whorls. Spiral cords form beads at intersections with axial ribs. Body whorl sculptured with six major spiral cords and many fine spiral lirae. Subsutural cord and two cords adjacent to siphonal constriction well developed and with prominent beads. Base of body whorl concave, sculptured with fine spiral lirae. Aperture ovate, a little less than one-fourth the shell length. Columella concave. Siphonal canal short, slightly turned to left, about 45° to shell axis. Shell somewhat vitreous, pink to white with white varices and subsutural band or dots of light brown. Columella light purple. Measurements (Table 10). Operculum unknown.

Radula: Unknown.

Anatomy: Unknown.

REMARKS.—This species has not received any attention since its description. Several specimens recently dredged near the Seychelles (Figure 13B-D) appear to be conspecific with the lectotype of *C. amirantium* from the Amirantes (Figure 13A). While there are some minor sculptural differences between the lectotype and the other specimens, the overall shell morphology, sculpture, and color are congruent with the type material. Sculptural variability in development of the axial ribs among three specimens from the Seychelles (Figure 13B-D) shows the phenotypic variation common to most *Cerithium* species. The rediscovery of *C. amirantium* at a depth of 35 m is comparable with the bathymetric data cited by E.A. Smith (1884:501) for *C. amirantium* in the original description.

Cerithium amirantium is not easily mistaken for other species with the exception of *C. tenellum* Sowerby, with which it is allopatric. The latter species differs only in its larger size and slightly different sculpture. When more comparative material is available, *C. amirantium* may prove to be an Indian Ocean phenotype of *C. tenellum*.

It would appear that *C. amirantium* is uncommon, at least in shallow water, but it is probably not uncommon on calcareous substrates from moderate depths associated with reefs and islands in the western Indian Ocean.

FOSSIL RECORDS.—Unknown as a fossil in the literature.

GEOGRAPHIC DISTRIBUTION.—Present records indicate this species is endemic to the Amirantes, Seychelles, and Mauritius islands.

SPECIMENS EXAMINED.—INDIAN OCEAN ISLANDS: 500–600 m, 11°28′5″S, 47°12′5″E, Benthedi sta DR-6, Îles Glorieuses (MNHNP); 440 m, 11°28′5″S, 47°17′7″E, Benthedi sta DS-10, W of Îles Glorieuses (MNHNP); 21°21′S, 65°52′E, Rodriguez Id, off Mauritius (USNM 716636).

Cerithium atromarginatum Dautzenberg and Bouge, 1933

FIGURES 14–16

Cerithium maculosum Mighels, 1845:22 [type not found; type locality: Oahu; not *Cerithium maculosum* Kiener, 1841].—Sowerby, 1865, pl. 14: fig. 97.—Tryon, 1887:137, pl. 26: figs. 75, 76.—Kobelt, 1898:216, pl. 38: figs. 10, 11.

Cerithium nassoides Sowerby, 1855:875, pl. 183: figs. 200, 201 [lectotype, largest of 2 syntypes herein selected: BMNH 1964411; type locality: Sandwich Islands; 14.4 mm × 6.7 mm; not *Cerithium nassoides* Grateloupe, 1832]; 1865, pl. 12: fig. 83.—Tryon, 1887:137, pl. 26: fig. 76.—Kobelt, 1898:216, pl. 38: figs. 10, 11.—Couturier, 1907:155.

Cerithium nassoide var. *minor* Couturier, 1907:155 [holotype: MNHNP, no number; type locality: Rikitea; Makapon; not *C. minor* C. Moore, 1866].

Cerithium atromarginatum Dautzenberg and Bouge (ex Vignal), 1933:304–305 [new name for *C. maculosum* Mighels, 1845, and *C. nassoides* Sowerby, 1855, both preoccupied].—Lamy, 1938:137.—Steele, 1957:112.—Tinker, 1958:36, figs.—Kay, 1979:121, fig. 45F.

Cerithium (Conocerithium) atromarginatum Dautzenberg and Bouge.—Maes, 1967:113, pl. 6: fig. L.

Cerithium bavayi Vignal.—Cernohorsky, 1972:69, pl. 15: fig. 9 [in part, left-hand figure only].

Cerithium (Conocerithium) aff. *C. egenum* Gould.—Ladd, 1972:40, pl. 9: fig. 11.

Cerithium (Thericium) atromarginatum Dautzenberg and Bouge.—Rehder, 1980:36–37.

DESCRIPTION.—*Shell* (Figure 14): Shell small, stocky, conical-acute, with broad base, reaching 15.5 mm length, 6 mm width, and comprising 8–10 inflated, angulately nodose whorls. Protoconch I (Figure 14I) smooth, 1.5 whorls; protoconch II (Figure 14I) 3.5 whorls, sculptured with two spiral cords and subsutural plications. Microscopic, prosocline axial striae between spiral cords, becoming opisthocline presuturally. Early teleoconch whorls sculptured with fine spiral striae (Figure 14F). Teleoconch whorls weakly sculptured with 11–13 smooth, crowded, spiral cords; sometimes without sculpture. Dominant spiral cord in middle of each whorl. Spiral cords crossed with many subsutural axial plaits and by broad axial ribs extending anteriorly from mid-whorl. Body whorl large, broad, sculptured similar to other teleoconch whorls, but having numerous, fine spiral striae and a few spiral cords on shell base. Base of body whorl slightly constricted at anterior siphon. Varix opposite outer lip of aperture. Aperture

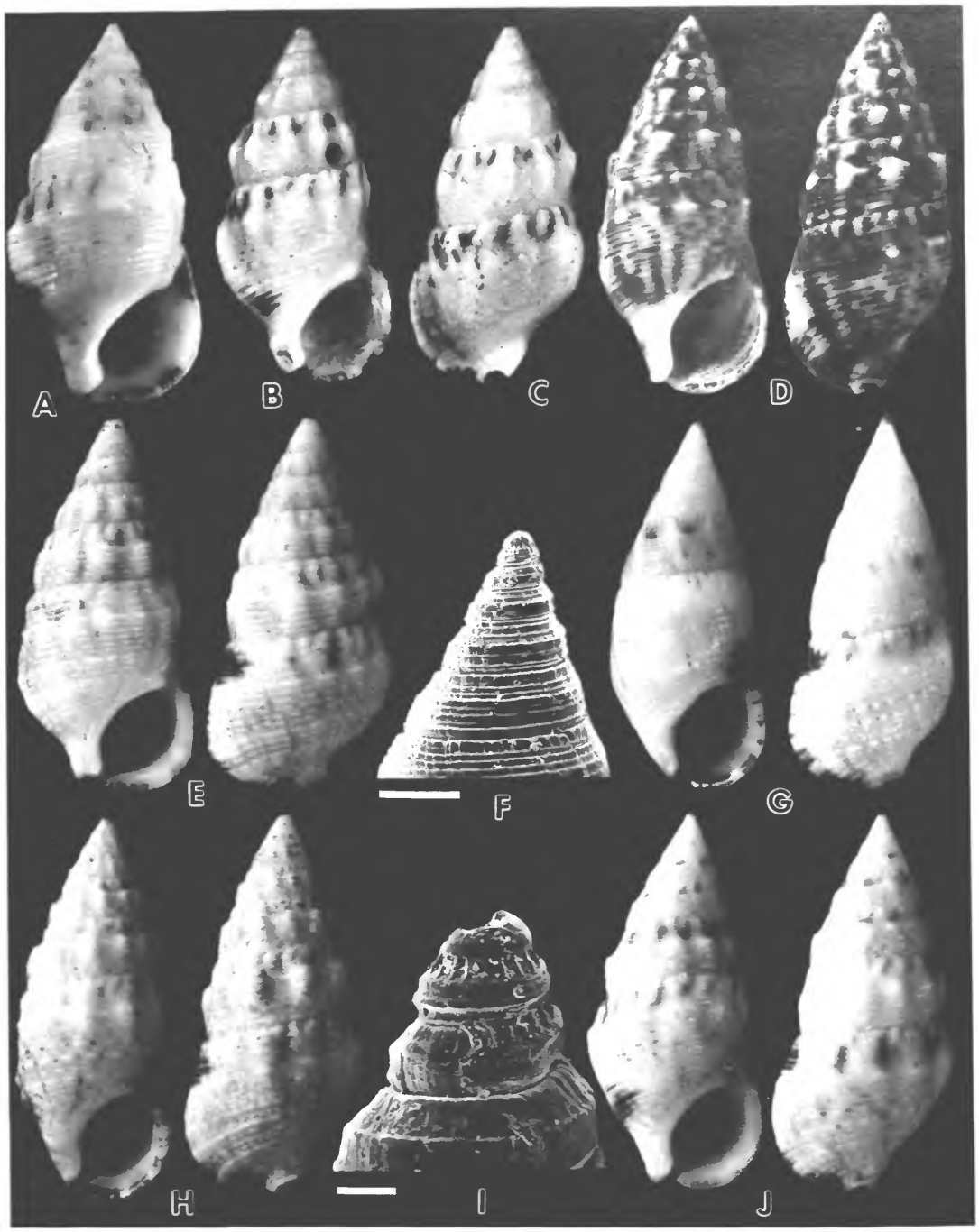


FIGURE 14.—*Cerithium atromarginatum* Dautzenberg and Bouge, figuring type specimens of synonymous taxa and showing morphological variability: A, Enewetak Atoll, Marshall Ids, (USNM 543357); B, holotype of *Cerithium bavayi* Vignal, 9.7 mm (MNHNP); C, lectotype of *Cerithium nassoides* Sowerby, Sandwich Ids, 14.4 mm (BMNH 1964411); D, apertural and abapertural views, Tahiti, 10.9 mm (USNM 791370); E, apertural and abapertural views, Mombassa, Kenya, 15 mm (USNM 595102); F, detail of early whorl sculpture, Rongelap Atoll, Marshall Ids (bar = 0.5 mm; USNM 582416); G, apertural and abapertural views, Rongerik Atoll, Marshall Ids, 11 mm (USNM 586327); H, apertural and abapertural views, Lifu, Loyalty Ids, 12.9 mm (USNM 423323); I, detail of protoconch, Rongerik Atoll, Marshall Ids, SEM (bar = 100 μm; USNM 582416); J, Rongerik Atoll, Marshall Ids, 12.6 mm (USNM 586327).

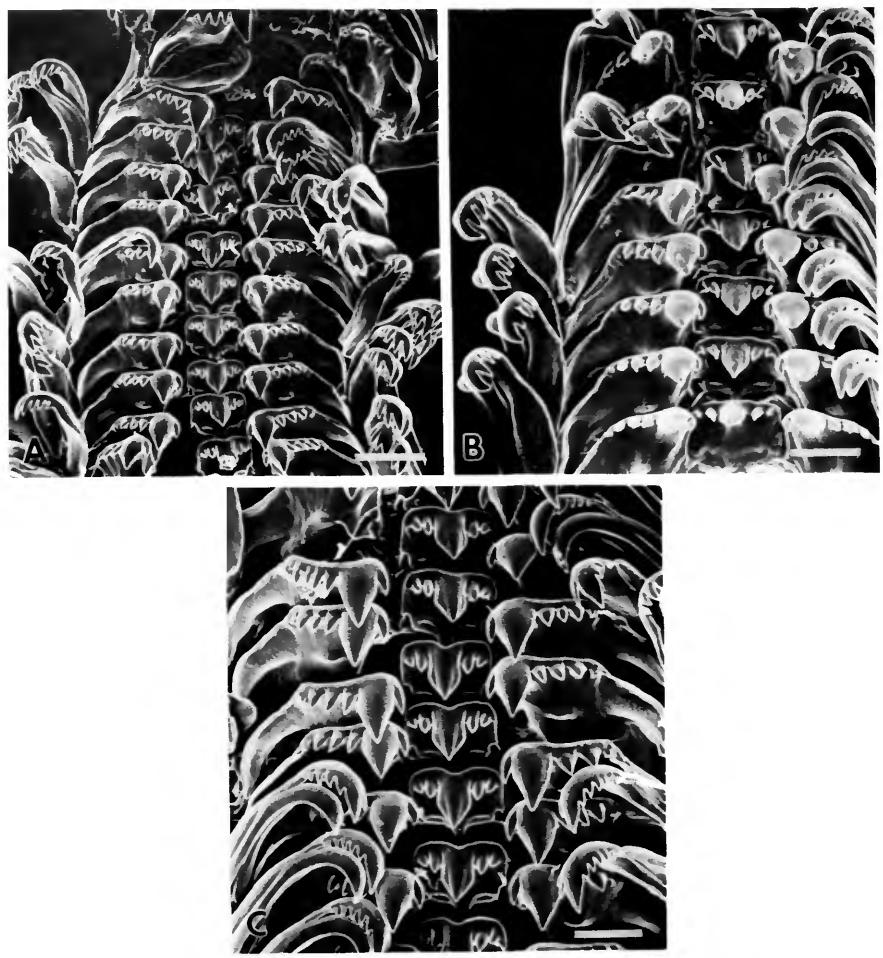


FIGURE 15.—Radula of *Cerithium atromarginatum:* A, radula with marginal teeth folded back (bar = 60 μm); B, half row (bar = 38 μm); C, detail of rachidian and lateral teeth (bar = 38 μm).

TABLE 11.—Shell morphometrics of *Cerithium atromarginatum.*

Character	$\bar{x}$ (n = 15)	sd	v	Range
Shell length	10.7	2.5	6.2	7.1–15.5
Shell width	4.8	1.2	1.4	2.2–6.0
Aperture length	3.5	1.1	1.2	2.2–6.0
Aperture width	2.5	0.6	0.4	1.8–3.6
Number whorls	8.9	0.8	0.6	8–10

ovate, large, a little more than one-third the shell length. Columella concave with slight callus. Anterior canal short, well defined. Anal canal defined by parietal columellar plait extending well into shell aperture. Outer lip convex, smooth, slightly thickened at edge and with very small denticles at interior edge. Shell color white with variable brown spots, dots and blotches. Large, reddish brown blotch at posterior end of outer lip; anterior part of outer lip frequently reddish brown. Brown axial flammules or blotches consistently between subsutural plaits and small spiral dots or dashes occasionally on spiral cords. Some shells nearly melanistic (Figure 14D). Measurements (Table 11). Periostracum thin, tan. Operculum corneous, thin, light tan, nearly transparent, paucispiral, with eccentric nucleus.

Radula (Figure 15): Type-1 radular ribbon (Figure 3A). Rachidian tooth (Figure 15B,C) squarish, anteriorly convex, with slight concave central depression. Basal plate with basal-lateral, lunule-shaped ridge on each side and with central, posterior extension. Cutting edge with spade-shaped main cusp flanked on each side with two small denticles. Lateral tooth (Figure 15B,C) trapezoid, having basal plate with large, posteriorly extending central ridge, notched inner edge, and long, lateral, posterior extension. Central ridge bears small, blunt denticle. Cutting edge of lateral tooth with long, pointed main cusp, single inner flanking denticle, and 3 or 4 outer, flanking denticles. Marginal teeth (Figure 15B,C) with long,

thin shafts, broad, spatulate bases, and curved apices with long, pointed main cusps at tips. Inner marginal tooth with three inner pointed, flanking denticles and three outer-flanking denticles. Outer marginal tooth same, but without outer flanking denticles.

Anatomy: Animal flesh color, flecked with yellow, white, and tan. Sides of foot, head, snout, and tentacles pink; very small red dots on snout and tentacle tips. Anterior sole with deep propodial groove. Females with wide, ciliated groove emerging from distal pallial oviduct and terminating in lateral glandular pit (ovipositor) on right side of foot. Snout highly extensible. Dorsal and lateral mantle edge with white papillae, mantle roof green.

Type-A pallial oviduct configuration (Figure 4A). Albumen gland thick, white; distal, white capsule gland. Sperm gutter with large opening in anterior medial lamina, becoming narrow tube in medial lamina edge, enlarging posteriorly to form large, spermatophore bursa. Small, lobate seminal receptacle in outer wall of proximal medial lamina adjacent to spermatophore bursa. No connection between bursa and seminal receptacle observed. Seminal receptacle of medial lamina directly across from seminal receptacle of lateral lamina. Lateral lamina of pallial oviduct thin, with distal opening into long, thin tube leading to proximal seminal receptacle.

Pair of small, glandular salivary glands lying behind nerve ring, each becoming simple tube passing through nerve ring and opening into dorsal-lateral buccal cavity.

SYNONYMIC REMARKS.—This species has been known as *Cerithium atromarginatum* in the current literature. The name *atromarginatum* Dautzenberg and Bouge, 1933, was proposed as a replacement name for *C. maculosum* Mighels, 1845, and *C. nassoides* Sowerby, 1855, both preoccupied taxa. An earlier name, *C. minor* Couturier, 1907, heretofore unnoticed in the literature, but also preoccupied, was proposed as a varietal name for *C. nassiodes* Sowerby. Cernohorsky (1972:69) considered *C. atromarginatum* (cited as *C. bavayi*) and *C. egenum* to be conspecific; thus, only the left hand figure (pl. 15: fig. 9) is *C. atromarginatum*. The fossil shell identified and figured by Ladd (1972:30, pl. 9: fig. 11) as *C.* aff. *egenum* is clearly *C. atromarginatum*.

ECOLOGY.—*Cerithium atromarginatum* occurs in intertidal, seaward, high energy habitats. In Hawaii, it lives on red algae or is buried in sand patches under rubble in tide pools and sandy algal mats on solution benches (Kay, 1979:121). This species was a common element of the seaward reef platform at Fanning Island, Line Islands (Kay, 1971:264). Rehder (1980:37) found it in similar habitats on Easter Island. At Pago Bay, Guam, I collected this species on the mid-tidal algal turf on a raised reef flat. I observed a large population living just below the high tide mark, on a seaward solution bench at Shark's Cove near Pupukea, Oahu, Hawaii. The species was common around the mat-like sandy roots of brown algae and in sandy interstices of the rocky substrate. In this high-energy environment, snails emerged on a rising tide and crawled about on the substrate and algal branches. This population lived in microsympatry with the equally abundant *C. egenum* Gould, which moved about more rapidly than *C. atromarginatum*.

Taylor (1984:283) wrote that *C. atromarginatum* is preyed upon by the thaidids, *Muricodrupa funiculus, Morula nodicostata, Morula uva,* and *Chronia fiscella* at Pago Bay, Guam. *Cerithium atromarginatum* is the main prey of *Muricodrupa funiculus* in the Sudanese Red Sea (Taylor and Reid, 1984:191). *Cerithium atromarginatum* has planktotrophic larvae as can be seen in SEM micrographs (Figure 14F,I), which clearly show the sinusigeral notch. Taylor (1975:98) found veligers of this species in the plankton of Kaneohe Bay, Oahu, Hawaii, from May through August and noted that veligers settled readily in seawater tables and grew rapidly. Ripe gonads were present in females I dissected in June. Metamorphosis occurs when the larval shell attains a length of 325 μm and 3 to 3.5 whorls are complete (Taylor, 1975:98; Kay, 1979:121).

DISCUSSION.—This small species is readily identified by its stout shape, sculpture of subsutural axial plaits, numerous, smooth spiral lirae, and central row of nodules on each whorl. The whitish yellow shell color, reddish brown spot at the upper edge of the outer lip, small, subsutural brown spots, and occasional weak axial maculations on the body whorl are all distinctive.

Cerithium atromarginatum may be confused with *C. egenum* Gould, with which it is geographically and ecologically sympatric. The latter species, however, is smaller, more slender, and lacks the subsutural plaits. Moreover, the spiral lirae of *C. egenum* are more granulose, no spot occurs on the posterior end of the outer lip, and a distinctive row of axial flammules is present on the base of the body whorl.

Variation in sculpture and color are common in this species. Some phenotypes are very nodulose (Figure 14D,E,H) while others are smooth, lacking all trace of nodules (Figure 14G). Shell color is generally a whitish yellow, but some specimens are covered with brown maculations and are nearly melanistic (Figure 14D). Rehder (1980:37) noted that Easter Island specimens are darker than most specimens from other localities.

Cerithium atromarginatum has been allocated to several other genera. However, the Type-A pallial oviduct (Figure 4A) is identical to that of *C. nodulosum*, the type species of *Cerithium*; moreover, the other anatomical features of *C. atromarginatum* are typical of *Cerithium* species and do not support its placement in another genus. The shell morphology of *C. atromarginatum* is similar to species of *Clypeomorus* Jousseaume, 1888; however, although *Clypeomorus* species live in similar intertidal habitats, they usually are larger and have an overall beaded aspect. In addition, the layout of their pallial gonoducts differs from that of *C. atromarginatum* (see Houbrick, 1985:30). Some authors (Maes, 1967:113) have placed *C. atromarginatum* in the subgenus *Conocerithium* Sacco, 1895, which was proposed for a small fossil Miocene species from Italy that has an overall stout shell with broad

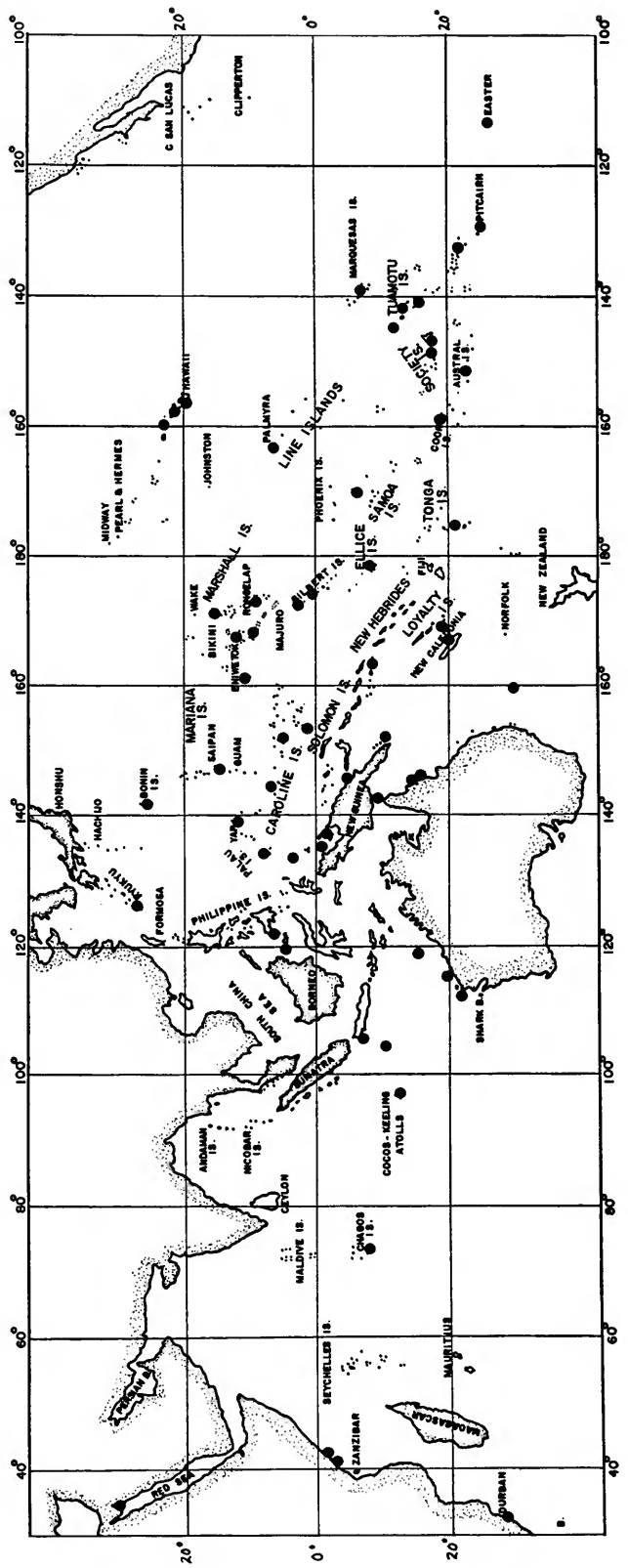


FIGURE 16.—Geographical distribution of *Cerithium atromarginatum*.

axial ribs. This poorly defined subgenus is distinguished only by its small, stout shape and axial ribs, shell characters that should be accorded little more than specific weight.

FOSSIL RECORDS.—Ladd (1972:40, pl. 9: fig. 11) figured an upper Miocene fossil from Enewetak Atoll, Marshall Islands (cited as *C.* aff. *egenum*), which is clearly *C. atromarginatum*.

GEOGRAPHIC DISTRIBUTION (Figure 16).—Indo-Pacific region from east Africa to Hawaii and Easter Island.

SPECIMENS EXAMINED.—EAST AFRICA: Scottburg, Natal, South Africa (WAM); Ukunda, Diani Beach, Kenya (ZMA); Malindi, 121.6 km N of Mombasa, Kenya (USNM 595102). RED SEA: Eilat, Gulf of Aqaba (USNM 672282). INDIAN OCEAN ISLANDS: E of Minni Minni, Diego Garcia, Chagos Archipelago (USNM 702130); S end, Direction Id, Cocos Keeling Ids (USNM 656271); S end, Home Id, Cocos Keeling Ids (USNM 656421); (WAM); off airstrip, SW side of West Id, Cocos Keeling Ids (ANSP); Ethel Beach, Christmas Id (WAM); Dolly Beach, Christmas Id (WAM); Flying Fish Cove, Christmas Id (WAM). JAPAN: Hahajima, Ogasawara (ANSP). RYUKYU ISLANDS: Itoman Reef, Okinawa (LACM 27329); Onna Flat, Okinawa (LACM 29244). PHILIPPINES: Isle 0.4 km NW of Tara Id (USNM 240335); Bolong, near Sangali, Sulu Sea (USNM 775138); Simaluc Id, Tataan Ids, Tawitawi (USNM 239643). INDONESIA: Pulau Panaitan, W Java (ZMA).

WESTERN AUSTRALIA: SE corner of Clerke Reef, Rowley Shoals (WAM); SE reef, S of Passages, Clerke Reef, Rowley Shoals (WAM); NW corner of Clerke Reef, Rowley Shoals (WAM); Citadel Rock, Kendrew Id, Dampier Archipelago (WAM); inner reef, Boat Bay, Kendrew Id, Dampier Archipelago (WAM); W side of Kendrew Id, Dampier Archipelago (WAM); 5 km SW of Yardie Creek, North West Cape (WAM); Mangrove Bay area, North West Cape (WAM). QUEENSLAND, AUSTRALIA: Murray Id, Torres Starit (AMS); Low Isles, near Port Douglas (AMS); No. 2 Bank, Michaelmas Reef, NE of Cairns (AMS); NE Herald Cay (AMS); Caloundra (AMS). NEW GUINEA: 1.6 km E of Biak, Irian Jawa (ANSP); Mios Woendi Id, Schouten Ids, Irian Jawa (USNM 542713); Massas Id, Madang (AMS); Kuia Id, Lusangay Id, Trobriand Gp, NE of Samarai, Papua (AMS); off Kaibala Village, N end of Kirwina Id, Trobriand Gp, Papua (AMS). SOLOMON ISLANDS: Su-u (AMS); San Cristobal Id (AMS). LOYALTY ISLANDS: Lifu (AMS, USNM 423297, 423303, 423315, 423323, 423331). NEW CALEDONIA: Thio (AMS). LORD HOWE ISLAND: (AMS). BONIN ISLANDS: Bonin (USNM 343865). MARIANA ISLANDS: Lagoon, W of Saipan (USNM 595510). PALAU: Palau (USNM 636592); E Babelthaup (USNM 620970); Ngargersiul Id (ANSP). CAROLINE ISLANDS: Yap (USNM 630815); NW end, Falerik Id, Ifaluk Atoll (USNM 616614); Elato Atoll (USNM 590965); 1.6 km W of Torongahai, Kapingamarangi (USNM 611067); Kapingamarangi Atoll, SE Caroline Islands (WAM); reef at Mutunlik, Kusaie Id (USNM 609484); Touhou Id (USNM 622318); Round Rock, Helen Channel, Helen Reef (ANSP).

MARSHALL ISLANDS: Enewetak Atoll, numerous localities (USNM 543357, 580856, 581131, 581532, 581731, 581779, 581822, 581823, 582187, 582618, 584367, 587275, 607260, 743890, 821847); Bikini Atoll, numerous localities (USNM 579168, 579313, 579448, 579480, 579515, 579567, 580167, 580195, 580309, 580383, 580424, 580522, 580951, 581337, 584789, 585193, 585634, 586084, 586949); Rongelap Atoll, numerous localities (USNM 580841, 582110, 582316, 582416, 582444, 583411, 583985, 584127, 584543, 585583); Rongerik Atoll, numerous localities (USNM 582919, 583419, 583518, 594657, 584928, 586327, 586354); Ailuk Id, Ailuk Atoll (USNM 615134); Temo Id, Likiep Atoll (USNM 615821); Lae Id, Lae Atoll (USNM 614904); Kwajalein Atoll (USNM 587352); W side Pinglap Ids, Jaluit Atoll (USNM 756847). GILBERT ISLANDS: Apamama (USNM 434000); Teiro Id, Abaiang Atoll (AMS).

HAWAIIAN ISLANDS: Kealia, Kauai (USNM 339335); Kailua, Oahu (ANSP); Kiwaula, near Kaena Pt, Oahu (ANSP); Rabbit Id, Oahu (ANSP); Kailua Bay, Oahu (WAM); Kawaiba, Oahu (AMS); Kuhuku, Oahu (AMS); Sharks Cove, Pupukea, Oahu (LACM 27697); Mokuleia, Oahu (USNM 485536); Pupukea Beach, near Waiamea Bay, Oahu (USNM 484658); N shore, Kahuku, Oahu (USNM 767555); Paumalau, Oahu (USNM 612412); W side Kahe Pt Beach, Oahu (USNM 777995); E side, Uluapu City, Mokapu, Oahu (USNM 655503); Waikiki, Oahu (USNM 343494); Honokowai, Maui (USNM 339334); Keei, Hawaii (USNM 409145); Punaluu, Hawaii (USNM 420899); Hookena, Hawaii (USNM 420891); Honaunau, Hawaii (USNM 343493); 8 km SW of Kapoho, Hawaii (USNM 409104); Keokea, Hilo, Hawaii (USNM 339333). LINE ISLANDS: Palmyra Id (AMS, USNM 348472). ELLICE ISLANDS: Reef flat near village, Vaitupu (USNM 686083); Funufuti Atoll (AMS). TOKELAU ISLANDS: Tokelau Islet, NE Nukunong (USNM 768618). TONGA: Niuafo'ou Id, N of Ninafoo Id (USNM 519015). COOK ISLANDS: Reef, N tip of Aitutaki (ANSP). AUSTRAL ISLANDS: Moerai, W of wharf, Rurutu (USNM 684120); E coast, Motu Motihia, Tubuai (USNM 705529). SOCIETY ISLANDS: NW Motu, Fareone, NW Mooréa (USNM 630553); Taone, Tahiti (USNM 673430); Mahina, Tahiti (USNM 791370, 775935).

TUAMOTU ARCHIPELAGO: Maiai Id, Tikahau Atoll (USNM 629530, 652534); N of Temao Pier, Makatea (USNM 753686); Takaroa (USNM 790072); Fakarava Id (USNM 348903); Makemo Id (USNM 348795); Raroia, numerous localities (USNM 697818, 698289, 698361, 698593, 711666, 711789, 720156, 720312, 720480, 720506, 721042, 721067, 722468, 723024, 723055, 723333, 753659, 753665, 753668, 753669, 753670, 753671, 753674); NE side, Tepukamaruia Id, Takume (USNM 753688); near Hikitaki Id, Amanu Id (USNM 671800); Vahi Tahi (USNM 753684); W part of Northeast Id, Anuanuraro Atoll (USNM 725242). GAMBIER ISLANDS: Motu Tarauru-roa, Mangareva (USNM 638244). PITCAIRN ISLAND: NW side off Pt Christian (USNM 731757); N side,

below Adamstown (USNM 756850); Isaacs Rock (USNM 789299). MARQUESAS ISLANDS: Taiohae Bay, Nuku-hiva (USNM 700237); Tahuata (USNM 775620). EASTER ISLAND: Te Peka Peka, La Perouse Bay (USNM 756028); Te Raa Raa, S Hanga Piko (USNM 751614).

Cerithium balteatum Philippi, 1848

FIGURES 17–20

Cerithium planum Anton, 1838:66 [no figure; type not found; type locality: not given; nomen dubium].—Philippi, 1849:7, pl. 1: fig. 18.—Sowerby, 1855:862, pl. 181: figs. 111–113; 1865, pl. 12: fig. 79.—Kobelt, 1895:187, pl. 34: fig. 10.—Cernohorsky, 1972:65, pl. 14: fig. 7 [not *Cerithium planum* Anton, 1838; is *C. balteatum* Philippi, 1848].

Cerithium balteatum Philippi, 1848:22–23 [type not found; type locality unknown; neotype, herein selected: USNM 695399, Georgia Cove, Rambi Id, Vanua Levu, Fiji, 13.3 mm × 5.4 mm]; 1849:4, pl. 1: fig. 10.—Sowerby, 1855:862–863, pl. 181: figs. 116, 117; 1865, pl. 11: fig. 72a,b.—Tryon, 1887:131, pl. 23: figs. 2, 3.—Kobelt, 1895:189–190, pl. 34: figs. 16, 17.

Cerithium invaginatum Gould, 1849:120, pl. 10: fig. 169 [holotype: USNM 5569; type locality: Fiji].—Sowerby, 1865, pl. 10: fig. 64a,b.—Tryon, 1887:131, pl. 23: fig. 97.—Kobelt, 1895:189, pl. 34: figs. 14, 15.

Cerithium coronatum Sowerby, 1855:863, pl. 181: fig. 118 [holotype: BMNH 1986285; type locality: Philippines; not *Cerithium coronatum* Bruguière, 1792]; 1865, pl. 8: fig. 48a,b.—Tryon, 1887:131.

Cerithium custos Bayle, 1880:244 [new name for *Cerithium coronatum* Sowerby, 1855].

Cerithium nigrobalteatum E.A. Smith, 1884:65, pl. 5: fig. n. [holotype: BMNH 1882.12.6.85; type locality: Prince of Wales Channel, Torres Strait].—Cernohorsky, 1978:52, pl. 13: fig. 7.

Cerithium planum Philippi [sic].—Tryon, 1887:131, pl. 23: figs. 97–99.

Cerithium planiusculum Kobelt, 1895:188, pl. 34: fig. 11 [name proposed for *Cerithium planum* Anton, 1838, as depicted by Sowerby (1855, pl. 181: figs. 111–113) and Sowerby (1865, pl. 12: fig. 79) but not *Cerithium planum* Anton, 1838, as depicted by Philippi (1849, pl. 1: fig. 18)].

Cerithium balteatum Philippi.—Cernohorsky, 1972:65, pl. 14: fig. 5 [not *Cerithium balteatum* Philippi; is *C. phoxum* Watson, 1880].

Cerithium (Thericium) schmidti Ladd, 1972:30, pl. 9: figs. 13, 14 [holotype: USNM 650470, paratype USNM 650420; type locality: Tagpochau Limestone of Saipan, Miocene].

DESCRIPTION.—*Shell* (Figures 17, 18): Shell fusiform, elongate, pagoda-shaped, comprising about 12 convex whorls, reaching 27.7 mm length and 8.1 mm width. Protoconch (Figure 18C) comprises 2.5 smooth whorls. Early teleoconch (Figure 18D) sculptured with two major spiral cords, minor spiral lirae, and wide, straight, axial ribs. Adult teleoconch sculpture extremely variable, generally comprising 0–4 major, spiral cords, many fine spiral striae and incised lines, and 0–18 axial ribs. Presutural spiral thread frequently beaded. Major spiral cords drawn out, thickened, forming beads or nodes where axial ribs cross spirals. Axial ribs very wide in some specimens, dominant on middle whorls, sometimes weak on penultimate and body whorls. Suture deeply impressed, wide postsutural ramp on adult whorls. Former varices thick, randomly distributed. Body whorl sculptured with 6 or 7 spiral, beaded cords and weak, colabral axial ribs. Two weak, beaded to spinose spirals define margin of basal constriction of body whorl. Base of body whorl deeply excavated, sculptured with many fine, spiral lirae. Aperture ovate, about one-fourth the shell length. Anterior canal well developed, long, tubular, slightly reflected to left of shell axis. Anal canal small, well defined by parietal columellar tooth. Columella concave, white, with narrow callus. Outer lip of aperture convex, finely crenulate, with weak, elongate, interior denticles. Shell color highly variable, generally with brown bands over white background. Nodes and ribs usually white. Early whorls bluish between presutural axial ribs. Anterior canal frequently dark brown; wide, presutural, brown, spiral band common. Measurements (Table 12). Periostracum thin.

Radula (Figure 19): Type-2 radular ribbon (Figure 3B) very small, about one twenty-first the shell length. Rachidian tooth (Figure 19C,D) triangular-shaped; basal plate narrower than anterior front and with pair of basal lunule ridges and with posteriorly extending, long, central ridge. Cutting edge of rachidian tooth with long central pointed cusp, flanked on each side by 2 or 3 small pointed denticles. Lateral tooth (Figure 19D) with broad basal plate having strong central ridge, and long, lateral-posterior, outer extension. Cutting edge of lateral tooth with large, blunt main cusp, small inner flanking denticle and 3 or 4 outer flanking denticles. Marginal teeth (Figure 19A,B) with long, narrow, curved shafts, hooked, comb-like apices and narrow bases. Inner marginal tooth apex with long spoon-shaped main cusp, 2 or 3 inner flanking denticles, and 1 or 2 outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Unknown.

SYNONYMIC REMARKS.—The nomenclatural history of this species is complex, as a perusal of the above synonymy will show. This is due to several missing type specimens of key taxa, the absence of clear illustrations of some types, and extreme intraspecific variation in shell sculpture.

Cerithium planum Anton has long been linked with this species, but is herein considered a nomen dubium, as the type is not extant, and the original description did not include a figure or type locality. Philippi's (1848) figure of *C. planum* was recopied by Kobelt (1895) but the Philippi figure is equivocal and is surely not the same species as those depicted under the other names in the above synonymy. Indeed, the actual size of the shell depicted by Philippi in Figure 18 is represented by a fine line that is no larger than 13 mm in length, next to the colored figure. The figures depicted by Sowerby (1855, 1865, 1866) and Tryon (1887) do not appear to be the same as Philippi's (1849) figure 18, while Kobelt's (1895) figure is a direct copy of Philippi's figure. Note that Tryon (1887) erroneously attributed the name *planum* to Philippi. Cernohorsky (1972:65) considered *C. invaginatum* Gould to be a form of *C. planum*, and is the only recent author to use the latter name.

Another name commonly applied to this species is *Cerithium balteatum* Philippi. I was unable to find Philippi's type

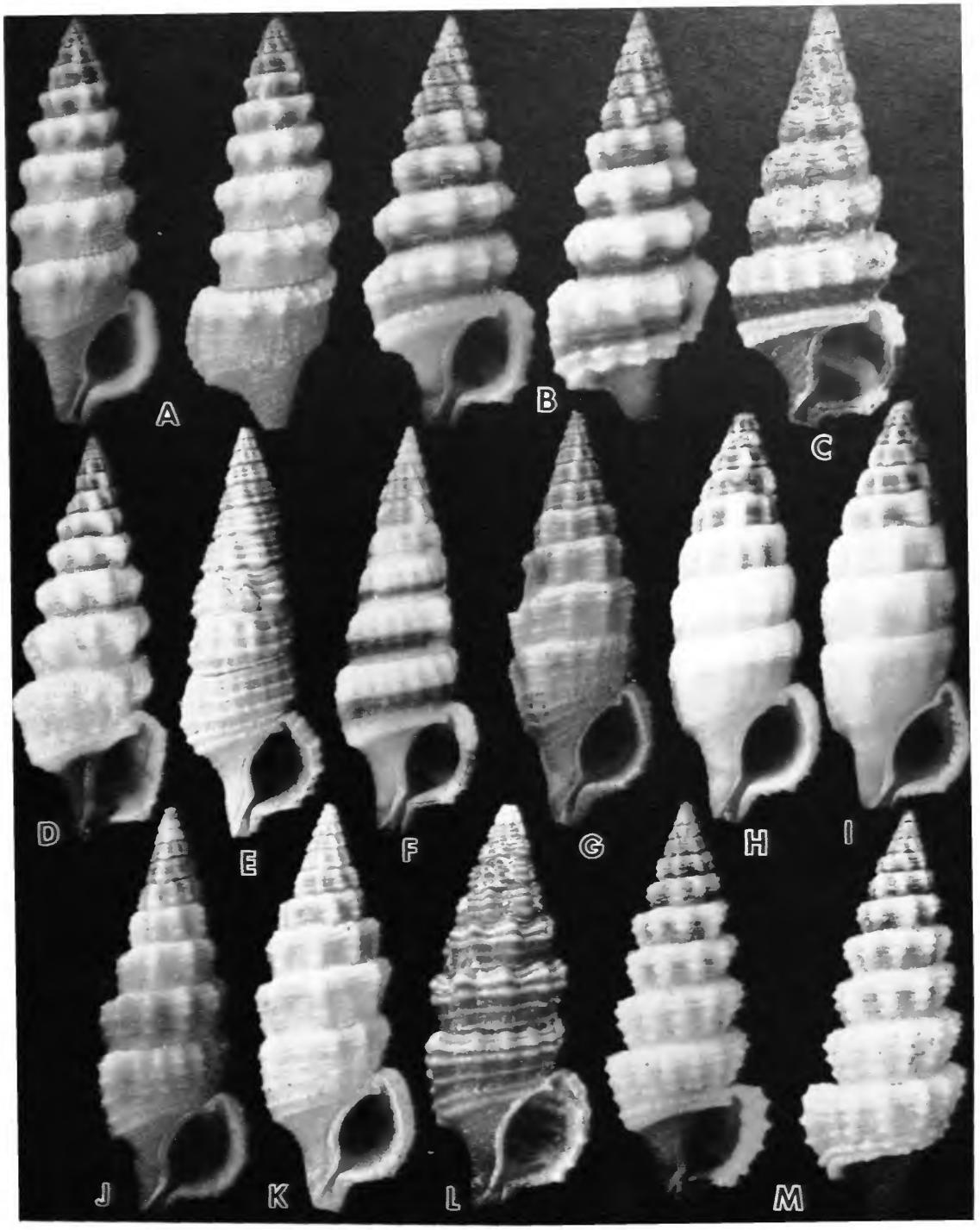


FIGURE 17.—*Cerithium balteatum* Philippi, figuring types of synonymous taxa and showing wide morphological variability: A, holotype of *Cerithium coronatum* Sowerby, Philippines, 21.7 mm (BMNH 1986285); B, neotype of *Cerithium balteatum* Philippi, Georgia Cove, Rambi Id, Vanua Levu, Fiji, 13.3 mm (USNM 695399); C, holotype of *Cerithium nigrobalteatum* E.A. Smith, Torres Strait, Australia, 14.5 mm (BMNH 1882126685); D, holotype of *Cerithium invaginatum* Gould, Fiji, 20.5 mm (USNM 5569); E, weakly sculptured phenotype, Nouméa, New Caledonia, 18.1 mm (USNM 784289); F, Momi Bay, Fiji, 14.2 mm (USNM 66047); G, melanisitic morph, Kajoe Raji, Celebes, Indonesia, 22.2 mm (ZMA); H,I, Subic Bay, Luzon, Philippines, 16.2 mm and 18.2 mm (DMNH 4229); J, Nuku'alofi, Tongatapu, Tonga, 16.4 mm (USNM 683971); K, Kajoe Raji, Celebes, Indonesia, 18 mm (ZMA); L, Nuku'alofa, Tongatapu, Tonga, 16.3 mm (USNM 683971); M, Delambre Reef, Western Australia, 19.6 mm (WAM).

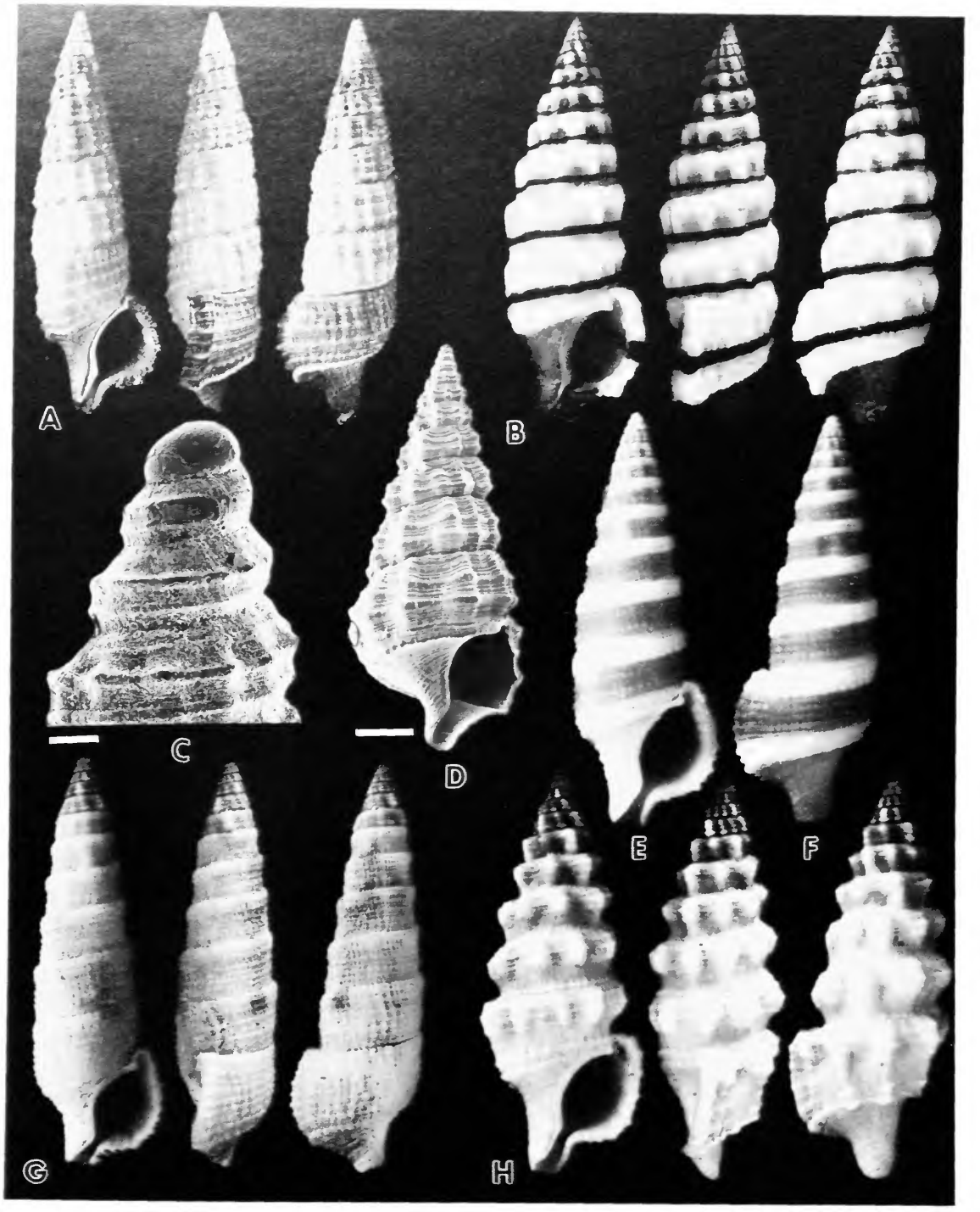


FIGURE 18.—*Cerithium balteatum* Philippi, showing wide phenotypic variability: A, apertural, side, and abapertural views of weakly sculptured phenotype, Nouméa, New Caledonia, 25.9 mm (MNHNP); B, apertural, side, and abapertural views of banded morph, Calamian Gp, Palawan, Philippines, 19.2 mm (LACM 76753); C,D, SEM of protoconch (C) and early whorl sculpture (D), NW Cape, Western Australia (bars = 115 μm and 1.76 mm; both WAM 1024-84); E-G, apertural, side, and abapertural views of finely beaded, slender morphs, Efate Id, New Hebrides, (E,F) 24.8 mm, (G) 25.4 mm (both USNM 787009); H, apertural, side, and abapertural views of highly nodulose phenotype, Viti Levu, Fiji, 21.4 mm (USNM 824818).

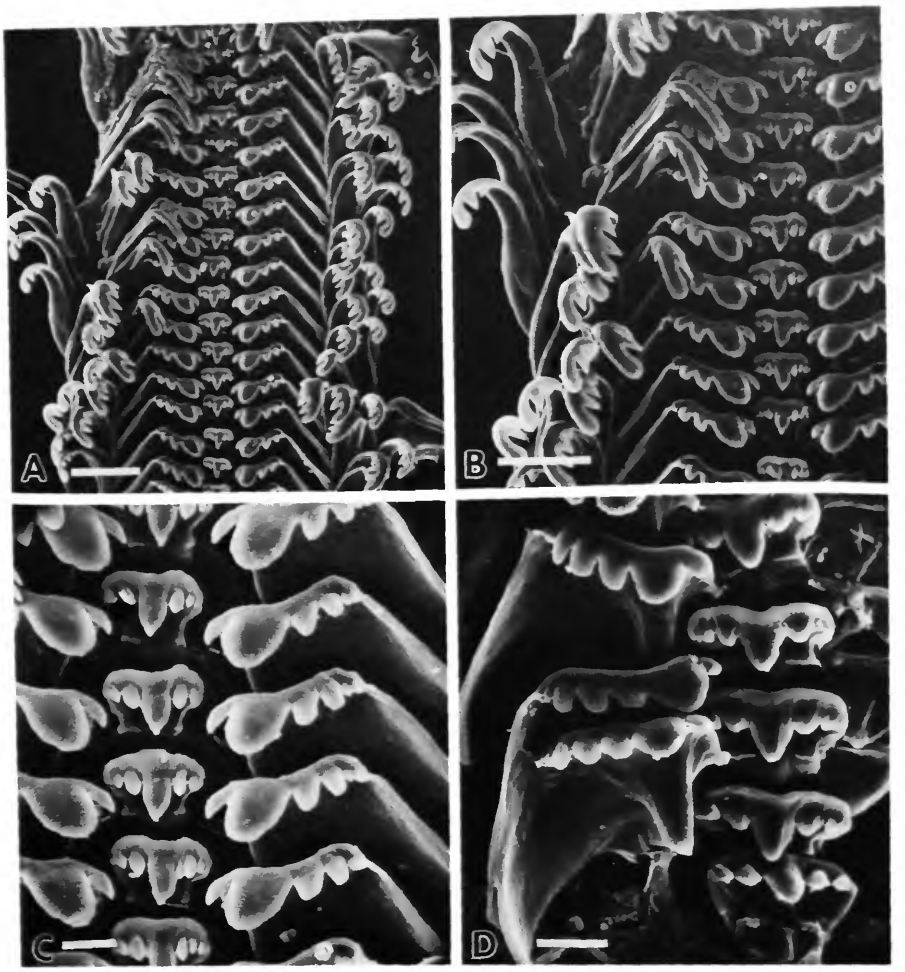


FIGURE 19.—Radula of *Cerithium balteatum* Philippi: A, section of ribbon with marginal teeth spread back, Delambre Id, Western Australia (bar = 75 μm; WAM 454-76); B,C, half row (B) and detail of rachidian and lateral teeth, Delambre Id, Western Australia (bars = 100 μm and 40 μm respectively; WAM 454-76); D, detail of rachidian and lateral teeth, Tawitawi, Philippines (bar = 30 μm; USNM 274223).

TABLE 12.—Shell morphometrics of *Cerithium balteatum*.

Character	$\bar{x}$ (n = 17)	sd	v	Range
Shell length	17.3	4.7	22.2	11.8-27.7
Shell width	6.0	1.2	1.5	4.1-8.1
Aperture length	4.2	1.1	1.2	2.6-6.4
Aperture width	3.2	0.7	0.5	2.0-4.1
Number whorls	12.4	1.1	1.1	11-14
Number spiral cords	3.1	1.3	1.6	0-4
Number axial ribs	10.8	3.9	15.5	0-18

specimen(s), but although he gave no locality in the original description, he subsequently figured the species well enough (1849, pl. 1: fig. 10) to allow its identification. Note the close resemblance of this figure to Sowerby's (1855) figures 116, 117. As Philippi's *balteatum* appears to be a name commonly used for this species, I herein designate a specimen from Rambi Id, Vanua Levu, Fiji (USNM 695399), as the neotype of *C. balteatum* (Figure 17B). It should be noted that what Cernohorsky (1972) has figured as *C. balteatum* is a specimen of *Cerithium phoxum* Watson, 1869. The name *Cerithium nigrobalteatum* E.A. Smith, 1884, was proposed for a phenotype with more inflated whorls and with black knobby spiral bands (Figure 17C), and is herein considered a synonym of *Cerithium balteatum*. Another morph with large axial knobs and concavely excavated whorls near the suture was called *Cerithium invaginatum* by Gould (1849) (Figure 17D), and a similar morph was named *C. coronatum* by Sowerby (1855) (Figure 17A). The later name is preoccupied by a fossil species

and was given a replacement name, *C. custos*, by Bayle (1880). These three taxa should be regarded as synonyms of *C. balteatum*. Another name that was applied to morphs such as those figured by Sowerby (1855, 1865) is *Cerithium planiusculum* Kobelt, 1895. Kobelt noted that Sowerby's figures of *C. planum* Anton were not the same as the figure of *C. planum* given by Philippi (1849) and proposed a separate name for them. The nominal species, *planiusculum*, is herein regarded as a synonym of *C. balteatum*. I have examined the types of the Saipan fossil, *Cerithium schmidti* Ladd, 1972, and find them to be conspecific with Recent *C. balteatum*. Ladd (1972:30) stated that Julia Gardner noted that the fossils of *C. schmidti* from Saipan showed a wide variation in outline and sculpture, which is typical of *C. balteatum*.

ECOLOGY.—I have not observed living specimens of this species and as specific habitat records are sparse, not much can be said about the ecology of *Cerithium balteatum*. It appears to be a shallow-water sand dweller and is found on coral and sand substrates in inshore, coastal habitats, and on shallow, offshore shelfs. The protoconch (Figure 18C) of few whorls lacks sculpture and a sinusigeral notch, indicating a direct kind of development, perhaps explaining the great variability in shell morphology between populations. The ecocline observed in shell morphology from inshore to offshore populations may be due to differential selective forces and poor dispersal ability of young.

DISCUSSION.—The distinguishing characters of this species are a pagoda-like shell sculptured with an acute presutural ramp, and the frequently darkly colored, deeply excavated shell base with constricted anterior canal, separated from the body whorl by two beady-spinose spiral cords (Figure 17A,B,D). The early whorls are strongly angulate and sculptured with 2 dominant, subcentral, nodulose spiral cords and eight axial ribs.

Two species that resemble *Cerithium balteatum* and occur sympatrically with it are *Cerithium torresi* E.A. Smith, and *Rhinoclavis (Proclava) sordidula* (Gould). *Cerithium torresi* differs in having more cancellate sculpture and in lacking the excavated shell base and the narrow, axially oriented anterior canal of *C. balteatum*. *Rhinoclavis sordidula* differs in having a weak central columellar plait and only three spiral cords per whorl. *Cerithium africanum*, new species, from the western Indian Ocean, bears superficial resemblance to *C. balteatum* and has a similar constricted base (Figure 9A–G). However, *C. africanum* has a stocky shell with angulate, overhanging whorls producing a fir tree outline. In contrast to *C. balteatum*, it has only three nodulose spiral cords per whorl, the strongest of which is postsutural.

Cerithium balteatum shows extreme intraspecific variation in shell form and sculpture. Some phenotypes depart sharply from the generalized diagnosis given in the above paragraph, and have received separate names. There are basically three kinds of morphological shapes with intergrades found between each: (1) a slender form with finely cancellate sculpture, moderately inflated whorls and a moderately impressed suture (Figure 17E; Figure 18A). This form is very much like *Rhinoclavis (Proclava) sordidula* (Gould), with which it is sympatric and frequently found in mixed lots in museum collections. The latter species differs from it in having a median columellar plait and in other sculptural details (Houbrick, 1978b:69). The name *Cerithium turritum* Sowerby, 1855, a synonym of *Rhinoclavis sordidula*, is often applied to this phenotype in older lots of museum collections. It appears to occur on continental shelfs at depths of 15–30 m on fine silty, sandy bottoms and is common off shore in northern Queensland and Northern Territory, Australia; (2) a highly nodulose phenotype with angulate whorls sculptured with wide axial ribs, strong spiral cords and a deeply impressed suture and presutural ramp (Figure 17A-D, G-M; Figure 18B,H). This knobby phenotype is best known as *Cerithium invaginatum* Gould (Figure 17D) or *C. coronatum* Sowerby (Figure 17A). It occurs in shallow-water, near-shore environments along continental coasts and is common around Torres Strait, Fiji, and the Philippines; (3) a smoother phenotype with straight sided whorls, deeply impressed suture and presutural ramp, sculptured with wide axial ribs and fine spiral striae that may be nearly lacking (Figure 18E–G). This phenotype is most commonly found in off shore, shallow-water, carbonate sand habitats associated with coral reefs. Comparison of many lots from throughout the range reveals many intergrades among these phenotypes, strongly suggesting that they comprise a complex of one variable species showing strong ecophenotypic variation.

FOSSIL RECORDS.—Recorded from the Miocene of Saipan by Ladd (1972:38), under the name *Cerithium schmidti* Ladd, 1972.

GEOGRAPHIC DISTRIBUTION (Figure 20).—*Cerithium balteatum* is found mainly in the western tropical Pacific, but also occurs in Southeast Asia, Indonesia, and Western Australia, extending eastward through New Guinea, Australia, and Melanesia. It occurs in southern Japan, the Ryukyu Islands, and throughout western Micronesia.

SPECIMENS EXAMINED.—THAILAND: Sriracha, SE Thailand (USNM 405888); Koh Maprao, (USNM 361339). JAPAN: 6 km NE of Kuzu-saki, 26°19.2'N, 127°44.8'E (AMS). RYUKYU ISLANDS: Seawall at channel off Kadena Yacht Club, Okinawa (USNM 821014, 852192); Baten Ko, Buckner Bay, Okinawa (USNM 594136); Okinawa (USNM 670925). PHILIPPINES: Subic Bay, Zambales, Luzon (DMNH 4234, MCZ); 27.4–54.8 m, Nasasa Bay, San Antonio, Zambales, Luzon (AMNH); Villa Carmen, Bataan Prov, SW Luzon (LACM 76761); Polillo Reef, Polillo Id, E Quezon, Luzon (AMS); Cabaloa, Polillo Gp, Quezon, Luzon (LACM 76749, 76771); Matabungkay, 115 km SSW of Manila, Luzon (AMS); 1.8–9.1 m, Batangas Bay, Batangas Prov, SW Luzon (AMNH, LACM 76785); Albay Prov, Luzon (WAM); Tabaco, Albay Prov, E side Luzon (ANSP 230832); Punta Engano, Mactan Id, Cebu (USNM 845805); SW end Mactan Id, E Cebu (LACM 84-158); 146.2 m, Mactan Id, Cebu (AMNH 203364); 3.6–4.2

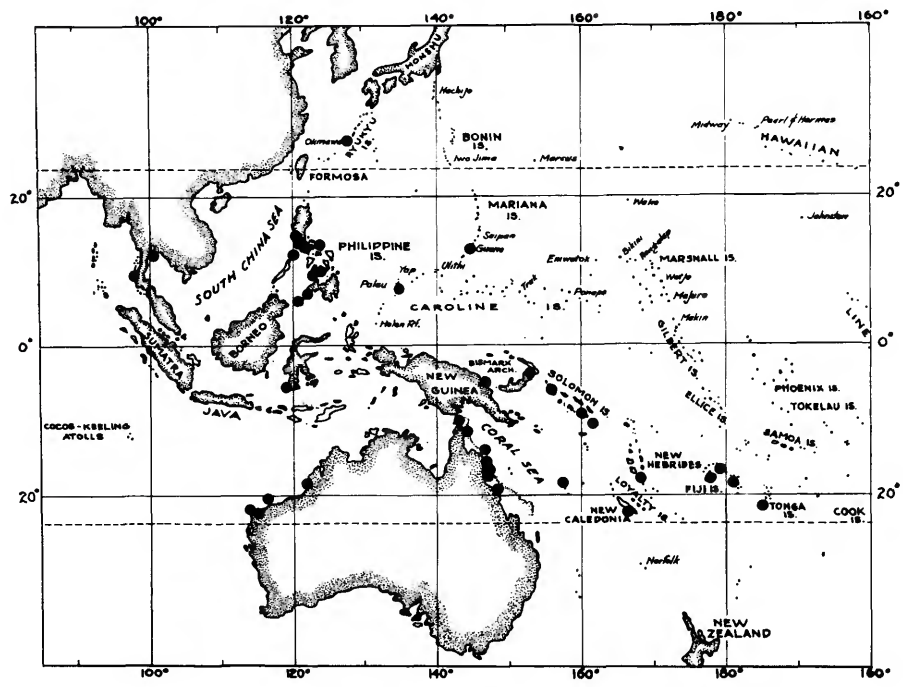


FIGURE 20.—Geographical distribution of *Cerithium balteatum* Philippi.

m, E side of Jagoliao Id, NW end of Bohol Id (ANSP); W side of Hadayan Id, NW end of Bohol Id (ANSP); Catbalogan, Samar (USNM 243727); 18 m, 06°53′10″N, 122°02′50″E, NE side of Little Santa Cruz Id, Mindanao (USNM 812161); 3.7 m, Calamian Gp, Palawan (LACM 76753); Culion, Calamian Gp, Palawan (LACM 76775); 38.4 m, USBF sta 5142, NE of Jolo Jolo (USNM 235623); 18.3 m, USBF sta 5159, off Bakun R, Tawitawi (USNM 236260, 236265); 18.3 m, USBF sta 5159, off Tinaka Id, Tawitawi (USNM 274223). INDONESIA: Kajoe Ragi, Celebes (ZMA).

WESTERN AUSTRALIA: Broome (AMS C68507, MCZ; NMV); Cape Frezier, Admiral Bay (WAM); NE side Shall Id, Passage Ids (WAM); Delambre Id (WAM 454-76); sand flats, Anchorage Bay, Rosemary Id, Dampier Archipelago (WAM); 25.6 km W of Eaglehawk Id, Dampier Archipelago (WAM); W of Flat Id, near Onslow (WAM); Mangrove Bay, Sandover Rock, NW Cape (WAM, WAM 1024-84); near Charles Knife Road, Exmouth Gulf (WAM); Exmouth Gulf (AMS C69351); 25 km N of Ningaloo homestead, North West Cape (WAM 1869-82); Cockatoo Id (NMV); Wapet Landing (WAM 3454-67). NORTHERN TERRITORIES, AUSTRALIA: Palm Bay (ZMA).

QUEENSLAND, AUSTRALIA: Murray Id, Torres Strait (AMS, MCZ); Goode Id, Torres Strait (AMS C49333); Thursday Id, Torres Strait (AMS); Hospital Pt, Thursday Id (AMS C105905); Friday Id, Torres Strait (AMS); Reef N of Terry Beach, W side of Prince of Wales Id, Torres Strait (AMS C109728); Albany Passage, Torres Strait (AMS); 5.5–21.9 m, off Albany Id, *Challenger* Exp (BMNH 87291667); Mabiag Id, Torres Strait (WAM); Portland Roads (NMV); No. 1 reef, Howick Gp, N of Cooktown (AMS C41317); Hope Id, SE of Cooktown (AMS C29687); Lizard Id (DMNH 32199, USNM 766816, 766944, 766946, 766949, 806000); lagoon, Lizard Id (AMS C105240); S side South Id, on face fringing reef, Lizard Id (AMS); Bird Islet, Lizard Id (AMS); 12°51′S, 143°49′E, reef N side of Bligh's Boat Passage (AMS); 13°37′S, 144°05′E, W side of Creech Reef (AMS); 13°45′S, 144°16′E; 14°25′S, 144°47.9′E; 14°24.9′S, 144°50.1′E; 16°39.2′S, 145°57.6′E; 14°36.8′S, 145°28.7′E; 11°4′S, 143°21.4′E; 15°39.5′S, 145°29.4′E; 14°25′S, 144°48.6′E; 16°40.4′S, 145°57.8′E (all AMS); 0.8 km W of North Direction Isle (AMS); 10.9–18.3 m, near Cairns reef (USNM 348646, 367721); Low Isles, near Port Douglas (AMS C76027, C117170, C117179); Low Id, off Port Douglas (NM G2534); Spur Reef, E of Norman Reef, N of Cairns (AMS); Michaelmas Cay, off Cairns (AMS); Moore Reef, E of Cairns (AMS); N side Wheeler Reef, NE of Townsville (AMS); Little Broadhurst Reef, E of Townsville (AMS); 55 m, 21°23′90″S, 158°59′60″E, *Chalcal* sta D55, Chesterfield-Bellona Plateau, Coral Sea (MNHNP); NW side, Macgillivray Cay (AMS); 9 m, Carter Reef (DMNH 31462). NEW SOUTH WALES, AUSTRALIA: Twofold Bay (NMV).

NEW GUINEA: Manokwari, NW West Irian (ANSP 249629, ZMA); 6–12 m, Yassi II reef, offshore from Nagada, Astrolabe Bay, Madang Prov, Papua (LACM 80-13); 15–40 m, 4°12′S, 152°13′E, Nodup, Rabaul, Papua (AMS). SOLOMON ISLANDS: Numa Numa Plantation, E coast of Bouganville Id,

56 km N of Kieta (AMS); reef, NE of Honiara, Guadalcanal (DMNH); East Pt, Imall Nggela Id, Florida Gp (AMS); Aaki Harbor, W coast of Malaita Id (AMS); San Cristobal, Brazier Exp (BMNH). NEW HEBRIDES: 168°19′06″E, 17°44′44″S, NW corner of Erakor lagoon, Efate Id (USNM 786937, 787009, 787114). NEW CALEDONIA: Oubactche (AMS C4034); 30 m, 22°21′S, 166°38′E, ORSTOM sta 16; 11 m, 22°26′S, 166°23′E, sta 22; 19 m, 22°17′S, 166°24′E, sta 261; 20 m, 22°13′S, 166°22′E, sta 272; 9 m, 22°12′S, 166°23′E, sta 273; 19 m, 22°14′S, 166°18′E, sta 275; 30 m, 22°17′S, 166°16′E, sta 277; 29 m, 22°21′S, 166°27′E, sta 279; 11 m, 22°16′S, 166°32′E, sta 290; all Secteur de Nouméa (MNHNP); Nouméa (AMS C3716); 7.3–21.9 m, Nouméa (ANSP); S side, Baie de Citron, Nouméa (ANSP); 22 m, 22°09′S, 166°07′E, ORSTOM sta 170; 20 m, 22°02′S, 166°03′E, sta 178; 18 m, 22°01′S, 166°00′E, sta 192; 17 m, 21°60′S, 165°59′E, sta 201; 14 m, 21°54′S, 165°53E, sta 210; 12 m, 21°55′S, 165°53′E, sta 211; 9 m, 22°12′S, 166°23′E, sta 273; all Baie de St Vincent (MNHNP); 35 m, 22°28′S, 166°31′E, ORSTOM sta 78; 32 m, 22°20′S, 166°49′E, sta 143; 29 m, 22°33′S, 166°40′E, sta 154; 23 m, 22°32′S, 166°38′E, sta 155; 32 m, 22°36′S, 166°42′E, sta 231; all Île Ouen, Baie du Prony (MNHNP); 35 m, 22°36′S, 166°48′E, ORSTOM, sta 299, Grand Récif Sud (MNHNP).

FIJI: Fiji Islands (USNM 87968); Albert Cove, NW Rambi Id, Vanua Levu (USNM 695205); Georgia Cove, Rambi Id, Vanua Levu (USNM 695362, 695399); Nadi Bay, Viti Levu (AMS, ANSP); 9–13.5 m, off Nadi, Viti Levu (USNM 638428); shallows off Sali Sali, Viti Levu (USNM 694482); Viti Levu Bay, NE Viti Levu (USNM 824818); Yakuilau Id, W Viti Levu (USNM 660356); 2 m off Yakuilao Id, W Viti Levu (USNM 660333); Malolo Reef, NW side Viti Levu (LACM 74-45); 7 m off Momi Bay off Naselesele Pt, N end of Taveuni (USNM 695479); S of Ketei, lagoon E side of Totoya Id (USNM 686565, 686604); E of Korolevu Bay, Kandavu (USNM 696114); W of Ngaloa Id, Kandavu (USNM 696383). MARIANAS: Guam (AMNH). PALAU: Near ferry dock, Koror Id (ANSP); NE part of Urukthapel Id (ANSP); 3.2 km NE of Gamudoko Id, off Urukthapel Id (ANSP); inside reef at Eil Malk (ANSP). TONGA: 3.6–4.5 m, Luangahu Id, Ha'apai Gp (LACM 72-151); 2.4 km from Nuku'alofa, Tongatapu (USNM 683971); Nukualofa (ANSP).

Cerithium caeruleum Sowerby, 1855

FIGURES 21–24

Cerithium tuberculatum Lamarck, 1822:75 [lectotype and one paralectotype herein selected: MHNG 1097/37; type locality: Red Sea; not *Cerithium tuberculatum* Brown, 1827, nor *Strombus tuberculatus* Linné, 1758].

Vertagus schroteri Mörch, 1852:58 [refers to Schröter, 1783, pl. 3: fig. 7; holotype: ANSP 17599; type locality: Red Sea, Arabia].

Cerithium caeruleum Sowerby, 1855:866, pl. 179: figs. 61, 62 [lectotype, herein selected: BMNH 19862841, 33 mm; 5 paralectotypes BMNH 19862842-6, type locality: Red Sea]; 1865, pl. 2: fig. 8.—Tryon, 1887:127, pl. 22: figs. 55, 56.—Jousseaume, 1930:282.—Moazzo, 1939:170.

Cerithium coeruleum [sic] Sowerby.—Kobelt, 1891:84–85, pl. 16: figs. 5, 6.

Cerithium caeruleum var. *minima* Fischer and Vignal in Fischer, 1901:109, pl. 4: fig. 8 [holotype: MNHNP, no number; type locality: Djibouti; 21 mm].

Clypeomorus caeruleum (Sowerby).—Taylor and Reid, 1984:201.

DESCRIPTION.—*Shell* (Figures 21, 22A–K): Shell large, solid, stocky, knobby, reaching 41.5 mm length and 19.2 mm width, and comprising 8–12 angulate, nodulose whorls. Protoconch 1 (Figure 22K) comprising 1.5 smooth whorls; protoconch 2 with sinusigeral notch and final 2 whorls sculptured with subsutural plicae and 3 fine, spiral lirae. Early teleoconch whorls (Figure 19F) sculptured with 2 or 3 spiral cords, numerous fine spiral lirae, and weak axial ribs. Adult teleoconch whorls angulate, sculptured with numerous spiral lirae separated by incised spiral lines, fine, colabral axial lines, and with two dominant spiral cords; small, beaded, belt-like, subsutural cord, and very large, nodulose, median cord. Median spiral cord of penultimate whorl with 8–12 large nodes and wide sutural ramp. Nodes sometimes spiny and axially drawn out. Suture slightly impressed. Body whorl large, wide, elongate, with weak siphonal constriction. Body whorl microsculpture same as on adult whorls, but with 4 or 5 major nodulose, beaded, or nearly smooth, spiral cords. Aperture ovate, a little more than one third the shell length. Columella concave with moderate thick callus. Anterior siphonal canal short, strongly reflected to left of shell axis. Anal canal deep, defined by parietal columellar plait. Outer lip thick, angulate, folded into weak inner denticles. Shell color grayish blue flecked with white; nodes black, early whorls white. Measurements (Table 13). Periostracum tan. Operculum dark brown, thick.

Radula (Figure 23): Type-1 radular ribbon robust, long, about one-fifth the shell length. Rachidian tooth (Figure 23D) squarish; basal plate with pair of posterior lunule-shaped ridges and weak, central, posterior projection. Cutting edge of rachidian with large, triangular, pointed main cusp, flanked on either side by two, sometimes three, blunt, very small denticles. Lateral tooth (Figure 23A,B) with basal plate having large central ridge with pustule on central-basal portion of ridge and long, narrow outer posterior extension. Cutting edge of lateral tooth with large triangular major cusp, one inner flanking denticle and 2 or 3 outer flanking denticles. Marginal teeth (Figure 23A,B) with wide shafts, narrow bases, and curved, hooked, blade-like apices bearing long pointed tips. Inner marginal tooth with 2 or 3 inner flanking denticles and 1 or 2 outer, flanking denticles; outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Osphradium extending length of ctenidium, not turning away from ctenidium at inhalant siphonal canal. Type-A pallial oviduct (Figure 4A). Paired salivary glands tightly lying mostly anterior to nerve ring on each side of buccal mass, but originating behind and passing through nerve ring.

SYNONYMIC REMARKS.—In the literature, this species is most commonly called *Cerithium caeruleum* Sowerby, 1855,

FIGURE 21.—*Cerithium caeruleum* Sowerby, figuring type specimens of synonymous taxa: A, lectotype of *Cerithium tuberculatum* (Linné), Red Sea, 33.2 mm (MHNG 1097/37); B, lectotype of *Cerithium caeruleum* Sowerby, Red Sea, 33 mm (BMNH 1986284/1); C, holotype of *Cerithium caeruleum* var. *minima* Fischer and Vignal, Djibouti, 21 mm (MNHNP); D, paralectotype of *Cerithium caeruleum* Sowerby, Red Sea, 37.1 mm (BMNH 1986284/1); E, holotype of *Cerithium schroteri* Mörch, Arabia, (ANSP 17599).

but it is clearly evident from examination of the lectotype of *Cerithium tuberculatum* Lamarck, 1822 (Figure 21A), that the two taxa are conspecific and that Lamarck's name has priority. However, Lamarck's taxon is a secondary homonym of *Strombus tuberculatus* Linné, 1758 (not *Strombus tuberculatus* Born, 1778). Bruguière (1789:15) subsequently combined Linné's name, *tuberculatus*, with the genus *Cerithium*. The taxon, *Strombus tuberculatus* Linné, has a complex synonymic history and is here regarded as a nomen dubium (for more detailed discussions, see Dodge, 1956:289–290 and Houbrick, 1978c:645; 1985:74). The next available and valid name is *Vertagus schroteri* Mörch, 1852, of which the holotype (Figure 21E) is conspecific with Lamarck's *Cerithium tuberculatum* and which has the same type locality. The little-known name, *schroteri*, has never been applied to this species by subsequent authors. *Cerithium caeruleum* Sowerby, 1855 (Figure 21B) is the next available name and the one commonly used for this species. Rather than strictly apply the principal of priority and disturb stability, I prefer to use Sowerby's (1855) name, *caeruleum*, and am referring the case to the Commission for a ruling (Art. 79c, Code). A more complete synonymy of *Cerithium caeruleum* is presented by Moazzo, 1939:170. The varietal name *minima*, was proposed by Fischer and Vignal in Fischer (1901:109) for a small, beach-worn specimen (Figure 21C), which is herein regarded as a synonym.

ECOLOGY.—This species usually occurs in large populations on intertidal rocky shelfs with a thin covering of sediment, and is frequently mentioned in ecological studies. Yaron (1979:235) and Mastaller (1979:46) recorded it to be common in the upper intertidal zone on beach stones and slabs in the

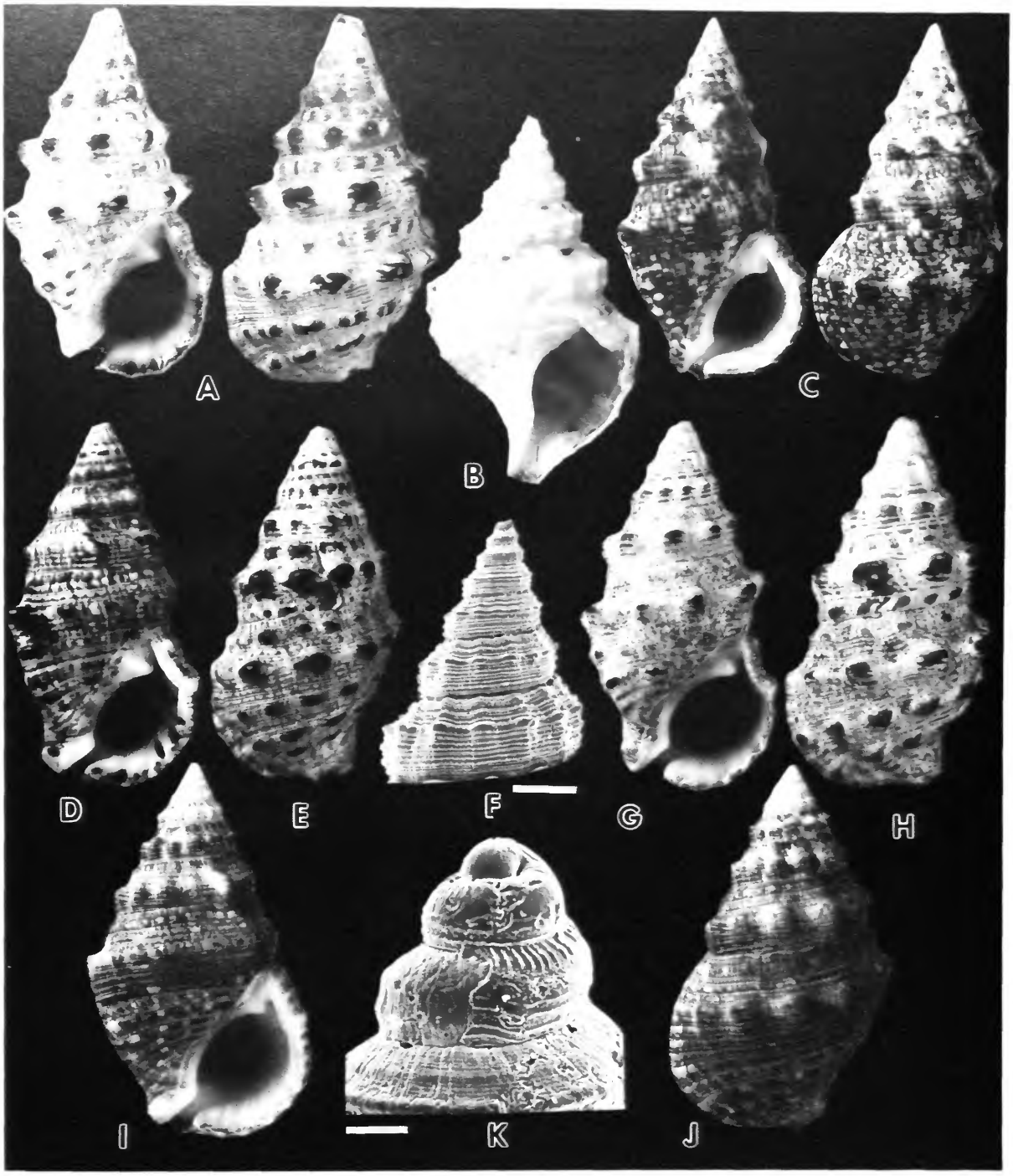


FIGURE 22.—*Cerithium caeruleum* Sowerby, showing morphological diversity: A, apertural and abapertural views of typical, nodulose phenotype, Uroa, Zanzibar, 34.8 mm (USNM 597267); B, immature shell, Port Sudan, Sudan, 7.3 mm (BMNH); C, apertural and abapertural views of weakly sculptured phenotype, Muscat, Oman, 30.5 mm (USNM 798220); D,E, Nossi Satrana, near Tulear, Madagascar, 35.6 mm (USNM 776772); F, SEM of early whorls (bar = 0.15 mm); G,H, apertural and abapertural views, N of Halieb, Egypt, 35.1 mm (USNM 788168); I,J, apertural and abapertural views of weakly sculptured phenotype, Muscat, Oman, 26.8 mm (USNM 798220); K, SEM of protoconch (bar = 68 μm).

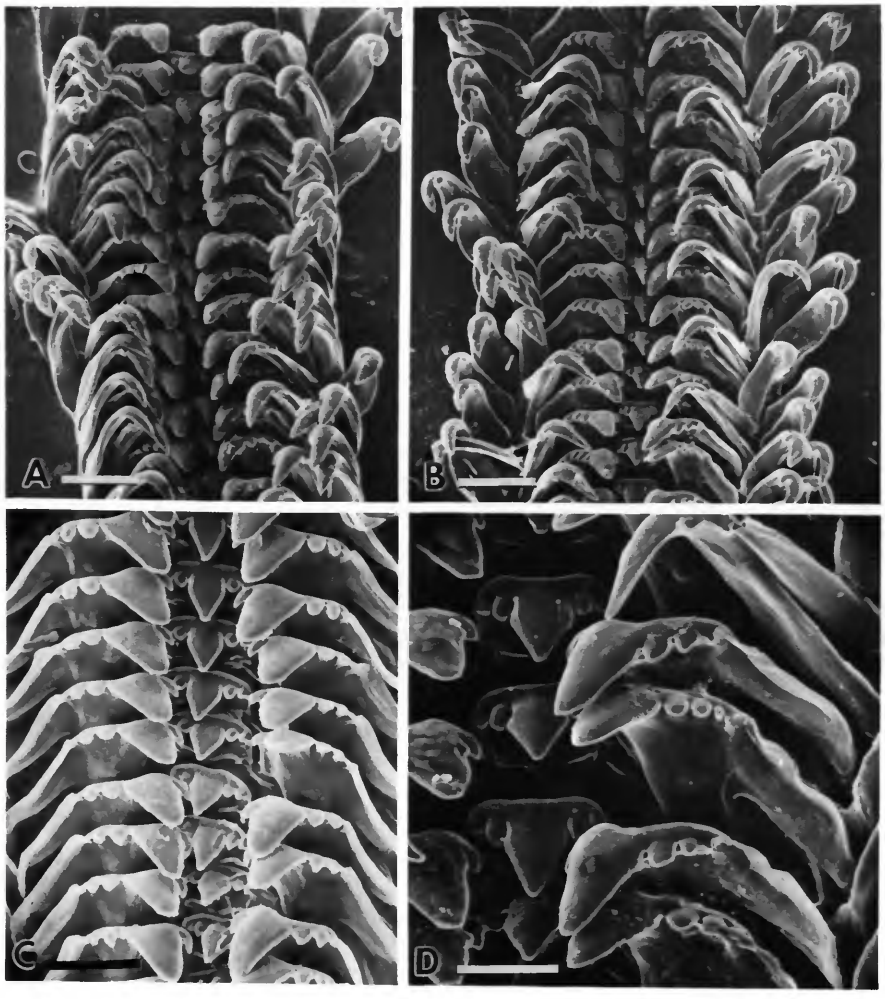


FIGURE 23.—Radula of *Cerithium caeruleum* Sowerby, SEM: A,B, part of ribbon showing marginals in natural retracted position (A), and folded back to expose other teeth (B), Dahab, Gulf of Aqaba (bar = 200 μm; AMNH); C, detail of rachidian and lateral teeth, Tulear, Madagascar (bar = 200 μm; USNM 708775); D, detail of rachidian and lateral teeth, Dahab, Gulf of Aqaba (bar = 50 μm; AMNH).

Gulf of Aqaba. Ayal and Safriel (1981:62) found populations with densities as high as 300 per m^2 along the Sinai coast, while Taylor and Reid (1984:190) recorded densities up to 54 per m^2 near Port Sudan, Sudan. Chelazzi and Vannini (1980:576–577) documented its vertical zonation and algal associations on intertidal rocky platforms in southern Somalia. A comprehensive account of the ecology of *C. caeruleum* occurs in Ayal and Safriel (1982a:308), who studied cerithiid habitats in the Sinai peninsula, Red Sea. They recorded that *C. caeruleum* lived to the lee of wide platforms in solution basins and tidal pools on surfaces covered with sediment, and was very active during ebbs, but aggregated or burrowed during flows. *Cerithium caeruleum* occurs along a wide range of environmental gradients and occupies a wide vertical range. It lives above a wide band of *Clypeomorus petrosa gennesi* (cited as *Cerithium tuberculatum*) and below *Clypeomorus bifasciata* (cited as *Clypeomorus moniliferum*). (A table, Ayal and Safriel, 1982a:310, table 2, documents the varied, intertidal, sediment-covered substrates that comprise the habitat of this species.) Fish-foraging appears to be responsible for the habitat segregation observed in *C. caeruleum* (Ayal and Safriel, 1982a:314). In the Gulf of Aqaba, Hulings (1986:323) recorded its occurrence in the *Tetraclita* (mid-littoral) zone on smooth, fossil reef bottoms and other slabs having a sand cover. In this environment, the vertical zonation of *Cerithium caeruleum* was between *Clypeomorus bifasciata* (Sowerby, 1855) and *Clypeomorus petrosa gennesi* (Fischer and Vignal, 1901), respectively.

TABLE 13.—Shell morphometrics of *Cerithium caeruleum*.

Character	$\bar{x}$ (n = 16)	sd	v	Range
Shell length	33.4	4.7	22.1	25.4–41.5
Shell width	16.9	2.0	3.9	12.1–19.2
Aperture length	13.2	1.9	3.5	10–16
Aperture width	9.4	1.3	1.7	7–11.4
Number whorls	9.3	1.2	1.4	8–12
Number spiral cords	2.2	0.4	0.2	2–3
Number axial ribs	10.1	1.2	1.4	8–12

The egg capsules of *C. caeruleum* each have a diameter of 150 μm, and there is an incubation period of 4–5 days prior to hatching (Ayal and Safriel, 1982b:399). Reproductive studies and growth statistics calculated by Ayal and Safriel (1982b: 395) provide evidence that this species lives from 90 to 120 days in the plankton and has a seven-year life history.

According to Ayal and Safriel (1982a), foraging fish are the major predators of juvenile *Cerithium caeruleum* in the Sinai Red Sea. Taylor and Reid (1984:190) found the muricid, *Muricodrupa funiculus*, to be the major predator of adult populations in the Sudanese Red Sea. They observed that aggregative feeding by *Muricodrupa* on adults of *C. caeruleum* was common, with as many as five predators being involved. Adult prey were attacked through the aperture, while smaller individuals were usually drilled through the spire. Due to the thick outer lip and heavily armored shell, it is unlikely that adults can be eaten by most crabs.

Examination of the protoconch (Figure 22K) shows a sinusigeral notch and sculpture indicative of planktotrophy. Hulings (1986) found the sex ratio of males to females in a Gulf of Aqaba population to be 1:6. The major period of reproduction was from April through August. The pale yellow egg masses are arranged in a continuous linear series of tightly folded strings measuring 4 mm high and 50 mm long, and are deposited on clumps of algae or pebbles. Individual egg capsules, 0.15 mm in diameter, contain a zygote 0.09 mm in diameter and are suspended in a gelatinous matrix. Free swimming veligers hatched within 4 to 6 days following deposition (Hulings, 1986:323).

Ritte and Pashtan (1982) have documented high levels of genetic polymorphism in populations of *C. caeruleum* from the Red Sea.

DISCUSSION.—This common intertidal species is confined to east Africa, Madagascar, and the Arabian peninsula and is unlikely to be confused with any other *Cerithium* species. It is distinguished by its squat, knobby shape; and as indicated by its name, *caeruleum*, a grayish blue color with spiral rows of black tubercles.

The overall shape and sculpture of *C. caeruleum* are much like those seen in members of the genus *Clypeomorus* Jousseaume, and several authors have assigned this species to *Clypeomorus* (Taylor and Reid, 1984:201), but the resemblance is superficial, as pointed out earlier in this monograph. *Cerithium caeruleum* is generally much larger than most *Clypeomorus* species. In size and overall morphology, it most closely resembles the sympatric species, *Clypeomorus petrosa gennesi* (Fischer and Vignal, 1901), which is also an intertidal, hard-substrate species. However, *Cerithium caeruleum* is larger, less pupiform, lacks the whorl sculpture of three tightly beaded spiral cords, and is distinctly more angulate in outline than *Clypeomorus petrosa gennesi*. There are also significant differences in the radulae of these two species (see discussion of *C. petrosa gennesi* in Houbrick, 1985:81–82). There is a remarkable convergence in shell morphology between *Cerithium caeruleum* and the batallariid, *Batillaria sordidia* (Gmelin, 1791), family Potamididae. The overall color and shell sculpture of *Cerithium caeruleum* are very close to those observed in *Batillaria sordida* (see Houbrick, 1978c, for discussion and figures of *B. sordida*). These two taxa have been confused in the past, and consequently the range of *Cerithium caeruleum* has been erroneously recorded to include China (E.A. Smith, 1891:416). The two species are widely allopatric, *B. sordida* being confined to the Pacific coast of China.

Intraspecific morphological variation occurs in shell size and strength of sculpture. Due to the harsh intertidal environment, protoconchs are normally eroded, as is much of the shell sculpture. The largest specimens I have seen are from Zanzibar and northwestern Madagascar, while the smallest ones came from the Persian Gulf, where the shells were more slender and less knobby than typical. Some morphs are quite knobby (Figure 22A,E,H) while others may be smoother, especially on the body whorl (Figure 22C,I,J). Immature specimens (Figure 22F) are fusiform with large, wide body whorls and resemble immature specimens of *Cerithium echinatum* Lamarck.

FOSSIL RECORDS.—Abrard (1942:60, pl. 6: fig. 24) recorded this species from the Pleistocene of Obock, Somalia.

GEOGRAPHIC DISTRIBUTION (Figure 24).—This species is confined to the continental margins of the western Indian Ocean where it is found as far south as Natal and Madagascar. It also occurs on Aldabra Atoll and in the Red Sea and Persian Gulf, extending eastward to the coasts of Pakistan and western India.

SPECIMENS EXAMINED.—EAST AFRICA: Durban, Natal, South Africa (BMNH, NM 6576, USNM 380891); Inhambane, Mozambique (NM F9460); SW Conduncia Bay, S of Choca, Mozambique (NM H1883); Ilha Rolas, Mozambique (AMS C127491); Mboa Maji, Tanzania (USNM 703950); Ras Mjimwema at Magogoni, Tanzania (USNM 703876); 2.4 km NW of Magogoni, Eastern Prov, Tanzania (AMS C100042); Ras Msimbazi Bay, Dar es Salaam, Tanzania (USNM 703919); Oyster Bay, 3 km N of Dar es Salaam, Tanzania (AMS); Oyster Bay, 6.4 km N of Dar es Salaam, Tanzania (USNM 703802); NW corner of Mbudya Id, 16 km N of Dar es Salaam, Tanzania (AMS C115925, C123796); Dar es Salaam (BMNH); N reef, Dar es Salaam (ANSP); Tanga, Tanzania (ANSP); Dembiani, 3.2 km N of Kizimkazi, SW Zanzibar (ANSP); Fumba, SW

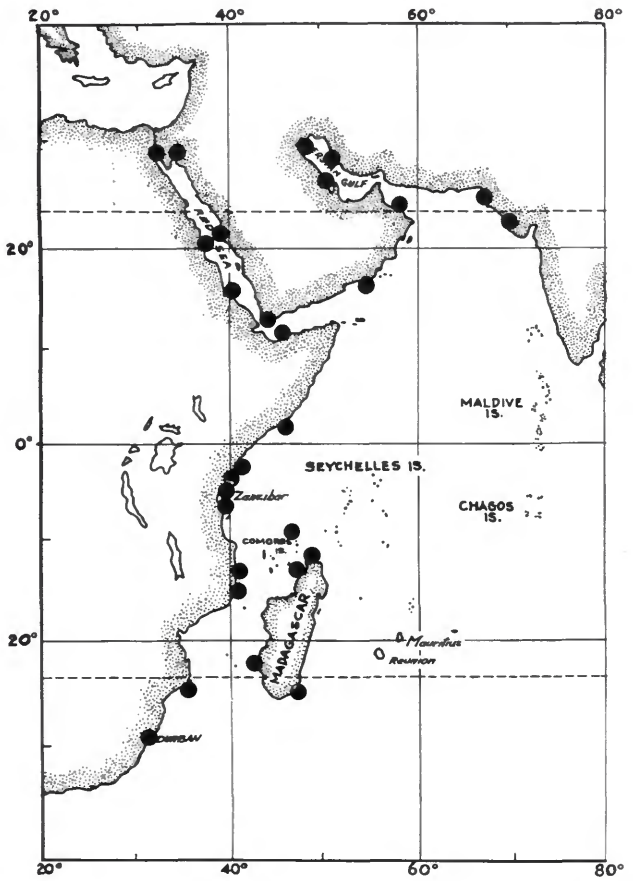


FIGURE 24.—Geographical distribution of *Cerithium caeruleum* Sowerby.

Zanzibar (ANSP); 3.2 km N of Fumba, SW Zanzibar (AMS); Pange Id, Zanzibar (ANSP); Bawe Id, Zanzibar (USNM 597195); Chango Id, W Zanzibar (AMNH); Kibweni, W Zanzibar (BMNH); Uroa Zanzibar (USNM 597267); Chwaka, E Zanzibar (ANSP); Diana Beach, Kenya (USNM 604257); SE pt, off Nyal Estates, Mombassa, Kenya (ANSP); Twige, Mombassa, Kenya (ANSP); Mombassa, Kenya (BMNH, USNM 604676); Kiziti Id, S of Shimoni, Kenya (AMS C117198); Shimoni, Kenya (AMNH); 6.4 km SE of Gedi, Kelifi District, Kenya (AMNH); Malindi, 121.6 km N of Mombassa, Kenya (USNM 595119); Malindi, Kenya (ZMA); 30 km SW of Mogadiscio, Somalia (AMNH); Mogadiscio, Somalia (USNM 673808); 14 km N of Mogadiscio, Somalia (ANSP).

RED SEA: Suez, Egypt (USNM 77357); Gulf of Suez, Egypt (USNM 23073); Abu-Zenima, Gulf of Suez, Egypt (USNM 798127); A-Tur, Gulf of Suez, Egypt (USNM 794190); 64 km S of Suez, Egypt (USNM 793767); 32 km N of Halieb, Egypt (USNM 788168, 797706); Dahab, Gulf of Aqaba, Egypt (USNM 794182); Ras Abu Galum, Gulf of Aqaba, Egypt (USNM 794176); Ras-Burka, Gulf of Aqaba, Egypt (USNM 794185); Eilat, Gulf of Aqaba, Israel (USNM 671281); Aqaba, Israel (AMNH, ANSP); Nuweiba, Sinai, Israel (AMS); Aqaba, Gulf of Aqaba, Jordan (USNM 841318); Mersa Ar-Rakiyai, 60 m N of Pt Sudan, Sudan (BMNH); Port Sudan, Sudan (USNM 770722); fringing reef by lighthouse, Port Sudan, Sudan (AMNH, BMNH); Abiad Bay, Entedebir Id, 50 km S of Massawa, Ethiopia (ANSP); Entedebir, Eritrea, Ethiopia (USNM 672283); Gubat Ashra Reef, 8 km N of Jidda, Saudi Arabia (USNM 591777); Jidda Harbor, Saudi Arabia (USNM 637025); near Jidda, Saudi Arabia (USNM 852250). GULF OF ADEN: Ras Boridly, Aden (ANSP); Bandar Sheikh Lil', Aden (USNM 679408); Berbera, Gulf of Aden, Somalia (USNM 133618, 133630).

ARABIAN SEA: Salalah, Dhofar Prov, Oman (AMNH). PERSIAN GULF: Kuwait (BMNH, USNM 618441); Injifa Shore, near Kuwait (USNM 796234); Ras Tanura, Saudia Arabia (USNM 636996); Bushire, Iran (BMNH). GULF OF OMAN: Muscat, Oman (AMNH, USNM 657374, 798220); Omani Beach, Muscat, Oman (AMS C124946); Mina al Fahal, 64 km W of Muscat, Oman (AMS); Ras al Hamra, Oman (NM G1419). MADAGASCAR: Baie d'Ambare (USNM 776772); Ambariobe, Nossi Bé (USNM 719905); Nossi Tanikely, 6.4 km S of Nossi Bé (ANSP); Nossi Ve Id, SSW of Tulear (USNM 708775, 709418, 862320, 862321, 862322, 862323); Nossi Ve, 32 km SSW of Tulear (AMS C100094); Nossi Satrana, SSW of Tulear (USNM 708664); Nossi Satrana, 40 km SSW of Tulear (AMS C137159); bay, S side of Nossi Iranja, 51.2 km SW of Nossi Bé (AMS C171836); N of Ambovombe (AMNH); Ft Dauphin (WAM). INDIAN OCEAN ISLANDS: Île Picard, Aldabra Atoll, Seychelles (USNM 837622). PAKISTAN: Karachi (AMNH); Manora Beach, Sind (USNM 605738). INDIA: Okha, Gujerat (AMNH); N side of Akha Pt, Gulf of Kutch (ANSP).

Cerithium citrinum Sowerby, 1855

FIGURES 25–27

Cerithium citrinum Sowerby, 1855:855–856, pl. 79: fig. 66 [lectotype, herein selected: BMNH, 19861681; 2 paralectotypes 198616823; type locality: Masbate, Philippines]; 1865, pl. 1: fig. 1.—Tryon, 1887:123, pl. 20: figs. 21, 23.—Kobelt, 1893:110–111, pl. 27: figs. 2, 3.—Kira, 1962:27, pl. 13: fig. 21.—Springsteen and Leobrera, 1986:59, pl. 13: fig. 4.

DESCRIPTION.—*Shell* (Figure 25): Shell tall, turreted, comprising 13–17 inflated whorls and reaching 50 mm length and 19.6 mm width. Protoconch unknown. Early teleoconch whorls purplish blue. Adult teleoconch whorls sculptured with broad, inflated, colabral axial ribs; 8–11 ribs on penultimate whorl. Each whorl with about 13 overriding, thin, spiral threads and deeply incised spiral lines. Numerous microscopic spiral lirae and incised lines overlying larger spirals. Suture deeply incised. Body whorl wide, with weak axial ribs except for varix opposite outer lip of aperture. Base of body whorl excavated by

FIGURE 25.—*Cerithium citrinum* Sowerby, showing phenotypic variation: A, lectotype of *Cerithium citrinum*, Masbate, Philippines, 38.1 mm (BMNH 19861681); B-E, Wheeler Reef, NE of Townsville, Queensland, Australia, 38.1 mm (AMS C117182); F, Batt Reef, E of Port Douglas, Queensland, Australia, 40.2 mm (AMS C117181); G, N of Vunu Pt, Tavenui, SW Fiji, 41.1 mm (USNM 695629); H, Centipede Reef, NE of Townsville, Queensland, Australia, 29.7 mm (AMS); I, Lizard Id, Queensland, Australia, 38.9 mm (USNM 766738).

strong siphonal constriction, sculptured with numerous spiral lirae. Aperture ovate, about one-fourth the shell length. Columella concave with thick columellar callus and distinct columellar lip. Anterior canal very long, tubular, thin, reflexed and slightly twisted to left of shell axis. Outer lip highly inflated, thickened at edge, strongly crenulated, with many internal denticles and strong tooth at base of outer lip, adjacent to canal. Anal canal well developed, flanked by distinct parietal columellar tooth extending well into aperture. Shell color white-lemon to darker yellow, especially on axial ribs, sometimes with diffuse brown blotches. Anterior canal frequently brown or dark blue, especially at anterior. Aperture usually bright yellow. Measurements (Table 14). Periostracum not evident. Operculum corneous, thin, dark tan and with eccentric nucleus.

Radula (Figure 26): Type-1 radular ribbon (Figure 3A) small, about one-twelfth the shell length, comprising about 60 rows of teeth. Rachidian tooth (Figure 26B-D) rectangular-hexagonal with pair of posterior basal ridges and weak, median, posterior projection on basal plate; top of rachidian convex with cutting edge having chisel-shaped central cusp flanked on each side by two pointed denticles. Lateral tooth (Figure 26D)

TABLE 14.—Shell morphometrics of *Cerithium citrinum*.

Character	$\bar{x}$ (n = 15)	sd	v	Range
Shell length	38.9	7.4	54.5	27.6–50
Shell width	14.5	3.3	10.6	8–19.6
Aperture length	10.0	1.9	3.4	6.8–12.7
Aperture width	7.7	1.3	1.8	5.6–10.2
Number whorls	14.7	1.3	1.8	13–17
Number axial ribs	9.7	0.8	0.6	8–11

rhomboidal with large central posteriorly projecting buttress and long, posterior, lateral extension on basal plate; cutting edge with large pointed main cusp, one inner flanking denticle and 3 or 4 pointed, outer flanking denticles. Marginal teeth (Figure 26C) with wide shafts and tapering hook-like tips, serrated with slender, pointed denticles. Inner marginal tooth with blade-like central cusp, 3 inner flanking denticles and 3–5 outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Body flesh colored, flecked with brown. Snout long; foot long, narrow. Mantle edge lined with small papillae. Inhalant siphon thick, darkly pigmented within. Osphradium greenish brown near mantle edge. Ctenidium narrow, comprised of long triangular filaments. Hypobranchial gland white, with narrow, glandular, transverse ridges. Buccal mass large, jaws large. Type-A pallial oviduct (Figure 4A); anterior seminal receptacle of lateral lamina a very long tube, extending posteriorly to point opposite posterior seminal receptacle of medial lamina.

FIGURE 26.—Radula of *Cerithium citrinum* Sowerby, SEM, Lizard Id, Queensland, Australia (USNM 766738): A, ribbon with marginals folded back (bar = 0.14 mm); B, detail of rachidian and lateral teeth (bar = 38 μm); C, dentition of tips of marginals (bar = 43 μm); D, cusps of lateral teeth (bar = 43 μm).

SYNONYMIC REMARKS.—In the original description of *C. citrinum*, Sowerby (1855:855-856) pointed out that the shell figured by Kiener (1841, pl. 4: fig. 1) under the name *C. columna* Sowerby, was conspecific with it, and I am in agreement with him, as it looks very much like the lectotype of *C. citrinum* (Figure 25A). Tryon (1887:123) considered *C. siphonatum* Sowerby to be synonymous with *C. citrinum*, but the former is an elongate phenotype of *C. columna* Sowerby (see illustrations of *C. columna*, Figures 31-33). Tryon also cited *C. bicolor* Hombron and Jacquinot as a synonym, but that taxon is synonymous with *C. suturale* Philippi. Finally, Tryon (1887:123) suggested that *C. citrinum* and the synonyms he associated with it were "probably mere varieties of *C. columna*." I do not agree with Tryon (see "Discussion" below).

As may be seen above in the synonymy of *C. citrinum*, the species is not figured in many recent shell books and is not well known. It is frequently misidentified as *Cerithium columna* Sowerby or *C. rostratum* Sowerby in private collections and museums.

ECOLOGY.—*Cerithium citrinum* is not a common species and does not appear to occur in large populations as do many other cerithiids. Museum records indicate that it occurs subtidally in lagoons and back reefs among patches of sand and rubble associated with marine angiosperm grass beds.

DISCUSSION.—The distinguishing characters of this species are a long, thin, twisted anterior canal, a slender, gracefully formed, lemon-yellow shell sculptured with broad, inflated axial ribs and overriding spiral threads and incised spiral lines. This species most closely resembles *Cerithium rostratum* Sowerby, which is a much smaller species that has wider, beaded, spiral bands and lacks an excavated shell base. *Cerithium citrinum* is also similar to some elongate phenotypes of *Cerithium columna* (Figure 31B,E; Figure 32A,B; Figure 33A,B), but does not have angulate whorls nor a beaded subsutural cincture; moreover, the radula of *C. columna* (Figure 34A-F) is entirely different from that of *C. citrinum* (Figure 26A-D).

The shell morphology of this species does not show much intraspecific variation (Figure 25A-I). Individuals from various parts of the range are all quite similar, although the spiral sculpture of the body whorl is stronger on specimens from the western Indian Ocean. There is more variation in color: some specimens are nearly white while other are intensely yellow. Some shells are more brown than yellow.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 27).—*Cerithium citrinum* occurs from East Africa, Madagascar, and southern India to Western Australia and is found throughout the Indian Ocean Islands. Although there are no records from Indonesia, it undoubtedly occurs there because there are also records from SE Asia; in the western Pacific, it is found from southern Japan south through the Philippines to Australia and throughout Melanesia as far east as Fiji. The one record from Hawaii needs reconfirmation.

SPECIMENS EXAMINED.—EAST AFRICA: Durban, South Africa (NM 1035, USNM 368022, 380889); Bazaruto Id, Mozambique (NM G4990); Mozambique (USNM 629032); Mozambique City, Mozambique (ANSP); NE Conducia Bay,

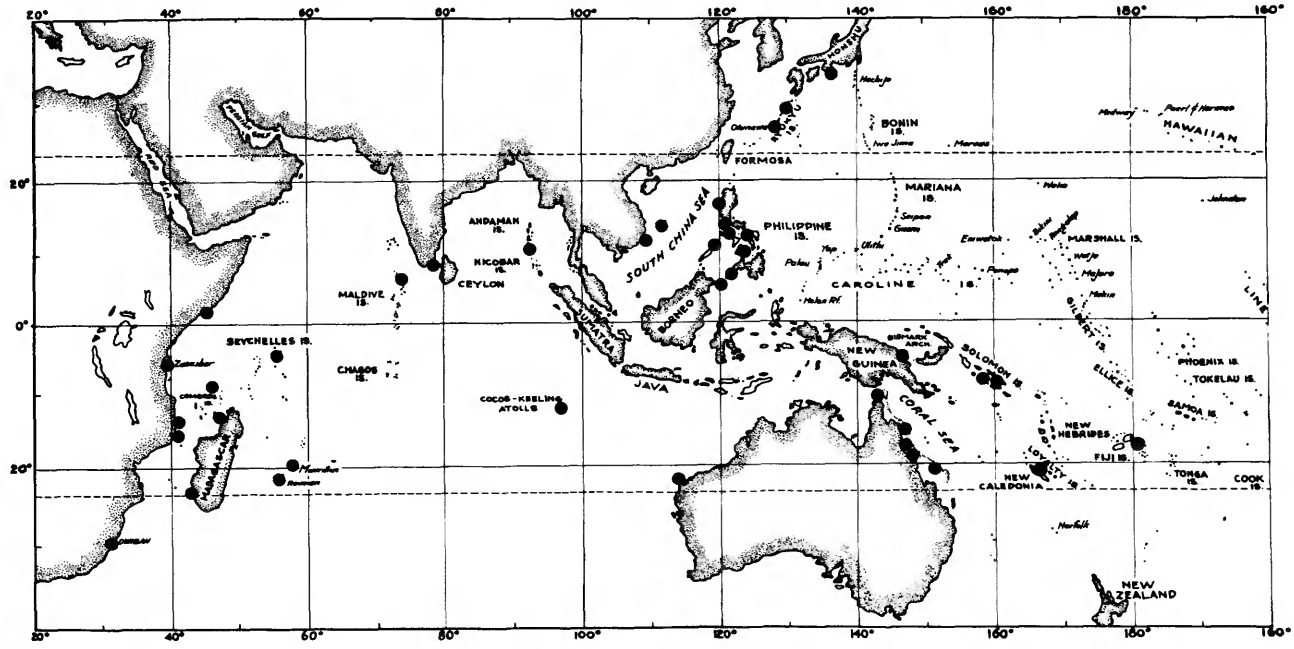


FIGURE 27.—Geographic distribution of *Cerithium citrinum* Sowerby.

Namalungo, Mozambique (NM H1868); Zanzibar (AMNH); Chango Id, W Zanzibar (ANSP); Kizimkazi, SW Zanzibar (ANSP); Mogadiscio, Somalia (USNM 862857). MADAGASCAR: 1.6–3.2 km S of Nossi Iranja, 51.2 km SW of Nossi Bé (ANSP); Tulear (MNHNP). INDIAN OCEAN ISLANDS: Île Malabar, Passe Houareau, Aldabra Atoll, Seychelles (USNM 837465); Aldabra lagoon, Aldabra Atoll, Seychelles (USNM 838349); Île Picard, Aldabra Atoll, Seychelles (USNM 837646, 837750, 837834, 837838, 837849); Mahé, Seychelles (BMNH); Mauritius (NMV); 58–70 m, 21°00′S, 55°15′E, off Reunion (MNHNP); S half of Kindikolu Id, Miladummadul Atoll, Maldives (ANSP); Cocos Keeling Ids (AMS); SW side West Id, Cocos Keeling Ids (USNM 656199).

INDIA: E Tuticorn (BMNH); Mannar (BMNH). ANDAMAN ISLANDS: Port Blair (BMNH). VIET NAM: Nha Trang, S Viet Nam (LACM 109992). S CHINA SEA: 54.8–91.4 m, Macclesfield Bank (BMNH 18944518). JAPAN: 2 m, intertidal, Cape Bansho-zaki, near Seto Marine Lab, Wakayama Pref, Honshu (LACM 82-19); Kii, Honshu (USNM 343863); Oshima, Osumi (USNM 343862). RYUKYU ISLANDS: Onna Village, Katabaru, Yakata, Okinawa (USNM not cataloged). PHILIPPINES: La Union Pt, Lingayen Gulf, Luzon (AMNH, USNM 634116); Baler Bay, Quezon Prov, Luzon (AMNH); Anirong, Polillo Gp, Quezon Prov, Luzon (LACM 76833); Bagac, Bataan Prov, Luzon (USNM 774973); Talaga Cove, Bataan Prov, SW Luzon (LACM 76787); Mataco Pt, Batangas Prov, SW Luzon (LACM 76834); Cubi Pt, Subic Bay, Luzon (USNM 842618); Lubang, Lubang Ids, Mindoro (LACM, MCZ); Cape Calavite, Mindoro (LACM 76836); Calapan, Mindoro (MCZ); Romblon Id, Tablas Ids (WAM); Cowit, Marinduke (AMS); Gaspar Id, Tres Reyes Gp, Marinduke (AMS); Cave Pt, N Samar (LACM 76909); Marintok-Mobo, Masbate, Masbate (AMNH); Punto Enganio, Mactan Id, Cebu (USNM 845807); Silino Id, Mindanao (USNM 244016); Zamboanga, Mindanao (USNM 233165, 713791); N Palawan (LACM 76832); Doc Can Id, Sulu Archipelago (WAM); Pearl Bank, near Zal Id, Sulu Archipelago (WAM); Laminusa, Sulu Archipelago (LACM 34709); Bongao Channel, SW end Sanga Sanga Id, Sulu Archipelago (ANSP).

WESTERN AUSTRALIA: Viaming Head Light, North West Cape (LACM 64-46); Pt Quobba (WAM 451-76). QUEENSLAND, AUSTRALIA: 9–15 m, Murray Id, Torres Strait (AMS); 3–6 m, NW tip of reef N of no. 5 bank reef, 13°40′S, 144°09′E (AMS); 16 m, N end of reefs off no. 5 bank reef, 13°46′S, 144°17′E (AMS); Lizard Id (USNM 766738); Low Isles, near Port Douglas (AMS C76027); 36.5 m, off Spur Reef, E of Norman Reef, N of Cairns (AMS); Batt Reef, E of Port Douglas (AMS C117181, AMS); NE Herald Cay, Coral Sea (AMS C69064); Wheeler Reef, NE of Townsville (AMS C117182); 11 m, N side of Wheeler Reef, NE of Townsville (AMS); Broadhurst Reef, E of Townsville (AMS); Centipede Reef, NE of Townsville (AMS); North West Id, Capricorn Gp (AMS); Lindeman Id, Whitsunday Passage (AMS); Frederick Reef (AMS); Fairfax Id, Bunker Gp (AMS C69053); Bowen (AMS); Green Id (AMS). NEW GUINEA: S end of Massas Id, Madang, Papua (AMS). SOLOMON ISLANDS: Tineti Pt, Florida Id (WAM); 7.5–33.0 m, Dry Sand Cay, S of Mbankia Id, Russell Ids, Central District, 9°09′S, 159°11.5′E (LACM 78-75). NEW CALEDONIA: Poindimie (AMS). FIJI: N of Vuna Pt, SW Taveuni (USNM 695629). HAWAII: Koloa, Kauai (LACM).

Cerithium claviforme Schepman, 1907

FIGURES 28–30

Cerithium claviforme Schepman, 1907:187–188, pl. 9: fig. 5, 5a [holotype: ZMA 3-06-003, 4 paratypes; type locality: Kajoe Ragi, Celebes, Indonesia: post-Tertiary].

DESCRIPTION.—*Shell* (Figure 28): Shell conical-ovate, solid, tapering, comprising 15 weakly inflated, knobby whorls and reaching 26.8 mm length and 12.8 mm width. Outline of early whorls slightly concave, becoming convex on central and adult whorls. Protoconch unknown. Early teleoconch whorls (Figure 28F) angulate, sculptured with strong, colabral, axial ribs and two spiral cords with broad subsutural ramp. Adult teleoconch sculptured with two adapical, major, spinose, beaded spiral cords, a thin presutural, beaded cord, and numerous spiral threads. Beads unite forming 11 or 12 axial plicae between major spiral cords, but usually not extending to suture on either side. Subsutural ramp marking limits of weak suture. Body whorl elongate, with varix opposite outer lip of aperture. Body whorl sculptured with four major beaded spiral cords; sometimes with weak central axial plications, and with numerous spiral threads, some enlarged and beaded. Shell base with weak siphonal constriction and numerous fine spiral threads. Aperture ovate, a little over one-third the shell length. Columella concave with slight columellar callus. Anterior siphonal canal short, turned slightly to left of shell axis. Anal canal well defined, marked by columellar parietal tooth extending well into shell aperture. Outer lip thickened at edge, enameled and nearly smooth, but with very weak crenulations and weak inner incised spiral lines. Shell color chestnut to light tan with white spirals, and darker brown spots on spiral cords. Beads white or brown. Anterior siphonal canal dark brown. Aperture and columella white to gold. Measurements (Table 15) Periostracum not evident. Operculum (Figure 28D) ovate, tan, paucispiral with eccentric nucleus, and with distinct attachment scar on obverse.

Radula (Figure 29): Type-1 radular ribbon (Figure 3A) short, one-ninth the shell length. Rachidian tooth (Figure 29B) triangular-square, with pair of posterior, lunule-shaped ridges and triangular posterior extension on basal plate. Cutting edge of rachidian with triangular, pointed main cusp flanked on each side by two small denticles. Lateral tooth (Figure 29A,B) having long posterior lateral extension and wide, long central buttress on basal plate. Cutting edge of lateral tooth with spade-shaped

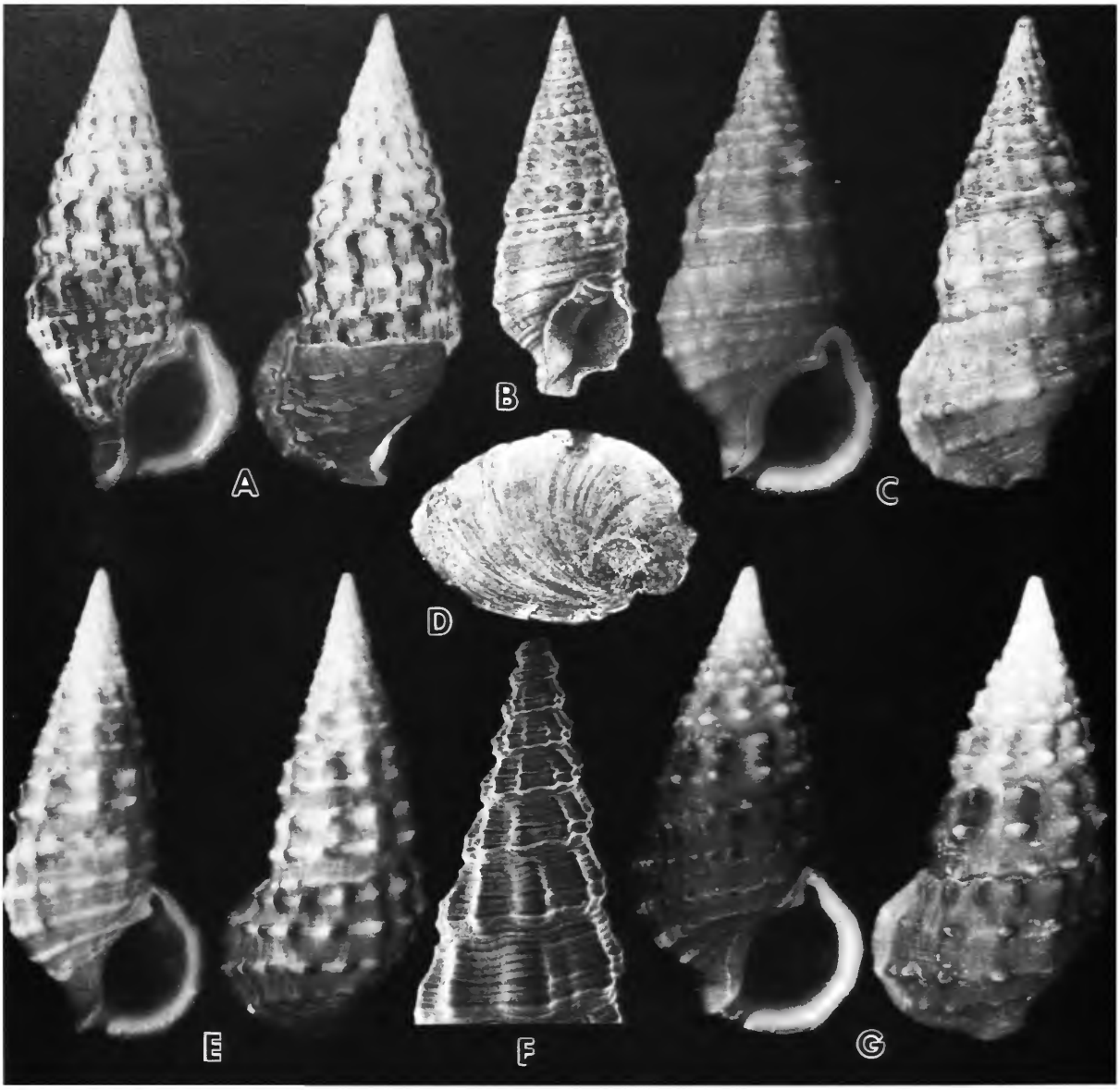


FIGURE 28.—*Cerithium claviforme* Schepman, showing morphological variation: A, Medren Id, Enewetak Atoll, Marshall ids, 31.5 mm (USNM 821796); B, holotype of *Cerithium claviforme*, Schepman, 1907, pl. 11: fig. 5; C, paratype of *Cerithium claviforme*, Kajoe Ragi, Celebes, Indonesia, late Tertiary, 24.2 mm (ZMA); D, operculum, Medren Id, Enewetak Atoll, Marshall Ids (USNM 828726); E, Palmyra Id, Line Ids, 31.3 mm (ANSP 315954); F, detail of early whorl sculpture and protoconch, SEM Korak Id, S Babelthuap, Palau (ANSP 203895); G, N end Kranket Id, Madang, Papua New Guinea, 21 mm (AMS C117187).

main cusp, one inner flanking denticle, and two outer flanking denticles. Marginal teeth (Figure 29A) with wide shafts and bases, and curved apices with blunt, spatulate tips. Inner marginal tooth with three inner flanking denticles and one outer flanking denticle. Outer marginal tooth same, but lacking outer flanking denticle.

Anatomy: Preserved animal cream colored with dusky gray, transverse lines and blotches. Mantle edge with long papillae and with very deep, inhalant siphonal notch creating posterior fold on left side of mantle. Mantle cavity organs typical of cerithiids, but anterior osphradium not separated from ctenidium near mantle edge. Pallial gonoducts unknown.

TABLE 15.—Shell morphometrics of *Cerithium claviforme*.

Character	$\bar{x}$ (n = 11)	sd	v	Range
Shell length	22.6	3.8	14.7	19.1–26.8
Shell width	10.4	1.6	2.7	7.1–12.8
Aperture length	6.3	1.2	1.5	3.7–7.8
Aperture width	4.5	0.9	0.8	2.6–5.3

SYNONYMIC REMARKS.—*Cerithium claviforme* is very poorly known and as seen in the synonymy above, has not been mentioned in the literature since its description. The holotype (Figure 28B) and four paratypes (Figure 28C) from Celebes are well colored, have shiny apertures, and appear to be Recent specimens, but as they are labeled "Posttertiair," they are probably subfossils.

ECOLOGY.—*Cerithium claviforme* lives at moderate subtidal depths in lagoons and passes associated with coral reefs. It has been taken by SCUBA divers on the ledges and walls of pinnacles in atoll lagoons. At Enewetak Atoll, it is not uncommon at night in these habitats (Scott Johnson, pers. comm.).

DISCUSSION.—This species is easily recognized by the concave outline of the upper whorls, the two rows of brown to white spiral beads, a distinctive chestnut color with white bands and brown spots, and by the yellow aperture. It may be confused with some phenotypes of *C. zonatum* Wood, but *C. zonatum* has more spiral cords and many sharp, spiny beads. *Cerithium claviforme* is also similar in shape to *C. pacificum*, new species. (Figure 100A–J), particularly in the concavity of its upper whorls.

Cerithium claviforme is not common in museum and private collections; consequently, the full range of variation is not well understood at this time. The sculptural pattern is fairly constant and varies only in the development of the minor spiral threads. The intensity of the brown-chestnut pigment and especially the spiral pattern of white bands and brown dots is quite variable. Throughout the range, the color of the aperture in freshly collected specimens is frequently bright yellow.

FOSSIL RECORDS.—The Indonesian type specimens (Figure 28B,C) are probably subfossils. There are no records of Recent specimens from Indonesia.

GEOGRAPHIC DISTRIBUTION (Figure 30).—This species occurs in the western Pacific from the Ryukyus south through the Philippines and western Carolines to Indonesia and New Guinea. It is also found in the central Pacific from the Marshall Islands east to the Line Islands.

SPECIMENS EXAMINED.—RYUKYU ISLANDS: 20–24 m, 26°20′48″N, 127°44′48″S, sea wall at Kadena Yacht Club Channel, Kadena, Okinawa (USNM 812931). PHILIPPINES: USBF Sta 5159, 18.3 m off Tinaka Id, Tawitawi (USNM 236267, 274224). INDONESIA: Kajoe Ragi, Celebes [fossil] (ZMA). NEW GUINEA: Duke of York Id, Papua (AMS); 3–6 m, inlet, N end of Kranket Id, Madang, Papua (AMS C117187). PALAU: 36.6–45.7 m, 1.6 km S of Korak Id, S Babelthuap (ANSP 203895). MARSHALL ISLANDS: 15 m, on ledge and cliff walls of Medren Pinnacle, Medren Id, Enewetak Atoll (USNM 821796, 828726, 828727); 10 m, pinnacle in Enewetak lagoon, Enewetak Id, Enewetak Atoll (USNM 821844); 54–60 m, Bikini lagoon, Bikini Atoll (USNM 862514, 862515). LINE ISLANDS: Palmyra Id (ANSP 22035, 315954, USNM 862516).

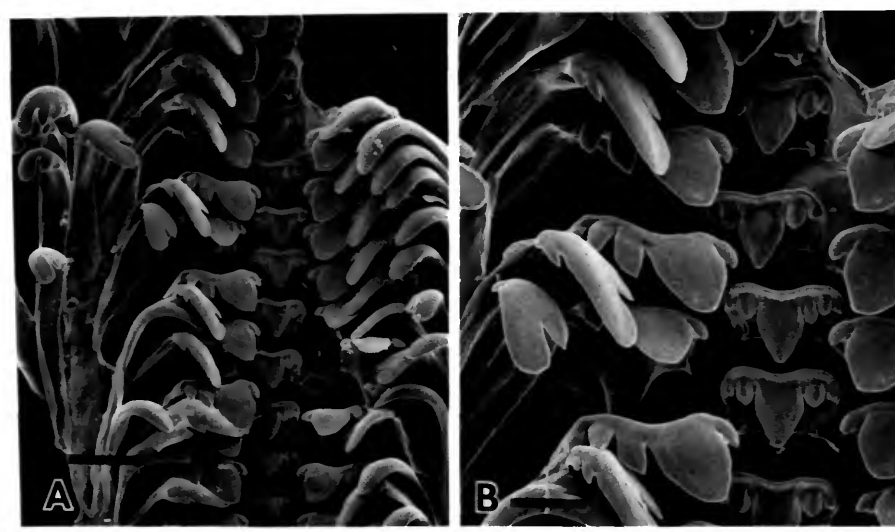


FIGURE 29.—Radula of *Cerithium claviforme* Schepman from Medren Id, Enewetak Atoll, Marshall Ids (USNM 828726): A, radula with left marginals folded back (bar = 37 μm); B, rachidian and lateral teeth (bar = 75 μm).

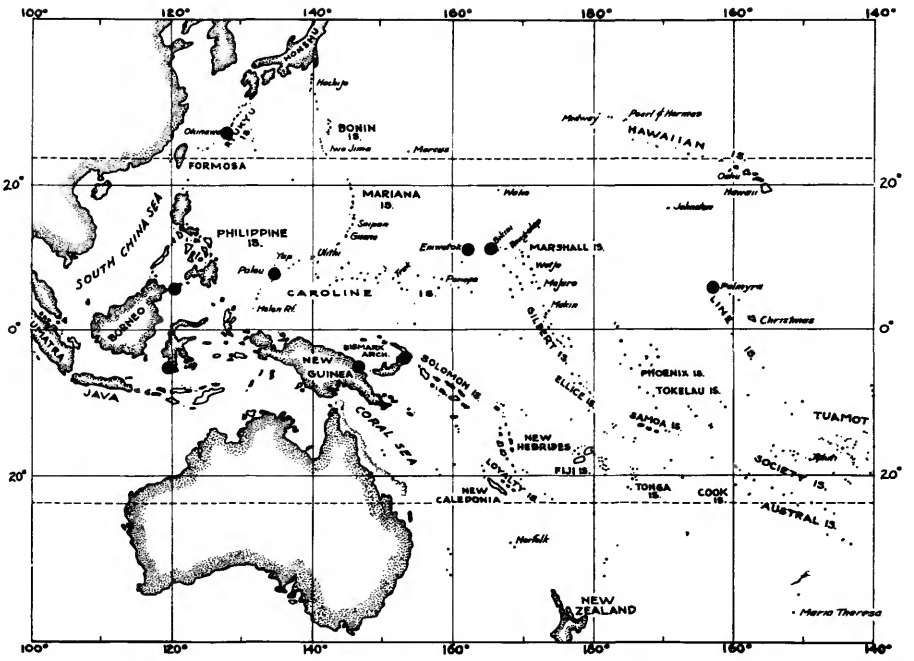


FIGURE 30.—Geographic distribution of *Cerithium claviforme* Schepman.

Cerithium columna Sowerby, 1834

FIGURES 31-36

Murex torulosa Linné, 1767:1226 [type not found; type locality not cited; nomen dubium].—Dodge, 1957:199-201.

Cerithium torulosum Bruguière, 1792:482 [2 probable syntypes MHNG 109736, larger selected as lectotype; type locality: not cited; 32 mm and 29.6 mm].—Lamarck, 1822:74-75.—Tryon, 1887:147, pl. 28: figs. 50, 52, 53.

Cerithium columna Sowerby, 1834:273, pl. 213: fig. 7 [neotype herein selected: BMNH 19862841, 40.2 mm, figured specimen of Sowerby (1855, fig. 56); type locality: Philippines]; 1855:855, pl. 178: figs. 55-58; 1865, pl. 1: fig. 2.—Tryon, 1887:123, pl. 20: figs 17-20.—Kobelt, 1891:85, pl. 16: figs 7, 8.—Salvat and Rives, 1975:268, fig. 60.

Cerithium torulosum (Linné).—Sowerby, 1855:857, pl. 179: fig. 64; pl. 180: fig. 92 [fig. 64 is not *Cerithium torulosum* Bruguière, 1792].—Deshayes, 1863:95.—Salvat and Rives, 1975:269, fig. 64.

Cerithium fusiforme Sowerby, 1855:862, pl. 180: figs. 16, 17 [holotype: BMNH 1986170; type locality: Philippines, 22.2 mm]; 1865, pl. 8: fig. 47.—Tryon, 1887:130 [not *Cerithium fusiforme* Leymerie, 1844].—Springsteen and Leobrera, 1986:62, pl. 13: fig. 18 [not *Cerithium fusiforme* Sowerby, 1855; is *Cerithium lissum* Watson, 1880].

Cerithium menkei Deshayes, 1863:97, pl. 38 [incorrectly cited on p. 97 as pl. 11]: fig. 15 [holotype not located, Deshayes' fig. 15 herein selected to represent lectotype; type locality: Reunion, 23 mm × 10 mm].—Tryon, 1887:123, pl. 20: fig. 19.

Cerithium siphonatum Sowerby, 1865, pl. 13: fig. 90a,b [holotype: BMNH 1986182; type locality, not cited; 17 mm × 7 mm].—Tryon, 1887:123, pl. 20: fig. 23.—Kobelt, 1893: 127, pl. 24: figs. 4, 5.

Cerithium sandvichense Sowerby, 1865, pl. 6: fig. 37a,b [holotype: BMNH 1986179; type locality: Sandwich Islands (Hawaii); 28 mm × 12 mm]; 1866, supplementary plate, pl. 12: fig. 305.—Tryon, 1887:127, pl. 22: fig. 58.—Kobelt, 1895:184, pl. 34: figs. 4-5.—Salvat and Rives, 1975:269, pl. 62.—Rehder, 1980:36, pl. 6: fig. 3.

Vertagus torulosus Sowerby, 1865, pl. 5: fig. 25a,b [type not found, Sowerby's fig. 25b herein selected to represent lectotype; type locality: Society Islands).

Cerithium cylindraceum Pease, 1869:77 [holotype: ANSP 17703; type locality: Paumotus; 25.8 mm - 8.1 mm].

Cerithium sculptum Pease, 1869:77, pl. 8: fig. 8 [holotype: ANSP 17592; type locality: Paumotus; 31 mm × 12.8 mm].—Tryon,1887:125, pl. 21: fig. 37.

Cerithium proditum Bayle, 1880:246 [new name for *Cerithium fusiforme* Sowerby, 1855; not *Cerithium proditum* Bayle, 1880:249].

Cerithium citrinoide Kobelt, 1893:122-123, pl. 23: figs. 6, 7 [holotype: SMF 228-197; type locality: Philippines; 38.5 mm × 13.3 mm].

Cerithium peasi Dautzenberg and Bouge, 1933:310 [new name for *Cerithium cylindraceum* Pease, 1869].

Cerithium munitoides Habe, 1964:43, pl. 13: fig. 1 [holotype: NSMT 54852, paratype NSMT 54853; type locality: Okinoerabu-shima, Kagoshima, Kyushu, Japan; 18.8 mm × 6.8 mm].

Cerithium (Cerithium) salebrosum Sowerby.—Ladd, 1972:37, pl. 9: fig. 12 [not *Cerithium salebrosum* Sowerby, 1855; is *Cerithium columna* Sowerby, 1834].

Cerithium (Thericium) salebrosum Sowerby.—Ladd, 1972:39, pl. 9: fig. 12 [not *Cerithium salebrosum* Sowerby, 1855; is *C. torulosum* Linné, 1767].

Cerithium (Cerithium) aff. *C. columna* Sowerby.—Ladd, 1972:39, pl. 10: fig. 2 [not *Cerithium columna* Sowerby, 1834; is *Cerithium munitum* Sowerby, 1855].

DESCRIPTION.—*Shell* (Figures 31-33): Shell turreted, fusiform, broad or slender, comprising 9-13 highly angulate to straight-sided whorls frequently dorso-laterally flattened. Shell reaching 50 mm length and 20.8 mm width. Protoconch (Figure 33H) comprises 3 whorls and with deep sinusigeral notch at lip edge; protoconch 1, comprising 1 smooth whorl; protoconch 2, red-brown with strong, buttress-like, subsutural, axial plicae and two spiral threads and interspace with microscopic chevron-shaped axial riblets crossing anterior spiral thread. Early teleoconch whorls sculptured with many finely incised

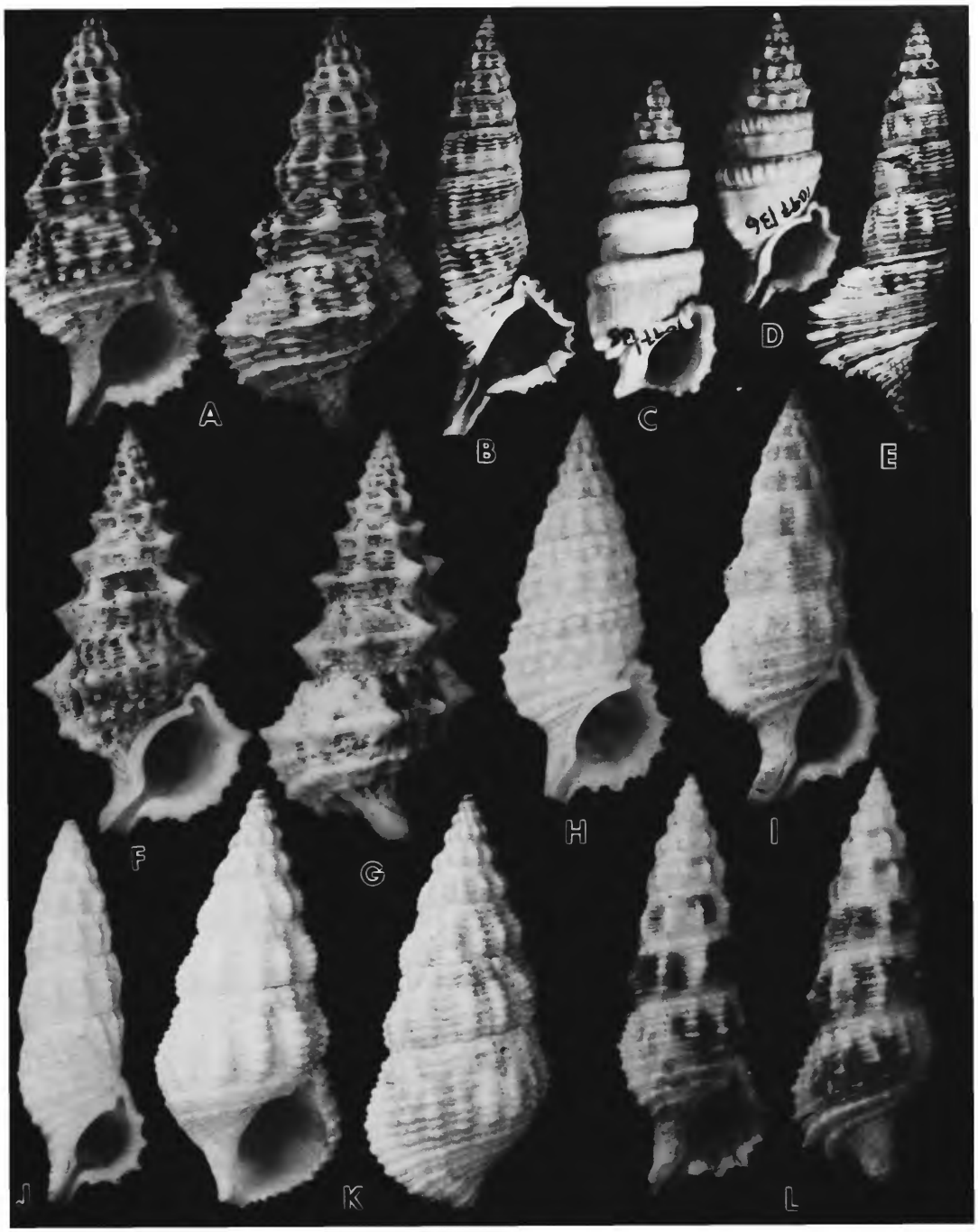


FIGURE 31.—Types of nominal species synonymous with *Cerithium columna* Sowerby: A, neotype of *Cerithium columna* Sowerby, shell figured by Sowerby (1855) in Thes. Conch., fig. 26, Philippines, 40.2 mm (BMNH 1986284/1); B,E, holotype of *Cerithium citrinoide* Kobelt, Philippines, 38.5 mm (SMF 228-197); C, lectotype of *Cerithium torulosum* Bruguière, with hand-written label of Lamarck, 32 mm (MHNG 109736); D, paralectotype of *Cerithium torulosum* Lamarck, 29.6 mm (MHNG 109736); F,G, specimen labeled *Cerithium menkei* Deshayes, from St Pierre, Réunion, closely resembling figured type, 35 mm (MNHNP); H, holotype of *Cerithium sculptum* Pease, Paumotus, 31 mm (ANSP 17592); I, holotype of *Cerithium siphonatum* Sowerby, 17 mm (BMNH 1986182); J, holotype of *Cerithium cylindraceum* Pease, Tuamotus, 25.8 mm (ANSP 17703); K, holotype of *Cerithium sandvichense* Sowerby, Hawaii, 28 mm (BMNH 1986179); L, holotype of *Cerithium fusiforme* Sowerby, Philippines, 22.2 mm (BMNH 1986170).

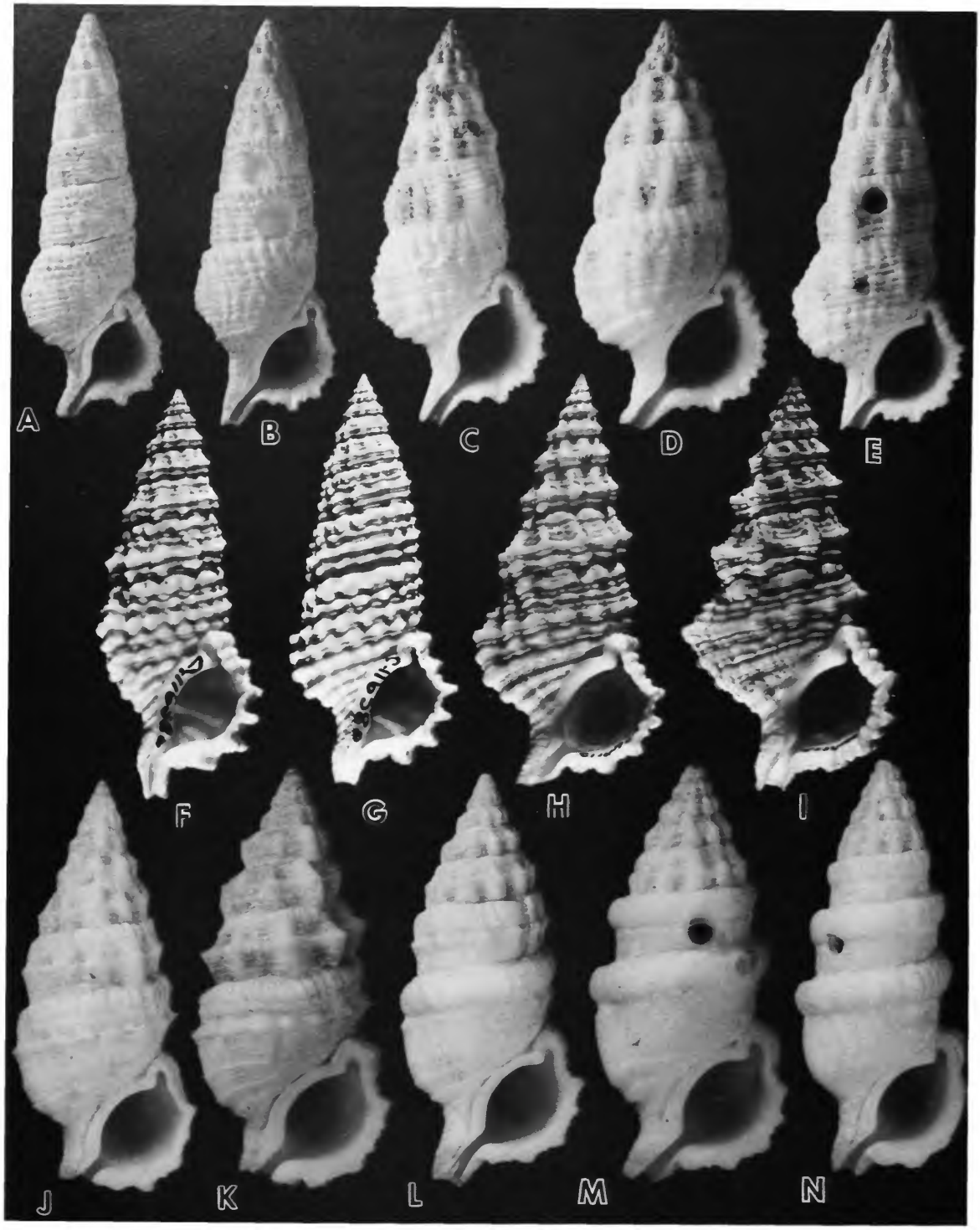


FIGURE 32.—*Cerithium columna* showing phenotypic variability in shell shape and sculpture within populations: A-E, individuals of population from Olhuvei Islet, S Male Atoll, Maldives, (A) 36.9 mm, (B) 30.8 mm, (C) 26.8 mm, (D) 19.8 mm, (E) 27.2 mm (LACM 841); F,G, Lizard Id, Queensland, Australia, (F) 40 mm, (G) 42.4 mm (AMS C116580); H,I, Rudder Reef, Port Douglas, Queensland, Australia, (H) 41.1 mm, (I) 36.8 mm (AMS C114902); J-N, individuals of population from Mauritius, including *torulosum* morphs (L-N), (J) 22 mm, (K) 23 mm, (L) 29.7 mm, (M) 22.3 mm, (N) 25 mm (MCZ 4090).

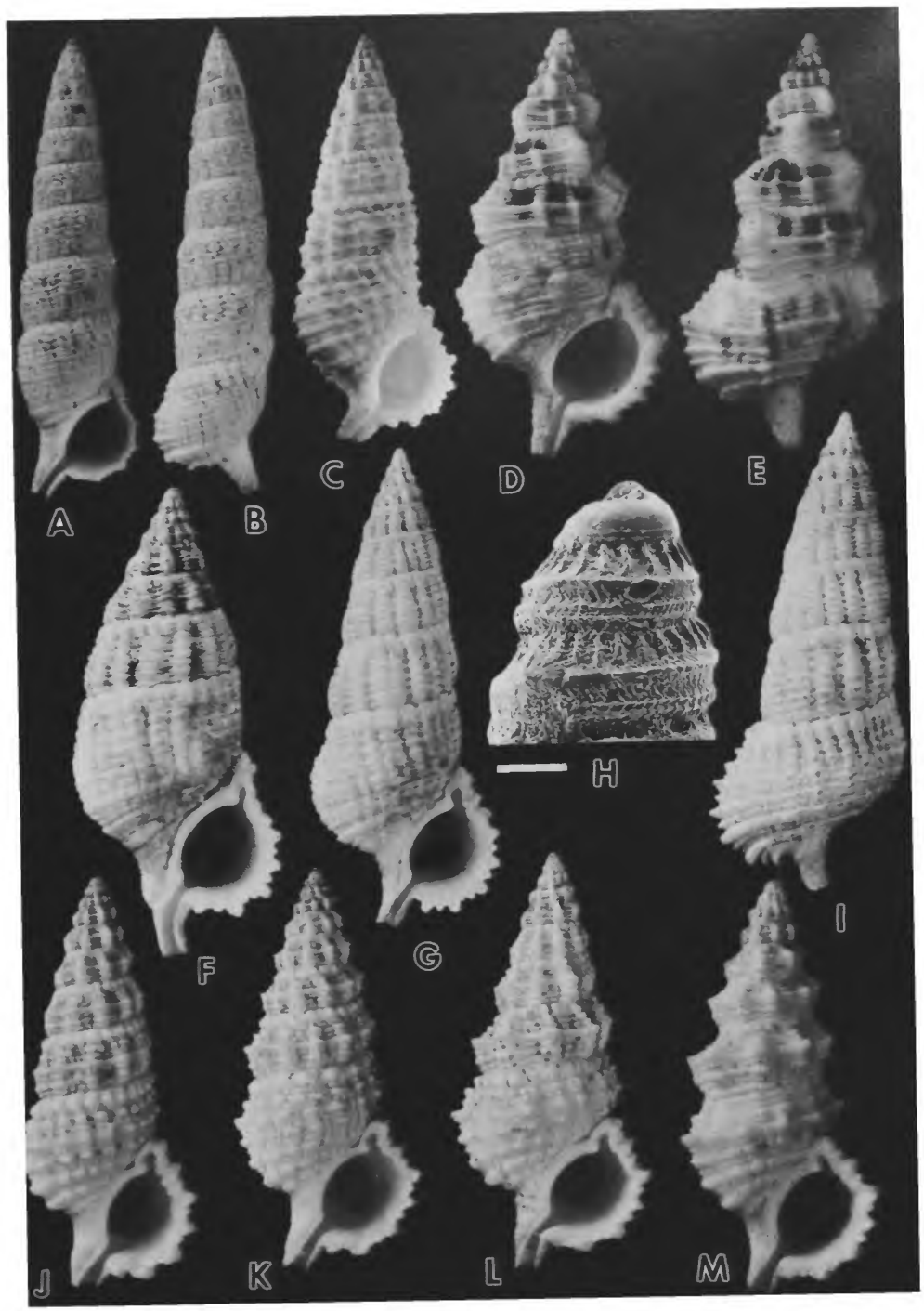


FIGURE 33.—*Cerithium columna* Sowerby showing phenotypic variability: A,B, extreme, elongate morph from Enewetak Atoll, Marshall Ids, 42.9 mm (USNM 821849); C, Sand Id, Enewetak Atoll, Marshall Ids, 35 mm (USNM 809774); D,E, Vaititti, Tuamotus, 31.3 mm (USNM 613289); F, *sandvichense* morph, Mauke Id, Cook Ids, 23.8 mm (USNM 869018); G,I, slender *sandvichense* morph, Mauke Id, Cook Ids, 37 mm (USNM 869018); H, SEM of protoconch showing axial and spiral sculpture, Rongelap Atoll, Marshall Ids (bar = 75 μm; USNM 585582); I–M, individuals from population ranging from quiet lagoon (F,G, 35.1 mm and 38.1 mm, respectively) through inlet (H, 39.9 mm), to reef front (I, 40.6 mm), Sand Id., Enewetak Atoll, Marshall Ids (USNM 795123).

spiral lines, earliest whorls with two spiral cords, rapidly increasing in number and tightly adpressed; two peripheral cords becoming dominant and nodulose to spinose in adult teleoconch; other spiral cords becoming coarser and varying in thickness, but major cords smoothly beaded; 1–14 spiral cords and many fine microscopic spiral striae (Figure 34A). Penultimate whorl with up to 18 axial ribs, usually strong and angulate at periphery. Subsutural band of beads varying in intensity, sometimes fusing to form thick, subsutural, spiral cord. Large, strong varices randomly placed on teleoconch. Suture deeply impressed and broad, subsutural ramp in some phenotypes. Body whorl large, broad, with excavated base and sculptured with numerous spiral striae and cords, larger of which sometimes with beads, nodes or spines. Large, broad varix on body whorl opposite outer lip of aperture. Anterior siphonal canal well developed, long, moderately tubular, reflected dorsally to left of shell axis. Anal canal well developed, bordered by strong parietal columellar plait. Aperture fusiform, ovate, between one-third and one-fourth the shell length. Outer lip thick at edge, strongly crenulate, and deeply furrowed internally, forming labial denticles that continue well into aperture. Columella concave, with heavy callus and thick columellar lip. Shell color usually white, occasionally cream, light yellow, or pink, and finely speckled and blotched with brown or purple. Juvenile whorls bluish black. Aperture and columella white. Measurements (Table 16). Periostracum thin.

Radula (Figure 34B-F): Type-1 radular ribbon (Figure 3A) 15 percent of shell length. Rachidian tooth (Figure 34E,F) rectangular with wide basal plate, pair of lunate basal ridges, and short, mid-posterior extension; anterior front convex and cutting edge with large spade-shaped central cusp flanked on each side by two, very small denticles. Lateral tooth (Figure 34E) with broad central, posterior projecting buttress bearing small papillae, and with short lateral, posterior extension; cutting edge with large, pointed, major cusp, one inner flanking denticle, and 3 outer flanking denticles. Marginal teeth (Figure 34B-E) short, with broad bases, sharply curved and serrated at tips. Inner marginal tooth with long, pointed, main cusp, 3 pointed, inner flankingdenticles, and 2 outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy (Figure 35): Head-foot pale to dark yellow-green with white and pink blotches and flecked with tiny black dots. Foot wide, crescent-shaped anteriorly, with deep anterior mucus gland. Females with ciliated groove and bulbous, glandular ovipositor on right side of foot. Mantle edge papillae green or white with tiny white spots beneath each papilla and evenly spaced white lines between each group of 5 papillae. Inhalant siphon pink, white with pink spots within. Snout massive, bilobed at tip. Mantle green. Osphradium tan; ctenidium white, narrow, comprising long triangular to finger-like filaments. Hypobranchial gland thick, pale green, divided into transverse ridges. Paired salivary glands comprise thin, uncoiled tubes running through nerve ring. Large esophageal gland present. Ovary whitish orange. Type-A pallial oviduct (Figure 4A; Figure 35) with short sperm gutter (Figure 35, sg) at edge of anterior medial lamina leading into elongate, enlarged spermatophore bursa (Figure 35, sb). Elongate, tubular anterior seminal receptacle (Figure 35, asr) in anterior lateral lamina (Figure 35, ll).

TABLE 16.—Shell morphometrics of *Cerithium columna*.

Character	$\bar{x}$ (n = 66)	sd	v	Range
Shell length	33.7	8.1	65.8	11.2–50
Shell width	13.7	4.1	16.6	4.1–20.8
Aperture length	10.3	2.8	7.5	2.4–15.4
Aperture width	7.8	2.1	4.6	3.2–11.9
Number whorls	11.0	0.6	0.4	9–13
Number spiral cords	7.0	3.2	10.3	1–14
Number nodes	9.5	4.1	17.0	0–18

SYNONYMIC REMARKS.—This highly variable species has been the recipient of many names and is best known as *Cerithium columna* Sowerby, 1834, which had been thought to be the earliest available name. However, an earlier name of Linné (1767) has priority: *Cerithium torulosum* (Linné, 1767). Linné (1767:1226) proposed the name *Murex torulosa* for a *Cerithium* species but did not cite any figure references or type locality. As the type material is not extant, this nominal species is considered a nomen dubium, even though the brief description indicating the thick spiral cords on the whorls might be considered adequate to identify this taxon, as there is no other *Cerithium* species with sculpture quite like it. The history of this taxon has been thoroughly discussed by Dodge (1957:199–200) who remarked that the description of Linné (1767:1226) was so good that "...it cannot be improved." *Murex torulosa* is regarded by Dodge as one of the few Linnaean mollusks that can readily be identified even without any locality data or references, but this seems extreme to me.

The difficulties arising in the synonymic history of this taxon stem from the fact that *C. torulosum* is a minor morphological variation, perhaps a monstrosity, of the common *Cerithium columna* Sowerby, of authors. Linné's (1767) taxon can be further pinned down by Bruguière's (1792:482) comments about *Cerithium torulosum*, a species he attributed to his own authorship. Bruguière (1792:482) cited *Murex torulosa* Linné in his synonymy of *Cerithium torulosum* Bruguière, and presented several figure references to identify it. Thus, if the identity of *Murex torulosa* of Linné is accepted as unequivocal, Bruguière's name would become a secondary homonym. Despite Bruguière's (1792:482) attribution of the name *torulosum* to his own authorship (as is evident by the use of the word "nobis"), he has obviously not described a new taxon, but has merely made a new combination by transferring the name *torulosa* Linné from *Murex* to *Cerithium*. Bruguière's collection was passed on to Lamarck and the latter's collection is today housed in the Geneva Museum of Natural History. In this

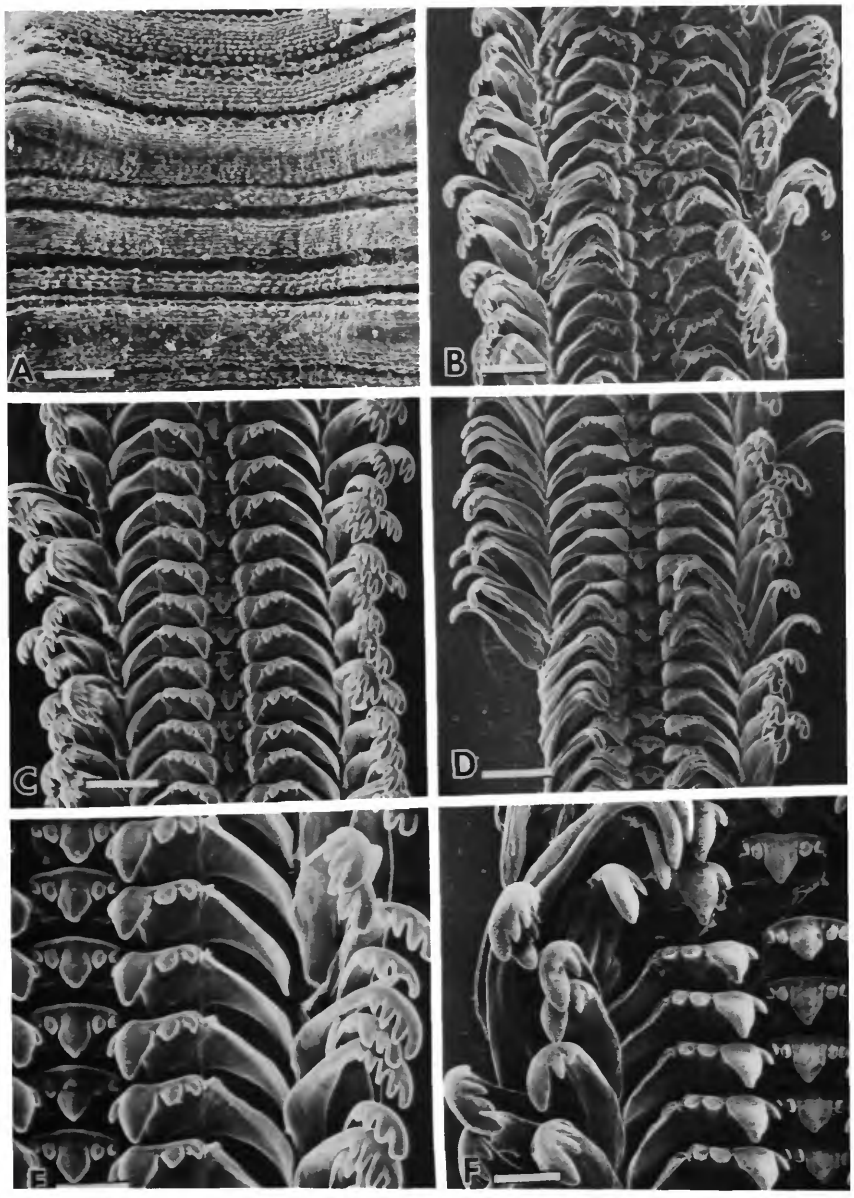


FIGURE 34.—SEM of sculptural details and radula of *Cerithium columna* Sowerby: A, microscopic beaded spiral sculpture comprising spiral striae, Rongelap Atoll, Marshall Ids (bar = 87 μm); B, radular ribbon with marginals turned back, Ras Burka, Gulf of Aqaba (bar = 140 μm; USNM 585582); C, radular ribbon with reflexed marginals, Sand Id, Enewetak Atoll, Marshall Ids (bar = 140 μm; USNM 794184); D, radula, Koromiri Id, Rarotonga (bar = 110 μm; ANSP 278675); E, rachidian, lateral, and marginal teeth, Sand Id, Enewetak Atoll, Marshall Ids (bar = 60 μm; USNM 801401); F, rachidian, lateral, and marginal teeth of *menkei* morph, Mauritius (bar = 60 μm; AMS C130101).

collection are two specimens with a hand-written label of Lamarck's bearing the name *Cerithium torulosum* Bruguière. These are the probable types of Bruguière and the larger (32 mm long) is herein designated as the lectotype of *Cerithium torulosum* Bruguière, 1792 (Figure 31C). Dodge has discussed the figure references of later authors pointing out that nearly all of these references are easily identifiable with the Linnaean description of *Murex torulosa*. As Dodge (1957:199) indicated,

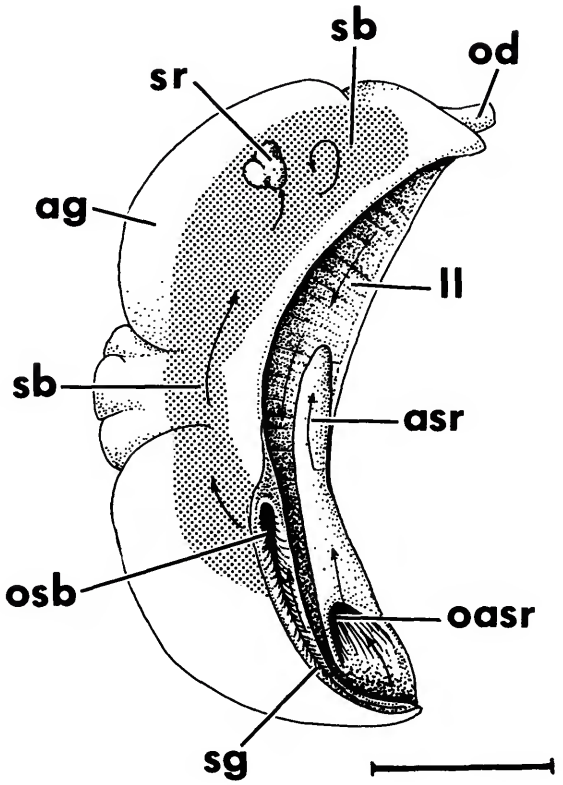


FIGURE 35.—Pallial oviduct of *Cerithium columna* oriented with anterior at bottom (bar = 1 mm); arrows denote cilliary currents. (Abbreviations: *ag* = albumin gland; *asr* = anterior seminal receptacle; *ll* = lateral lamina; *oasr* = opening to anterior seminal receptacle; *od* = coelomic oviduct; *osb* = opening to spermatophore bursa; *sb* = spermatophore bursa; *sg* = sperm gutter; *sr* = seminal receptacle.)

two distinct shell forms have been given the name *torulosum*, at least since the middle of the nineteenth century; one conforms to the Linnaean description while the other lacks the revolving thick cord and is instead covered with spiral nodes. Dodge (1957:200) however, erred in assuming that the two were distinct species; they are, in fact, two phenotypes of the same species (see below). Sowerby (1855:857) was the first to figure the two forms of this species. He attributed the name *torulosum* to Linné and in the *Thesaurus* (1855, pl. 180: fig. 92) figured a specimen that closely resembles both the figure references of Bruguière's (1792:482) *Cerithium torulosum* and his types in the Geneva Museum. In addition, Sowerby (1855, pl. 179: fig. 64) figured another shell, which he also called *Cerithium torulosum* (Linné), that differs greatly from the *torulosum* of Linné (1767) and Bruguière (1792). It is without doubt what is today known as *Cerithium columna* Sowerby of authors.

It seems that Sowerby's concept of *Cerithium torulosum* (Linné) is based on two different phenotypes selected by him to illustrate the wide variety of sculpture found in the species. Sowerby (1855:857) remarked that the species "is remarkable for its tendency to exaggerate the natural prominence of the whorls at the suture into a sort of swelled cord, leaving the greatest part of several whorls plain." He further commented that in Hanley's collection there was a "monstrosity" with this swelling continued for several whorls. Sowerby (1865, pl. 5: fig. 25a,b) later remarked that the thick corded variety was of "an irregular growth peculiar to this species." Having examined a series of shells from Mauritius showing all degrees of this condition (Figure 32J-N), I agree with Sowerby's assessment and believe that the shells described by Linné and Bruguière are indeed phenotypic extremes in which the nodes have become fused to form thick, swollen spiral cords. These unusual phenotypes grade into typical *columna* forms, forming a continuum down to the finely beaded phenotypes figured and named as *torulosum* by Sowerby (1855) on pl. 179: fig. 64.

Cerithium columna Sowerby, 1834, is based on a shell that is an intermediate between the extremes of the two *torulosum* phenotypes figured by Sowerby in the *Thesaurus* (Sowerby, 1855, pl. 179: fig. 64; pl. 180: fig. 92). This phenotype has well-developed spiral nodes and its sculpture is by far the most common sculptural pattern seen throughout the Indo-Pacific. Examination of Sowerby's figured specimens (1855, pl. 178: figs. 55–58) and thousands of specimens convinces me that *Cerithium columna* is conspecific with the putative *C. torulosum* (Linné). The name *columna* is herein chosen as the valid one as the name *torulosum* has been used only by Salvat and Rives (attributed to Linné; 1975:269) since its proposal by Bruguière, while *columna* has been the commonly used name of all other authors. Because this is a common, well-known species, it is believed that strict application of the rule of priority would cause nomenclatural instability. A petition to suppress the name *torulosum* in favor of *columna* has been submitted to the ICZN. One of Sowerby's (1855, pl. 178: fig. 57) figured specimens is herein selected as the neotype of *Cerithium columna* Sowerby (BMNH 19862841, 40.2 mm) (see Figure 31A).

Another synonym of *Cerithium columna* is *C. fusiforme* Sowerby, 1855. This taxon represents an elongate, brown-blotched phenotype (Figure 31L). The name *fusiforme* is preoccupied, and was given the replacement name *Cerithium proditum* by Bayle (1880:246). A similar morph was named *C. cylindraceum* Pease (Figure 31J). The morphologies of the types of *Cerithium siphonatum* Sowerby, 1865, 1866 (Figure 31I) and *C. sculptum* Pease, 1869 (Figure 31H) are identical and both taxa are conspecific with *C. torulosum* (Linné). Elongate forms such as these are common throughout Polynesia. An extremely elongate phenotype of *Cerithium torulosum* from the Philippines was given the name *Cerithium citrinoide* Kobelt, 1893 (Figure 31B,E) but similar morphs exist throughout the Indo-Pacific and I have examined numerous specimens with intermediate shell morphology (Figure 32A-E) between these extremely elongated morphs and the less elongated, beaded

shells of *C. torulosum*, as depicted by Sowerby (1855:179, fig. 64). I thus regard *Cerithium citrinoide* as a synonym of *C. torulosum*. *Cerithium sandvichense* Sowerby, 1865, 1866 (Figure 31K), an ignored taxon revived by Rehder (1980:36), is also considered conspecific with *C. columna* (see "Discussion" below).

ECOLOGY.—This common species is frequently mentioned as a component of the shallow-water molluscan fauna in ecological studies of reef environments. Although *C. columna* is found in many varied, intertidal to subtidal reef environments, it generally occurs in sand-rubble habitats behind off-shore reefs and in well-oxygenated lagoons. This appears to be its preferred habitat throughout an extensive geographical range. Around the Sinai Peninsula, Red Sea, where fish predation is intense, it occurs on the mid-littoral of rocky, open shores in cracks and fissures or in algal-covered pools and on subtidal soft substrates (Ayal and Safriel, 1981:62–63; 1982a:308, 314). On Red Sea reefs off Sudan, Taylor and Reid (1984:187) recorded that it comprised 4.5 percent of the mollusks found in sand and 3.4 percent of the sand-rubble Mollusca. Maes (1967:112) found it to be common on algal-covered rocks in sheltered parts of seaward reefs of Cocos Keeling Islands. *Cerithium columna* lives partially buried or on the surface of coarse sand in low intertidal and subtidal habitats around Lizard Island, Queensland, Australia (pers. obs.). In Guam, it lives on protected, seaward platforms and benches where it is common in sandy patches associated with algal turf (pers. obs.). Here, it is frequently found with *Clypeomorus nympha* Houbrick, 1985, although the latter species tends to live more in the mid- to high intertidal zones. Demond (1957:291–292) recorded *C. columna* to be common in sand pockets on windward reef flats throughout Micronesia. In Hawaii, it occurs on similar intertidal and shallow subtidal habitats (pers. obsr.), but has been dredged off Oahu at a depth of 90 m (Demond, 1957:291). Richard and Salvat (1972:1548) found *C. columna* comprised 2 percent of the molluscan fauna of the fringing reefs of Tiahura, Moorea, Society Islands. At Easter Island, the easternmost outpost of the Indo-Pacific Province, Rehder (1980:35) recorded that *C. columna* was found on reef flats in shallow tide pools, on a thin sandy substrate bound by algal filaments. Thus, published reports about *C. columna*, ranging from the Indian Ocean and the Red Sea to sites in French Polynesia in the South Pacific, confirm that this species lives in similar habitats throughout its wide geographic range.

Cerithium columna has been recorded as a prey item of *Cymatium nicobaricum* in Guam (Taylor, 1984:283), and of the muricid, *Muricodrupa funiculus*, in the Red Sea (Taylor and Reid, 1984:187). In Guam, the crab, *Eriphia sebana*, commonly eats *C. columna* (Vermeij, pers. comm.).

The egg mass of this species is unknown, but the highly sculptured protoconch (Figure 33H) with deep sinusigeral notch described above, is indicative of a planktonic larval phase in life history. The planktonic larval stage of Hawaiian populations taken from April through August has been described by Taylor (1975:96, pl. 11: figs. c–e). The larval snail is white and has an unpigmented, bilobed, unequal velum. Metamorphosis occurs when 3.25 whorls of the larval shell are complete.

DISCUSSION.—*Cerithium columna*, although exceedingly variable, is best recognized by its nodose, angulate, axial ribs and coarse, nodulose, beaded spiral cords and incised spiral lines, both large and minute (Figure 34A). The long siphonal canal, flaring crenulated apperture, and a tendency for dorsal-ventral flattening of the shell are also characteristic. The bright green, pink-spotted animal is unique among *Cerithium* species. The short lateral extensions of the lateral radular tooth are also distinctive.

Cerithium columna exhibits a wide diversity of shell phenotypes and is perhaps the most variable of all *Cerithium* species. As demonstrated by the above synonymy, many names have been proposed for various phenotypes, resulting in a complex and confusing taxonomic history. Resolution of the range of variation in shell morphology required the examination of thousands of lots of museum specimens from an enormous geographic range, plus extensive field studies of living populations. In addition, radular comparisons using SEM were made between different phenotypes, and anatomical studies were conducted on populations from Lizard Id and Magnetic Id, Queensland, Australia, Guam, Fiji, Hawaii, and Enewetak Atoll, Marshall Islands. The results, while not conclusive, suggest that the *C. columna* complex constitutes a single, variable species. The species comprises a huge complex of forms that has been difficult to statistically analyze and to resolve within the context and goals of this monograph. More detailed, careful developmental studies and anatomical and radular comparisons need to be made between the many populations throughout the vast range. In addition, biochemical techniques may prove useful in understanding genetic variability.

Shell variability is frequently observed within a single population from a given site, but the phenotypes comprising the population are closely correlated with differences in local microhabitats. For example, possible ecoclinal variation was observed in a population of *C. columna* from Enewetak Atoll, Marshall Islands. This population, from the north end of Enewetak Id, extends from a seaward, high-energy, intertidal, reef-bench habitat dominated by algal mats, into a shallow inlet that comprises a subtidal reef flat subject to strong currents, and terminates in shallow, subtidal, sandy substrate associated with the quiet waters on the lagoon side of the island. Individuals living on the seaward, high-energy bench are usually stocky, have a low length/aperture length ratio, and are highly sculptured with angular spiral rows of sharply pointed nodes (Figure 33M). Conversely, snails from the sandy lagoon microhabitat have longer, more slender shells, a high length/aperture-length ratio, are sculptured with numerous spiral and axial beads, and have long siphonal canals (Figure 33J). Individuals from the inlet, a reef flat environment of rubble and

coarse sand, are intermediate in shape and sculpture (Figure 33K,L) between the predominant phenotypes of the other two microhabitats. The free-swimming veliger phase in the life history of *C. columna* results in constant recruitment to all three habitats. Thus, all phenotypes and their various intergrades occur throughout the ecocline at Enewetak, but presumably, each microhabitat exerts selective pressure so that the most favorable phenotype is dominant at a given habitat. This has not been quantitatively demonstrated, but examination of Figure 33J-M, offers visual support to this hypothesis.

Intraspecific variation, similar to that described in the Enewetak population above, has been observed in populations of *C. columna* from many other Indo-Pacific regions. All of the phenotypic varieties thus far examined are linked to each other by a series of morphological intergrades, and no phenotype appears to constitute a discrete geographic population that would qualify for subspecific recognition. An example of intergradation in shell sculpture between two very different phenotypes in one population from Mauritius is shown in Figure 32J-N, where typical *columna* phenotypes merge into *torulosum* phenotypes. Note that the early whorls are quite similar. A similar intergrading series from the Maldives is seen in Figure 32A-E, where *citrinoide* and *fusiforme* phenotypes are linked to typical *columna* phenotypes by intermediate forms. The same situation exists, although to a lesser degree, in phenotypes given the name *Cerithium sandvichense* by Sowerby (Figures 31L, 33F,G,I), in which sculpture of low axial ribs crossed by numerous unequal spiral cords and lirae is seen. As this phenotype appears to be limited to the SW tropical Pacific (Rehder, 1980:36), a case could perhaps be made for subspecific recognition of the *sandvichense* morphs, but intergrades with typical *columna* morphs coexist with it (e.g., USNM 789292, 789595). Given the extreme phenotypic plasticity of *C. columna*, it is unlikely that the trivial sculptural details defining *C. sandvichense* are valid criteria for specific or subspecific recognition. Moreover, no differences between the radula of *C. columna* and *sandvichense* phenotypes were discerned. *Cerithium sculptum* Pease (Figure 31H) is also regarded as conspecific with *C. columna*, being merely an extreme beaded form from sandy habitats that intergrades into more typical *columna* phenotypes (Figure 32F-I).

A conchological feature uniting all phenotypes is the similarity of the juvenile and early adult whorls, which are purple or bluish in most morphs and which may be seen in nearly all the figured specimens herein. Major sculptural differences in all phenotypes appear only on the last 3 or 4 whorls of the teleoconch.

Cerithium columna most closely resembles *C. dialeucum* (Figures 46, 47A,B), which differs from it in having a less solid, darker, more tapered shell, with more well-defined axial ribs and smooth beads on the finer spiral cords and lirae. *Cerithium citrinum* Sowerby (Figure 25) also looks like *C. columna*, but the former has many more fine spiral cords, an elongate, tubular siphonal canal, and lacks the angulate axial ribs and subsutural beaded cord of the latter species. Some dwarfed individuals of *C. columna* may resemble *C. balteatum* Philippi (Figures 17, 18), but the latter species may be distinguished from the former by its deeply excavated shell base and tightly constricted siphonal canal.

FOSSIL RECORDS.—Despite the fact that *C. columna* is one of the most common and widespread cerithiid species living today, there are few fossil records of it in the literature. It has been recorded from Pliocene-Holocene drill holes at Enewetak and Bikini Atolls, Marshall Islands (Ladd, 1972:37), and a doubtful record from the Pliocene-Pleistocene limestone of Guam was cited by Ladd (1972:39, pl. 10: fig. 1), but the identity of the specimens is equivocal.

GEOGRAPHIC DISTRIBUTION (Figure 36).—This species has one of the widest Indo-Pacific distributions among *Cerithium* species, being found from the Gulf of Suez in the Red Sea, to Easter Island, at the far eastern extreme of the Province. There are records of *C. columna* from virtually every continental shore and island group in this vast area.

SPECIMENS EXAMINED.—EAST AFRICA: Durban, South Africa (USNM 368023); Kizimkazi, SW Zanzibar (ANSP); Pange Id, Zanzibar (ANSP); N of Chwaka, Zanzibar (ANSP); Twiga, Mombassa, Kenya (ANSP); SE of Gedi, Kilifi, Kenya (AMNH); Mogadiscio, Somalia (USNM 673807). RED SEA: Eilat, Gulf of Aqab, Israel (USNM 671283, 672284); Aqaba, Gulf of Aqaba, Jordan (USNM 841307); Na am-Marsa el Et, Sinai (AMNH); Ras Burka, Gulf of Aqaba, Egypt (USNM 794184); Gulf of Suez (USNM 23004); near Jidda, Saudi Arabia (USNM 852249); S side Dissei Id, off Massawa, Ethiopia (AMS); Massawa, Ethiopia (ANSP). PERSIAN GULF: Ras Tanura, Saudi Arabia (AMNH, ANSP). GULF OF OMAN: Muscat, Oman (AMNH, ANSP, USNM 657346, 657379).

INDIAN OCEAN ISLANDS: Île Picard, Aldabra Atoll, Seychelles (USNM 837469, 837760); North West Bay, Seychelles (ANSP); Anse Louis, Seychelles (ANSP); Anse aux Pins, SE Mahé, Seychelles (ANSP); Seychelles (USNM 634724); SW Cap Malherueux, N Mauritius (ANSP); S side Tombeau Bay, Mauritius (ANSP); Port Louis, Mauritius (AMNH); Jerome Pt, SE of Makelbourg, E Mauritius (ANSP); Le Chaland, SE Mauritius (AMS C130101, C142389); Flic en Flacq, W Mauritius (ANSP); N of Black River Bay, W Mauritius (AMS); St Pierre, La Reunion (MNHNP, USNM 306317, 862868); W side Olhuveli Islet, S Male Atoll, Maldive Islands (LACM 84-1); Feridu Id, Ari Atoll, Maldives (ANSP); Maro Id, Fadiffolu Atoll, Maldives (ANSP); N Malosmadulu Atoll, Maldives (ANSP); Diego Garcia, Chagos Archipelago (BMNH, USNM 702189, 842617); Home Id, Cocos Keeling Ids (ANSP); Pulo Siput, Cocos Keeling Ids (ANSP); Pulo Panjang, Cocos Keeling Ids (USNM 589144); Cape Ianjong Pagi, West Id, Cocos Keeling Ids (USNM 656380); "Trannies," N tip West Id, Cocos Keeling Ids (ANSP).

THAILAND: Goh Sindarar Nua (Chance Id) (USNM 661321, 661355); Goh Phi Phi (Pipidon) (USNM 661499);

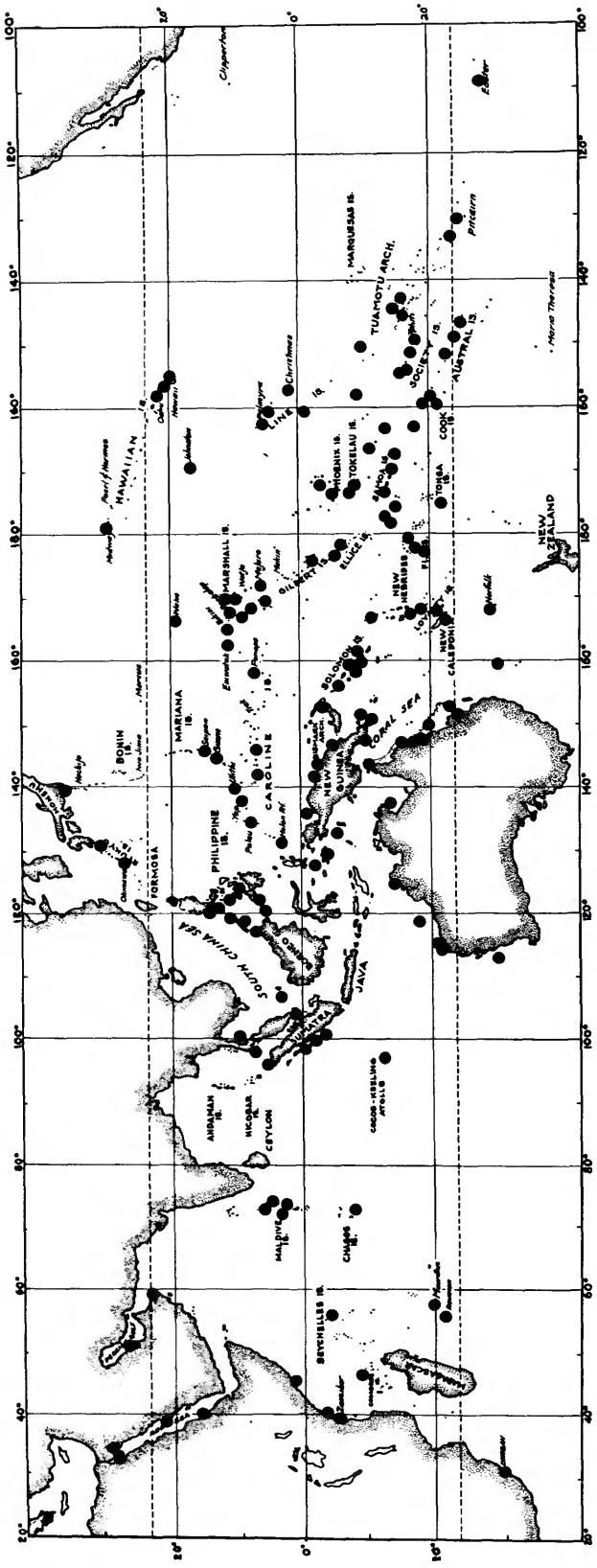


FIGURE 36 (left).—Geographical distribution of *Cerithium columna* Sowerby.

Goh Similan (USNM 661452); Koh Tao (USNM 405702, 405959, 419637, 419642, 862859). MALAYSIA: Singapore (USNM 770610); Sibuan Id, N Borneo (USNM 657668); Kudat Bay, Sabah, N Borneo (AMNH); Tigabu Id, Kudat District, Sabah, N Borneo (USNM 632199). JAPAN: Kanazawa (USNM 169777); Sagami Bay (ANSP). RYUKYU ISLANDS: Maesato, Ishigaki-shima (ANSP, USNM 613729); Ora Wan, Okinawa (USNM 593544); S of Kadena, Okinawa (ANSP); Nakadomari, Okinawa (AMNH); Naha Airfield Reef, Okinawa (ANSP); Okuma, Kunigami-Gun, Okinawa (USNM 670652); Shioya, Shanawan Bay, Okinawa (USNM 489134); Kue Reefs, Okinawa (ANSP); Okinawa (USNM 617514, 670890); Cape Tekopi, W side Samberbaba (ANSP); Ukibara-shima, E of Okinawa (USNM 670493); NE coast Theya Shima (ANSP).

PHILIPPINES: Sabtang Id, Batanes Gp (USNM 243912); Maculabo Id, Luzon (USNM 239792); Nasugbu, Luzon (USNM 232860); Maricaban Id, Luzon (USNM 232980); Camp Wallace, La Union, Luzon (USNM 233098); Calapan, Mindoro (USNM 862864); Gigmoto, Cataduanes (ANSP); Cataingan Bay, Dumurug Pt, Masbate (USNM 243833); Tara Id (USNM 243757, 243773, 243784); Lalaan, Negros (USNM 313478); Guijulugau Id, Negros (USNM 244053); Guijulugan, Negros (USNM 862858); Magallanes Bay, N end Mactan Id, Cebu (ANSP); Pangalao, Bohol (USNM 845791); E side Jagoliao Id, NW Bohol (ANSP); Hadayan Id, Bohol (ANSP); Opol, Mindanao (USNM 243715); Little Santa Cruz Id, Zamboanga, Mindanao (USNM 244033); Tanubigan Ids, Mindanao (USNM 619823); Murcielagos Bay, Mindanao (USNM 232901); Port Langcan, Dumaran Id, Palawan (USNM 243874); Tagbayag Bay, Palawan (USNM 244185); Puerto Princesa, Palawan (USNM 862863); Melampaya Bay, NW Palawan (AMNH); Jolo Id (USNM 233110, 233111); Bubuan Id, Jolo (USNM 243662, 243665); Simaluc Id, Tataan Id, Tawitawi (USNM 239704); Tabaan, Tawitawi (USNM 233210); between Siasi and Bongao Ids, Sulu Archipelago (USNM 313886); Bongao Channel, SW end Sanga Sanga Id, Sulu Archipelago (ANSP). INDONESIA: Pulau Boenta, off Acheh Head, NW Sumatra (USNM 661811); Siantan, Anamba Ids (USNM 598136, 611751); Pulau Bai, Batu Gp, off Sumatra (USNM 654488, 654650); Pulau Penju, S of Sumatra (USNM 661911); Pulau Siburu, N of Sipora, SW of Sumatra (USNM 654741, 654776, 654827); Pulau Melila, off Sumatra (USNM 661954); Mega Mentawai Ids, SW of Sumatra (USNM 655044); Pulau Stupai, Mentawai, SW of Sumatra (USNM 655112, 655151); S coast Gomumu Id, S of Obi, Moluccas (USNM 746424); Pombo Id, Haruku Strait, E of Ambon, Moluccas (USNM 746557); Waratneu Id, Tajundu, Kai Ids, Moluccas (USNM 746769).

WESTERN AUSTRALIA: S end Gun Id, Houtman Abrolhos Ids (WAM); Mangrove Bay, NW Cape (WAM); Bill's Bay,

3.2 km S Pt Maud (WAM); N of Ningaloo Homestead, NW Cape (WAM); reef 1 km SW of Pilgonaman, NW Cape (WAM); N of Mandu Mandu Reef, NW Cape (WAM); reef W of Tantabiddi Creek, NW Cape (WAM); Bundegi Reef, NW Cape (WAM); between Cape Dupuy and Cape Maleuet, Barrow Id (USNM 694123); S of Passages, Clerke Reef, Rowley Shoals, off Broome (WAM); Walsh Pt, Admiralty Gulf (WAM); Corneille Id, Institut Ids (WAM); Condillac Id, Institut Ids (WAM). NORTHERN TERRITORY, AUSTRALIA: Darwin (AMNH). QUEENSLAND, AUSTRALIA: Murray Id (USNM 273849); Murray Id, Torres Strait (AMS); S side Thursday Id, Torres Strait (AMS); N side Terry Beach, Prince of Wales Id, Torres Strait (AMS); Yam Id, Torres Strait (AMS C105852); Piper Id, Cape York (AMS); Groote Eylandt, Gulf of Carpentaria (AMS); Lizard Id (AMS C116580, USNM 704777, 766736, 766749, 766803, 766882, 766958, 783883); Bird Id, Lizard Id (AMS); Bird Id (USNM 91060); Anchorage Bay, Lizard Id (USNM 795123); Rudder Reef, NE of Port Douglas (AMS); Pixie Reef, near Batt Reef, Low Isles, off Port Douglas (AMS); Low Isles (USNM 623071); Port Douglas (AMS, USNM 770613); Holmes Reef, off Cairns (AMS); Michaelmas Cay, off Cairns (AMS C53547); Green Id, off Cairns (AMS); Beaver Reef, Hinchinbrook Id (ANSP); Little Kelso Reef, NE of Townsville (AMS); Orpheus Id, Palm Id Gp, off Ingham (AMS); Challenger Bay, Palm Id Gp off Ingham (ANSP); Keeper Reef, NE of Townsville (AMS); Broadhurst Reef, E of Townsville (AMS); Sand Cay, Marion Reef, off Townsville, Coral Sea (AMS); Hayman Id, Whitsunday Gp (AMS, USNM 704903); Langford Reef, Whitsunday Passage (AMS); Hervey Ids (USNM 91058); W side N Kepple Id, Kepple Bay (AMS); Heron Id, Capricorn Gp (AMS, USNM 431839); One Tree Id, Capricorn Gp (AMS); Masthead Id, Capricorn Gp (AMS); Northwest Id, Capricorn Gp (AMS); off Gladstone (USNM 618191). NEW SOUTH WALES, AUSTRALIA: Norfolk Id (AMS); Lord Howe Id (AMS).

NEW GUINEA: Mios Woendi, Schouten Ids, Irian Jaya (USNM 542695); Abroeki Id, Maransabadi Id, Aoeri Ids, Geelvink Bay, Irian Jaya (ANSP); Mios Andan Besan, W of Weigeo Radja Ampat, Irain Jaya (AMS); Pai Id, Mios Woendi Atoll, Padaido Ids, Irian Jaya (ANSP); Manokwari, Irian Jaya (ANSP); W Sowek, Soepiori Id, Irian Jaya (ANSP); Motupore Id, Papua (USNM 796571); near Hollandia, Papua (USNM 611929); Celeo Id, 8 km off Aitape, Papua (USNM 593934); Port Moresby, Papua (AMS); Megiar Harbor, 48 km N of Madang, Papua (AMS); Mailu Id, Amazon Bay, SE Papua (AMS); Panab Id, Madang, Papua (AMS); Kuia Id, Lusancay Ids, Trobriand Gp, Papua (AMS); Duke of York Id, New Britain (AMS). SOLOMON ISLANDS: Saposa Id, NW Bougainville Id (ANSP); Arawa Bay, Bougainville Id (USNM 701053); Shortland Id, Bougainville Id (ANSP); Choiseul Id (ANSP); Hetakta Id, N side Santa Isabel (LACM 78-5987); Vitora Id, SE Santa Isabel (LACM 78-5246); Laulasi Id, S of Aoki, W coast Malaita Id (AMS); Pavuvu Id, Russell Gp (USNM 488307, 488361); Ghavutu Id, Nggela Sule, Florida Ids (LACM 78-6614); W of Pt Cruz, Honiara (AMS); Nudha Id, Indespensable Strait (LACM 78-6922); Reef Ids, Santa Cruz Gp (AMS). NEW HEBRIDES: SE coast Santos Id (USNM 787204, 787864); Tuki Tuki Pt, W Efate Id (USNM 824828); Hideaway Id, Mele Bay, Efate Id (AMS); Pointe d'Arbel, Efate Id (USNM 787534); Erakor Lagoon, SW Efate Id (USNM 824816); Efate Id (ANSP, USNM 787726); S of Black Beach, Tana (USNM 692454). LOYALTY ISLANDS: Cliffs, Îlots Deguala, Uvea Atoll (USNM 692967, 693064); Lifu (AMS).

NEW CALEDONIA: Île Ain, 4.8 km ENE Touho (ANSP); Plage de Poe, Bourail (ANSP); N Dumbea Pass, Nouméa (ANSP); Laregnere Reef, E of Nouméa (ANSP); Île Cesar, Anse Vata, Nouméa (AMS); Touaourou (USNM 724648); 8 km S of Touaourou (USNM 784393). FIJI: Off Oinafa Id, NE coast Rotuma (USNM 686202, 686203); Hapmafau Bay, S coast Rotuma (USNM 686184); Albert Cove, NW Rambi Id, Vanua Levu (USNM 695234, 695287, 695354, 695392); W of Ngaratoka Pass, Vanua Levu (USNM 695114); N side Verevere Id, Vanua Levu (USNM 694960); reef off Waiyevo, Taveuni (USNM 695528); S end Taveuni (USNM 695710); SW of Tulane Harbor, Koro (USNM 695856); Yewa Id, Yasawa Gp (AMS); Tavutha Reef, N Viti Levu (USNM 824787); Yakuilau Id, off Nandi, Viti Levu (USNM 652936); Leleuvia Id, Viti Levu (USNM 666381, 666481); Cuvu Id, Nandronga, Viti Levu (USNM 616843); Suva, Viti Levu (USNM 531901); Laucala Bay, Suva, Viti Levu (USNM 790673, 790682); Makuluva, Viti Levu (USNM 531858); Waya Id, Kandavu (USNM 696229, 696302, 696333, 696338); Ndravuni Id, Kandavu (USNM 695931); Yaukuve Id, Kandavu (USNM 696017); Ono Id, Kandavu (USNM 696071); Vunisea Bay, Kandavu (USNM 697135); Yauravu Pt, Kandavu (USNM 696687, 697061, 697082); Matuku (USNM 686404, 686460).

MARIANA ISLANDS: Saipan (ANSP, USNM 602454); N Haputo Pt, Tweed's Cave, Guam (USNM 851138); Tumon Bay, Guam (USNM 620360); Apra Bay, Guam (USNM 243622, 243741, 862862, 862866, 862867); N Tipalao Pt, Guam (USNM 842619, 842622); Cocos Id, Guam (USNM 847287); Pago Bay, Guam (USNM 774842, 853051). PALAU: Palau (USNM 636244, 636280); Kayangel Id (ANSP, USNM 489006); 1.6 km S of Namelaki Pass, Babelthuap Id (ANSP); Angaur Id (USNM 616974). HELEN REEF: Helen Id (ANSP). CAROLINE ISLANDS: Yap Id (USNM 591136, 591173, 630816); Asor Id, Ulithi Atoll (USNM 593211, 602381); Fasserai Ids, Ulithi Atoll (USNM 591116); Eauripik Atoll (USNM 590786); Sand Id, Metalanim Harbor, Ponape (ANSP); NW end Falaribald, Ifaluk Atoll (USNM 616623); Falalap Id, Ifaluk Atoll (USNM 616715); Elangalop Id, Ifaluk Atoll (USNM 616336); Falarik Id, Ifaluk Atoll (USNM 616222); Ifaluk Atoll (USNM 616331); Faraulep Atoll (USNM 590887); Elato Atoll (USNM 590963); Satawal Atoll (USNM 591011); Tapatuaitu, Kapingamarangi Atoll (USNM 610868, 611153); Touhou Id, Kapingamarangi Atoll (USNM 622310); Mutunlik,

Kusaie Id (USNM 609563). WAKE ISLAND: SE end, Wake Id (ANSP).

MARSHALL ISLANDS: Enewetak Atoll (many localities throughout: USNM 580730, 581126, 581372, 581725, 581942, 582054, 582190, 582273, 582288, 582310, 582591, 583582, 584372, 584393, 584790, 716366, 743894, 801401, 809772, 809774, 809775); Bikini Atoll (many localities throughout: USNM 579309, 579340, 579716, 579821, 579884, 579992, 580063, 580089, 580515, 580518, 580530, 580623, 581031, 583051, 583634, 585932); Burok, Rongelap Atoll (USNM 583993); Lomuilal Id, Rongelap Atoll (USNM 585678, 585797); Arbar Id, Rongelap Atoll (USNM 582450); Noen Id, Rongelap Atoll (USNM 585354); Kabelle Id, Rongelap Atoll (USNM 582402, 582425); Bock Id, Rongerik Atoll (USNM 594656); Bigonattam Id, Rongerik Atoll (USNM 586329, 586352); Rongerik Id, Rongerik Atoll (USNM 586223); Enyvertok Id, Rongerik Atoll (USNM 583521, 583533); Uterik Id, Uterik Atoll (USNM 615642); Taka Id, Taka Atoll (USNM 615463); Ailuk Id, Ailuk Atoll (USNM 615141); Wotho Id, Wotho Atoll (USNM 614263); Likiep Atoll (USNM 596143); Ujelang Id, Ujelang Atoll (USNM 614654, 768033); Kwajalein Atoll (USNM 587346, 614742); Ujae Id, Ujae Atoll (USNM 607287); Majuro Atoll (USNM 486659); Kabbenbock Id, Jaluit Atoll (USNM 659096, 659144); Enybor Id, Jaluit Atoll (USNM 659406, 659410, 659420); S of Jabor, Jaluit Atoll (USNM 659657); Jaluit Id, Jaluit Atoll (USNM 660240). GILBERT ISLANDS: (USNM 34580); Onotoa Atoll (USNM 607750); Spamama (USNM 433927).

HAWAIIAN ISLANDS: Midway Id (ANSP, USNM 613467); Sand Id, Midway Ids (USNM 606698); Honolulu Harbor, Oahu (USNM 339329, 339787); off Waikiki, Honolulu, Oahu (USNM 339330); off Kaanapali, Maui (USNM 339331); Keopea, Hilo, Hawaii (USNM 339328). LINE ISLANDS: Johnston Atoll (ANSP); Palmyra Id (ANSP, USNM 348469, 487399, 613467); Monounou Village, Washington Id (USNM 725832); E end, Washington Id (USNM 725799); S coast Washington Id (USNM 725770); London, Christmas Id (USNM 725896, 725950); Christmas Id (USNM 725870); Jarvis Id (ANSP); Penrhyn Id (AMNH); NW coast Vostok Id (USNM 726008); Wake Id, Caroline Id (USNM 726110); Wake Id, Caroline Id (USNM 726130); N shore of South Id, Caroline Id (USNM 726053); South Id, Caroline Id (USNM 726027, 726043). ELLICE ISLANDS: Nanumea (USNM 433798, 433802); Vaitupu (USNM 685914, 686056, 686162). WALLIS AND HOORN ISLANDS: Between Luanna and Fungalei Ids, Wallis Id (USNM 676462); Nukuhifala, Wallis Id (USNM 676283, 676394); E coast Faoia, Wallis Id (USNM 676131). HOWLAND-BAKER ISLANDS: Howland Id (USNM 677814); N side Baker Id (USNM 699776). PHOENIX ISLANDS: Canton Id (USNM 513322); Hull Id (USNM 13338). TOKELAU ISLANDS: N of Puka Islet, W side Nukunono Id (USNM 768620, 768746); S end Taulangapapa Islet, E side Nukunono Id (USNM 768665); Fenua Loa, S point Fakaofu Id (USNM 768186); lagoon, Fenua Loa, S point Fakaofu Id (USNM 768239). SWAINS ISLAND: NW coast Swains Id (USNM 768420, 768423).

SAMOA: Asau Harbor, Savaii (USNM 675770); Felialupo road, W side, Savaii (USNM 675963); Apia, Upolu (AMNH, USNM 573841, 620824, 702489); Ofu, Manua Ids (USNM 699420); Pago Pago (USNM 862860); Fugasa Bay, Tutuila (USNM 699384); 0.8 km E of Cape Fogausa, Tutuila (USNM 704637); Tutuila (USNM 862861); Asili, Tutuila (USNM 685560); Pt Deceit, Tutuila (USNM 699481); Faga-alu, Tutuila (USNM 699103); Fagaitua Bay, Tutuila (USNM 704677); Rose Atoll (USNM 513347, 513356); Matautu Pt, Apia, Upolu (USNM 697262). NINAF'OU: Ninaf'ou (USNM 383852, 519043, 519089). TONGA: (USNM 76773); Niutoua, Tongtapu (USNM 671939). COOK ISLANDS: Anchorage Id, Suvorov (USNM 704445, 704461, 704499); Tom's Id, Palmerston Atoll (USNM 685116, 685128); Bird Id, Palmerston Atoll (USNM 685271); North Id, Palmerston Atoll (USNM 685196); Palmerston Atoll (USNM 685174); N of Amuri, Aitutaki (USNM 791014); Akitua, Aitutaki (USNM 684833, 684888); Motu Maina, Aitutaki (USNM 685067); Akaiami, Aitutaki (USNM 697321); Auotu Id, Manuae Atoll (USNM 732436); Auotu Id, Hervey Ids (USNM 732464); Mauke Id (USNM 634587); Motu Tou, Rarotonga (USNM 684661); Tupapa, E of Avarua, Rarotonga (USNM 721462); Muri, Rarotonga (USNM 732554); Taakoka Id, Rarotonga (USNM 708648); S coast, near Avaavaroa Pass, Rarotonga (USNM 732584); Kumukumu, Mangaia (USNM 684366). AUSTRAL ISLANDS: Moerai, Rurutu (USNM 684054, 684080, 684119, 684242, 684312); islet opposite Pt Tanitoa, Tubuai (USNM 683794, 683798, 683863); NE coast, E of Tahueia, Tubuai (USNM 705482); NE coast Motu Toena, Tubuai (USNM 705595); near Mataura, Tubuai (USNM 676839); Motu Moturoa, Tubuai (USNM 683685, 683720); Motu Tuitui, Raevavae (USNM 732161); Motu Veiamanu, Raevavae (USNM 676820); Motu Mano, Raevavae (USNM 676768).

SOCIETY ISLANDS: W side, Bellinghausen (USNM 705195, 705222, 705246); Motu Ahi, Maupiti (USNM 706059, 706256, 706329, 706338); Motu Auera, Maupiti (USNM 706139, 706149, 706207); Îles Scilly (USNM 705332); Farepiti Pt, Bora Bora (USNM 613491); Uturoa, Raiatea (USNM 630130); Teffaao, Huahini (USNM 674847); N of Fare, Huahini (USNM 630372, 708239); Motu Pahare, Huahine (USNM 674897); Port du Bourayne, Huahine (USNM 630295); Motu Iruru, Huahine Atoll (USNM 675391, 675495); Avapaihi Pass, Huahine Atoll (USNM 674655, 819058); NE end Mopelia (USNM 705155); Motu Onetahi, Tetiaroa (USNM 705670, 705672, 705676, 705723, 705730, 705751, 705752, 705758, 705776); Motu Rimatuu, Tetiaroa (USNM 705958, 705977); Motu Tiaraunu, Tetiaroa (USNM 705820, 705861, 705865); W of Pt Hauru, Moorea (USNM 630495); Opunohu Bay, Moorea (USNM 630328); Nuaret Bay, Moorea (USNM 630717, 668442, 668775, 671414, 775932, 791336, 797267, 797268, 804439); Moorea (USNM 791374, 791376); Tahiti

(numerous localities, USNM 668895, 669551, 671666, 672809, 672918, 789089, 789267, 791342, 791343, 797266, 804437, 804441).

TUAMOTU ARCHIPELAGO: Temao Harbor, Makatea (USNM 629803); Matiti Id, Tikahau (USNM 629299, 629364, 629644); Tairapa Pass, Manihi Atoll (USNM 790175); Teiavaroa Pass, Takaroa Atoll (USNM 789993); W side Avatoru Pass, Rangiroa Atoll (USNM 782812); Anaa Atoll (USNM 775534, 775893, 789013); E side Kakapuka, Raroia (USNM 723056); E of Kakapuka, Raroia (USNM 723023); Garumaoa Id, Raroia (USNM 720201, 720333, 720366, 723339, 723368, 723399, 723435); Okaea Id, Raroia (USNM 722830); N end Oneroa Id, Raroia (USNM 721184); N of Tekatikati Id, Raroia (USNM 721267); Patapata Id, Raroia (USNM 723190); Gavarivari Id, Raroia (USNM 723253, 723285); Opakea Id, Raroia (USNM 722383, 723098, 723102); Montufano Id, Raroia (USNM 721246); Otapoki Id, Raroia (USNM 720622); Ngarumaea Id, Raroia (USNM 697831, 697844); Otikaheru Id, Raroia (USNM 720679); Tatakoto Atoll (USNM 782709); Vahitahi (USNM 613289). GAMBIER ISLANDS: Motu Tepapuri (USNM 726357, 726368); S side Aukena (USNM 776433); Motu Tarauru-roa, Mangareva Id (USNM 638237). PITCAIRN ISLANDS: Oeno Atoll (USNM 789560, 789621). EASTER ISLAND: Near Vaihu (USNM 769729).

Cerithium coralium Kiener, 1841

FIGURES 37–41

Cerithium coralium "Dufresne" Kiener, 1841, pl. 8: fig. 3 [holotype: not located; type locality: Indian Ocean; neotype, herein selected: USNM 634420, Tap, Caroline Islands, 37.7 mm × 12.9 mm]; 1842:32–33.—Sowerby, 1855:863, pl. 179: fig. 63.

Cerithium granosum Kiener, 1841:1, pl. 4: fig. 3 [lectotype, herein selected: MNHNP, no number, 20 mm × 6.7 mm; type locality: Timor, erroneously cited "Red Sea" in description; not *Cerithium granosum* Borson, 1821, nor Valenciennes, 1832, nor Wood, 1848]; 1842:57–58 [may be *Cerithium scabridum*].—Sowerby, 1855:863, pl. 181: figs. 123, 124; 1865, pl. 11: fig. 73.—Tryon, 1887:132, pl. 23: fig. 9.—Kobelt, 1898:221, pl. 39: figs. 12, 13.

Cerithium ustum Hombron and Jacquinot, 1852, pl. 23: figs. 18, 19 [holotype: MNHNP, no number: type locality: Solomon Islands]; 1854:100.

Cerithium mitraeforme Sowerby, 1855:873, pl. 183: fig. 190 [holotype: BMNH 1986173; type locality not given; 18.4 mm × 6.2 mm]; 1865, pl. 11: fig. 74.—Tryon, 1887:132, pl. 23: figs. 5, 6.—Kobelt, 1898:214, pl. 38: fig. 4.

Cerithium corallinum [sic] Kiener.—Sowerby, 1865, pl. 5: fig. 29.

Cerithium corallinum [sic] Dufresne.—Tryon, 1887:125, pl. 21: fig. 36; pl. 24: fig. 46 [in error for *coralium* Kiener].

Cerithium (Ptychocerithium) ickei Martin, 1914:161–162, pl. 5: figs. 128–129 [holotype: RMGM Leiden ST107566; type locality: Miocene of East Borneo; not *Cerithium ickei* Vignal, 1908].

Cerithium nanggulanense Vignal, 1915:136 [new name for *Cerithium ickei* Martin, 1914].

Cerithium duffieldi Iredale, 1929:278 [new name for *Cerithium granosum* Kiener, 1841].

Cerithium (Ptychocerithium) nanggulanense.—Martin, 1931:38, pl. 5: fig. 13.

Cerithium eojavanum Altena, 1938:208 [new name for *Cerithium nanggulanense* Martin, 1914].

Cerithium (Thericium) coralium Kiener.—Wissemma, 1947:61–62.—Ladd, 1982:32, pl. 37: figs. 6–8.

Cerithium (Thericium) ruppelli Philippi.—Ladd, 1972:38, pl. 9: fig. 16 [not *Cerithium ruppelli* Philippi, 1848].

Cerithium rubus Martyn.—Popenoe and Kleinpell, 1978, pl. 2: figs. 23, 24 [not *Cerithium rubus* Martyn, 1786; is *C. coralium* Kiener, 1841].

Clypeomorus coralium (Kiener, 1841).—Springsteen and Leobrera, 1986:62, pl. 13: fig. 17.

DESCRIPTION.—*Shell* (Figures 37, 38A–G): Shell strong, elongate, turreted, comprising 12–18 straight-sided whorls, attaining 48.1 mm length and 16 mm width. Protoconch Figure 38E) with 4 sculptured whorls and sinusigeral notch. Early teleoconch (Figure 38G) elongate, comprising sharp shell apex, sculptured with two spiral cords gradually becoming beaded and crossed by weak axial riblets. Ribs becoming stronger and colabral as whorls increase in size. Adult teleoconch whorls sculptured with three major beaded spiral cords crossed by 11 to 21 axial ribs, and with many fine spiral threads and incised lines. Beads on spirals aligned with axial ribs. Number of axial ribs twice the usual number. Varices randomly distributed. Suture deeply impressed; narrow postsutural ramp on each whorl. Body whorl wide, sculptured with 5 or 6 beaded, spiral cords, numerous fine spiral striae, usually lacking axial ribs, and with strong varix opposite outer lip of aperture. Body whorl weakly constricted at base. Aperture fusiform, narrow, a little less than one third the shell length. Columella moderately concave with thick callus and columellar lip. Anterior siphonal canal short, thick, broad, only slightly reflected. Anal canal deep, flanked by strong parietal columellar callus and tooth. Outer lip thick at edge, crenulate and with inner elongate denticles; wide posterior sinus formed where outer lip joins penultimate whorl. Shell color dark brown to dirty gray, sometimes striped with brown or dirty white; beads dark. Aperture white, sometimes brown. Measurements (Table 17). Periostracum brown. Operculum dark brown, thick, corneous and ovate with eccentric nucleus.

Radula (Figure 39): Type-1 radular ribbon (Figure 3A) very small, short, about one-ninth the shell length. Rachidian tooth (Figure 39B,D) rectangular, with central, posterior, triangular extension and pair of posterior, basal lunate ridges on basal plate. Front of rachidian tooth concave; cutting edge with large spade-shaped main cusp flanked on each side by 2, or 3 small denticles. Lateral tooth (Figure 39B–D) with broad basal plate, strong central ridge, and long posterior lateral extension. Cutting edge of lateral tooth with large main cusp, one inner flanking denticle, and 3 or 4 outer flanking denticles. Marginal teeth (Figure 39C) with wide bases and central shafts, curved apices, and sharp tips. Inner marginal tooth with long sharp main cusp, 2 or 3 inner flanking denticles and 1 or 2 outer flanking denticles. Outer marginal tooth same, but without outer flanking denticles.

Anatomy: Body long, slender, comprising 6 or 7 whorls. Head-foot dirty gray over light orange background. Head with broad, short, blackish snout, rounded dorsally and flat

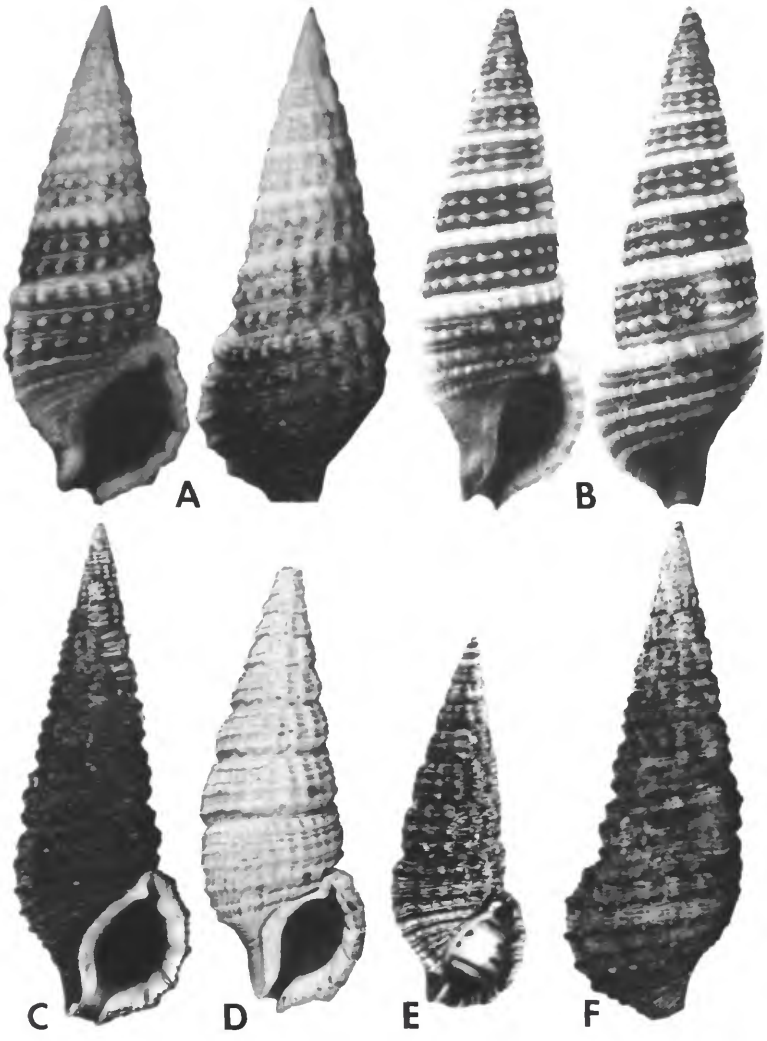


FIGURE 37.—Types of nominal taxa synonymous with *Cerithium coralium* Kiener: A, lectotype of *Cerithium granosum* Kiener, 20 mm (MNHNP); B, holotype of *Cerithium mitraeforme* Sowerby, 18.4 mm (BMNH 1986173); C, F, neotype of *Cerithium coralium* Kiener, 37.7 mm (USNM 634420); D, holotype of *Cerithium ickei* Martin, 24 mm (RMGM ST 107566); E, holotype of *Cerithium ustum* Hombron and Jacquinot, Solomon Ids, 28 mm (MNHNP).

ventrally. Cephalic tentacles each with long, wide peduncle and short, thin shaft striped transversely with black. Eyes tiny, black, bordered with large black band. Mantle edge yellow, fringed with many fine, long papillae. Inhalant siphon black along edge and with deep orange interior. Small papillae in mantle cavity at inhalant siphon.

Osphradium narrow, tall, bipectinate. Gray ctenidium long, narrow and with very long, finger-like filaments. Hypobranchial gland orange, thin, lacking transverse folds. Salivary glands originating behind nerve ring, passing through it, and

TABLE 17.—Shell morphometrics of *Cerithium coralium*.

Character	$\bar{x}$ (n = 22)	sd	v	Range
Shell length	22.7	5.1	26.3	15.1–32.3
Shell width	8.3	1.7	2.9	5.3–11.2
Aperture length	6.9	1.8	3.1	4.5–10.5
Aperture width	4.5	1.1	1.3	3.0–6.8
Number of whorls	13.6	1.4	2.0	12–18
Number spiral cords	3.0	–	–	3
Number nodules	15.9	2.8	7.6	11–21

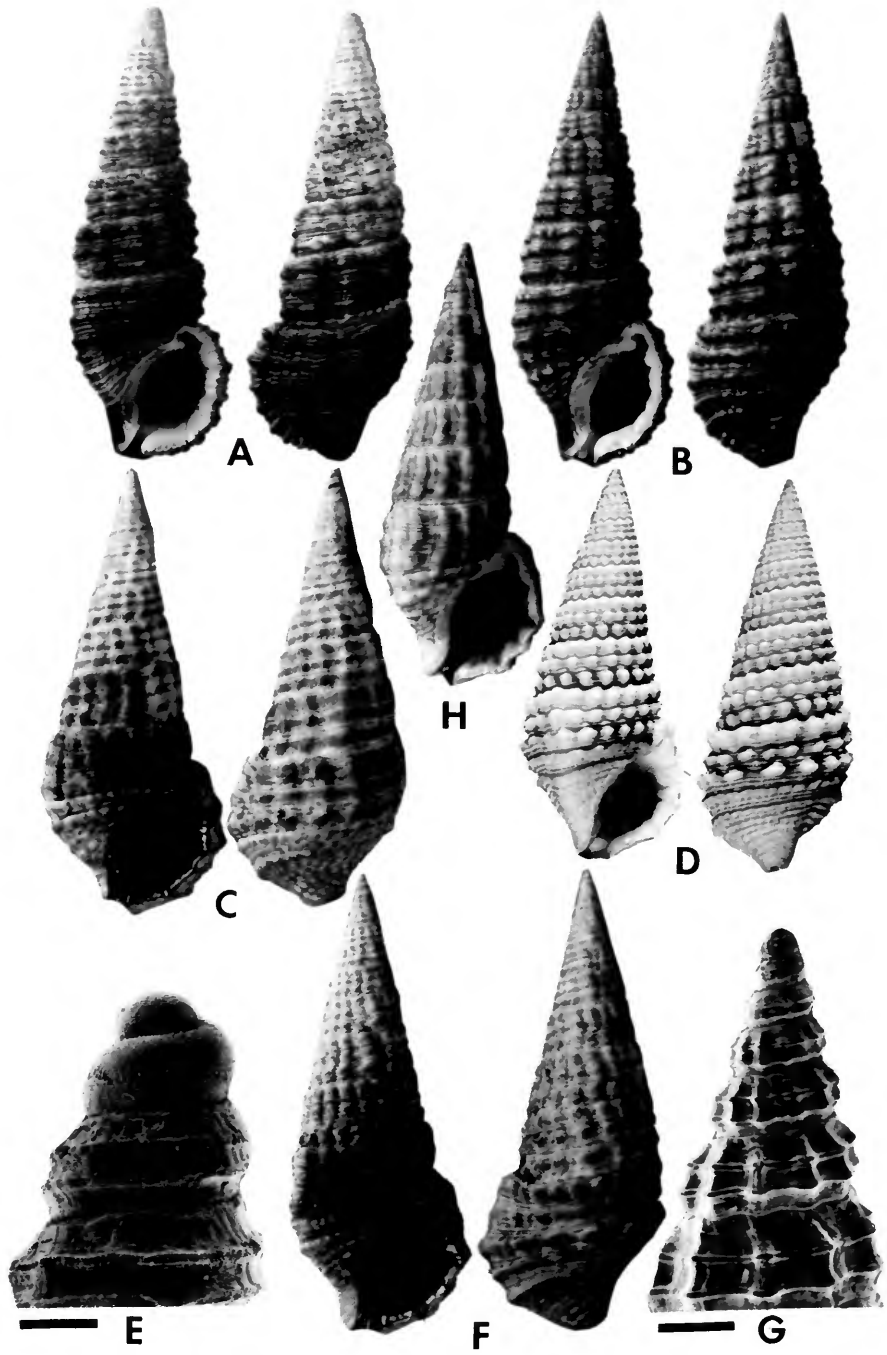


FIGURE 38.—*Cerithium coralium* Kiener showing phenotypic variability: A, Chance Id, Thailand, 48.5 mm (USNM 661414); B, Cebu, Cebu, Philippines, 33.7 mm (USNM 243797); C, Magenta Estuary, New Caledonia, 21.9 mm (USNM 862532); D, albinistic morph, Losuia, Kuriwina Id, Trobriand Gp, Papua, 23.4 mm (AMS C87944); E, SEM of protoconch, Manila Harbor, Luzon, Philippines (bar = 88 μm; USNM 244137); F, Linapacan, Philippines, 22.9 mm (USNM 243854); G, SEM of early whorl sculpture, Manila Harbor, Luzon, Philippines (bar = 0.3 mm; USNM 244137); H, morph with strong axial ribs, 20 mm.

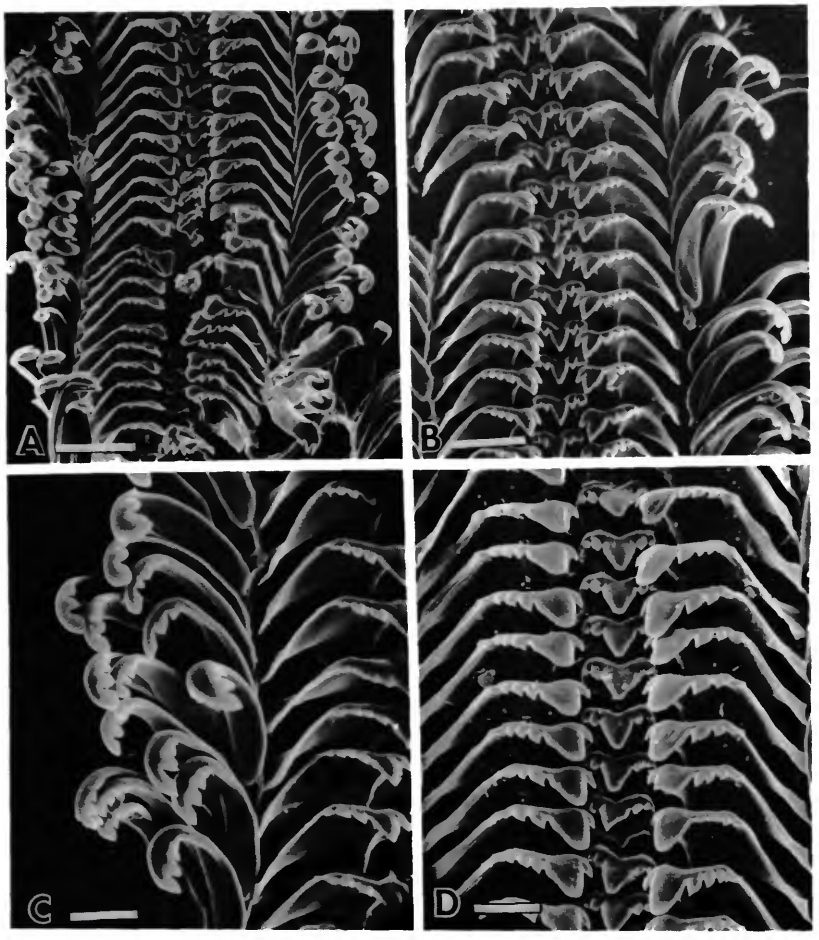


FIGURE 39.—Radula of *Cerithium coralium* Kiener: A, Radula with marginals spread open, Goh Sindarar, Naa, Thailand (bar = 0.15 mm; USNM 661414); B, Polillo Id, E Quezon, Luzon, Philippines (bar = 75 µm; ANSP 229481); C, marginal teeth (bar = 70 µm, same data as B; ANSP 229481); D, rachidian and marginal teeth (bar = 75 µm, same data as A; USNM 661414).

becoming tightly coiled on buccal mass near exit of glands into oral cavity. Small esophageal gland present.

Type-C pallial oviduct (Figure 4C) with long sperm gutter opening into white spermatophore bursa (Figure 40); spermatophore bursa yellow at posterior end of medial lamina. No seminal receptacle in medial lamina. Lateral lamina thin, with wide ciliated area comprising sperm gutter at anterior end (Figure 40, lsg) partially covered by thin flap of tissue (Figure 40, f) leading into small seminal receptacle (Figure 40, osr) at posterior of lateral lamina. Oviductal groove deep and glandular at posterior end of pallial oviduct.

Nervous system having RPG ratio (Davis et al., 1976:263) of 0.64.

SYNONYMIC REMARKS.—The holotype of *C. coralium* has not been found, but Kiener's description and illustration of it (1841:32, pl. 8: fig. 3) are so good that there is no doubt as to the identity of this taxon. Moreover, the shell figured by Sowerby (1855, pl. 179: fig. 63) in the *Thesaurus* as *C. coralium* matches Kiener's illustration perfectly. However, after describing *C. coralium*, Kiener described a very similar species on page 57, *C. granosum*. The syntypes of *C. granosum* Kiener are probably those collected by Peron and Lesueur and are unequivocally conspecific with *C. coralium*. Although the type locality of *C. granosum*, "Red Sea" (Kiener, 1842:57), is incorrect (*C. coralium* does not occur there), the label with the syntypes cites Timor as the locality. I herein select the specimen measuring 20 mm in length and 6.7 mm in width as the lectotype of *C. granosum* (Figure 37A).

The name *granosum* is preoccupied, and as the name *coralium*, commonly used for this species by numerous authors

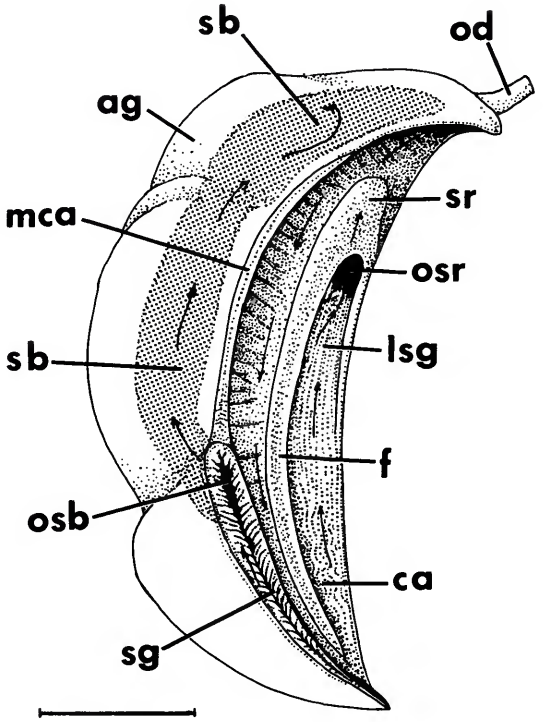


FIGURE 40.—Pallial oviduct of *Cerithium coralium*, oriented with anterior at bottom (bar = 0.75 mm; arrows denote ciliary currents). (Abbreviations: *ag* = albumin gland; *ca* = ciliated area forming broad gutter leading to seminal receptacle; *f* = thin fold of tissue overlying part of ciliated area; *lsg* = lateral lamina sperm gutter ; *mca* = medial lamina ciliated area, interacting with cilaited area of lateral lamina; *od* = coelomic oviduct; *osb* = opening to spermatophore bursa; *osr* = opening to seminal receptacle; *sb* = spermatophore bursa; *sg* = sperm gutter; *sr* = seminal receptacle.)

over many years, precedes the description of *granosum* by some 25 pages, I herein designate a specimen from Yap, Caroline Islands (USNM 634420), as the neotype of *C. coralium* (Figure 37C,F).

Sowerby (1865, pl. 5: fig. 29) misspelled the name *coralium* as *corallinum* and this mistake was followed by Tryon (1887:125), but the latter name has no validity.

I have examined the holotypes of *C. ustum* Hombron and Jacquinot, 1852 (Figure 37E) and *C. mitraeforme* Sowerby, 1855 (Figure 37B), and consider both taxa to be conspecific with *C. coralium*.

The Indonesian fossil species, *Cerithium ickei* Martin, 1914 (Figure 37D), appears to be identical to *C. coralium*. As Martin's taxon is preoccupied, several replacement names have been proposed for it and these also fall into the synonymy of *C. coralium*. Martin (1931:38) referred *C. ickei* (cited as *C. nanggulanense* Vignal) to the subgenus *Ptychocerithium* Sacco, 1895, but this is a poorly defined, equivocal category based on an Italian fossil type species, and is of doubtful taxonomic or systematic utility. The fossil depicted by Ladd (1972:38, pl. 9: fig. 16) as *C. ruppelli* Philippi, is *C. coralium*.

ECOLOGY.—*Cerithium coralium* is an epifaunal species of intertidal, estuarine, mangrove habitats where it occurs in large populations on nearly liquid muddy or sandy substratum, between pneumatophores of *Avicennia*, and commonly on soft bare mud in front of the mangrove fringe. In this ecotope, it is commonly associated with various potamidid snails with which it is somewhat convergent in shell shape and sculpture. *Cerithium coralium* frequently is found with *Cerithidea cingulata* (Gmelin) (a potamidid), *Clypeomorus bifasciata* (Sowerby) and *Clypeomorus pellucida* (Hombron and Jacquinot). At Piti Bay, Guam, populations of *C. coralium* occur at the flocculent mud-water interface of a mud flat, seaward of a *Clypeomorus bifasciata* population. In Hong Kong, I found *C. coralium* living with *Clypeomorus pellucida* and *Cerithidea cingulata* among dwarf mangroves.

Several ecological studies have been made on this species: Vohra (1971:694), in an ecological study of zonation along a sandy shore in Singapore, found *C. coralium* to be common on sticky, sandy areas overgrown with *Halophila ovalis*. Studies exist on the respiration (Rao and Rao, 1984), starvation metabolism (Rao et al., 1987), and seasonal changes in the levels and content of biochemical constituents (Rao et al., 1988) of *C. coralium* populations in India. Fecal pellets and stomach contents reveal that this species is a deposit feeder and feeds on diatoms and microalgae comprising the detritus in these habitats. The feeding biology of *C. coralium* in Hong Kong was studied by Yipp (1980), who found that it lives in areas of high organic content and is a deposit feeder in competition with *Cerithidea cingulata*. The stomach and rectal contents of *C. coralium* comprised microalgae, filamentous algae, macroalgae, and vascular plant material, and there was a notably high diatom content (Yipp, 1980:714–717).

Very little is known about the reproductive biology and life history of *C. coralium*. The protoconch is usually eroded, even in very small snails. A few partially eroded protoconchs each comprised three whorls and a sinusigeral notch (Figure 38E), indicating at least a partial planktonic larval phase. According to Sreenivasan (in litt.) there is a planktonic stage in life history and settling takes place at the three-whorled stage.

DISCUSSION.—The distinguishing characters of this species are a tall, tapering, dark brown shell comprising straight-sided whorls each sculptured with 3 aligned beaded spiral cords and a spindle-shaped aperture with thickened parietal callus, deep anal canal, and flaring, crenulated, thick outer lip with a wide posterior sinus. Shell length in adults is highly variable.

The anatomy of *C. coralium* differs from that of other *Cerithium* species in the layout of the pallial oviduct (Type-C, Figure 4C). The wide ciliated area and thin, flap-like sperm gutter at the anterior of the lateral lamina as well as the posterior seminal receptacle of the lateral lamina (Figure 40) are unique among *Cerithium* species. The absence of a seminal

receptacle in the medial lamina is also unusual. The cephalic tentacles are noteworthy in having long peduncular bases and thin tips. The thin hypobranchial gland is poorly developed and produces only a small amount of mucus compared with those of other *Cerithium* species.

Cerithium coralium is a widespread species and displays considerable intraspecific variation in shell sculpture. Spiral elements and beads dominate, but some individuals display distinct axial ribbing (Figure 38H). The largest specimens are from Indonesia and SE Asia (Figure 38A). Individuals from populations in SE Asia, Indonesia, Western Australia, and the Philippines tend to have large brown shells sculptured with fine spiral threads and with beads drawn out to form spiral cords (Figure 38A,B,F). The sinus in the outer lip is broad and shallow and the parietal area is only moderately thickened. Along the eastern Australian coast, individuals are smaller and the shell has fewer spiral striae and a thicker parietal callus. The outer apertural lip is more crenulate and has a deeper, more pronounced sinus. Populations from southern Queensland and New South Wales comprise individuals with stocky shells and wide apertures. Shells from silty, gray sand flats in Queensland (AMS C41329, Annam River, near Cooktown, Queensland; AMS C67084 Kepple Bay, Queensland) and New Guinea (AMS C87944) have white shells. The unusual phenotypes described above are very unlike typical *C. coralium*, but intergrades occur in Queensland and in SE Asia. Although the larvae of *C. coralium* are planktotrophic, the environment of a given area no doubt selects those variants best suited to it; thus, local differences in shell sculpture and shape may be ecophenotypic responses to environment. Sculptural variations between populations from some adjacent localities exist, but there is also an overall geographic clinal change in shell size and sculpture as one moves from the extensive mangrove habitats of the tropical, continental Indo-Pacific to more limited subtropical habitats found among low coral islands and atolls in the Pacific.

In the field, *C. coralium* is not likely to be confused with other *Cerithium* species because few live in similar estuarine habitats. It may be misidentified as a potamidid and is frequently considered as a *Batillaria* or *Cerithidea* species. Occasional populations of *Cerithidea cingulata* (Gmelin), *Clypeomorus bifasciata* (Sowerby, 1855), *Cerithium zonatum* (Wood), and *Cerithium torresi* E.A. Smith, occur in estuarine biotopes in sympatry with *C. coralium*. In such a situation, the shells of all species are usually dark brown, highly eroded, and convergent in general shape and sculpture. Careful inspection is necessary to separate these species when collected together, as they are frequently lumped into single lots in museum collections. This is further compounded by mixing of shells of different taxa by hermit crabs. Careful field observation usually resolves this difficulty because these species live in slightly different habitats. For example, *Clypeomorus bifasciata*, while it may be more elongate than normal due to the low energy environment, and look very similar to eroded *C. coralium*, lives only at the high intertidal zone, usually on mangrove roots or rocks along the shoreline. *Cerithium zonatum* is usually found in grass beds, stones, or branches in this environment, while *C. torresi* lives on sand flats bordering or marginal to mangroves. None of these species, however, live on the mid-tidal mud flats in microsympatry with *C. coralium*, with the exception of some *Cerithidea* species. The latter are potamidids and have a round, multispiral operculum with central nucleus.

The batillariid, *Velacumanthus australis*, is very similar to *C. coralium* in shell morphology, but the shell of the former is thicker, larger, and has an undulating spiral sculpture and an anal canal more at the inner top of the outer lip. Moreover, *Velacumanthus*, in contrast to *Cerithium*, has a round, paucispiral operculum with a central nucleus. *Velacumanthus* is only sympatric with *C. coralium* in Queensland and the northern part of New South Wales.

FOSSIL RECORDS.—This species has been recorded from the Pliocene of Java, Sumatra, and Nias; the Pleistocene of Java; and the Holocene and Pleistocene of Taiwan (Wissema, 1947:62). Indonesian Pleistocene fossils of *C. coralium* were examined from Loloanaa, Nias Id, and Pangarengen, Java (both CAS). Pleistocene fossils have also been found in Bondoc Peninsula, Tayabas Prov., Philippines (CAS). Examination of the types of *Cerithium everwijni* Martin, *C. noetlingi* Martin, and *C. ickei* Martin (Figure 34D) convinces me that these are synonymous with *C. coralium* or close ancestors of it. Although I was unable to find the type of *C. samaranganum* Martin, it too is probably conspecific with *C. coralium*. *Cerithium coralium* has been recorded from the Pleistocene of the New Hebrides by Ladd (1972:38; cited as *C. ruppelli* Philippi; 1982:32, pl. 37: figs. 6–8). Altena (1941:23–24) listed various Neogene sites in Java, Sumatra, and Nias, where fossils have been found. In Timor it has been cited from Pliocene and Quaternary sites (Tesch, 1920:55; cited as *C. rubus* Martyn). Popenoe and Kleinpell (1978, fig. 3, pl. 2: fig 24; cited as *C. rubus* Martyn) recorded it from the Vigo Formation (Pliocene), Philippines.

GEOGRAPHIC DISTRIBUTION (Figure 41).—*Cerithium coralium* has a moderate Indo-West Pacific range, centered around the continental margins and large archipelagos of the Indian Ocean and western Pacific, where there are extensive mangrove habitats. In the Indian Ocean, it occurs in southern India and Ceylon eastward through SE Asia and Indonesia to Western Australia. In the western Pacific, it occurs from southern Japan and the Ryukyus south throughout the Philippines, New Guinea, and Melanesia, around northern and eastern Australia. It also occurs in western Micronesia, but the single record from the Marshall Islands probably represents an isolated, transient population. There is no doubt that the presence of mangrove swamps is a critical factor in distribution.

SPECIMENS EXAMINED.—INDIA: Alibag Beach, Bombay (AMNH); Chaupati Beach, Bombay (USNM 862527); Travancore (BMNH); near river mouth, Porto Novo (USNM 841363). CEYLON: (USNM 91116); Colombo Harbor (AMS). AN-

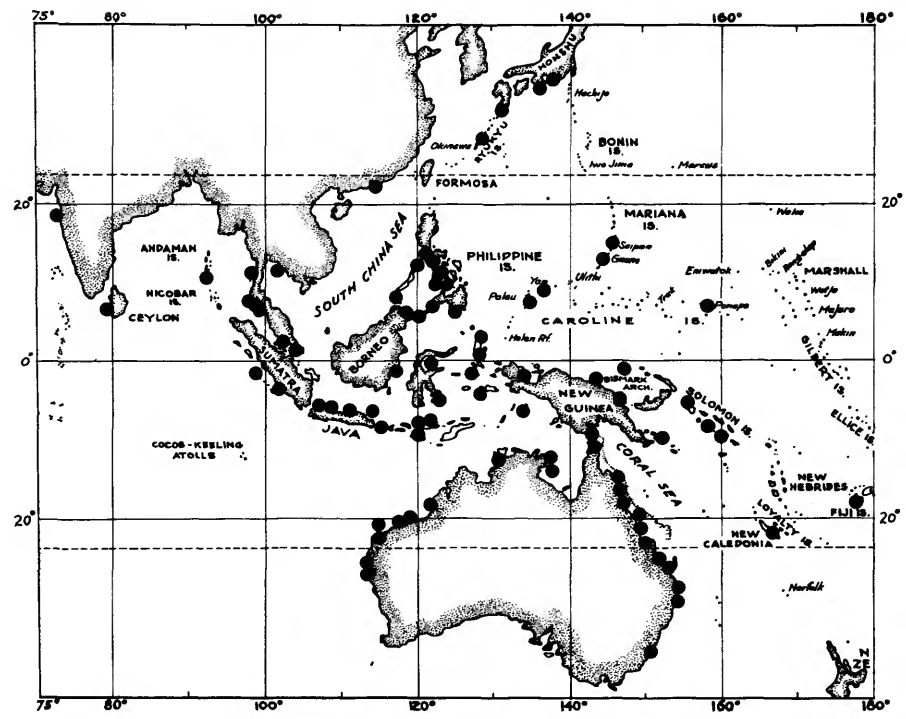


FIGURE 41.—Geographic distribution of *Cerithium coralium* Kiener.

DAMAN ISLANDS: Port Blair (NM F7196). BURMA: Mergui (BMNH). THAILAND: SW end Rawal Beach, Phuket, (LACM 85-4); Goh Sindarar Nua (Chance Id) (USNM 661406, 661414); Koh Kut, Gulf of Siam (USNM 405845). MALAYSIA: Pulau Lang Kawi (AMS); Port Dickson (ANSP); NW side of Cape Rachado (Tanjong Tuan) (AMS); Singapore (AMS, BMNH); Kranji, Singapore (ANSP); near Changi, Singapore Ids (WAM); Kampong Loyang, near Changi, NE Singapore (USNM 660666, 660668); Loyang Besar, Singapore (WAM); Telok Limau, Bako National Park, Sarawak (ANSP); Airport, Kudat, N Borneo (ANSP); Sandakan, Sabah, N Borneo (AMS, USNM 243748, 658119); Berhala Id, Sandakan, Sabah, N Borneo (ANSP, USNM 666824); Berhala Channel, Sandakan, N Borneo (USNM 657580); Po Bui Id, Sandakan, N Borneo (USNM 243695); Sim Sim, Sandakan, Sabah, N Borneo (AMNH, AMS, USNM 666764). CHINA: Inside end of Tai Tam Bay, Hong Kong (AMS, USNM 710606). JAPAN: Yokohama, Honshu (ANSP); Tosa, Honshu (ANSP); Kisame, Honshu (ANSP); Kii, Honshu (LACM); Kishiu (USNM 228219). RYUKYU ISLANDS: (ANSP, BMNH, USNM 343869).

PHILIPPINES: Numerous localities throughout archipelago (USNM); Manila Yacht Club, Manila, Luzon (ANSP); 8 km S of Cavite City, Luzon (WAM); Matabunkay Cove, 14 km S of Nasugbu, Batangas Prov, Luzon (ANSP 229481); near Panukulan, Balunga District, NW Polillo Id, E Quezon, Luzon (WAM); Barrio Lupi, Prieto Diaz, S Luzon (ANSP); Calapan, Mindoro (BMNH); San Jose, Mindoro (WAM); Cebu City, Cebu (BMNH); Bago, Negros (ANSP); Catbalogan, Samar (BMNH); Dapitan Bay, NW Mindanao (BMNH); Coron, Camalian Gp, Palawan (BMNH); Claredon Bay, S end of Balabac Id, Palawan (WAM); Doc Can Id Lagoon, Sulu Archipelago (WAM); Bongao Channel, SW end Sanga Sanga Id, Sulu Archipelago (ANSP). INDONESIA: Mentawai Ids, SW of Sumatra (USNM 655042); Benkoelen, Sumatra (USNM 363880); Sembuga, 14 km E of Balikpapan, E Kalimanton, Borneo (AMS); Taganak Id, Borneo (USNM 243941); Tjiperwagaran, Bantam, Java (USNM 260561); Pasar Ikan, Batavia Bay, Java (RMNH); Pruput, Bantam, Java (USNM 862527); Pekalongan, Java (ZMA); Jepara, Java (USNM 767483); Sepoeloe, N coast of Madoera (ZMA); Bali (AMS); Limbe Id, Gulf of Tomini, Celebes (USNM 243939); USBF sta 5642, SE of Tikola Pina, Buton Strait, Celebes (USNM 259796); Celebes (BMNH); Morotai Id, Moluccas (AMS); Rajahi Bay, Halmahera, Moluccas (BMNH); Mangrove River, Piajhi Bay, Halmahera (BMNH); Obi Latoe (RMNH); Amboena (BMNH); Kampong, Taberfane, S shore mouth of Maikoor R, Aru Islands (USNM 755614, WAM).

WESTERN AUSTRALIA: Dirk Hartog Id, Shark Bay (WAM); Weld Id (AMS); mouth of Bigota Creek, Barrow Id

(USNM 691791, WAM); 20°40'S, 115°25'E, between Cape Dupuy and Cape Malouet, Barrow Id (USNM 694107); E side of Withnell Bay, Dampier Archipelago (WAM); Back Beach, Dampier (WAM); Delambre Id, Dampier Archipelago (WAM); Port Hedland (AMS, USNM 801601); Cape Kerauden (WAM); Roebuck Bay, Broome (AMS); behind Buccaneer Rock (WAM); Lookout Hill, Broome (USNM 828809); Broome (AMS, WAM); Barred Creek, near Broome (BMNH, NM); Pelican Point, Carnarvon (WAM); Carnarvon (AMS).

NORTHERN TERRITORY, AUSTRALIA: Myilly Pt, Darwin (WAM); Fannie Bay, Darwin (AMS); Victoria, Port Essington (AMS); Groote Eylandt, Gulf of Carpentaria (AMS); Port Bradshaw, near Cape Arnhem (USNM 602122). QUEENSLAND, AUSTRALIA: Mapoon, Gulf of Carpentaria (AMS); Torres Strait (USNM 253559); N end of Yam Id, Torres Strait (AMS); Friday Id, Torres Strait (BMNH); Thursday Id (LACM); Hospital Pt, Thursday Id, Torres Strait (AMS); Red Island Point, Cape York (AMS); E end Saibai Village, Sabai Id, Torres Strait (AMS); Howick Gp (AMS); Starcke River, N of Cooktown (AMS); Annan River, Cooktown (AMS C41329); Four Mile Beach, Port Douglas (AMS); Buchan's Pt, N of Cairns (AMS); Yule Pt, Cairns (NMV); Cairns Harbor, Cairns (AMS); Ned Lee Creek, Magnetic Id, off Townsville (AMS, USNM 828826, 847054); Cockle Bay, Magnetic Id, off Townsville (USNM); Bowen (AMS); 3.2 km S of Bowen (AMS); Hook Id, Whitsunday Passage (AMS); Rockhampton, Keppel Bay (AMS); Yeppon (AMS); Pialba, Hervey Bay (AMS); Dundowran, Hervey Bay (AMS); Noosa River (AMS); Sandgate, Moreton Bay (AMS); Caloundra Head (BMNH); Currimundi Lake, near Caloundra (AMS C90092); Wynnum, near Brisbane (AMS); Cleveland, S of Brisbane (AMS); North Id, Pellew Gp (AMS). NEW SOUTH WALES, AUSTRALIA: Tweed Heads (NMV); Redbank River (AMS); Woolgooga, N of Coff's Harbor (AMS); Collaroy Beach (AMS); Ball Head, Goat Id, Port Jackson (AMS); Long Reef (AMS).

NEW GUINEA: Wandammen Bay, Irian Jaya (ZMA); Sorendidori, E side of Soepiori Id, Schouten Ids, Papua (ANSP); Nui Id, Madang Harbor, Papua (AMS C87941); SW of Losuia, Kiriwira Id, Trobriand Gp, Papua (AMS); Daru, Papua (AMS). ADMIRALTY ISLANDS: Manus Id (USNM 542858). SOLOMON ISLANDS: Choiseul Bay, Choiseul Id (ANSP); Wagina Id, Choiseul Id (AMS); Ata Id (AMS); Pavuvu Id, Russel Gp (USNM 862522); Guadalcanal (LACM). NEW CALEDONIA: 4.8 km N of Touho (ANSP); Pointe aux Long Cous, Nouméa (USNM 724207); Nouméa (NMV); Baie de l'Orphelinat, Nouméa (ANSP); Magenta Estuary (USNM 862532); 2 km S of Conception (USNM 724534, 774515). FIJI: Veiuto, near Suva, Viti Levu (WAM); Suva Pt, Suva, Viti Levu (USNM 532127, 532428); Laucala Bay, Suva, Viti Levu (USNM 794736, 794740). MARIANA ISLANDS: Tanapag Harbor, Saipan (ANSP); Apra Bay, Guam (USNM 243740, 301842, 301848, 774775). PALAU ISLANDS: Palau (USNM 636560); mouth of Garumisukan River, Karamando Bay, Babelthaup Id (ANSP); Airai, Babelthaup Id (USNM 862531); Gatun Dock, Palau (UGI); Arakabesan, Palau (UGI); Koror (ANSP). CAROLINE ISLANDS: Yap (CAS, USNM 634420); Nam Matoe Id, Ponape (ANSP, USNM 42358); New Matol Id, Ponape (USNM 631742). MARSHALL ISLANDS: Ebon Atoll (ANSP).

Cerithium crassilabrum Krauss, 1848

FIGURES 42–44

Cerithium crassilabrum Krauss, 1848:107–108, pl. 6: fig. 10. [Type originally at Stuttgart Museum, but subsequently lost (see Janus, 1961:2); type locality: Natal coast; not *Cerithium crassilabrum* Orbigny, 1850. Neotype herein designated: NM 7303, 15.9 mm × 6.8 mm, Coffee Bay, Transkei, South Africa.].—Kensley, 1973:79, fig. 266.—Kilburn and Rippey, 1982:54, pl. 11: fig. 3.

DESCRIPTION.—*Shell* (Figure 42): Shell stout, conical-turrate, comprising 10 moderately inflated, granulose whorls and attaining 17 mm length and 7 mm width. Protoconch unknown. Early teleoconch sculptured with about 6 spiral threads per whorl. Adult teleoconch whorls sculptured with three major beaded spiral cords with a minor beaded cord in each interspace. Two largest major cords at whorl periphery. Penultimate whorl angulate at periphery. Subsutural cord cincture-like with many rounded beads. Suture impressed, well defined. Body whorl large, wide, sculptured with 7 or 8 spiral cords, weakly beaded and with weak siphonal constriction at truncated base. Several weak varices irregularly placed. Aperture ovate, large, about one-third the shell length. Anterior siphonal canal very short and wide, strongly reflexed to left of shell axis. Anal canal well developed, bordered with weak parietal columellar tooth. Columella concave with thick callus and minor columellar lip. Outer lip thickened, smooth, and convex. Shell color flesh to tan with brown and white alternate spots on spiral cords. Beads white. Periostracum tan.

Radula (Figure 43): Type-1 radular ribbon (Figure 3A) robust, a little over one-seventh the shell length. Rachidian tooth (Figure 43B) square, having sharply pointed, central, posterior extension and pair of lunate ridges at base of basal plate. Front of rachidian tooth convex; cutting edge with large spade-shaped main cusp flanked on each side by two small denticles. Lateral tooth (Figure 43B) with broad basal plate having thick central ridge bearing small peg, and with long, basal-lateral projection. Marginal teeth (Figure 43A,B) short with broad stems, pointed bases, and serrated, curved apices. Inner marginal tooth with rounded main cusp, two sharp, flanking inner denticles, and one outer flanking denticle. Outer marginal tooth same, but lacking outer flanking denticle.

Anatomy (based on dried animal): Dorsal two-thirds of mantle edge papillate. Large, broad, muscular snout pigmented with dark brown, transverse stripes. Cephalic tentacles relatively long and thick. Paired jaws, each about 0.9 mm long. Pallial gonoducts unknown.

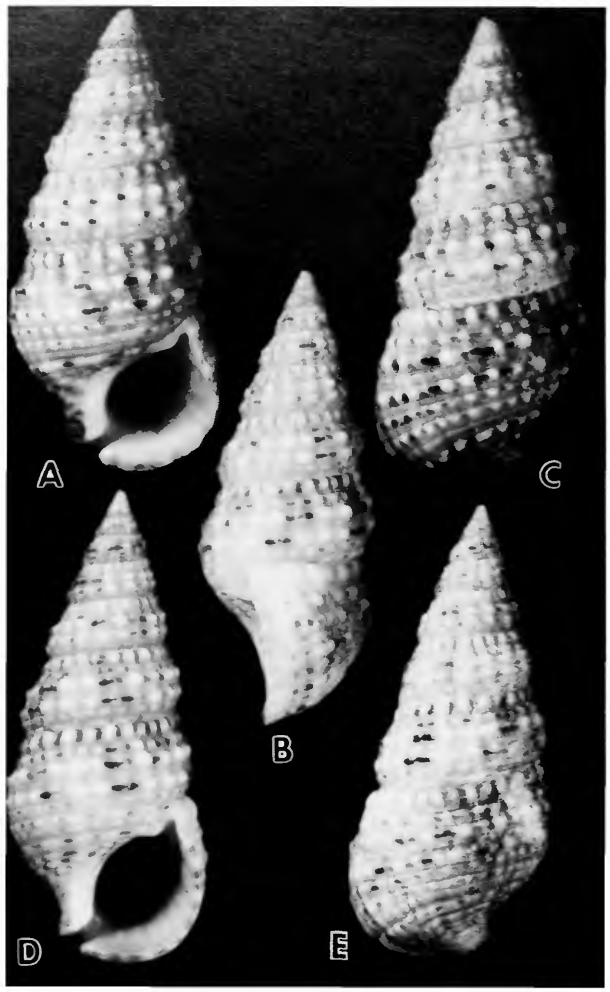


FIGURE 42.—*Cerithium crassilabrum* Krauss: A-C, neotype, Coffee Bay, Transkei, South Africa, 16 mm (NM 7303); D,E, Port Alfred, South Africa, 16.7 mm (ANSP 211671).

SYNONYMIC REMARKS.—Although the type material has been lost (Janus, 1961:2), the figure and description presented by Krauss (1848:107–108, pl. 6: fig. 10) are good enough to leave no doubt as to the identity of this unusual species. I designate the largest (NM 7303, 15.9 mm × 6.8 mm) of three specimens from Coffee Bay, Transkei, South Africa as the neotype of *C. crassilabrum* (Figure 42A-C).

ECOLOGY.—Little is known about this species, but data from museum specimens indicates an intertidal, algal-covered, hard substrate as the habitat. Kilburn and Rippey (1982:54) report that it lives in rocky tide pools among short, bushy algae and on the alga, *Padina*. According to collection data slips, *C. crassilabrum* sometimes burrows in sand. Nothing is known of the egg mass or kind of reproduction, and the protoconch is

FIGURE 43.—Radula of *Cerithium crassilabrum* from Salt Rock, Umhlali, South Africa (NM A192): A, radula with marginal teeth spread open (bar = 100 μm); B, detail of half row (bar = 50 μm).

unknown, but the restricted geographic distribution indicates direct development.

DISCUSSION.—*Cerithium crassilabrum* is not common in museum collections and is not well known in the literature. Only a few specimens have been available for examination, but there does not appear to be a great amount of intraspecific variation in shell sculpture. This small, squat species has a very restricted distribution and is not likely to be confused with any other *Cerithium* species. Its overall morphology most closely approaches that of some *Clypeomorus* species, such as *C. bifasciata* (Sowerby) (see Houbrick, 1985:23–41), with which it is geographically sympatric. The latter species is fatter, has fewer whorls, a more truncated base, and only three beaded, spiral cords without the granulose interspace threads. Although the shell of *C. crassilabrum* is similar to those of *Clypeomorus* species, the radula does not look like that of *Clypeomorus bifasciata*, and the sculpture of *C. crassilabrum* appears to be more like that observed in *Cerithium* species. For these reasons it is tentatively assigned to the genus *Cerithium* Bruguière, until the anatomy can be examined in detail.

Cerithium crassilabrum looks very much like the western Atlantic species, *Cerithium lutosum* Menke, and may be related to it.

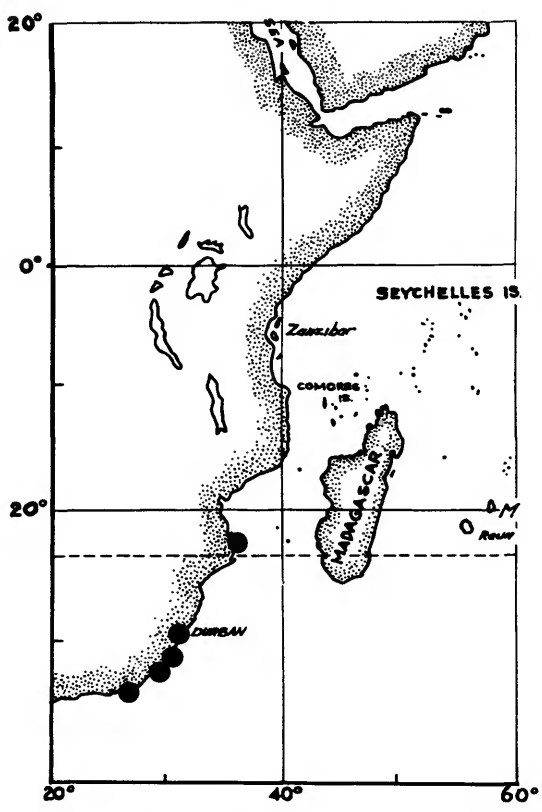


FIGURE 44.—Geographic distribution of *Cerithium crassilabrum* Krauss.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 44).—South eastern Africa, from Port Alfred, South Africa, north to Mozambique.

SPECIMENS EXAMINED.—EAST AFRICA: Port Alfred, South Africa (USNM 249689); Coffee Bay, Transkei, South Africa (NM 7303); Mzamba, Pondoland, South Africa (NM 7389); Margate, 17.8 km S of Port Shepstone, South Africa (ANSP 211671, 216514); Port Shepstone, South Africa (USNM 845794, WAM 1027-84); Tongaat, South Africa (NM A892); Salt Rock, Umhlali, South Africa (NM A192); North Reef, Bazaruto, Mozambique (NM G2138).

Cerithium dialeucum Philippi, 1849

FIGURES 45–50

Cerithium dialeucum Philippi, 1849:2–3 (14–15, pl. 1: fig. 5 [type not found; no locality given; neotype herein designated: USNM 862619, 34.3 mm × 14.2 mm, S side of Mathuata Id, N coast of Viti Levu, Fiji].—Sowerby, 1855:860, pl. 180: figs. 98, 99; 1865, pl. 3: fig. 18.—Tryon, 1887:130, pl. 23: figs. 87, 88.—Kobelt, 1895:167–168, pl. 31: figs. 8, 9.—Salvat and Rives, 1975:268, fig. 61.—Cernohorsky, 1978:51, pl. 13: fig. 4.

Cerithium suturale Philippi, 1849:2, (14), pl. 1: fig. 4 [type not found, no locality given; not *Cerithium suturale* Risso, 1826, nor Buvignier, 1843].—Sowerby, 1855:860, pl. 178: figs. 52, 53; 1865: pl. 8: fig. 54.—Tryon, 1887:123, pl. 20: fig. 24.—Kobelt, 1895:166–167, pl. 31: figs. 6, 7.

Cerithium striatum Hombron and Jacquinot, 1852, *Atlas;* pl. 23: figs. 16, 17 [holotype: MNHNP, no number, 23.3 mm × 18.1 mm; type locality: New Zealand (in error, herein corrected and restricted to Viti Levu, Fiji); not *Cerithium striatum* Deshayes, 1833, nor Lea, 1833, nor Giebel, 1848]; 1854:100.—Tryon, 1887:130.

Cerithium bicolor Hombron and Jacquinot, 1852, *Atlas*: pl. 23: figs. 14, 15 [holotype: MNHNP, no number, 24 mm × 10.5 mm; type locality: New Zealand, in error, herein corrected and restricted to Viti Levu, Fiji; not *Cerithium bicolor* C.B. Adams, 1845].

Cerithium kobelti Dunker, 1877:67; 1882:106, pl. 4: figs. 8, 9.—Kira, 1962:26, pl. 13: fig. 16.—Kuroda and Habe, 1971:113, pl. 16: figs. 7–9.—Shirai, 1980:276.

Cerithium (Proclava) kobelti Dunker.—MacNeil, 1960:41–42, pl. 11: fig. 21 [not *Cerithium kobelti* Dunker, 1877; is *Cerithium tenellum* Sowerby, 1855].

Cerithium ravidum Philippi.—Cernohorsky, 1972:64, pl. 14: fig. 2 [not *Cerithium ravidum* Philippi; is *Cerithium dialeucum* Philippi, 1849].

Cerithium (Cerithium) tenellum Sowerby.—Springsteen and Leobrera, 1986:63, pl. 14: fig. 10 [not *Cerithium tenellum* Sowerby, 1855; is *Cerithium dialeucum* Philippi, 1849].

DESCRIPTION.—*Shell* (Figures 45–47): Shell light, turreted, highly sculptured, comprising 13 or 14 inflated, angulate whorls reaching 34.8 mm length and 15.9 mm width. Protoconch unknown. Early teleoconch whorls (Figure 45D) with broad, sloping, subsutural ramp and sculptured with 2 spiral threads on third whorl, 3 on fourth whorl, and 4 on fifth whorl. Adult teleoconch sculptured with 4, sometimes 3 main, nodose spiral cords with single smaller spiral cord in each interspace, and many fine spiral striae, crossed over by strong axial ribs. Smaller, frequently beaded, spiral cords and crossover points strongly nodose or spinose, with dominant, most nodose cord on whorl periphery. Subsutural cincture or band produced by 2 or 3 small, beaded spiral threads. Penultimate whorl with 8–19 axial ribs. Thick, angulate varices randomly distributed over shell whorls. Suture impressed, distinct and wavy. Body whorl wide, with moderately excavated base and large, prominent varix opposite outer lip of aperture. Body whorl sculptured with broad subsutural cincture, 5 or 6 main, nodulose spiral cords, and numerous smaller, beaded spiral cords of varying strength. Aperture ovate, wide, about one-third the shell length. Columella concave with thick callus and well-defined lip. Anterior siphonal canal elongate, tubular, strongly constricted, reflected dorsally and to left of shell axis. Anal canal well defined, deep, bordered with strong, parietal, columellar tooth. Outer lip of aperture thick at edge, strongly crenulate, spirally toothed and grooved within. Shell color highly variable, but usually with white or tan background overlain by darkly pigmented brown, tan, purple-black stripes or bands. Dark spiral band frequently on subsutural cincture. Japanese specimens (*kobelti* morphs) usually with yellow beads or all yellow-tan. Protoconch dark purple. Aperture white; inside of outer lip of aperture with brown stripes. Measurements (Table 18). Periostracum tan, thin.

Radula (Figure 48): Type-1 radular ribbon (Figure 3A)

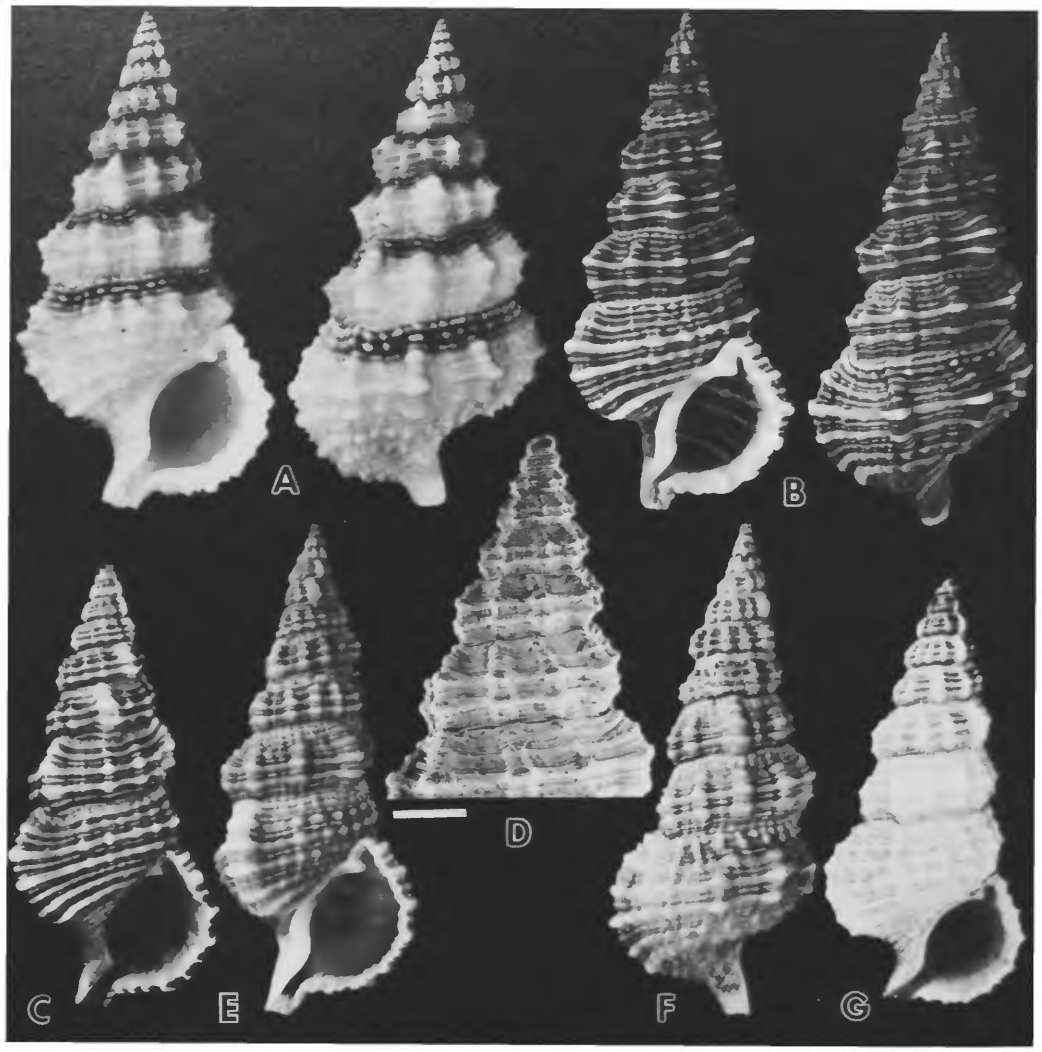


FIGURE 45.—*Cerithium dialeucum* Philippi, showing phenotypic variation: A, S Harald Bay, Ngau, Fiji, 28.2 mm (USNM 686625); B, Île de Brun, Nouméa, New Caledonia, 35 mm (AMNH 104218); C, holotype of *Cerithium striatum* Hombron and Jacquinot, 23.3 mm (MNHNP); D, SEM of early whorls and protoconch, Nouville, New Caledonia (bar = 0.43 mm; USNM 806089); E,F, Nouméa, New Caledonia, 36 mm (AMNH 104218); G, holotype of *Cerithium bicolor* Hombron and Jacquinot, 24 mm (MNHNP).

short, a little less than one-ninth the shell length. Rachidian tooth (Figure 48B,C) triangular with long median posterior projection and pair of basal ridges on basal plate. Anterior front of rachidian tooth concave; cutting edge with spade-shaped main cusp flanked on each side by two small, blunt denticles. Lateral tooth (Figure 48B,C) with strong, posteriorly projecting, buttress-bearing, small pustule, and long narrow, lateral, posterior projection. Marginal teeth (Figure 48B-D) with curved, serrated tips and spatulate bases. Inner marginal tooth with long, spoon-shaped main cusp, 3 inner flanking denticles, and 2 outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy (Figure 49): Head-foot pinkish with small white, orange, and brown flecks and larger blackish blotches. Deep ciliated groove on right side of female foot terminating in small, bulbous ovipositor. Snout thick, broad, bilobed. Cephalic tentacles broad at peduncular bases and relatively short. Eyes orange. Mantle edge fringed with elongate, tapering, pale yellow papillae. Inhalant siphon large, muscular, bright orange interiorly, and fringed with yellow papillae. Dorsal surface of

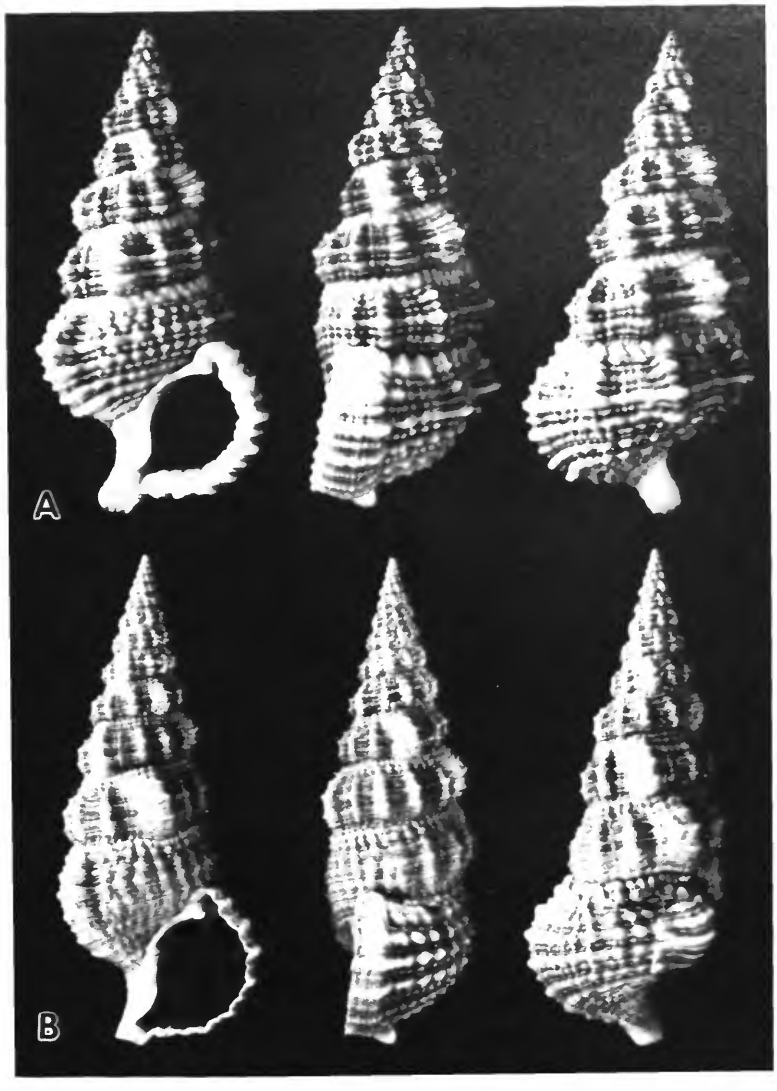


FIGURE 46.—*Cerithium dialeucum* Philippi: A, neotype of *Cerithium dialeucum* Philippi, S side Mathuata Id, Viti Levu, Fiji, 34.3 mm (USNM 862619); B, Inhaca Id, Delgado Bay, Mozambique, 39.5 mm (NM 6567).

TABLE 18.—Shell morphometrics of *Cerithium dialeucum*.

Character	$\bar{x}$ (n = 21)	sd	v	Range
Shell length	30.3	2.6	6.8	24–34.8
Shell width	12.7	1.3	1.6	10.9–15.9
Aperture length	9.6	1.2	1.5	6.1–12.3
Aperture width	6.9	0.8	0.7	5.9–9.4
Number whorls	13.4	0.5	0.2	13–14
Number spiral cords	3.8	0.4	0.2	3–4
Number axial ribs	12	2.5	6.5	8–19

mantle with long, narrow, orange stripes.

Osphradium tall, green, extending length of ctenidium. Ctenidium tan, narrow, comprised of long, tapering filaments. Hypobranchial gland brown, thick, glandular.

Buccal mass of moderate size with short radula and pair of semilunar jaws having scale-like surface. Salivary glands a pair of thin, uncoiled tubes running through nerve ring. Esophageal gland wide, well developed.

Type-B pallial oviduct (Figure 4B) with short, wide, anterior sperm gutter (Figure 49, sg). Sperm gutter with two openings

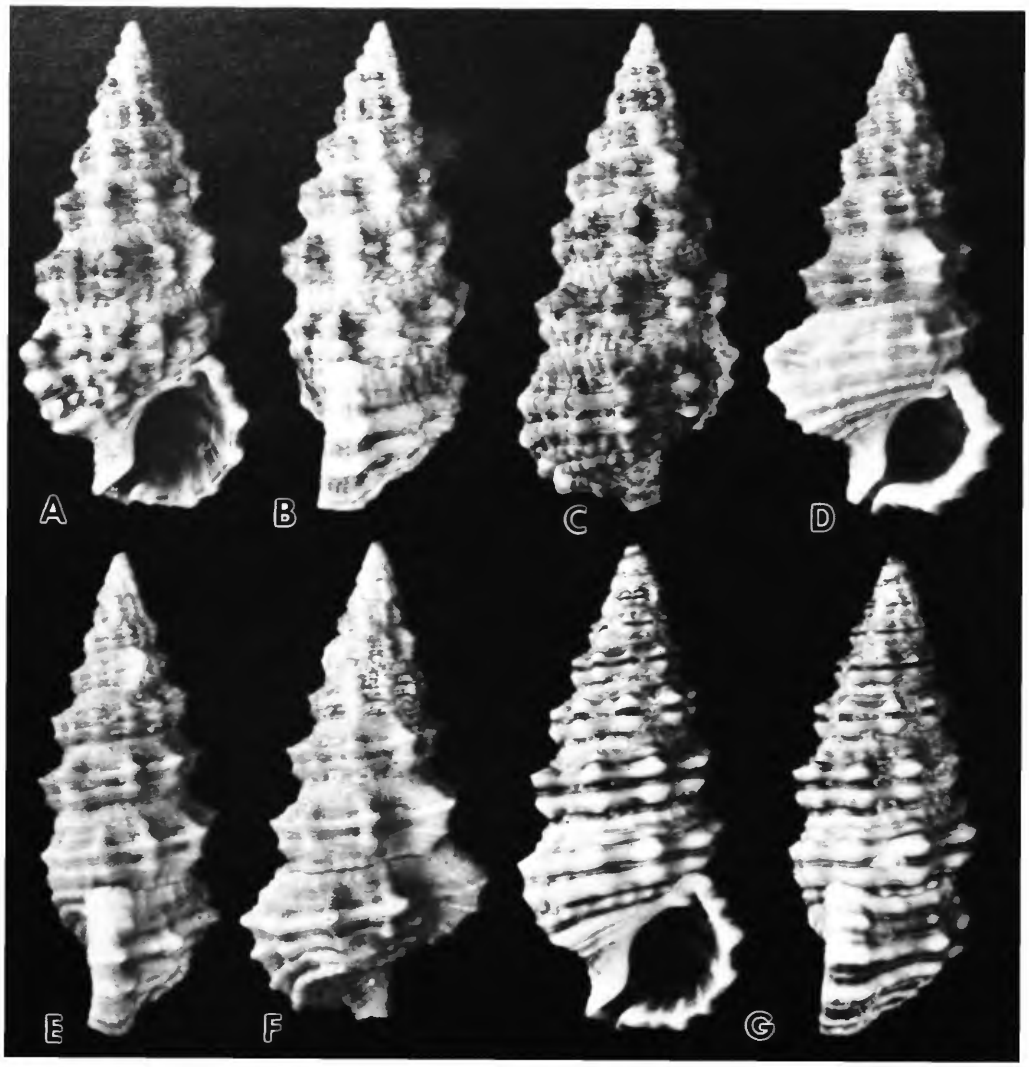


FIGURE 47.—*Cerithium dialeucum* Philippi, showing variability in sculpture and color: A–C, *kobelti* morph, Tosa, Japan, 22.8 mm (DMNH 15293); D–F, Mauritius, 26.1 mm (MCZ 23611); G, *kobelti* morph from Miyazaki, Kyushu, Japan, 23.3 mm (USNM 563789).

(Figure 49, osb, oasr); one to large spermatophore bursa (Figure 49, sb), extending length of medial lamina; the other opening (Figure 49, oasr) adjacent to first, becoming narrow, thin-walled tube in outer edge of medial lamina and leading into small posterior seminal receptacle (Figure 49, psr) at posterior edge of medial lamina. Free edge of medial lamina concave, especially in middle of lamina, and highly ciliated, forming broad sperm gutter (Figure 49, sg). Anterior edge of thin-walled lateral lamina with long ciliated tube probably functioning as anterior seminal receptacle (Figure 49, asr). Outside of tube highly ciliated and fitting into concave edge of medial lamina.

SYNONYMIC REMARKS.—This species, although relatively common throughout its range, is not usually cited in the literature, and also has been ignored in recent popular shell books. It is perhaps best known as *C. suturale* Philippi, 1849, a preoccupied name. Two other names, *C. striatum* (Figure 45C) and *C. bicolor* (Figure 45G), both of Hombron and Jacquinot, 1852, are likewise preoccupied. Philippi's figure of *C. suturale* (Philippi, 1849, pl. 1: fig. 4) is an excellent representation, leaving no doubt as to its identity. Philippi's figure 4 depicts a common color variation having a wide,

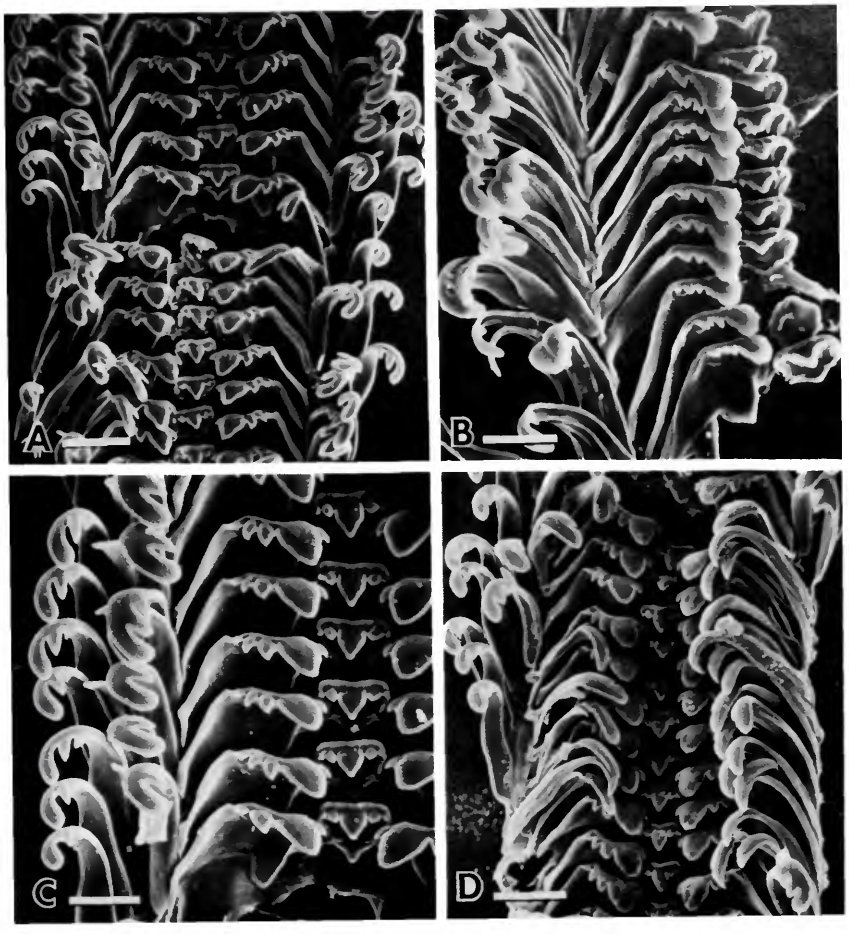


FIGURE 48.—Radula of *Cerithium dialeucum* Philippi: A, Port Moresby, Papua New Guinea (bar = 107 μm; AMS C81956); B, radula of *kobelti* morph, Hirado Hizen (bar = 30 μm; USNM 273180); C, half row with marginal teeth folded back (bar = 30 μm; AMS C81956); D, Tonghaven, N of Nouméa, New Caledonia (bar = 107 μm; ANSP 238481).

brown band at the suture. *Cerithium dialeucum* is very similar to *C. suturale* Philippi, 1849. Philippi's drawings of the comparative whorl sculpture between *C. suturale* and *C. dialeucum* are somewhat misleading because intergrades exist. Sowerby's figures of *C. dialeucum* (1855, pl. 180: figs. 98, 99) clearly resemble his depictions of *C. suturale* (pl. 178: figs. 52, 53). Moreover, Sowerby (1855:860) stated that only the black band at the suture separated the two taxa and that both forms had been found by Cuming on the Island of Ticao, Philippines. Thus, Philippi's (1849) figures of *C. suturale* and *C. dialeucum* are thought to represent the same species. These two nominal species are herein regarded as conspecific. *Cerithium dialeucum* is the earliest available name, and for the purpose of taxonomic stability, a neotype of *C. dialeucum* (USNM 862619) is designated (Figure 46A). Tryon (1887, pl. 23: figs. 87, 88) showed two figures of *C. dialeucum* with different sculpture and synonymized *C. striatum* Hombron and Jacquinot with it. Cernohorsky's (1978:51) figure of *C. dialeucum* looks more like *C. zonatum* (Wood). *Cerithium kobelti* Dunker (Figure 47A-G) is herein regarded as conspecific with *C. dialeucum*, but see "Discussion" below.

ECOLOGY.— Nothing has been published about the ecology of *Cerithium dialeucum*. It appears to be most common in terrigenous sediments in silty, protected bays associated with high islands and continental shores. This species lives in shallow, subtidal, habitats, usually on algal-covered rocks and rubble. I have found it on diverse substrates, such as red algae on submerged boulders at Bataan, Philippines; in *Enhalus* grass beds and rubble in Pago Bay, Guam; and on rocks along a sheltered lagoon in Nouville, Nouméa, New Caledonia. The fecal pellets are elongate cylinders composed of fine sediment. Eggs and larvae are unknown as is the protoconch, but the

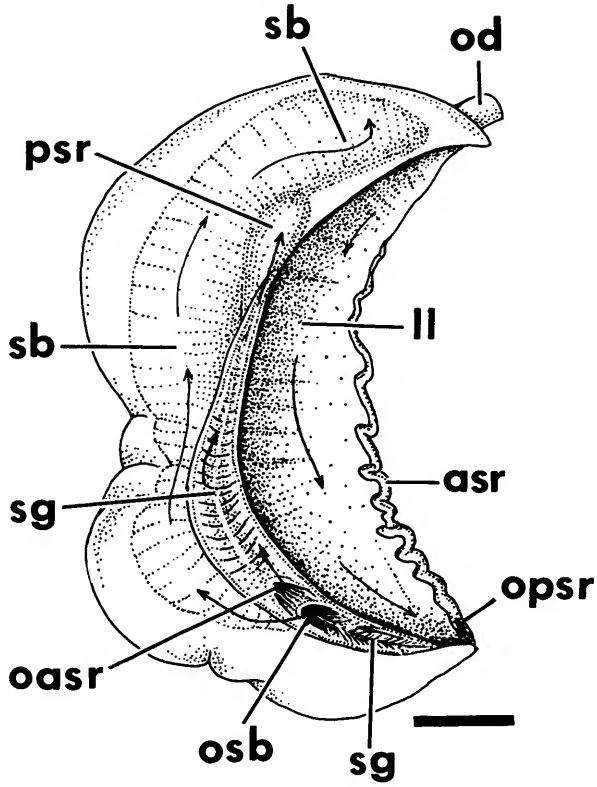


FIGURE 49.—Pallial oviduct of *Cerithium dialeucum*. (Arrows signify ciliary currents; bar = 1 mm). (Abbreviations: *asr* = anterior seminal receptacle; *ll* = lateral lamina; *od* = coelomic oviduct; *opsr* = opening of posterior seminal receptacle; *osb* = opening of spermatophore bursa; *psr* = posterior seminal receptacle; *sb* = spermatophore bursa; *sg* = sperm gutter.)

extensive geographic range and upper teleoconch whorls (Figure 45D) indicate indirect development. The Japanese form of this species, *C. kobelti* (Figure 47A-G), has been figured by Shirai (1980:276) crawling on a rocky, subtidal substrate covered with calcareous and red algae, a habitat similar to that observed in the Philippines. The chromosome number of the Japanese phenotype of this species is 2n = 18 (Nishikawa, 1962).

DISCUSSION.—*Cerithium dialeucum* is characterized by a tapering shell with angulate, spinose whorls sculptured with numerous spiral elements and by two, thin, closely set, beaded subsutural spiral cords that wind about the suture like a belt (Figure 45A-C). Prominent former growth varices are present. The body whorl is inflated and spinose with a crenulate outer lip on the round aperture. Color is extremely variable, ranging from patterns of wide white bands (Figure 45A) through narrow black and white striped forms (Figure 45B,C) to solid colors such as gold, brown, and yellow. Sculpture varies considerably, some phenotypes departing from the the usual spinose aspect (Figure 45A,B; Figure 47) and becoming finely beaded (Figure 46B). Development of the spiral spinose cords varies, some shells bearing more spiral cords than others. Phenotypes with three dominant spiral cords are common in New Caledonia, while those with four spiral cords are more prevalent in Queensland, Australia. There are specimens in which the the exact number of major spiral cords is indeterminate because of the variability and development of minor spirals between the majors. In general, there are 3 or 4 dominant spiral cords separated from one another by finer spiral threads and grooves. The interior of the aperture is distinctive in having spiral bands of pigment.

Cerithium kobelti Dunker, from Japan (Figure 47), appears to be a phenotypic variation of *C. dialeucum*, and does not attain the length of the latter. The nodes on the two dominant spiral cords of the former tend to be wider and smoother than those of *C. dialeucum*, and there are generally fewer axial ribs per whorl. The *kobelti* phenotypes are frequently pigmented with yellow nodes or may be totally yellow. The radula of *C. kobelti* is identical to that of *C. dialeucum*. The *kobelti* phenotypes appear to be geographically restricted to the Japanese islands and may qualify for subspecific status, but the conchological differences between them and the *dialeucum* forms are not statistically significant, and the anatomy of *kobelti* remains unknown. Thus, there is no reason to accord the Japanese phenotypes subspecific status at this time. Careful conchological and anatomical studies between the two phenotypes are needed.

Cerithium dialeucum is frequently confounded with *C. columna* Sowerby, but the latter is larger, with a more solid shell, a wider body whorl, and more convex whorls with fewer axial ribs. *Cerithium columna*, in contrast to the darkly pigmented *C. dialeucum*, is usually white with faint brown axial blotches. The shell surface of *C. columna* is dull, lacking the shiny aspect of the spiral cords on *C. dialeucum*.

Narrow phenotypes of *C. dialeucum* (Figures 45E,F; 46B) may be confused with *C. torresi* E.A. Smith, which is sympatric with the former. *Cerithium torresi* also has spiral pigmented stripes within its aperture, but has reduced varix formation. Overall, *C. torresi* is a smaller, more slender, tapering shell and is more finely beaded than *C. dialeucum*.

FOSSIL RECORDS.—*Cerithium dialeucum* is known from the Pleistocene of Japan (MacNeil, 1960:41-42). Holocene subfossils have been examined from Kudat, North Borneo, Malaysia (ANSP).

GEOGRAPHIC DISTRIBUTION (Figure 50).—This species has an Indo-West Pacific distribution. It occurs in the Indian Ocean along the continental shores of eastern Africa as far south as Durban, South Africa, throughout Madagascar and high Indian Ocean islands, east to SE Asia and the Indonesian Archipelago. In the Pacific, it occurs from Japan south to Australia and Melanesia, the Marianas and Fiji, east to Samoa.

SPECIMENS EXAMINED.—EAST AFRICA: Umhlah, Charles Pool, Thompson's Bay, South Africa (NM 9515); Durban Bay, Durban, South Africa (NM 6569, USNM 380856, 380888);

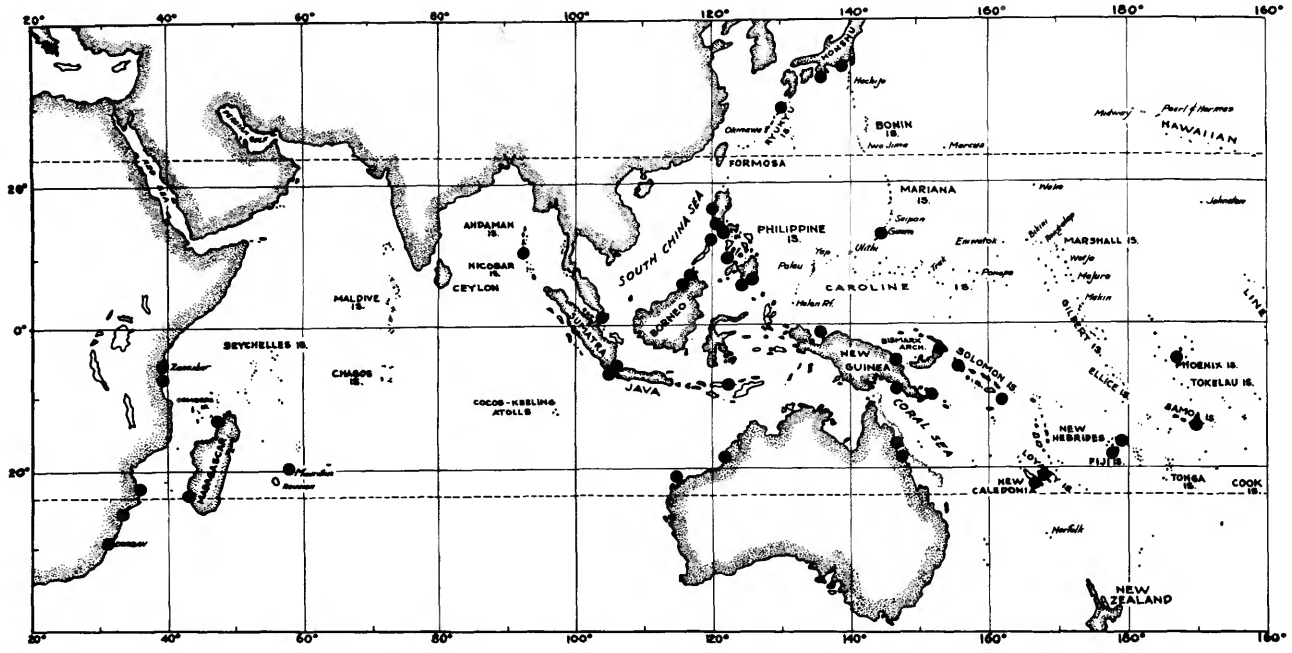


FIGURE 50.—Geographic distribution of *Cerithium dialeucum* Philippi.

Inhaca Id, Delgado Bay, Mozambique (NM 6567); Bartolomeu Dias, Sandy Estuary, Mozambique (NM G108); Bagamoyo, Eastern Prov, Tanzania (USNM 703992); Zanzibar (AMNH). INDIAN OCEAN ISLANDS: Nossi Bé, Madagascar (ANSP); Tulear, Madagascar (MNHNP); Ambariobe, Nossi Bé, Madagascar (USNM 719906); Nossi Kisimani, 19.2 km SSW of Nossi Bé (MCZ 265085); Mauritius (DMNH 100216, MCZ 23611, NM G45544); SW Cap Malheureux, N Mauritius (ANSP 344637); Grand Bay, NW Mauritius (DMNH 46139); Flic en Flacq, W Mauritius (ANSP 273202). ANDAMAN ISLANDS: Port Blair, South Andaman Id (BMNH); Long Id, Andaman Islands (BMNH). MALAYSIA: Sekudu Id, Strait of Johore (USNM 660690); Pu Setbarok, SW Singapore (WAM); Jesselton, N Borneo (USNM 658372); Kota Kinabalu [Jesselton], N Borneo (ANSP); Kudat Dist, N Borneo (USNM 666750).

JAPAN: Kaga-mura Yatsuka-gun, Shinane Pref, Nabuo Hirata (Japan Sea) (ANSP); Tsuruga (USNM 383561); Kominato, Chiba, Honshu (WAM); Tokyo Harbor, Honshu (ANSP); Hayama, near Kamakura, Sagami Bay, Honshu (ANSP); Hayama, near Yokohama, Honshu (MCZ); Choshaga Saki, Sagami (CAS); Sagami Bay, Honshu (DMNH); Kyoto, Honshu (ZMA); Tosa, Sima (ANSP, DMNH); Kii, Honshu (FSM, MCZ 145656, 209869, 209871); Nagasaki, Honshu (ANSP, USNM 228226); Wakagama (ANSP); Hirado, Hizen (ANSP, MCZ 43045, USNM 273180, 343864); Mogi (USNM 228255); Waki, Satsuma (USNM 363688). RYUKYU ISLANDS: Amami O-Shima (ANSP).

PHILIPPINES: W coast Palaui Id, Luzon (USNM 232917); Banan, Batangas Prov, Luzon (WAM); Talisian Cove, Talisian Prov, NW Luzon (LACM 76758); La Union Pt, Lingayen Gulf, Luzon (AMNH); 9.1–18.3 m, Baler Bay, Quezon Prov, Luzon (AMNH); 18.3–27.4 m, Nasasa Cove, Zambales Prov, NW Luzon (LACM 76783); Port Binang, Subic Bay, Luzon (USNM 232885); W shore Subic Bay, Luzon (USNM 543335); Villa Carmen, Bataan Prov, Luzon (WAM); Talaga, Bataan Prov, Luzon (WAM); Eman Pt, Morong, Bagok, Bataan Prov, Luzon (USNM 774779, 774926); Looc Bay, Bagac, Bataan Prov, Luzon (LACM 76808, USNM 774869, 774976); Moron, Bataan Prov, Luzon (ANSP); Manila, Luzon (USNM 303680); Mariveles, Luzon (USNM 233213); reef, E end of Sisiman Bay, Bataan Prov, Luzon (ANSP 230027); 1.8–5.5 m, Naic, Cavite Prov, SW Luzon (LACM 76808); Matabungkay, 11 km SSW of Manila, Luzon (AMS); Awasan Beach, Tagkawayan, Quezon Prov, Luzon (AMS); Tilik Bay, Lubang, Mindoro (AMNH); Lubang Id (USNM 243934); Calapan, Mindoro (MCZ); San Jose, Mindoro (WAM); Estero, Bagaong River, Mindoro (USNM 243808); Kawayan, NW Marinduque Id (AMS); 1–6 m, Ata Id, 2 km W of Kawayan, Marinduque (AMS); Cowit, Marinduque (AMS); 3.7–9.1 m, Marintoc-Mobo, Masbate, Masbate (AMNH); Dumurug Pt, Masbate (USNM 233001); Iloilo, Panay (USNM 383973); Guijulugau, Negros (USNM 232848, 244049); Davao, Mindanao (FSM); Sarangai Bay, Mindanao (USNM 233126); Ophol, Mindanao

(USNM 243714); 5.5–9.1 m, Laminangcong, Calamian Gp, Palawan Prov (AMNH); Busuanga (USNM 243955); 9.1–18.3 m, Coron Bay, Palawan (AMNH); Tagbayag Bay, Palawan (USNM 244180). INDONESIA: Teluk Betong, S Sumatra (ZMA); Putih, N coast of Java (WAM); Panaiton, W Java (ZMA); Jepara, Java (USNM 767487); Pruput, Bantam, Java (USNM 260584); on reef at Larantoeka, E Flores (ZMA); between Weri and Waibaloen, near Larantoeka, Flores (ZMA); off Kg Nalahia, Nusa Laut Id, 03°38′S, 128°47′E (WAM); S Moluccas (ZMA).

WESTERN AUSTRALIA: Broome (WAM); mouth of Bibata Creek, Barrow Id (USNM 691586). QUEENSLAND, AUSTRALIA: S end of Wonga Beach, N of Mossman (AMS); Cooya Beach, N of Mossman (AMS); Four Mile Beach, Port Douglas (AMS); Batt Reef, off Port Douglas (AMS); Buchan's Point, near Cairns (AMS); Happy Beach, near Cairns (AMNH); Bingil Bay, E of El Arish (AMS); Bingil Bay, Mission Beach (USNM 842685); Horseshoe Bay, Magnetic Id (USNM 824825); Goeffrey Bay, Magnetic Id, off Townsville (AMS, USNM 842874); Hook Id (AMS); Kepple Bay (AMS); Airlie Beach (AMS). NEW GUINEA: Selo Id, off NW reefs, Aitape, Papua (USNM 616002); Japen Id, Schouten Archipelago, Irian Jaya (AMS); Cape Tekopi, W side Samberbaba, Japen Id, Schouten Archipelago, Irian Jaya (ANSP 205145); Madang, Papua (AMS C95234); Kapa Kapa, 72 km N of Port Moresby, Papua (AMS C81956); Milne Bay, Port Moresby (USNM 543018); near Port Moresby (AMS); Gaire Beach, 48 km E of Port Moresby (AMS); d'Entrecasteaux Id, off SE Papua (MCZ); Rabaul, New Britain (AMNH); Duke of York Id, New Britain, Papua (AMS). SOLOMON ISLANDS: Beach reef, Tsimba Mission, 16 km S of Soraken Pt, Bougainville Id (ANSP); Buin Bay, Bougainville Id (USNM 631005); Ugi Id (USNM 600408); San Cristobal (AMS). NEW HEBRIDES: NW Efate Id (DMNH). LOYALTY ISLANDS: Lifu (AMS, USNM 423302). NEW CALEDONIA: Oubatche (AMS); Jadin Reef, N of Hienghene (AMS); Tuocarin Reef, S of Yate (AMS); Voh-Gatope Id (DMNH); Touho Bay, Nouméa (DMNH); Nouville, N part of Nouméa (USNM 806089); W side, S shore of Mt d'Or, near Nouméa (ANSP); Poindoime, Nouméa (AMS); Amadee Light House, Nouméa (DMNH 116910); off Chateau Reef, Nouméa (DMNH 116556); NE side Îsle de Brun, Nouméa (AMNH 104218); Baie de Prony (USNM 724874).

FIJI: SW end Tutu Id, Vanua Levu (USNM 695008); NW Rambi Id, Albert Cove, Vanua Levu (USNM 695182); Rambi Id, Georgia Cove, Vanua Levu (USNM 695374); Yakuilau Id, off Nandi Bay, Viti Levu (USNM 658798); Nadi, Viti Levu (AMS); Lautoka, Viti Levu (AMS); Sali Sali, Viti Levu (USNM 694439); S side Mathuata Id, Viti Levu (USNM 694350, 862619, neotype); W side Malake Id, Viti Levu (USNM 694572); Viti Levu Bay, Viti Levu (USNM 824800); Newtown Beach, Nadi Bay, Viti Levu (AMS, ANSP); Suva Harbor, Viti Levu (ANSP 77-36); Suva, Viti Levu (USNM 531901, 531909, 531959, 532017, 532492, 633164, 862621); Suva Pt, Viti Levu (USNM 532385, 862388); Laucala Bay, Suva, Viti Levu (USNM 790675); S of Harold Bay, Ngau (USNM 686625); S of Ketei, lagoon E side Totoya Id (USNM 686589). MARIANA ISLANDS: Asan Pt, Guam (CAS); Piti Bay, Guam (USNM 847293); Agat, Guam (USNM 862623); Alutom Id, Agat Bay, Guam (ANSP); Nimitz Beach, Anae Id, Guam (USNM 852052); Nimitz Beach, Guam (AMNH); E of Anae Id, Guam (USNM 710507); Port Merizo, Guam (ANSP); Merizo, Cocos Lagoon, Guam (LACM 77-18); off Umatae, Fouha Bay, Guam (USNM 774772). PHOENIX ISLANDS: Hulls Gp (USNM 862622). SAMOA: Tutuila (ANSP, USNM 488621); Pago Pago Harbor, Tutuila (AMS, USNM 574044); Faga-alu, Tutuila (USNM 699103, 862620).

Cerithium echinatum Lamarck, 1822

FIGURES 51–54

Strombus tuberculatus Linné, 1767:1213, no. 514 [type not located; type locality: "In Mare Mediterraneo;" no figure references, nomen dubium; not *Strombus tuberculatus* Born, 1778].—Dodge, 1956:289–290.

Rubus, Martyn, 1786, pl. 58 (Tonga) [non binomial].

Cerithium echinatum Lamarck, 1822:69–70 [lectotype, herein selected: MHNG 1097/18/1 and one paralectotype MHNG 1097/18/2; type locality: not given, herein restricted to Tulear, Madagascar; 42.6 mm];—Deshayes, 1843:291–292 [refers to Kiener, 1841, pl. 3: fig. 1].—Tesch, 1920:52–53, pl. 130: fig.173.—Salvat and Rives, 1975:268, fig. 58.

Cerithium mutatum Sowerby, 1834: No. 42 [no pagination, species 6, fig. 6; type not located, Sowerby's fig. 6 herein selected to represent the lectotype; type locality: not cited]; 1855:897.—Tryon, 1887:124, pl. 20: fig. 27.—Kay, 1979:122, fig. 45L.

Cerithium adansonii Bruguière.—Kiener, 1842:9–10, pl. 4: fig. 2 [not *Cerithium adansonii* Bruguière, 1792; is *C. echinatum* Lamarck, 1822].

Cerithium rubus Deshayes, 1843:310 [type not located, refers to Martyn, 1786, pl. 58; type locality: not cited; nomen dubium; not *Cerithium rubus* in sensu Sowerby, 1855, and later authors].

Cerithium album Hombron and Jacquinot, 1852, pl. 23: fig. 25 [holotype: MNHNP no number; type locality: Torres Straits; 37.5 mm × 18.3 mm]; 1854:101 [refers to Atlas, pl. 23: figs. 22, 23 in error: *alba* is fig. 25].

Cerithium tuberculiferum Pease, 1869:76–77 [type: not found, refers to Sowerby, 1865, pl. 2: fig. 11; type locality: Paumotus].—Kobelt, 1893: 100–101, pl. 20: figs. 3, 4.—Salvat and Rives, 1975:268, fig. 59.

Gourmya echinata (Lamarck).—Cox, 1927:85–86, pl. 18: fig. 3.

Cerithium (Thericium) mutatum Sowerby.—Ladd, 1972:37, pl. 9: fig. 6.

Cerithium (Cerithium) rubus Deshayes.—Rehder, 1980:34–35, pl. 6: figs. 1, 2.

Cerithium (Cerithium) echinatum (Lamarck).—Springsteen and Leobrera, 1986:60, pl. 13: fig. 6.

DESCRIPTION.—*Shell* (Figures 51, 52): Shell thick, heavy, robust, conical-turrate, comprising 11 to 13 nodose, inflated, angulate whorls and attaining 65 mm length and 26 mm width. Protoconch (Figure 52E) 3.5 whorls. Protoconch 1 smooth; protoconch 2 sculptured with subsutural riblets and two spiral cords, lower one weakly beaded. Lower half of protoconch whorls with microscopic sculpture of lattice-like opisthocline lines below second spiral cord. Deep sinusigeral notch at aperture lip of protoconch. Early teleoconch sculptured with two main spiral cords and several weaker spiral lirae (Figure

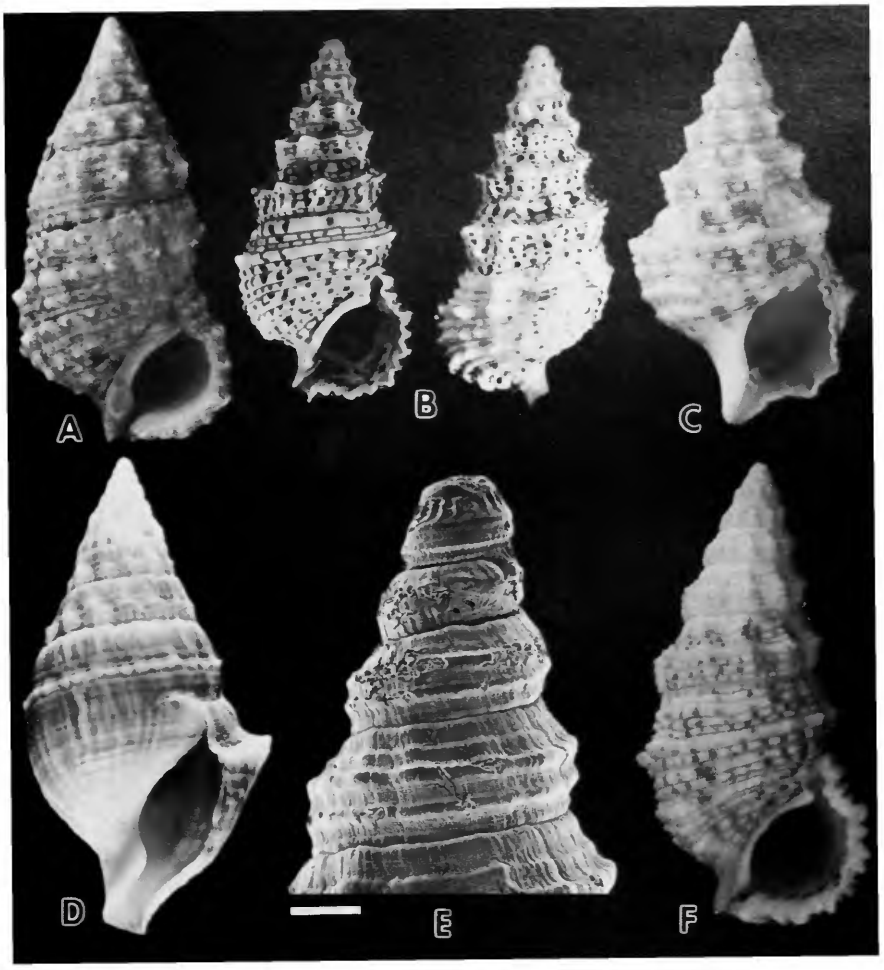
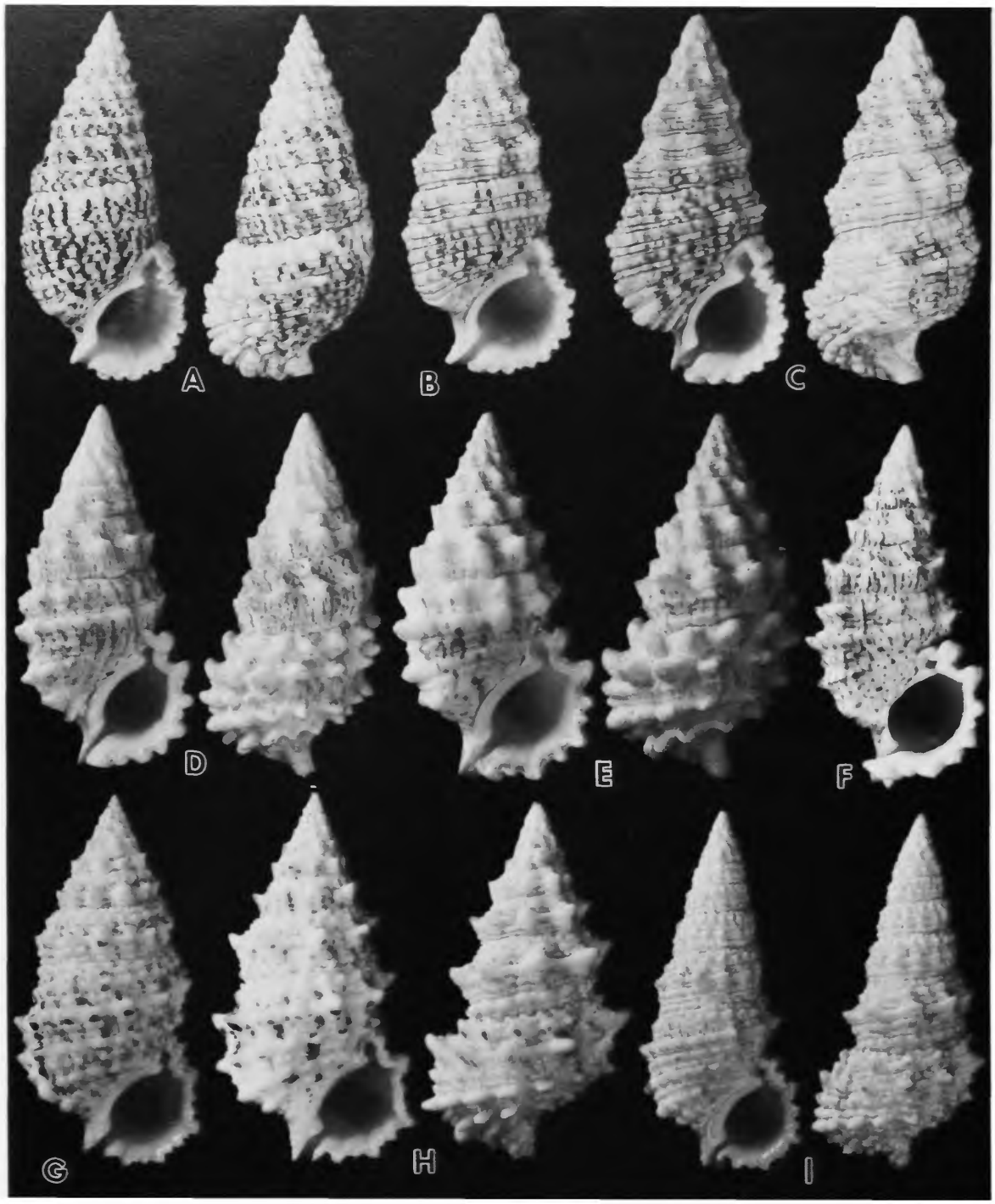


FIGURE 51.—Immature shells and types of nominal taxa synonymous with *Cerithium echinatum* Lamarck: A, holotype of *Cerithium album* Hombron and Jacquinot, Torres Strait, Australia, 37.5 mm (MNHNP); B, lectotype of *Cerithium echinatum* Lamarck, 42.6 mm (MHNG 1097181); C, immature shell from Dirk Hartog Id, Western Australia, 19.5 mm, (WAM 450-76); D, immature shell showing smooth sculpture from Broadhurst Reef, E of Townsville, Queensland, Australia, 19.2 mm (AMS); E, SEM of early whorls and protoconch from Mataire Id, Raroia, Tuamotus (bar = 0.14 mm; USNM 698605); F, possible syntype of *Cerithium mutatum* Sowerby (ANSP 17593).

51E) and becoming progressively spinose or nodular on second spiral cord of larger whorls (Figure 51D). Adult teleoconch sculptured with central spiral cord bearing large pointed nodes, incised spiral lines, and 3 or 4 minor, sometimes spinose, nodular, spiral cords. Penultimate whorl with 11–61 spiny nodes. Each whorl with broad subsutural ramp. Nodes and spines frequently drawn out axially, forming weak, broad ribs, especially on lower half of whorl. Suture deeply impressed. Body whorl very large, elongate. Aperture ovate, about one-third the shell length. Columella slightly concave with

FIGURE 52.—*Cerithium echinatum* Lamarck, showing phenotypic variation: A, weakly sculptured morph with incised spiral lines, Abrolhos Ids, Western Australia, 52,7 mm (USNM 801607); B, weakly sculptured morph with spiral incised lines, Barrow Id, Western Australia, 50.1 mm (USNM 691908); C, Rottnest Id, Western Australia, 42.4 mm (WAM 446-76); D, knobby morph, Gulf of Aqaba, Eilat, Israel, 51.1 mm (USNM 779992); E, highly sculptured *mutatum* morph with thickened spinose nodes, Gilbert Islands, 50.8 mm (USNM 76763); F, Tetiaroa, Society Islands, 54.5 mm (USNM 705661); G, finely spinose *rubus* morph, Raroia, Tuamotus, 43.2 mm (USNM 698256); H, finely spinose *rubus* morph, Tokelau, 35.8 mm (USNM 768659); I, slender, elongate *rubus* morph, Anumuraro, Tuamotus, 45.5 mm (USNM 725226).


A
B
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thick callus and well-developed lip. Anterior siphonal canal tubular, of moderate length, reflected dorsally and to left of shell axis. Anal canal large, formed by constriction of upper outer lip and bordered with large, parietal, columellar tooth extending well into aperture. Outer lip thick, highly crenulated and spinose at edge and with deep inner lines. Hook-like extension of base of outer lip crossing over, but not fused with anterior siphonal canal. Shell color white with tan or brown spiral lines, spots, and blotches. Brown to tan flamules sometimes present. Aperture white. Protoconch pink; juveniles yellow, tan, or brown. Measurements (Table 19). Periostracum tan, thin. Operculum thick, brown and paucispiral with eccentric nucleus.

Radula (Figure 53): Type-1 radular ribbon (Figure 3A). Rachidian tooth (Figure 53D) rectangular; basal plate with narrow central, posterior extension and with pair of posterior basal ridges. Top of rachidian tooth slightly rounded; cutting edge with large spade-shaped main cusp flanked on each side by two, sometimes three, small denticles. Lateral tooth (Figure 53D–F) with wide central ridge with basal node and long basal posterior extension on broad basal plate. Cutting edge of lateral tooth with long, pointed main cusp, one inner flanking denticle and 3 or 4 outer flanking denticles. Marginal teeth (Figure 53C, D) with long narrow shafts, broad bases, and hooked apices with sharp pointed tips. Inner marginal tooth with long main cusp, 3 or 4 inner flanking cusps, and 3 outer flanking cusps. Outer marginal tooth same, but without outer flanking cusps.

Anatomy: Head-foot large, muscular; animal green with maroon blotches, with white and pink spots on head, and with dark brown blotches and iridescent blue lines on foot. Cephalic tentacles slender, tapering, darkly pigmented at tips, and with broad peduncular bases. Eyes black, surrounded with orange. Snout wide, massive. Columellar muscle large, thick. Mantle edge scalloped and with many long, fine papillae. Top of mantle whitish orange, yellow and green. Inhalant siphon thick, muscular, darkly pigmented, and with many papillae along edge.

Osphradium yellow-brown, narrow, tall, tapering into inhalant siphon. Ctenidium white, long, very narrow, comprised of long, tapering, triangular filaments. Hypobranchial gland pale green, thick, wide, becoming narrow near exhalant siphon, and with transverse ridges. Rectum very wide.

Massive buccal mass with stout jaws. Thick, cord-like salivary glands passing through nerve ring, not distally coiled. Esophageal gland well developed, very wide. Stomach large, with extensive sorting area. Style sac and style short.

Type-A pallial oviduct (Figure 4A) with thick posterior albumen gland and with thick, white, median capsule gland. Sperm gutter opens at middle of medial lamina into large, posterior, spermatophore bursa. Small, orange seminal receptacle at dorsal-posterior of medial lamina opening into oviductal groove. Opening of anterior seminal receptacle of lateral lamina opposite opening to spermatophore bursa of medial lamina. Anterior seminal receptacle extending about two thirds length of lateral lamina.

SYNONYMIC REMARKS.—Lamarck's name, *C. echinatum*, is the earliest available one for this species, but his original description was without a figure and no locality was given. Later, he referred to Kiener's illustration of *C. echinatum* (1841, pl. 3: fig. 1) leaving no doubt as to the identity of his species. In Kiener's text (1842:8) the "seas of the Indies," the coasts of Madagascar, and the Seychelles, are cited as localities. There are two shells of *C. echinatum* in the Geneva museum with a handwritten label by Lamarck that exactly match Kiener's figures (1841, pl. 3: fig. 1, 1a). I herein select the larger (42.6 mm long) as the lectotype (Figure 51B) and restrict the type locality to Tulear, Madagascar. The holotype of *Cerithium album* Hombron and Jacquinot, 1852, is a worn, stocky phenotype (Figure 51A) that is conspecific with *C. echinatum*. The name *album* was first published in the *Atlas* (pl. 23: fig. 25) which dates from 1852 according to the individually stamped plates in the Paris Museum (Bouchet, pers. comm.). The text was written later, and therein Hombron and Jacquinot (1854:101) erroneously referred to *C. alba* as being illustrated in the *Atlas* on pl. 23: figs. 22, 23 (figure 25 is *alba*). Both Tryon (1887:101) and Kobelt (1898:102) also considered *C. album* to be conspecific with *C. echinatum*. Another name given to this species is *C. mutatum* Sowerby, 1834, and although no locality was given in the original description, and the type has not been found, there is a specimen in the collection of the Academy of Sciences, Philadelphia labeled "type" and "ex auctore," indicating that Sowerby had sent type material of his species to the Academy. This shell (Figure 51F) is clearly conspecific with Lamarck's *C. echinatum*. Sowerby (1855:858) later placed *C. mutatum* into the synonymy of *C. echinatum* Lamarck in the *Thesaurus*, although in the index to this work (p. 897), *mutatum* is listed as a variety of *echinatum*. Sowerby did not mention *mutatum* in his *Cerithium* monograph, subsequently published (1865) in *Conchologica iconica*. It is thus clear that Sowerby, after initially proposing the taxon *mutatum*, subsequently considered it to be a synonym of *C. echinatum*, or at best, a variety of that taxon. Tryon (1887:124) and Kobelt (1898:102) also considered *C. mutatum* to be conspecific with *C. echinatum*. Rehder's (1980:35) resurrection and application of the name *mutatum* to phenotypes of *C. echinatum*, in which there is extreme nodular development is thus contrary to the evidence of the probable

TABLE 19.—Shell morphometrics of *Cerithium echinatum*.

Character	$\bar{x}$ (n = 52)	sd	Range
Shell length	44.9	6.4	30.1–65
Shell width	20.2	2.4	13–26
Aperture length	15.4	3.1	10.2–23
Aperture width	11.1	1.9	7.9–16
Number whorls	11.9	0.4	11–13
Number nodes	23.7	13.0	11–16

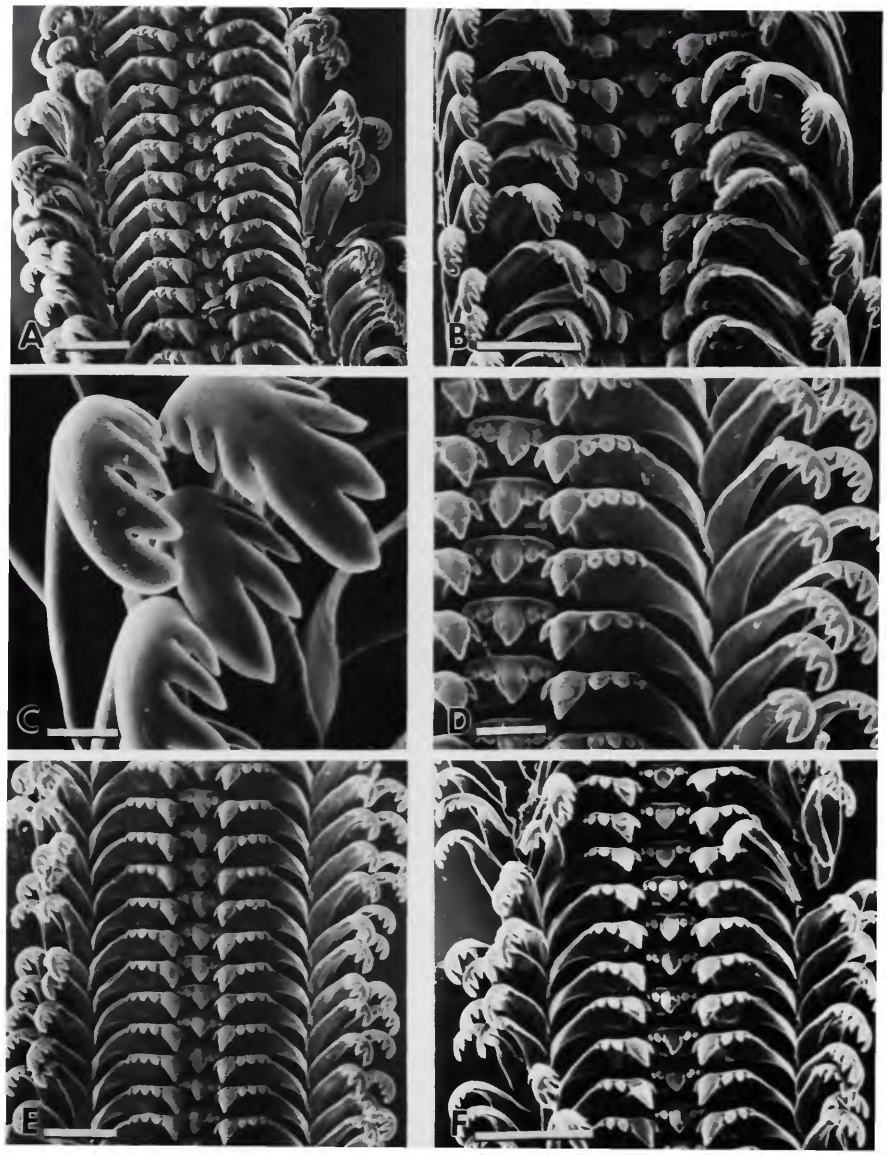

FIGURE 53.—Radula of *Cerithium echinatum* Lamarck: A, radular ribbon with marginal teeth spread open, Aqaba, Israel (bar = 0.23 mm); B, detail of half row, showing rachidian, lateral, and marginal tooth dentition, Papua (bar = 200 μm; AMS C95223); C, half row, Guam (bar = 650 μm; USNM 774767); D, radula with marginal teeth folded over ribbon, Guam (bar = 100 μm; USNM 774767); E, radula with marginal teeth spread back, Guam (bar = 170 μm; USNM 794046); F, radula with marginal teeth spread back, Tuamotus (bar = 200 μm; USNM 794046).

type material, the opinion of Sowerby himself, and the judgement of several other authors. I am thus of the opinion that *mutatum* is synonymous with *echinatum* (see my remarks in the following discussion). The name *C. tuberculatus* (Linné, 1758) has sometimes been applied to *C. echinatum*, but because of the abbreviated, equivocal description, and the lack of both type material and figure references, *C. tuberculatus* (Linné) is here considered a nomen dubium. *Cerithium tuberculatum* Born, 1778, is also erroneously applied to *C. echinatum* but the former name is a synonym of *Batillaria sordida* (Gmelin, 1791) (see Houbrick, 1978c:642). In lieu of the missing type of *C. tuberculiferum* Pease, examination of the figure of *C. adansonii* Bruguière, presented by Sowerby (1865, pl. 2: fig. 11) and referred to by Pease (1869:76–77) in his description,

leads me to conclude with Tryon (1887:101) that this taxon is identical with *C. echinatum*, merely being a more slender, spinose form of the latter species (called *C. rubus* Deshayes by Rehder (1980:34)).

The original description of *C. rubus* Deshayes, 1843, was without a figure or a type locality and the name was based on an earlier, non-binomial name of Martyn (1786), *Rubus*. Deshayes' (1843:310) first four figure references are to Martyn or to later citations referring to Martyn. The first of these (Martyn, 1786, pl. 58), is unequivocally identical to the spinose morphs of *C. echinatum* found in southeastern Polynesia; thus, *C. rubus* Martyn is a synonym of *C. echinatum*. Rehder (1980:34–35) recognized *C. rubus* as a distinct species, but I do not agree (see "Discussion" below).

ECOLOGY.—*Cerithium echinatum* is very common and lives on subtidal, rocky substrates, such as submerged solution benches and rocky areas of fringing reefs. At the western part of its range it is common along continental margins, high islands, and low-lying, coral-reef islands. The same is true of the western Pacific, but in Polynesia it is found only on the low coral atolls and islands, while at the extreme eastern end of its range it occurs around volcanic islands (Rehder, 1980:35). *Cerithium echinatum* occurs in moderate, subtidal depths, but is occasionally taken quite deep; however, in the eastern end of its range, on Pitcairn Island and Easter Island, it lives in tide pools (Rehder, 1980:35). Ayal and Safriel (1981:62; 1982a:308) recorded that *C. echinatum* is common in the Red Sea subtidally among boulders on the reef table and on algal-covered pebbles and hard surfaces rich in holes. In Guam and Hawaii I have found it to be common in depths of 3–30 m, off the reef crest. The shell of this species is frequently encrusted with coralline algae. Yaron (1979:233) recorded that *C. echinatum* "apparently feeds on the soft parts of corals," but this is surely erroneous, as no predatory *Cerithium* species is known, and *C. echinatum* has a style sac and crystalline style, indicative of herbivory. Gut contents of live-collected specimens comprised detritus, algal fragments, diatoms, and sand grains.

Although predation has not been directly observed, crushed adult shells (USNM 731775, 732050, 732055, 732064, 732260) have been taken from stomachs of fish such as *Diodon hystrix* and *Coris aygula* at Pitcairn and Ducie Islands, and in Rarotonga, Cook Islands. Despite the very thick and heavily armored shell, numerous museum specimens show evidence of peeling due to crab attacks, even on very large, robust shells (USNM 705816, 722942).

Little has been recorded about the reproductive biology or growth of *C. echinatum*, but the protoconch (Figure 51E) shows that a planktotrophic stage is present before settlement. Taylor (1975:99) described Hawaiian veligers of this species (cited as *C. mutatum*) found in the plankton from July until August. The veliger has a bilobed, unequal velum and a protoconch with a smooth apical whorl and two spiral keels on the abapical whorls, agreeing with the protoconch described and depicted herein from an adult shell (Figure 51E). Taylor (1975:99) found that metamorphosis occurred when two whorls were complete, but as the protoconch figured herein has 3 whorls, this is probably a variable feature. The egg mass is unknown.

DISCUSSION.—*Cerithium echinatum* is easily recognized by its large, heavy shell, stout shape, and a sculpture of several spiral rows of acute to robust nodes that are especially prominent on the body whorl. The shell base is concave, the outer lip strongly crenulate, and its base frequently projects over the anterior canal.

Considerable sculptural variability exists in this species over a broad geographic range, particularly in the number of spiral nodes. A broad, clinal change in shell morphology resulting in three major phenotypes may be discerned: (1) Phenotypes from the western Indian Ocean have only several rows of large, sharp nodes on the lower whorls and many incised spiral lines (Figure 52D). Populations from Western Australia comprise strongly pigmented individuals, with several spirals of smaller sharp nodes, and a strong pattern of spiral incised lines (Figure 52A–C). (2) Populations from the western Pacific, western Polynesia, especially those from calcareous habitats on coral reefs, are more robust, lack spiral lines, and have a coarse sculpture of thickened spinose nodes, especially on the body whorl (Figure 52E,F). These phenotypes were attributed to *C. mutatum* Sowerby by Rehder (1980:35; see "Synonymic Remarks," above), but specimens from coral reefs in the Red Sea are identical, indicating that these forms are ecophenotypes. (3) Populations of *C. echinatum* from southeastern Polynesia tend to be slender, with many short, pointed tubercles presenting an overall spinose appearance (Figure 52G–I). These phenotypes were given specific recognition by Rehder (1980:34–35), who called them *C. rubus* Deshayes (see "Synonymic Remarks," above). Similar forms occur in the western Pacific at Guam and in the Carolines.

After close examination of hundreds of lots of specimens from throughout the range, I was unable to consistently separate the three phenotypes described above into any meaningful geographic pattern that would indicate subspeciation, with the exception of the *rubus* phenotypes. These forms occur chiefly in southeastern Polynesia, and may be an incipient subspecies of *C. echinatum*; however, the presence of this phenotype in some western Pacific localities would seem to preclude subspecific status. Numerous intergrades, referred to by Rehder (1980:35) as an unnamed species coexisting with the *rubus* phenotype, occur between all phenotypes, and as there is no circumscribed geographic range for any of the phenotypes, subspecific recognition is not warranted. No differences in radular pattern between the different phenotypes were discerned. Convincing evidence for formal taxonomic recognition of these three phenotypes is lacking, and it is concluded that *C. echinatum* represents one, widespread, variable species. More detailed work utilizing statistics and biochemical techniques is needed on this species-complex.

Ontogenetic changes in shell morphology make identity of

immature or subadult shells difficult. Immature shells may be highly pigmented and are shaped differently from adults due to an abrupt appearance of spiny nodes and the lack of a fully developed apertural lip on the body whorl (Figure 48C,D).

The only species with which *C. echinatum* may be confused are *C. caeruleum* Sowerby (Figure 22A-K) and *C. columna* Sowerby (Figure 31). *Cerithium caeruleum* is sympatric with *C. echinatum* in the western Indian Ocean and differs in having a stockier gray-blue shell with dark brown nodules, a large aperture, and less defined suture. As there is a weak siphonal constriction, the shell base is not as concave. *Cerithium columna* is sympatric with *C. echinatum* throughout the latter species' geographic range but the former species is a smaller, more highly turreted, slender species with a deeper sutural impression, and has a longer, more attenuate siphonal canal. *Cerithium columna* has many spiral cords per whorl and, if present, only one larger row of nodes per whorl, while the body whorl has only two spiral nodose cords.

FOSSIL RECORDS.—In the western Indian Ocean, *Cerithium echinatum* has been reported from the Neogene and Pleistocene of Zanzibar (Cox, 1927:85-86, pl. 18: fig. 3). It has also been found in Tertiary and Quaternary deposits on Timor (Tesch, 1920:52-53, pl. 130: fig. 173). Ladd (1972:37) reported this species (as *C. mutatum*) from the Holocene of Enewetak Atoll, Marshall islands. Sub-Recent specimens of this species are in the Western Australian Museum, Perth.

GEOGRAPHIC DISTRIBUTION (Figure 54).—This species has one of the widest ranges known among *Cerithium* species. It occurs from the Red Sea and East Africa throughout the Indian Ocean, and in the Pacific, from southern Japan and the western Pacific south through Melanesia, and eastward throughout Micronesia and Polynesia, to Easter Island.

SPECIMENS EXAMINED.—EAST AFRICA: Durban, Natal, South Africa (USNM 368024); Inhaca Id, Mozambique (MCZ); Santa Carolina Id, Bazaruto Bay, Mozambique (ANSP, MCZ, USNM 656712); Ilha Do 180, Mozambique (AMS C125007); NW corner Mbudya Id, 16 km N Dar es Salaam, Tanzania (AMS C123791); Mbudya Id, 16 km N of Dar es Salaam, Tanzania (AMS C115924); Kizimkazi, Zanzibar (ANSP); Chukwani Place, SW Zanzibar (MCZ); Pange Id, W Zanzibar (ANSP); Mnazi Moja, Zanzibar City, Zanzibar (USNM 604409); Bawe Id, 6.4 km N of Zanzibar City, Zanzibar (USNM 597195); Bawe Id, Zanzibar (MCZ); outer reef, Kiwengwa, Zanzibar (ANSP); Malindi, 106.4 km N of Mombasa, Kenya (USNM 595038); Gesira, Somalia (ANSP); 30 km SW of Mogadiscio, Somalia (AMNH); Mogadiscio, Somalia (USNM 673796, 679344, 679372, 754955). RED SEA: Fara'um Id, Elat, Israel (USNM 769982, 769983, 779992); Aqaba, Gulf of Aqaba, Jordan (USNM 841308, 841314); El Himera, Gulf of Aqaba, Egypt (USNM 794179); Port Sudan, Sudan (USNM 770717). ARABIAN SEA: Abu Musa Id, 64 km NE of Sharjah, Oman (MCZ). MADAGASCAR: Nosy N'Tangam, W Nossi Bé (MCZ); Îlot Sable off SE Île St Marie (MCZ); Fort Dauphin (MCZ); Sarodrano (MCZ).

INDIAN OCEAN ISLANDS: Passe Dubois, Île Picard, Aldabra Atoll, Seychelles (USNM 837929); Passe Yangue, Île Picard, Aldabra Atoll, Seychelles (USNM 837569, 837749, 837850); Aldabra lagoon, Aldabra Atoll, Seychelles (USNM 837626); SE of South Id, African Ids, Amirantes (ANSP); 1.6 km NE of Anse Étoile, NE Mahé, Seychelles (ANSP); Anse aux Pins, Mahé, Seychelles (BMNH, MCZ); cove, N side of Sel Point, E Mahé, Seychelles (ANSP); La Digue, Seychelles (BMNH); Seychelles (USNM 633321, 634732, WAM); Pointe Fayette, E Mauritius (ANSP); Flic en Flacq, W Mauritius (ANSP); Flic en Flacq, Arsenal Bay, Mauritius (USNM 716513); 4 km SSE of Mahebourg, Mauritius (ANSP); Le Chaland, SE Mauritius (AMS C124560); Mauritius (MCZ); Rodriguez Id (BMNH); Reunion (ANSP, MCZ); Faro islet, NW of Filadu Id, Tiladummati Atoll, Maldives (ANSP); N Male Atoll, Maldives (ANSP); Dunidu Id, N of Male Town, NW tip of Gan, Addu Atoll, Maldives (ANSP); Maldives (WAM); Cocos Keeling Atoll (USNM 589152); Pulo Panjana, Cocos Keeling Atoll (USNM 679371); reef off Possession Point, Horsburgh Id, Cocos Keeling Atoll (ANSP); "The Rips," S end of Direction Id, Cocos Keeling Atoll (ANSP). THAILAND: (USNM 661462).

JAPAN: Kii (BMNH). RYUKYU ISLANDS: Oshima, Osumi (MCZ, USNM 343848); Osumi Peninsula, Kagoshima (USNM 563908); Akamaru-zaki, Okinawa (ANSP); 36.58 m, 26°30′00″N, 127°50′45″E, Horseshoe Cliffs, Onna Village, Okinawa (USNM 821340); S end of bay, 0.5 km SW of Onna Village, Okinawa (USNM 812948); Yakata, Katabaru, Onna Village, Okinawa (USNM 821036); sea wall at channel off Kadena Yacht Club, Okinawa (USNM 812994, 821059); Kita-Daito-Jima, Okinawa (USNM 563846, 679343); China Reef, Okinawa (AMNH); Okinawa (USNM 671097). TAIWAN: off Kao-Hsiung (ANSP). PHILIPPINES: Wawa, Nasugbu, Batangas Prov, Luzon (WAM); Caban Id, Luzon (USNM 808730); Sandoval Point, Bondoc Peninsula, S Quezon (WAM); SE Mompog Id, Mompog Pass, S Quezon (WAM); Salomague Id, E Marindique, S Quezon (WAM); Tilig, Lubang (USNM 243677); Calapan, Mindoro (AMNH); Cara Id, Lubane, Mindoro (WAM); off Buyong Beach, Mactan Id, Cebu (AMS C138702); Silino Id, Mindanao (USNM 244017); Zamboanga, Mindanao (AMNH); Corin Harbor, Busuanga, Palawan (MCZ); Doc Can Id, Sulu Archipelago (WAM); Boanga Channel, SW end, Sanga Sanga Id, Sulu Archipelago (ANSP); Sitanki, Sitanki Id, Tawitawi (USNM 243640). INDONESIA: Pulau Stupei, Mentawai Id, SW of Sumatra (USNM 655133); Taganak Id, Borneo (USNM 233247); Tg Tapan, Piru Bay, Ceram, Moluccas (USNM 746709); 3.2 km N of Tg Nuan, Jamdena Strait, Tanimbar, Moluccas (USNM 747581).

WESTERN AUSTRALIA: Wilson Bay, Rottnest Id (WAM); Mable Cove, Rottnest Id (WAM); S end of Houtman Abrolhos Ids (USNM 801607); S of Gun Id, Houtman Abrolhos Ids (WAM); outside reef, NW Gun Id, Houtman Abrolhos Ids (WAM); island between Eastern Id and Seal Id,

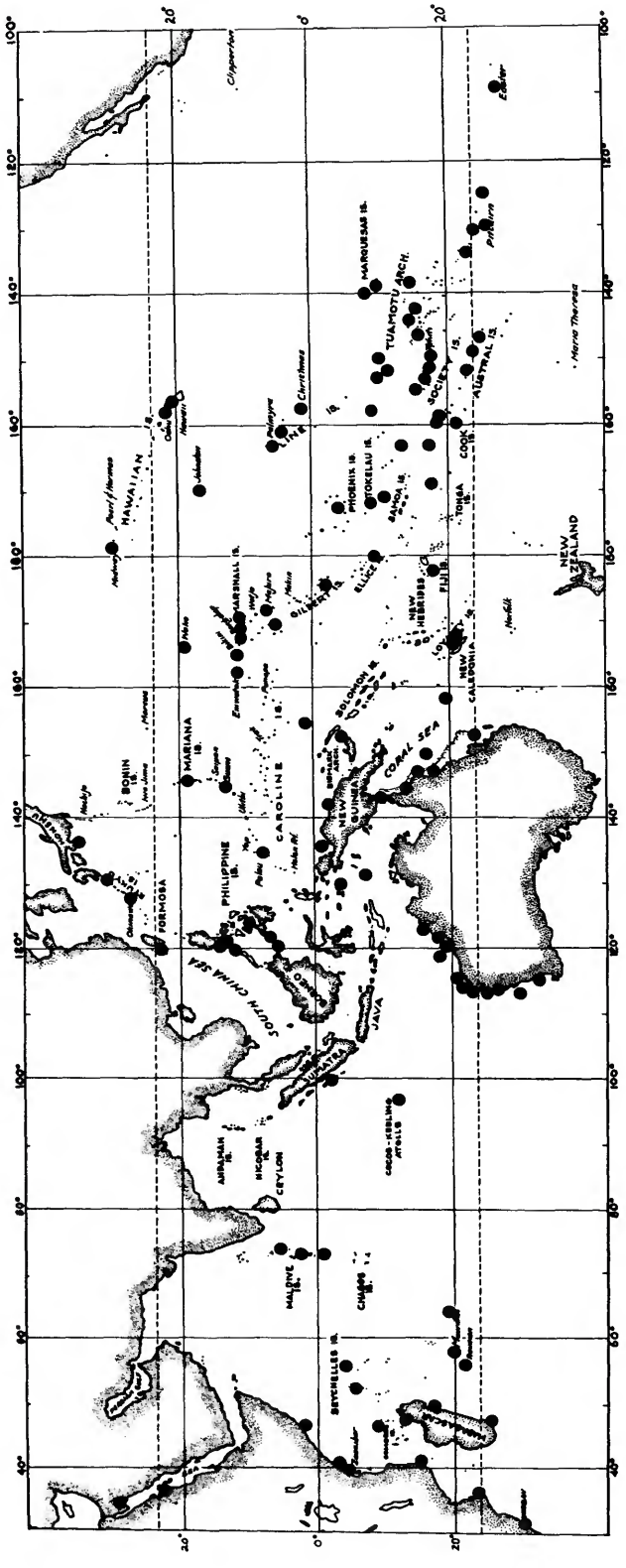

FIGURE 54 (left).—Geographic distribution of *Cerithium echinatum* Lamarck.

Houtman Abrolhos Ids (WAM); Williama, Useless Loop, Shark Bay (AMS); Surf Point, Dirk Hartog Id, Shark Bay (WAM); SE end of Dirk Hartog Id, Shark Bay (WAM); Sunday Id, SE side of Dirk Hartog Id, Shark Bay (WAM); West Point, Dirk Hartog Id, Shark Bay (WAM); Cape Boullanger, Dorre Id, Shark Bay (WAM); below Quobba light ("Blowholes"), N of Carnarvon (AMS, WAM); Quobba Station, 64 km N of Carnarvon (WAM); Point Quobba (ANSP, WAM); Cape Cuvier (ANSP); 6.4 km N of Red Bluff (ANSP); Mangrove Bay area, North West Cape (WAM); Bill's Bay, 3.2 km S of Point Maud (WAM); Maud's Landing, Point Maud (WAM); W of Point Cloates (WAM); W of Ningaloo Homestead, Point Cloates (WAM); reef, 1 km SW of Pilgonaman, North West Cape (WAM); North Mandu Mandu, North West Cape (WAM); Tantabiddi, North West Cape (WAM); 19.2 km S of Yardie Creek, North West Cape (WAM); reef front 5 km SW of Yardie Creek, North West Cape (WAM); Yardie Creek, North West Cape (WAM); 35.2 km S of Vlaming Head, near North West Cape (AMS, ANSP); Coral Bay, S of North West Cape (AMS C101973); Exmouth, North West Cape (WAM); W of Flat Id, off Onslow (WAM); Thevenard, off Onslow (WAM); Horrock's Beach (WAM); Beagle Id (WAM); E of Cape Poivre, Barrow Id (USNM 691749, WAM); Shark Point, Barrow Id (WAM); S end Flacourt Bay, Barrow Id (USNM 691908); between Cape Dupuy and Cape Malouet, Barrow Id (USNM 694124); W side of Kendrew Id, Dampier Archipelago (WAM); inner reef, Boat Bay, Kendrew Id, Dampier Archipelago (WAM); E side of Kendrew Id, Dampier Archipelago (WAM); off Museum Bay, Kendrew Id, Dampier Archipelago (WAM); N end of Kendrew Id, Dampier Archipelago (WAM); North Citadel Rock, Kendrew Id, Dampier Archipelago (WAM); North West Id, Montebello Ids (WAM); Broome (AMS, WAM); outside reef, NE of Clerke Reef, Rowley Shoals (WAM); Mermaid Reef, Rowley Shoals (WAM); Catamaran Bay, W side of King Sound, near Cape Leveque (AMS C71218).

QUEENSLAND, AUSTRALIA: Murray Ids, Torres Strait (MCZ); Wind Rain Id 11°36′S, 144°01′E (AMS); Agincourt Reef 12°29′S, 143°45′E (AMS); NW end, Long Sandy Reef 12°29′S, 143°45′E (AMS); SW corner of reef S of Hibernia Entrance 12°47′S, 143°48′E (AMS); Cat Reef 13°S, 143°51′E (AMS); Ham Cay 13°S, 145°52′E (AMS); SW end No 5 Sandbank Reef 13°14′S, 144°16′E (AMS); Princess Charolette Bay, Cape York Peninsula (WAM); NW end Ribbob Reef 14°40.5′S, 145°39.5′E (AMS); Lizard Id (WAM); Bird Islet, Lizard Id (AMS); Yonge Reef, E of Lizard Id (AMS); Batt Reef, off Port Douglas (AMS); NE Herald Cay, Coral Sea (AMS); Lihou Reef, E of Cairns, Coral Sea (AMS C168561); Wheeler Reef, NE of Townsville (AMS); Davies Reef, E of Townsville (AMS); Broadhurst Reef, E of Townsville (AMS C114897); 50 m, Chesterfield-Bellona Plateau, 19°10′37″S,

158°33′37″E (MNHNP); Centipede Reef, NE of Townsville (AMS); Penrith Id (AMNH); Saumarez Reef, Coral Sea, 21°50′S, 153°39′E (AMS); Tryon Id, Capricorn Gp (AMS); Lady Elliot Id (ANSP).

NEW GUINEA: Abroeki Isle, Maransabadi Id, Aeori Id, Geelvink Bay, Irian Jaya (ANSP); Biak, Irian Jaya (AMS); Seleo Id, off NW reefs, Aitape (USNM 615997); New Britain (AMS). LOYALTY ISLANDS: Cap des Pins, Lifu (AMS). NEW CALEDONIA: Poindimie (AMS). FIJI: Nadi Bay, Viti Levu (AMS); Manava Id, N of Viti Levu (USNM 824786, 824795). MARIANA ISLANDS: Agrihan Id (USNM 487959); Apra Harbor, Guam (USNM 620454); 10.67 m, off Orote Cliffs, Orote Pt, Guam (USNM 842631); Port Merizo (ANSP); 12.19 m, Manua Bay, Guam (USNM 774767); Guam (AMNH). CAROLINE ISLANDS: Kapingamarangi (USNM 610836, 610844); Ulithi (USNM 602379, 602380); N side of Ngariungs Ids, Kayangel Id, Palau (ANSP); 1.6 km S of West Passage, Babelthuap Id, Palau (ANSP). WAKE ISLAND: (AMNH, MCZ, USNM 13214, 657467); SE end, Wake Id (ANSP). MARSHALL ISLANDS: Rigili Id, Enewetak Atoll (USNM 580729); Jieroru Id, Enewetak Atoll (USNM 581369); NE end Yurchi Id, Bikini Atoll (USNM 582964); 60.97 m, lagoon, Bikini Atoll (USNM 584663); Bikini Id, Bikiki Atoll (USNM 580339, 583640, 585427); Yomyaran Id, Bikini Atoll (USNM 580621); Lomuilal Id, Rongelap Atoll (USNM 585680); Rongerik Id, Rongerik Atoll (USNM 586234); Bigonattam Id, Rongerik Atoll (USNM 586346); Uterik Id, Uterik Atoll (USNM 615644); Wotho Id, Wotho Atoll (USNM 614267, 614290); Ujae Atoll (USNM 614515); Kwajalein Atoll (USNM 486149); Ine Id, Arno Atoll (USNM 634997); between Sydneytown and Watchhouse, S of Jabor, Jaluit Atoll (USNM 659611). GILBERT ISLANDS: (USNM 76763); Onotoa Atoll (USNM 607652, 607673, 607719, 622645).

HAWAIIAN ISLANDS: Midway (USNM 634809); channel, Honolulu Harbor, Oahu (USNM 339770); Honolulu, Oahu (USNM 484786); Hanauma Bay, Oahu (USNM 531575); off Kaanapali, Maui (USNM 339326); off Launiupoko Camp, Maui (USNM 339327). LINE ISLANDS: Palmyra Id (USNM 348467, 348468, 487405); S coast, Washington Id (USNM 725759); Christmas Id (AMS); N side, W of North Pt, Starbuck Id (USNM 725963); South Id, Caroline Id (USNM 726019, 726046); N shore of South Id, Caroline Id (USNM 726006, 726054); Nake Id, S part of W coast of Caroline Id (USNM 726108, 726125); NW coast, Vostok Id (USNM 726009); Flint Id (ANSP); Sand Id (USNM 693927). JOHNSTON ISLAND: (ANSP). ELLICE ISLANDS: Lagoon, main island, Nukulailai (USNM 685825). PHOENIX ISLANDS: Canton Id (USNM 513277, 513292, 513293, 620008); Swains Id (USNM 513301, 769835). TOKELAU ISLANDS: Reef N of Fenualoa Islet, SW part of Atafu (USNM 768816); Tokelau Islet, NE Nukunono (USNM 768501); E end Taulangapapa Islet, E side Nukunono (USNM 768659); E side Nukunono (USNM 768949); SE Nukunono (USNM 768514, 769834); W point, Mulifenua, Fakaofu (USNM 768275); lagoon, Fenua Loa, S point Fakaofu (USNM 768233); S side, Fenua Fala, Fakaofu (USNM 768143, 768231); W side of Tukao, Manihiki Atoll (ANSP). SAMOA: Rose Id, Rose Atoll (USNM 513354, 513358, 704597, 704598, 704599, 708235). TONGA: Niuafou (USNM 383834, 519047); Opaahi, Niue (USNM 862418).

COOK ISLANDS: Bird Id, Palmerston Atoll (USNM 685281); reef S of Nivana Village, Rakahanga (USNM 704367); lagoon, NW of Anchorage Id, Suvarev (USNM 704052, 704432); reef flat, E side Anchorage Id, Suvarev (USNM 704501); lagoon, Aitutaki (USNM 732475); Motu Akaiami, Aitutaki (USNM 684997); Manuae Id, W side Hervey Id (USNM 732470); Auotu Id, Hervey Id (USNM 732429); N side, E of Avarua Harbor, Rarotonga (USNM 732260). TUBUAI ISLANDS: N coast, NW of Moerai, Rurutu (USNM 732323); W coast, off Avera Id, Rurutu (USNM 732329); N coast, Tubuai (USNM 732292); lagoon, NW of Motu Mano, Raevavae (USNM 732183, 732216). SOCIETY ISLANDS: W side, ocean reef, Bellingshausen (USNM 705205, 705207, 705227); SW side of Toopua Id, Bora Bora (USNM 731492); near Vaiore Bay, Tahaa (USNM 674127); 91–2.43 m, Île Mahea, off Hamene (ANSP); Motu Tipaemau, Raiatea (USNM 675170); Îlot Tipaemano, Raiatea (USNM 674041); W coast of Raiatea (ANSP); S tip Motu Pahare, Huahine (USNM 674882); Motu Farfone, Moorea (USNM 630756); Opunohy Bay, Moorea (USNM 630588); Atiue, Tahiti (ANSP); Punaavia Lagoon, Punaavia, Tahiti (AMS C71624); Patutoa, Tahiti (USNM 669546, 669705); N of Papeete, Tahiti (WAM); Fare Ute Pt, Papeete, Tahiti (USNM 668911); E side of Taunoa Pass, Tahiti (USNM 668811); Papara, Tahiti (USNM 791358); Pt Ovauaara, Tautira, Tahiti (USNM 674484); Motu Onetahi, Tetiaroa (USNM 705739); NE end, Motu Tiaraunu, Tetiaroa (USNM 705816); W part of Northeast Id, Anuanuraro (USNM 725246).

TUAMOTU ARCHIPELAGO: Matiti, Tikahau Atoll (USNM 629335, 629620, 679345); lagoon near main pass, Matiti Id, Tikahau Atoll (USNM 629630, 652490); W side Avatoru Pass, Rangiroa Atoll (USNM 731510, 782802, 782807); W side Tairapa Pass, Manihi (USNM 790192); Lagoon, main motu, Manihi (USNM 798728); reef, E end main motu, Manihi (USNM 790228, 798109); Anaa (USNM 775569); NE side, coral reef, Anaa (USNM 775871, 775882, 775896); Takaroa Atoll (USNM 789988); SW point of Takaroa Atoll (WAM); Makemo Id (USNM 348796); S of W part of Northeast Id, Anuanu Raro (USNM 725226); Garumaoa Id, Raroia (USNM 711738, 720177, 720202, 720305, 720320, 723309, 723411, 732653, 758396); S end of Garumaoa Id, Raroia (USNM 720326); Okaea Id, Raroia (USNM 722824); Oneroa Id, Raroia (USNM 721099, 721160); N of Tekatikati Id, Raroia (USNM 721283); Ngarumaoa Id, Raroia (USNM 697615, 697816, 698015, 698256, 698327, 698516); Onigehuihui, Raroia (USNM 722942); channel, SE end, Opakea Id, Raroia (USNM 723070, 723137); Tepatahiti Id, Raroia (USNM 723002); Kahingi Id, Raroia (USNM 720392); Raroia (ANSP); Vahitahi (USNM 613287, 613288); NE side, Tepu-

kaamaruia Id, Takume (USNM 723644, 723667, 723683); W of village, Tatakoto Atoll (USNM 782725); near landing, NW side Puka Puka (USNM 789876); reef flat, N side Puka Puka (USNM 789796, 789858).

GAMBIER ISLANDS: Outer reef edge, Motu Tenoko (USNM 726169); N part of barrier reef, Motu Tepapuri (USNM 726344, 731403); Motu Tarauru-roa, Mangareva (USNM 638186). PITCAIRN ISLANDS: Off sand cay, N end Oeno Id (USNM 789601); lagoon shore, W of NW Pt, Oeno Id (USNM 731560); lagoon near N coast, Oeno Id (USNM 731525); W side, Oeno Id (USNM 789582); off Christian's Pt, Pitcairn Id (USNM 731775, 731891); NW side, off Down Coconuts, Pitcairn Id (USNM 731867); SE coast off The Rope, Pitcairn Id (USNM 731655); off Bounty Bay, Pitcairn Id (USNM 731661); W Point, Down St Paul's, Pitcairn Id (USNM 731947); N side, below Adamstown, Pitcairn Id (USNM 731921).

DUCIE ATOLL: Western end, Ducie Atoll (USNM 732036); W end of large island, Ducie Id (USNM 732074); W side main boat passage, Ducie Atoll (USNM 732086). MARQUESAS: Anaho Bay, Nukuhiva (USNM 799534); Baie du Controleur, Nukuhiva (USNM 799546); Taiohae Bay, W side of Nukuhiva (USNM 799430, 799451); Île de Tahuata (ANSP, USNM 775595); S of Baie Hanavave, Fatu Hiva (USNM 798719, 798785); S side Omoa Bay, Fatu Hiva (USNM 798742). EASTER ISLAND: E of Hanga Tee, Vaihu (USNM 756100); Hanga Piko (USNM 751540, 751572, 769732).

Cerithium egenum Gould, 1849

FIGURES 55–57

Cerithium egenum Gould, 1849:121 [holotype: USNM 5571; type locality: "Wilson's Id" (Manihi, Tuamotus); 6 mm × 2.5 mm];—1852:151, pl. 10: fig. 17.—Sowerby, 1865, pl. 15: fig. 101 [not *Cerithium egenum* Gould, 1849].—Tryon, 1887:137, pl. 25: fig. 70.—Kobelt, 1898:243, pl. 42: fig. 13 [not *Cerithium egenum* Gould, 1849].—Kay, 1979:121, fig. 45G.

Cerithium rarimaculatum Sowerby, 1855:875, pl. 183: fig. 204 [holotype: BMNH 1975625; type locality: Debu, Philippines; 11 mm]; 1865, pl. 15: fig. 103.—Tryon, 1887:139, pl. 26: fig. 91.—Kobelt, 1898:216, pl. 38: fig. 9.

Cerithium strictum Hedley, 1899:433–434, fig. 22 [holotype: AMS C5942; type locality: Funafuti Atoll, Ellice Islands, 7 mm × 3 mm].

Cerithium bavayi Vignal, 1902:304, pl. 8: figs. 7, 8 [holotype: MNHNP, no number; type locality: New Caledonia; 9.7 mm × 1 m].—Cernohorsky, 1972:69, pl. 15: fig. 9 [in part, right hand figure only].—Salvat and Rives, 1975:270, fig. 68.

Cerithium bavayi var. *denticulata* Vignal, 1902:305 [holotype: MNHNP; type locality: New Caledonia; not *Cerithium denticulatum* Lamarck, 1804].

Cerithium (Conocerithium) egenum Gould.—Maes, 1967:113, pl. 6: fig. K.—Ladd, 1972:39, pl. 9: figs. 9, 10.

Cerithium (Conocerithium) bavayi Vignal.—Cernohorsky, 1972:69, pl. 15: fig. 9 [in part, right hand figure only].

Cerithium (Thericium) egenum Gould.—Rehder, 1980:37, pl. 6: fig. 4.

DESCRIPTION.—*Shell* (Figure 55): Shell small, narrow, turreted, comprising 9–11 weakly inflated, sometimes angulate adult whorls, and reaching 11.5 mm length and 4.8 mm width. Protoconch (Figure 55K) of 3 whorls; protoconch 1 smooth; protoconch 2 with elaborate sculpture and sinusigeral notch. Protoconch sculpture comprising two spiral cords, subsutural, colabral, axial plaits; minute opisthocline axial plaits beneath first spiral cord, and presutural, orthocline, axial riblets beginning before and crossing over second spiral cord. Early whorls (Figure 55B) sculptured with 5 or 6 spiral cords, incised spiral striae, and tiny spiral threads. Central spiral cord enlarging on successive whorls. Adult teleoconch sculptured with 5–7 raised, flat-surfaced, unequal, spiral cords and incised spiral lines. Subsutural and central spirals sometimes with up to 13 beads becoming angulately nodose at periphery. Minor spiral cords sometimes pustulose. Suture slightly impressed, distinct. Body whorl elongate, concave subsuturally, becoming convex adapically, with moderately excavated base and with prominent varix opposite outer lip of aperture. Body whorl sculptured with numerous spiral cords and striae, angulate at center and with central spiral band of subsutural beads or nodes. Aperture ovate, about one-third the shell length. Columella concave, with slight columellar callus and weak parietal plait defining anal canal. Anterior siphonal canal very short, turned to left of shell axis. Outer lip smooth. Shell color white with axial chestnut-brown markings on base; sometimes with irregular brown blotches or spirals on upper whorls. Measurements (Table 20). Periostracum light tan, thin. Operculum thin.

Radula (Figure 56): Type-1 radular ribbon (Figure 3A) long, about one-half the shell length. Rachidian tooth (Figure 56B) triangular with rounded sides, pair of fine posterior ridges, and narrow, triangular, posterior extension; cutting edge with large, pointed, central, main cusp flanked on each side by two sharp denticles. Lateral tooth (Figure 56B) with long lateral, posterior extension, and with broad, central, basal buttress bearing weak central pustule; cutting edge with large, pointed main cusp, one inner flanking denticle and 3 or 4 outer flanking denticles. Marginal teeth (Figure 56A,B) spatulate, with curved spoon-like, serrated tips. Inner marginal tooth with long main cusp, 4 inner flanking denticles and 2 or 3 outer flanking denticles. Outer marginal tooth same, but without outer flanking denticles.

Anatomy: Animal whitish yellow with yellow spots on head, cephalic tentacles, and sides of foot. Dorsal-posterior part of snout and cephalic tentacles, especially peduncles, dark brown, and sides of foot with brown blotches. Sole of foot with yellow spots and with deep anterior pedal mucus gland. Snout moderately elongate. Mantle edge with short yellow papillae and roof of mantle at inhalant siphon darkly pigmented, thickened, and folded where ctenidium ends.

Osphradium wide in proportion to ctenidium, flesh-colored, extending length of ctenidium, but separated from it by thin area of mantle, and turning sharply away from ctenidium at inhalant siphon. Ctenidium narrow, grayish yellow with black edges, comprised of long, triangular filaments. Hypobranchial gland with gray papillate texture, partially covering rectum;

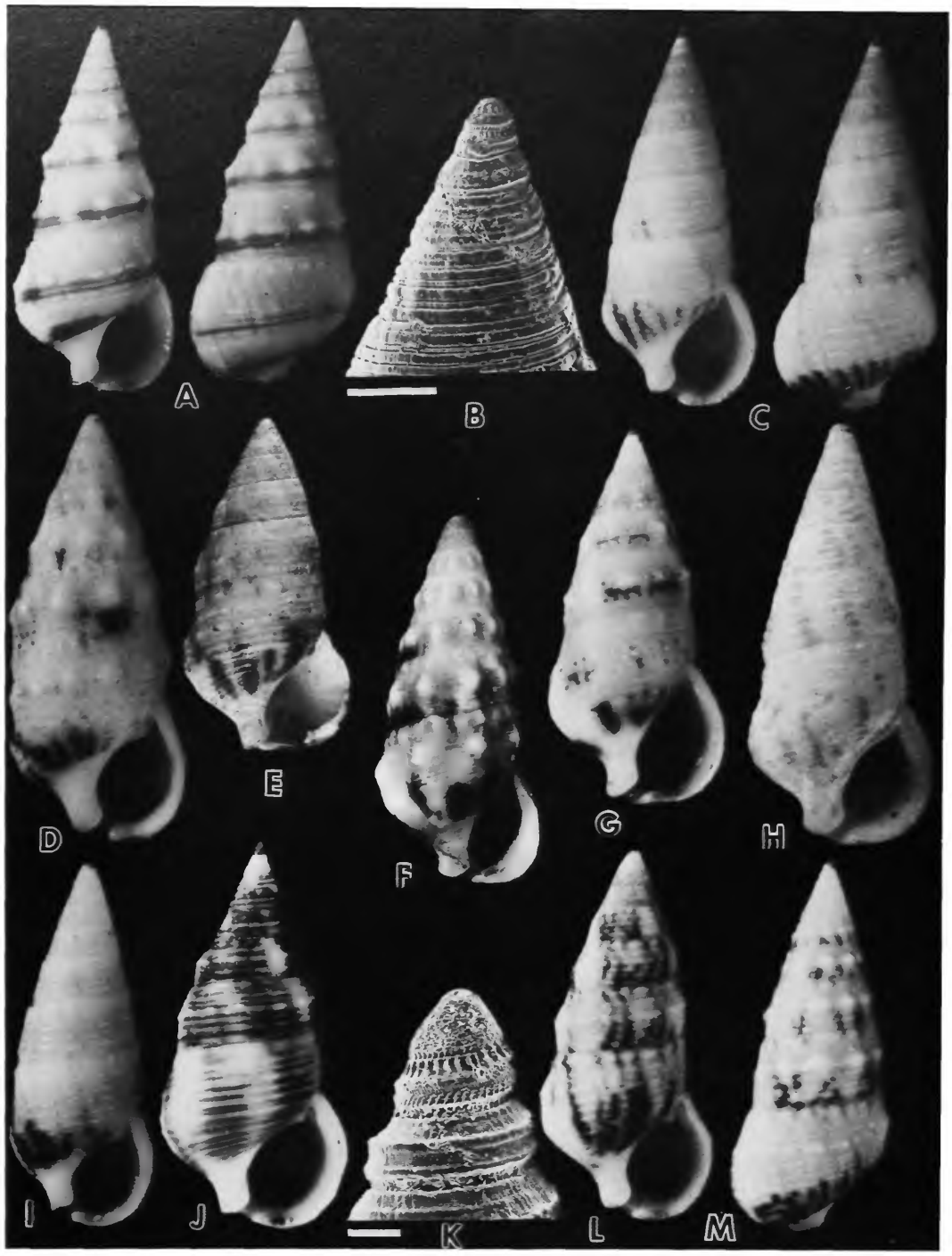

FIGURE 55.—*Cerithium egenum* Gould, showing phenotypic variation and types of nominal taxa synonymous with it: A, Raroia, Tuamotus, 8.9 mm (USNM 723335); B, SEM of early whorls and protoconch from Rongelap Atoll, Marshall Islands (bar = 400 μm; USNM 582426); C, Raroia, Tuamotus, 8 mm (USNM 723335); D, holotype of *Cerithium bavayi denticulata* Vignal, Lifu, Loyalty Ids, 10 mm (MNHNP); E, holotype of *Cerithium bavayi* Vignal, New Caledonia, 9.7 mm (MNHNP); F, holotype of *Cerithium rarimaculatum* Sowerby, Cebu, Philippines, 11 mm (BMNH 1975625); G, Tahiti, Society Islands, 6.2 mm (USNM 791371); H, holotype of *Cerithium egenum* Gould, Wilson's Island, Tuamotus, 6 mm (USNM 5571); I, Rongelap Atoll, Marshall Islands, 6 mm (USNM 582426); J, Paumalu, Oahu, Hawaii, 6.8 mm (USNM 485483); K, SEM of early whorls and protoconch from Rongelap Atoll, Marshall Islands (bar = 100 μm; USNM 582426); L, Tahiti, Society Islands, 9.6 mm (USNM 791371); M, Raroia, Tuamotus, 8.2 mm (USNM 723335).

TABLE 20.—Shell morphometrics of *Cerithium egenum*.

Character	$\bar{x}$ (n = 14)	sd	v	Range
Shell length	9.1	1.9	3.5	6.4–11.5
Shell width	3.9	0.8	0.6	2.9–4.8
Aperture length	2.7	0.5	0.3	2.1–3.6
Aperture width	2.0	0.4	0.2	1.3–2.5
Number whorls	10.1	0.7	0.5	9–11
Number spiral cords	5.8	0.6	0.3	5–7
Number beads	8.1	4.5	20.4	0–13

very wide, swollen near anus. Inner mantle adjacent to anus and distal end of pallial gonoduct black.

Buccal mass comparatively large with pair of large jaws. Paired salivary glands originating behind nerve ring as swollen masses, passing through it, uncoiling, and emptying on upper anterior surface of buccal mass. Esophageal gland present.

Type-B pallial oviduct (Figure 4B) with anterior white capsule gland and posterior albumen gland. Posterior seminal receptacle near edge of inner side of spermatophore bursa and connected by narrow duct along edge of medial lamina to anterior sperm gutter. Anterior seminal receptacle of lateral lamina a small, anterior, narrow pouch.

SYNONYMIC REMARKS.—Despite the use of the name *C. bavayi* Vignal by some authors, Gould's (1849) name is the earliest available one. Maes (1967:113) was the first to recognize that *C. egenum* Gould, represents this species. There is no question that the holotype of *C. egenum* matches Gould's original description, despite some discrepancies between the original color diagnosis and the holotype (see Rehder, 1980:37–38, for detailed comments). The holotype of *C. egenum* (Figure 55H) is badly eroded, but not likely to be confused with any other *Cerithium* taxon. Rehder pointed out that Ladd (1972:39) erred in citing the Caroline Islands as the type locality. The present name of Wilson's Island, the cited type locality, is Manihi Id, Tuamotus. Examination of the holotypes of *C. rarimaculatum* Sowerby (Figure 55F), *C. strictum* Hedley, *C. bavayi* Vignal (Figure 55E), and *C. bavayi denticulata* Vignal (Figure 55D) shows that all four are conspecific with *C. egenum*. Cernohorsky's (1972:69, pl. 15: fig. 9) treatment of *C. bavayi* is based on a mixed concept of *C. egenum* and *C. atromarginatum*, as demonstrated by his fig. 9.

Several authors (Maes, 1967:113; Cernohorsky, 1972:69) have referred *C. egenum* to the subgenus *Conocerithium* Sacco, 1895, which is a poorly defined taxon here regarded as congeneric with *Cerithium* (see discussion under *Cerithium atromarginatum*, "Synonymic Remarks," p. 28).

ECOLOGY.—A population at Shark Bay, Oahu, Hawaii, occurs in apparent microsympatry with *C. atromarginatum* on an intertidal solution bench in pools filled with brown, bushy algae and algal-covered pebbles (pers. obs.). Snails of this population are very active and quickly move over the substrate and crawl on algal strands. Kay (1979:121–122) recorded that this species burrows in sand in tide pools and on solution benches in Hawaii. This species has been found in the stomach and gut of the fish, *Coris aygula* at Pitcairn (USNM 731787) and Rapa (USNM 725710). Drilled specimens, indicative of naticid predation, and shells "peeled" by crab claws are not uncommon.

The protoconch of 2.5 sculptured whorls with sinusigeral notch (Figure 55K) indicates a planktotrophic larval phase in the life history. Kay (1979:121–122) recorded that veligers are bilobed and metamorphose when three to three and one-quarter

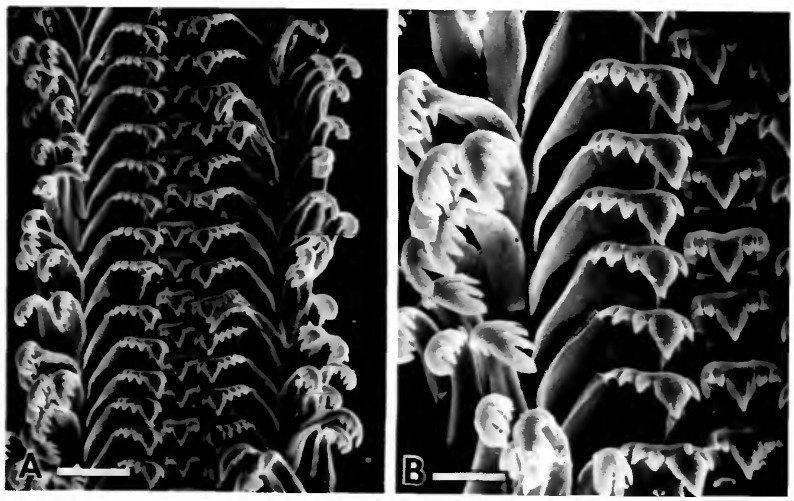

FIGURE 56.—Radula of *Cerithium egenum* Gould, Tuamotus (USNM 629778): A, radula from Raroia, Tuamotus (bar = 75 μm); B, same (bar = 45 μm).

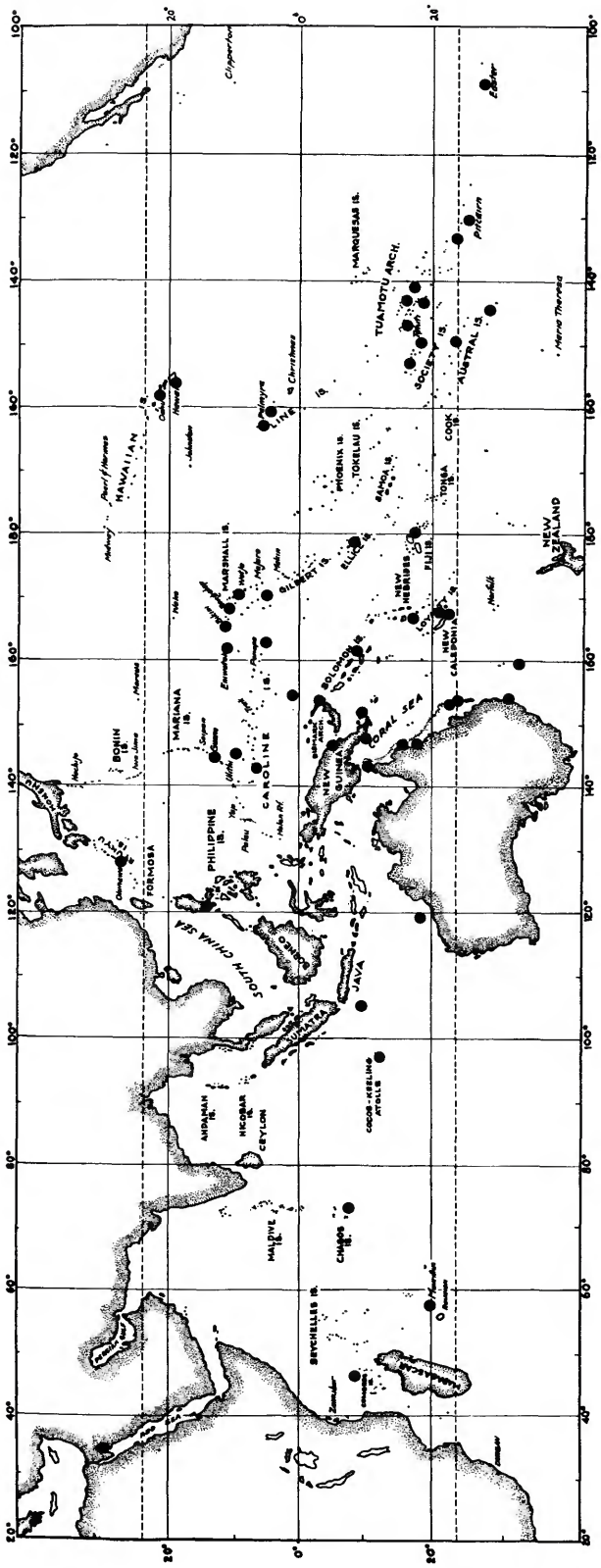

FIGURE 57 (left).—Geographic distribution of *Cerithium egenum* Gould.

whorls are complete, at a length of 500 µm. The egg mass is unknown.

DISCUSSION.—The distinguishing characters of this species are a small, slender shell, sculptured with fine, unequal, spiral lirae, and a grayish white shell color with chestnut brown axial marks on the lower part of the whorls and shell base.

This species shows moderate interspecific variation in shell sculpture. The subsutural and central spiral cords are strongly beaded or nodulose, producing angulate whorl peripheries in some individuals (Figure 55A,D,F,L,M), while other individuals may completely lack nodes and beads (Figure 55C,I). Some phenotypes have pronounced spiral cords and spiral striae (Figure 55J). Shell color also varies somewhat, with some individuals being banded (Figure 55A), and others being darkly pigmented throughout (Figure 55J). However, most specimens have the distinctive axial markings on the shell base.

Cerithium egenum should be closely compared and contrasted with its sympatric congener, *C. atromarginatum* (Figure 14). The salient differences between these two species have been discussed above, under *C. atromarginatum* (which see). It is not surprising that these two species are frequently found mixed in collections as they are similar in size and color and live in virtual microsympatry. Anatomically and reproductively, *C. egenum* differs from *C. atromarginatum* in having the medial seminal receptacle closer to the inner edge of the medial lamina, and a shorter seminal receptacle in the inner lamina.

Another species with which *C. egenum* may be confused is *Bittium zebrum* (Kiener, 1841), which also occurs in sand pockets among rocky, algal-covered tide pools. The latter species is usually smaller, highly colorful, and has more granular sculpture with many varices and axial ribs.

FOSSIL RECORDS.—This species has been recorded as a Holocene fossil from drill holes on Bikini and Enewetak Atolls, Marshall Islands (Ladd, 1972:39–40).

GEOGRAPHIC DISTRIBUTION (Figure 57).—*Cerithium egenum* has a very wide Indo-Pacific distribution, ranging from the Red Sea throughout the Indian Ocean and the Pacific, eastward to Hawaii, the Tuamotus, Pitcairn Island, and Easter Island.

SPECIMENS EXAMINED.—RED SEA: Ophir Bay, Gulf of Elat, Israel (USNM 779996, 780061). INDIAN OCEAN ISLANDS: Île Picard, Aldabra Atoll, Seychelles (USNM 838050, 838320); Le Chaland, 4 km S of Mahebourg, SE Mauritius (AMS); Diego Garcia, Chagos Archipelago (USNM 761918); reef off SE end West Id and Pulo Maria, Cocos Keeling Islands (USNM 656223); Christmas Id (AMS); Flying Fish Cove, Christmas Id (WAM). RYUKYU ISLANDS: Susami, Wakayama Prefecture (USNM 666614); Okinawa (USNM 2037). PHILIPPINES: Matabungkay, 115 km SSW of Manila, Luzon (AMS).

WESTERN AUSTRALIA: SE corner of Clerke Reef, Rowley Shoals (WAM); mouth of Greenough River (AMS).

QUEENSLAND, AUSTRALIA: 14.4–24 km off Murray Id, Torres Strait (AMS); Murray Id, Torres Strait (AMS); Lizard Id (AMS); Rocky Id, Cape Flattery (AMS); Arlington Reef, NE of Cairns (AMS); Palm Id, N of Townsville (AMS); Keeper Reef, NE of Townsville (AMS); Tryon Id, Capricorn Gp (AMS); W end Heron Id (AMS); Lady Musgrave Id, Bunker Gp (AMS); Lady Elliot Id (AMS); NW side of Macgillivray Cay (AMS); Mooloolaba Beach (AMS); Caloundra (AMS). NEW SOUTH WALES, AUSTRALIA: Woolgoolga (AMS); Lord Howe Id (AMS). NEW GUINEA: S of Kalibobo Pt, Madang (AMS); Port Moresby (AMS); off Kaibala Village, N end Kiriwina Id, Trobriand Gp (AMS); N tip of Buriwadi Id, Trobriand Gp (AMS); New Ireland, Bismark Archipelago (AMS). SOLOMON ISLANDS: Laulasi Id, S of Aoki, W coast of Malaita Id (AMS). NEW HEBRIDES: Bushman's Bay, E Malekula (USNM 824837). LOYALTY ISLANDS: Lifu (USNM 423300, 423301, 423317). NEW CALEDONIA: Touaourou (USNM 784142). FIJI: N of Vuna Pt, SW Taveuni (USNM 695655).

MARIANA ISLANDS: Apra Harbor, Guam (USNM 851002). CAROLINE ISLANDS: Between Elengalap and N end Falerik Id, Ifaluk Atoll (USNM 616511, 616564, 616574); SW Falerik Id, Ifaluk Atoll (USNM 616528, 616529, 616585, 616708, 616721); reef at Mutunlik, Kusaie Id (USNM 609488); 1.6 km W of Torongahai, Kapingamarangi (USNM 610802, 611068). MARSHALL ISLANDS: Enewetak Atoll, numerous localities (USNM 542819, 581736, 582186, 582271, 582284, 582285, 582317, 582617, 584128); Bikini Atoll, numerous localities (USNM 579169, 579281, 579315, 579516, 580346, 580382, 580524, 580949, 582622, 585192, 586082); Rongelap Atoll, numerous localities (USNM 580840, 582111, 582404, 582426, 582600, 583407, 585584); Back Id, Rongerik Atoll (USNM 594659); Ailuk Id, Ailuk Atoll (USNM 756848); Jaluit Atoll (USNM 659215, 659504, 659755, 660073, 660109). HAWAIIAN ISLANDS: Shark Bay, near Sunset Beach, Oahu (USNM 836896); Paumalu, Oahu (USNM 485483, 612411); Mokapu Pt, Oahu (USNM 361566); Keokea, Hilo (USNM 339338). LINE ISLANDS: Palymra Id (USNM 348474, 360631); W of Manounou village, Washington Id (USNM 725827).

ELLICE ISLANDS: Funafuti (AMS). AUSTRAL ISLANDS: Moerai, Tubuai (USNM 684107); S Pointe Ruea, Baie Puoro, Rapa (USNM 725710); off SE island, Îles Morotiri (USNM 725671). SOCIETY ISLANDS: Mahini, Tahiti (USNM 775934, 791369, 791371). TUAMOTU ARCHIPELAGO: Temao Harbor, Makatea (USNM 629778, 629827); Anaa (USNM 819773); ocean reef, 3.2 km W of village, Takaroa (USNM 790080, 790081); Makemo Id (USNM 348797); Raroia, numeous localities (USNM); NE side, Tepukaamaruia Id, Takume (USNM 723640, 723641, 723649, 723685); near Hikitake Id, Amanu Atoll (USNM 671794); Vahi Tahi (USNM 613183, 613184); Mururoa (USNM 819774); Puka Puka (USNM 789809); Matiti Id, Tikahau (USNM 629287, 629337, 819894); Takarava Id (USNM 348909). GAMBIER ISLANDS: NW coast, Aukena Id (USNM 726260). PITCAIRN ISLANDS: Off Christian's Point, Pitcairn Id (USNM 731787); N side, below Adamstown, Pitcairn Id (USNM 731920). EASTER ISLAND: S of Hanga Kioe, Tahai (USNM 756849); N Hanga Piko, SW coast (USNM 751603); E of Hanga Tee, Vaihu (USNM 756126).

Cerithium flemischi Martin, 1933

FIGURES 58–60

Cerithium flemischi Martin, 1933:29–30, pl. 4: figs. 30, 31 [holotype: RMGM, not numbered; type locality: Ktolemando strata, asphalt beds of Buton Id, Indonesia (Lower Miocene); 35.5 mm].

DESCRIPTION.—*Shell* (Figure 58): Shell elongate, turreted, slender, with apical angle of 20 degrees comprising 16–19 straight-sided whorls, and reaching 52.2 mm length and 13.9 mm width. Protoconch (Figure 58E) about two and a half whorls, brown. Protoconch 1 one smooth whorl; protoconch 2 sculptured with subsutural row of pustules, two median smooth spiral cords, and covered with tiny raised dots, and with deep sinusigeral notch. Early teleoconch whorls (Figure 58D,I) with strong, colabral axial ribs. Adult teleoconch whorls slightly constricted subsuturally and sculptured with 2 or 3 dominant spiral beaded cords, several tiny, smooth lirae, and fine spiral striae. Beads point toward shell apex and aligned forming 10–12 slightly slanting, colabral axial ribs (Figure 58H). Smaller, more weakly defined spiral beaded cord sometimes present subsuturally. Varices randomly distributed as broad axial ribs. Suture distinct, impressed, straight, with thin, smooth, suprasutural spiral cord. Body whorl (Figure 58F) thin-shelled, slightly inflated and sculptured with two main, beaded spiral cords and weak subsutural cord with slight axial plications. Base of body whorl moderately constricted with broad, shallow, short, anterior siphonal canal that is pointed to left of shell axis. Weak anal canal present. Large varix present opposite outer lip of aperture. Aperture circular-ovate, a little more than one-fifth the shell length. Columella concave with thin parietal callus and lip. Outer lip of aperture smooth, thin, slightly sinuous, flaring at suture (Figure 58F). Shell color dull whitish brown; aperture, beads, and spiral cords white. Weak, tan, spiral bands sometimes present. Measurements (Table 21). Periostracum thin, dark brown, sometimes colorless. Operculum thin, brown, corneous, paucispiral, ovate with subcentral to central, slightly sunken nucleus. Attachment scar on obverse elongate, ovate, occupying about one third of operculum.

Radula (Figure 59): Type-3 radular ribbon (Figure 3C) short, robust, about one-tenth the shell length. Rachidian tooth (Figure 59D) squarish, rounded anteriorly, with long ridge and short, central extension at posterior of basal plate; cutting edge with short, central main cusp flanked on both sides with 1 or 2 small denticles. Lateral tooth (Figure 59B,C) with short, lateral, posterior extension, and thick, central buttress having transverse ridge on broad basal plate; cutting edge of lateral tooth with large, pointed main cusp, one inner flanking denticle and

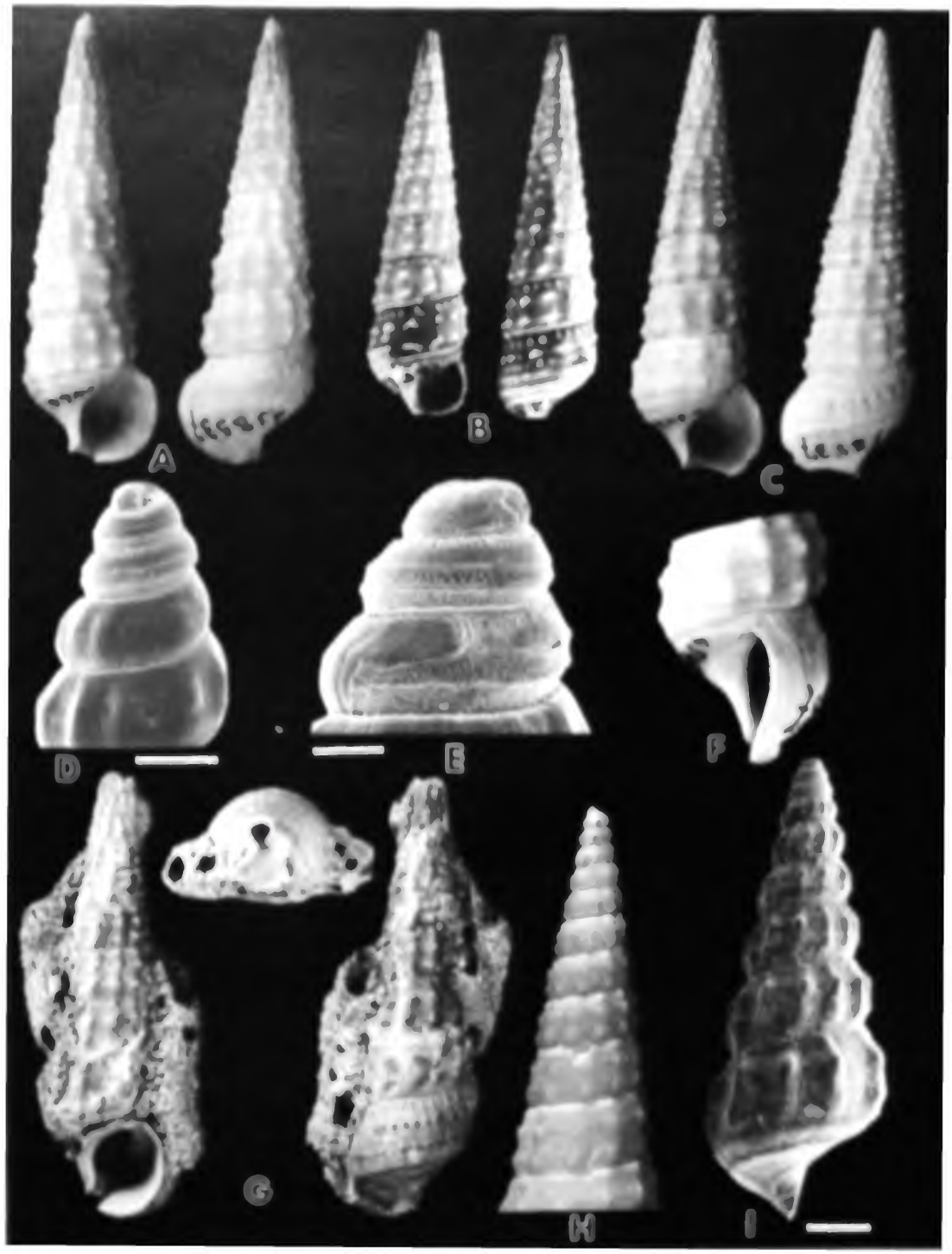

FIGURE 58.—*Cerithium flemischi* Martin, showing phenotypic variation: A, Lagonoy Gulf, Luzon, Philippines, 40.5 mm (USNM 238537); B, lectotype of *Cerithium flemischi* Martin, 35.7 mm (RGM); C, Lagonoy Gulf, Luzon, Philippines, 48 mm (USNM 238537); D, SEM of protoconch and early whorls (bar = 300 μm); E, SEM of protoconch (bar = 70 μm; USNM 238537); F, detail of outer lip of aperture (USNM 238537); G, apertural, adapertural and anterior views of shell with worm tubes as found in situ, 1354N, 11958E, Philippines, 45.7 mm (MNHNP); H, early whorls, Lagonoy Gulf, Philippines (USNM 238537); I, SEM of immature shell, Magabalo Id, Mindanao, Philippines (bar = 0.5 mm; USNM 276883).

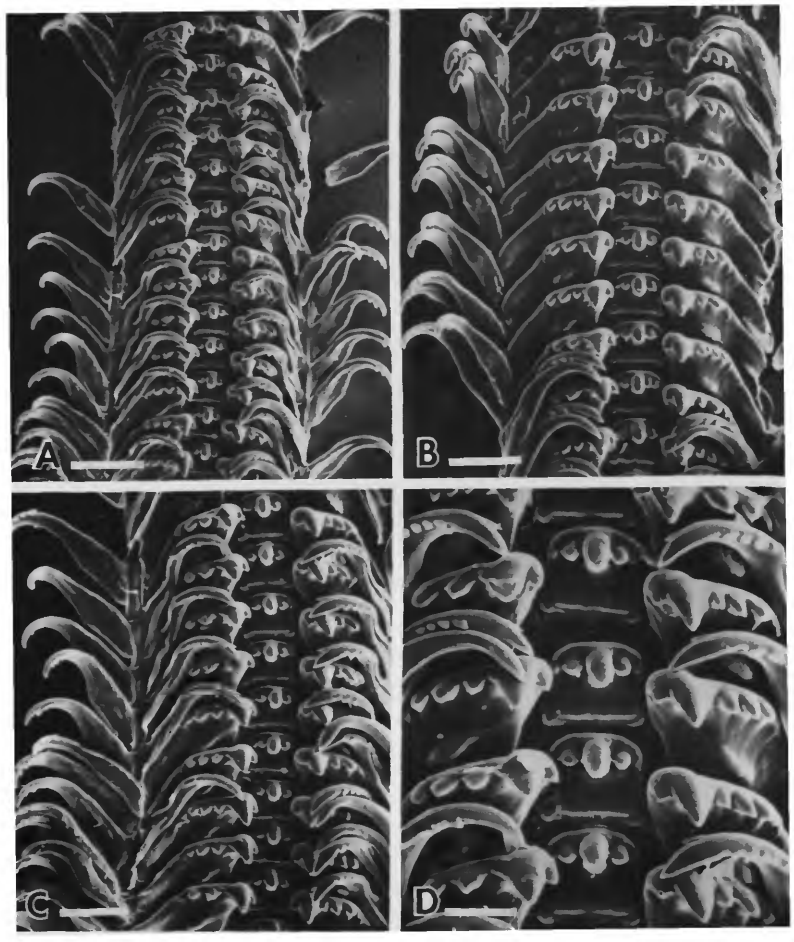

FIGURE 59.—Radula of *Cerithium flemischi* K. Martin, Batan Id, Lagonoy Gulf, Luzon, Philippines (USNM 238517): A, radula with marginal teeth spread back (bar = 50 μm); B, same (bar = 100 μm); C, radula with right marginals covering ribbon (bar = 100 μm); D, rachidian and lateral teeth (bar = 150 μm).

3 or 4 outer flanking denticles. Marginal teeth (Figure 59B,C) with narrow shafts and curved, serrated tips. Inner marginal tooth with sharp tip, 3 inner flanking, sharp denticles and 3 or 4 outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

TABLE 21.—Shell morphometrics of *Cerithium flemischi*.

Character	$\bar{x}$ (n = 10)	sd	v	Range
Shell length	40.6	7.1	50.6	31.5-52.2
Shell width	10.9	1.9	3.7	8.5-13.9
Aper ture length	8.4	1.7	2.9	6.1-10.7
Aperture width	6.6	1.5	2.2	4.5-8.5
Number whorls	17.1	1.0	1.0	16-19
Number spiral cords	2.8	0.4	0.2	2-3
Number axial ribs	11.7	0.8	0.7	10-12

Anatomy (preserved animal): Animal cream-white with narrow foot having well-developed, deeply cleft, crescent-shaped, anterior pedal, mucus gland. Snout thick, long; cephalic tentacles long, each having large black eye at broad peduncular base. Columellar muscle, long, about three whorls. Visceral mass with very large stomach, occupying 2.5 whorls. Mantle edge with small papillae and well-developed inhalant siphon.

Mantle cavity deep. Osphradium dark brown, arranged in tight, sinuous folds; ctenidium narrow, long.

Buccal mass elongated, situated well behind snout. Paired salivary glands comprised of thick, convoluted tubes passing through nerve ring. Wide esophageal gland with thick glandular transverse folds. Large stomach relatively simple interiorly with weak sorting ridges and folds, a long, thin central ridge nearly dividing stomach chamber in half, and with large, broad style sac. Fecal pellets ovoid, well compacted.

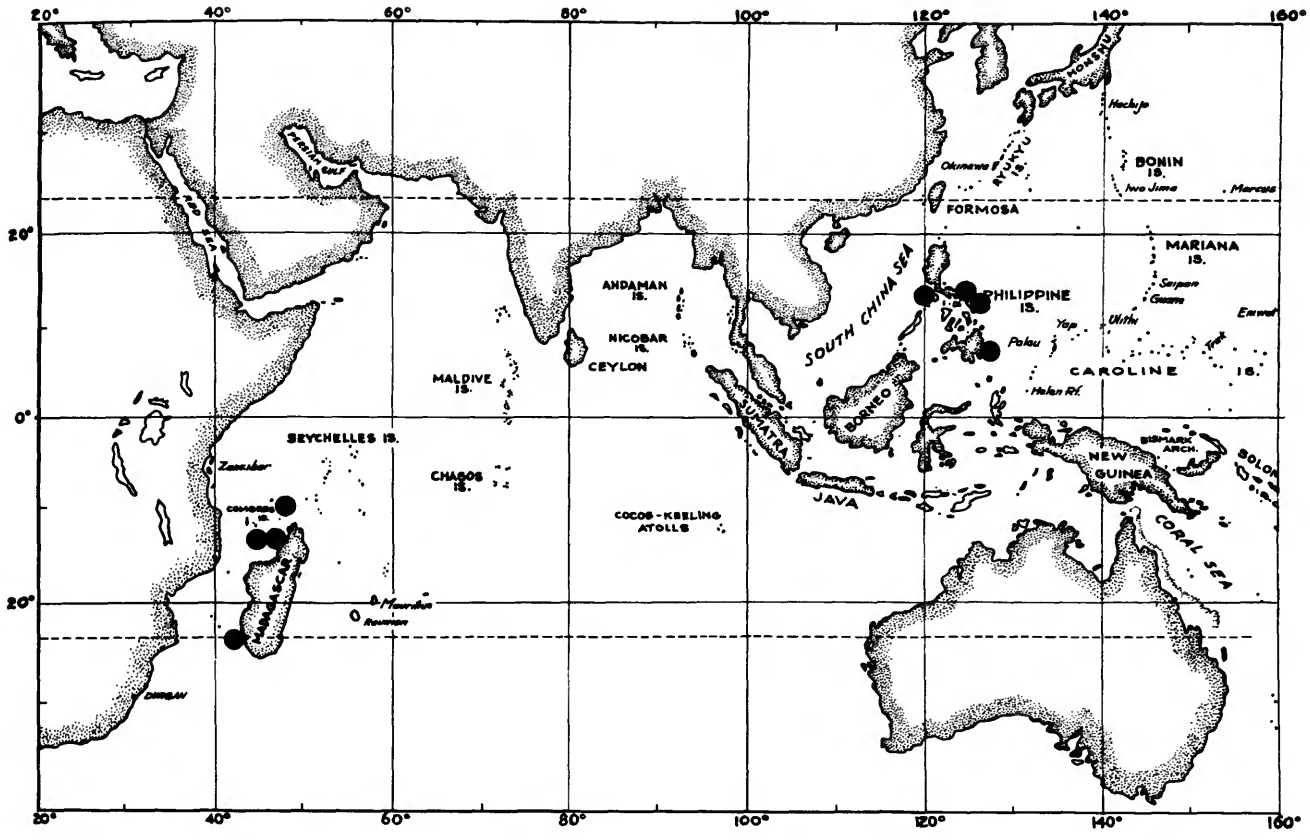

FIGURE 60.—Geographic distribution of *Cerithium flemischi* Martin.

Pallial oviduct (?) Type-B (Figure 4B), very long and having medial lamina with long, deep bursa posteriorly divided by longitudinal ridge. No seminal receptacle seen in lateral lamina.

SYNONYMIC REMARKS.—*Cerithium flemischi* was originally described as an Indonesian fossil by Martin (1933:29–30), who was apparently unaware that it was still living offshore, on shelf habitats. There is no doubt that the fossil holotype (Figure 58B) and live-collected specimens from the Philippines (Figure 58A,C,G,H) and Indian Ocean are conspecific.

ECOLOGY.—This species lives on offshore shelfs on sandy bottoms (to 1300 m) and is difficult to obtain without dredging apparatus. Despite its ratchet sculpture (sensu Signor, 1983), most live-collected specimens have eroded dorsal surfaces and apices, are covered with a dark brown periostracum, and have sandy worm tubes along the sides of the shell (Figure 58G), indicating a permanent surface habitat rather than a burrowing one. Large, coarse pieces of algae and marine angiosperm grasses in the stomach indicate that this species eats decaying plant material and algae which drifts to the bottom. Few drilled shells or repair marks indicative of crab attacks have been seen. Protoconch morphology (Figure 58D,E) indicates a pelagic larval stage in life history.

DISCUSSION.—This species is distinguished by a large, tapering, dull, white shell sculptured on the penultimate whorl with a small, subsutural spiral, beaded cord, and two main, thin spiral lirae and rows of rounded beads. The small rounded aperture with its expanded, rounded, outer lip and short, shallow, anterior, siphonal canal are also noteworthy characters. The nearly circular operculum with subcentral nucleus, the long columellar muscle, elongated snout and buccal mass, large but simple stomach with weak sorting ridges, and long, central, thin ridge, and the tightly folded osphradium are also notable characters. The division of the posterior spermatophore bursa by longitudinal ridge is an unusual feature of the pallial oviduct. Freshly collected specimens are covered with a dark brown to blackish periostracum. Although rare and poorly known in museum collections, *C. flemischi* does not appear to be uncommon in its deep-water habitat.

Cerithium flemischi is very close in shell form and sculpture to *C. gloriosum* (Figure 61), which is a smaller species with more inflated whorls, a rounded shell base, and a porcelaneous texture. Both species are sympatric in the western Indian Ocean. *Cerithium gloriosum* is sculptured with three main, spiral, sharply beaded cords per whorl, but lacking the fine

spiral striae seen in *C. flemischi*. Both species share similar anatomical features, have very similar radulae, and live in similar habitats: it is probable that they are closely related.

FOSSIL RECORDS.—*Cerithium flemischi* has been recorded from the lower Miocene of Buton, Indonesia (Martin, 1933: 29–30). I have examined specimens collected by A.J. Kohn from the Late Pleistocene Nakasi Beds of Saunitabu, Viti Levu, Fiji.

GEOGRAPHIC DISTRIBUTION (Figure 60).—From the Mozambique Channel, Indian Ocean, and the Philippines. This species probably occurs in suitable deep water habitats throughout the Indo-West Pacific. Fossil records indicate a wider range in the past.

SPECIMENS EXAMINED.—MADAGASCAR: 695 m, Anton Bruun Sta 365D, 23°20′S, 43°32′E, 42.42 km off Tulear (USNM 775062); 850–1125 m, 13°50′S, 47°17′7″E, Mozambique Channel (MNHNP); 1250–1300 m, Chalutage Sta 142, 13°45′6″S, 47°34′2″E, Mozambique Channel (MNHNP). INDIAN OCEAN ISLANDS: 700 m, Benthedi Sta 58, 12°47′S, 44°56′6″E, W of Grande Passe de l'Ouest, Mayotte (MNHNP); 520 m, Benthedi Sta DR-28, 12°38′S, 45°11′9″E, E Passe M'Zambo, Mayotte (MNHNP); 1300–1480 m, Benthedi Sta DR-40, 12°56′S, 45°18′2″E, E Récif Bendele, Mayotte (MNHNP); 520–830 m, Benthedi Sta DR-37, 12°53′8″S, 45°16′2″E, E Récif Bandele, Mayotte (MNHNP); 460–500 m, Benthedi Sta DR-06, 11°28′5″S, 47°12′2″E, W of Îles Glorieuses (MNHNP); 440 m, Benthedi Sta DS-10, 11°28′5″S, 47°17′7″E, W of Îles Glorieuses (MNHNP); 625 m, Benthedi Sta DS-122, 11°32′S, 47°23′2″E, SE of Îles Glorieuses (MNHNP).

PHILIPPINES: 745.8 m, USBF Sta 5450, off Batan Id, Lagonoy Gulf, Luzon (USNM 238517); 1032.8 m, USBF Sta 5460, off Siabat Pt, Lagonoy Gulf, Luzon (USNM 238537); 970 m, Musorstom Sta CP-56, 13°54′N, 119°57′E, off Mindoro (MNHNP); 865 m, Musorstom Sta CP-55, 13°54′N, 119°58′E, off Mindoro (MNHNP); 750–925 m, Musorstom Sta 49, 13°49′N, 120°00.5′E, off Mindoro (MNHNP); 548.4 m, USBF Sta 5446, NW of Bagtag Id, Samar (USNM 244130, 289094); 80.4 m, USBF Sta 5235, off Nagubat Id, E Mindanao (USNM 276899); 903 m, USBF Sta 5236, off Magabao Id, E Mindanao (USNM 276883); 694.4 m, USBF Sta 5238, off Pt Lambajon, E Mindanao (USNM 258117).

Cerithium gloriosum, new species

FIGURES 61–63

DESCRIPTION.—*Shell* (Figure 61): Shell tall, elongate, comprising 13–16 weakly inflated teleoconch whorls and reaching 28.4 mm length and 8.3 mm width. Protoconch (Figure 61B) 3.5 whorls with sinusigeral notch. Protoconch 1 smooth; protoconch 2 sculptured with row of subsutural spiral pustules, two spiral cords and tiny, microscopic dots. Early teleoconch sculptured with 2 spiral cords, pointed beads, and axial riblets presenting spinose-reticulated appearance. Adult teleoconch whorls smooth, shiny, with slight pre- and postsutural ramps and sculptured with three beaded spiral cords and weak, presutural, spiral thread. Beads pointing towards apex and aligned colabrally forming 13–16 weak, opisthocline, axial ribs. Varices occasionally present. Suture moderately impressed, well defined. Body whorl with large varix opposite outer lip of aperture; sculptured with 5 or 6 main, spiral cords, and several weak, minor spiral striae; first three adapical cords sometimes beaded. Base of body whorl weakly constricted. Aperture ovate, about one-fourth the shell length. Columella weakly concave with slight callus and weak, anterior lip. Anal canal a very weak parietal indentation. Anterior siphonal canal wide, very short, and slightly turned to left of shell axis. Outer lip of aperture thin, smooth, and convex, slightly pendant anteriorly. Shell color porcelaneous white with occasional faint traces of brown bands or splotches. Aperture white. Measurements (Table 22). Periostracum not seen. Operculum thin, corneous, and paucispiral with nearly central nucleus.

Radula (Figure 62): Type-3 radular ribbon short, about one-ninth the shell length. Rachidian tooth (Figure 62C,D) square, with posterior ridge and short, median, posterior extension on basal plate; cutting edge with short main cusp flanked by 1 or 2 denticles on each side. Lateral tooth (Figure 62B–D) with basal plate having short lateral-posterior extension and wide central buttress with short, median, transverse fold on ridge. Marginal teeth (Figure 62A,B) with broad bases and stems and narrow, curved, serrated tips. Inner marginal tooth with pointed tip, 2 or 3 inner flanking denticles, and 2 outer flanking denticles; outer marginal tooth same, but lacking outer flanking denticles.

Anatomy (preserved animal): Animal white, having narrow foot with deep, well-developed, anterior pedal, mucus gland. Snout broad, short; cephalic tentacles stout, short with large black eye on each cephalic peduncle. Deep longitudinal groove separating sole from rest of foot. Mantle edge with small papillae. Osphradium straight, narrow, brown, and with irregularly shaped leaflets. Pallial oviduct long, narrow, with large bursa in medial lamina. Stomach large, nearly 2.5 whorls in length.

HOLOTYPE.—MNHNP, not numbered, Figure 61A,D (26.4 mm × 7.0 mm).

PARATYPES.—MNHNP, over 200 specimens, not numbered; USNM 862327, Figure 61C,E,F (both lots same locality as holotype).

TYPE LOCALITY.—Îles des Glorieuses (11°28′5″S, 47°12′E, 500–600 m; BENTHEDI Sta DR-06).

ETYMOLOGY.—Named for the Îles Glorieuses, where large numbers of this species have been dredged.

REMARKS.—The distinguishing characters of this species are the rounded shell base, distinct suture, and porcelaneous texture sculptured with three spiral cords of pointed nodules aligned to form opisthocline axial ribs. The extremely short, broad, anterior, siphonal canal and the weak anal canal are also

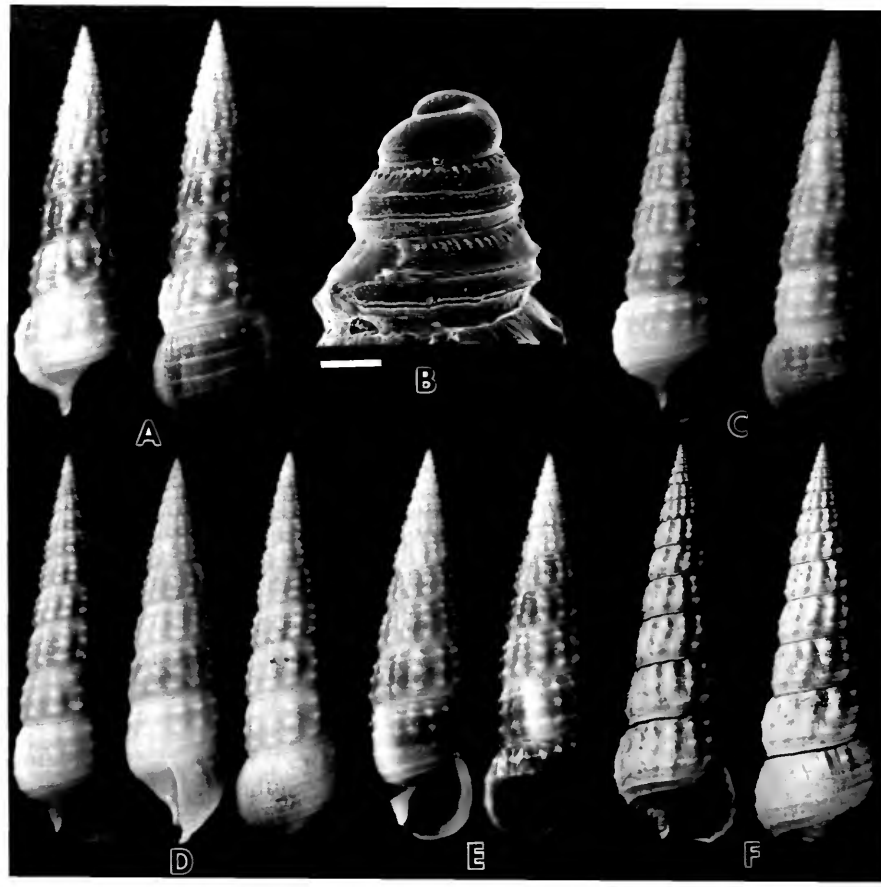

FIGURE 61.—*Cerithium gloriosum*, new species, 500–600 m, 1128S, 4712E, Îles Glorieuses: A, paratype, Îles Glorieuses, 24.6 mm (USNM 862327); B, SEM of protoconch (bar = 0.15 mm; USNM 862327); C, paratype, 28.4 mm (USNM 862327); D, holotype, 26.4 mm (MNHNP); E, paratype, 23.4 mm (USNM 862327); F, paratype, 24 mm (USNM 862327).

noteworthy. The nearly circular operculum and subcentral nucleus are unusual, but are characters shared by other deep-water cerithiids. The radula is notable in having a ridge on the posterior of the rachidian basal plate (Figure 62D), and a transverse ridge on the buttress of the lateral tooth (Figure 62B–D). The shell differs somewhat from those of other large, deep-water cerithiids in being smaller, less slender, and in having a more rounded shell base, a prominent dorso-lateral body whorl varix, and several distinct former varices. *Cerithium gloriosum*, new species, is morphologically close to *C. flemischi* Martin, *C. ophioderma* (Habe), and *C. matukense* Watson. In contrast to *Cerithium flemischi*, which it most closely resembles, the shell of *C. gloriosum*, new species, lacks an evident periostracum. *Cerithium gloriosum*, new species, has a porcelaneous, white shell with occasional faint traces of brown banding or splotches. Spiral sculpture between the nodes is more distinct on the early teleoconch whorls. Axial riblets are numerous, and where they cross the spiral cords, nodules become more spinose, especially on the early teleoconch whorls, presenting a reticulate sculpture. In contrast to *Cerithium matukense* and *C. flemischi*, the outer lip is less rounded, the body whorl not as inflated, the outer lip of the aperture less flaring, and the base of the body whorl is only mildly constricted. *Cerithium gloriosum*, although known only

TABLE 22.—Shell morphometrics of *Cerithium gloriosum*.

Character	$\bar{x}$ (n = 14)	sd	v	Range
Shell length	24.4	2.5	6.4	18.9–28.4
Shell width	7.1	0.6	0.4	6–8.3
Aperture length	5.5	0.5	0.3	4.3–6.4
Aperture width	3.7	0.4	0.2	2.7–4.3
Number whorls	14.9	0.8	0.7	13–16
Number spiral cords	3	–	–	3
Number axial ribs	13.9	0.9	0.8	13–16

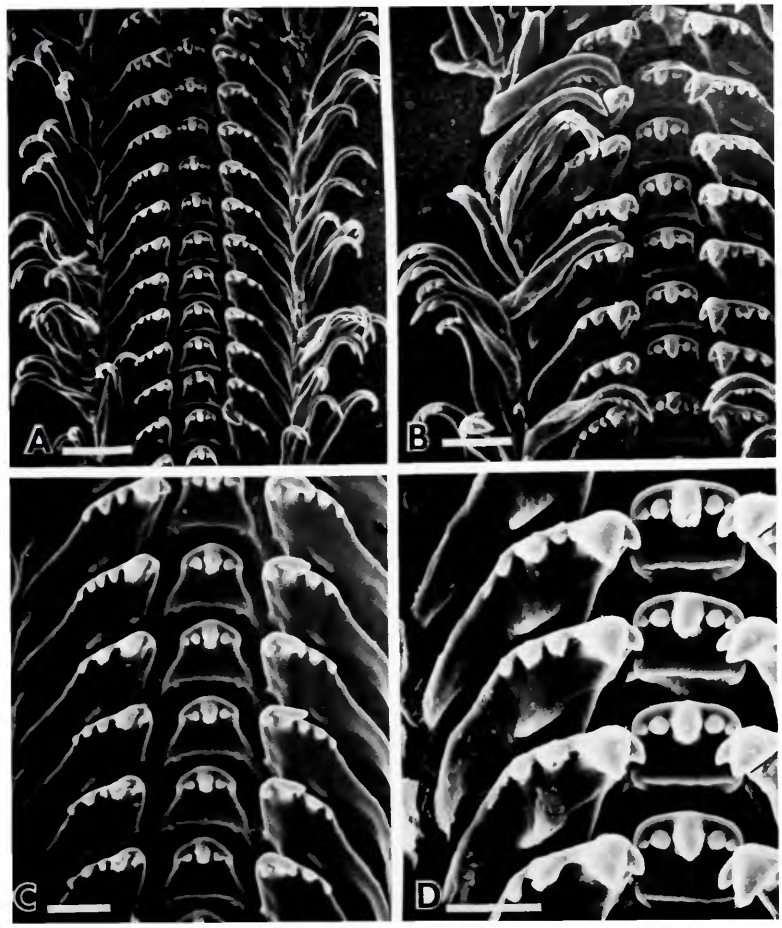

FIGURE 62.—Radula of *Cerithium gloriosum*, new species, Îles Glorieuses, type-lot (USNM 862327): A, radula with marginals spread back (bar = 100 μm); B, half row (bar = 100 μm); C, rachidian and lateral teeth (bar = 50 μm); D, detail of rachidian and lateral dentition (bar = 40 μm).

from poorly preserved specimens, appears to be anatomically very similar to *C. flemischi*.

Specimens from Borneo are more nodulose than those from the western Indian Ocean and when more material is available for comparison, they may prove to be a separate species.

A noteworthy anatomical feature of this species is the groove around the circumference of the foot, separating the sole from the rest of the foot, which is also seen in *C. flemischi*.

ECOLOGY.—*Cerithium gloriosum*, new species, is a deep-water species living on sandy bottoms at depths ranging from 250 to 600 m. Although the shell has ratchet sculpture (sensu Signor, 1983), it does not appear to be a complete burrower as many live-collected specimens have worm tubes comprised of cemented sand grains on the sides of the shell, suggesting that they live on the surface of the substrate, with only the ventral sides of the whorls in the sand. Few of the dredged specimens from the Mozambique Channel had broken apertures or repair marks, suggesting that crab predation is not common. Shells dredged off Borneo had drilled tips indicative of naticid predation. Protoconch morphology (Figure 58B) indicates a pelagic larval stage in life history.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 63).—This species has been found off the Comoro islands in the Mozambique Channel, and off Borneo, Indonesia. It probably occurs in suitable deep-water habitats throughout the Indo-West Pacific.

SPECIMENS EXAMINED.—INDIAN OCEAN ISLANDS: 200–500 m, Benthedi Sta DR-38, 12°54′8″S, 45°15′6″E, Mayotte (MNHNP); 500 m, Benthedi Sta ST-34, 12°53′7″S, 45°16′1″E, Mayotte (MNHNP); 275–400 m, Benthedi Sta DR-33, 11°53′5″S, 45°16′3″E, E Passe Longogori, Mayotte (MNHNP); 1300–1480 m, Benthedi Sta DR-40, 12°56′S,

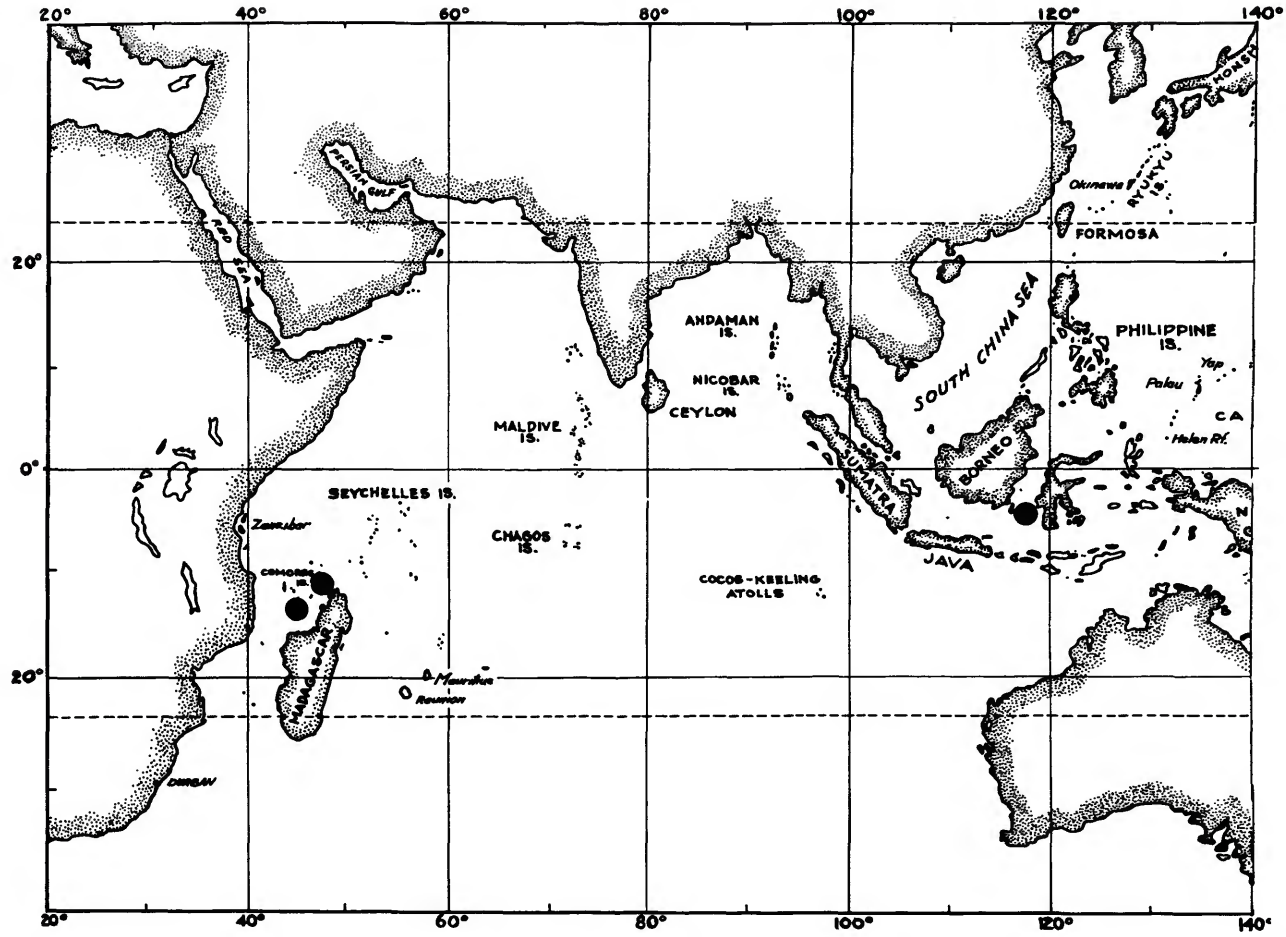

FIGURE 63.—Geographic distribution of *Cerithium gloriosum*, new species.

45°18′2″E, E Récif Bandele, Mayotte (MNHNP); 500–600 m, Benthedi Sta DR-06, 11°28′S, 47°12′E, Îles Glorieuses (type-lot) (MNHNP); 440 m, Benthedi Sta DS-10, 11°28′5″S, 47°17′E, Îles Glorieuses (MNHNP, USNM 862327); 440 m, Benthedi Sta DS-16, 11°28′5″S, 47°17′7″E, W of Îles Glorieuses (MNHNP); 250 m, Benthedi Sta DR-08, 11°29′2″S, 47°18′2″E, Îles Glorieuses (MNHNP); 700 m, Benthedi Sta 123F, 11°31′8″S, 47°23′5″E, Îles Glorieuses (MNHNP); 335–390 m, Benthedi Sta DS-120, 11°30′S, 47°24′7″E, SE Îles Glorieuses (MNHNP). INDONESIA: 557.5 m, BCF Sta 5592, 4°12′44″N, 118°27′44″E, off Silungan Id, Borneo (USNM 278958).

Cerithium interstriatum Sowerby, 1855

FIGURES 64–66

Cerithium interstriatum Sowerby, 1855:876–877, pl. 184: fig. 216 [lectotype, herein selected: BMNH 10971028112; no locality given, Honolulu, Hawaii, herein selected as type locality; 13 mm × 5 mm]; 1865, pl. 14: fig. 93.—Kay, 1979:122, fig. 451.

Cerithium clavis Sowerby, 1865, pl. 14: fig. 94 [lectotype, herein selected: BMNH, 19861691, 15.9 mm × 4.8 mm; 1 paralectotype 19861692; no locality].—Kobelt, 1898:227, pl. 40: fig. 5.—Schepman, 1909:161–162.—Kay, 1979:122.

Cerithium thaanumi Pilsbry and Vanatta, 1905:576; 1906:787, fig. 1 [holotype: ANSP 85855; type locality: Hilo, Hawaii, 14.2 mm × 4.5 mm].

DESCRIPTION.—*Shell* (Figure 64A–G, I–M): Shell elongate, slender, small, reaching 16.6 mm length and 5.4 mm width, and comprising 11–14 weakly inflated whorls sculptured with 3 spiral weakly beaded cords. Protoconch (Figure 64F) comprising 3.5 whorls; protoconch I smooth, one whorl; protoconch II sculptured with subsutural plications and two spiral cords, papillate on final whorl; sinusigeral notch in aperture lip of protoconch II. Early teleoconch (Figure 64I) whorls cancellate due to axial ribs crossing spirals. Teleoconch whorls sculptured with 3 or 4 major, beaded, spiral cords, thin spiral, subsutural

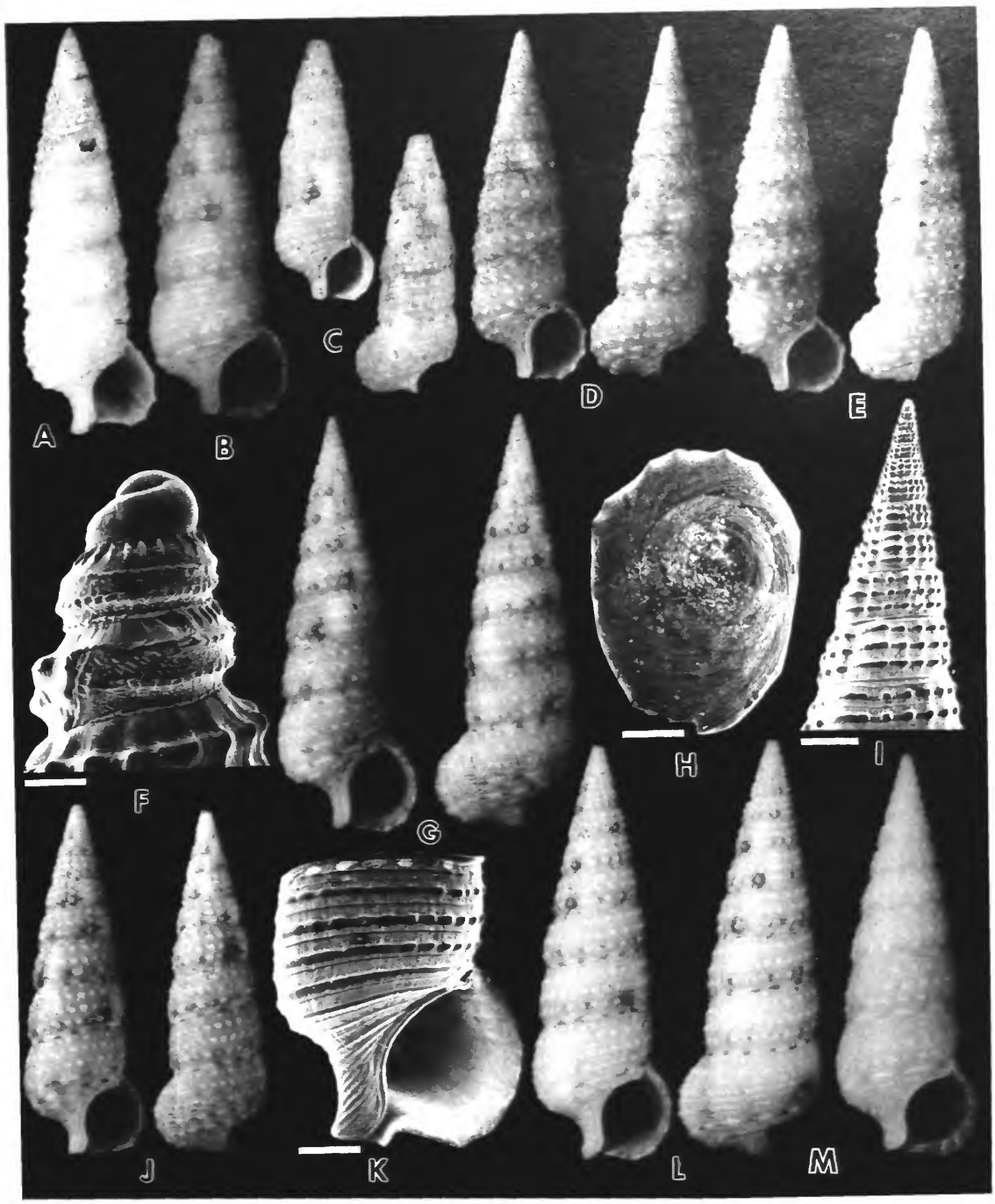

FIGURE 64.—*Cerithium interstriatum* Sowerby, with types of nominal taxa synonymous with it and showing morphological variation: A, lectotype of *Cerithium clavis* Sowerby, 15.9 mm (BMNH 19861691); B, holotype of *Cerithium thaanumi* Pilsbry and Vanatta, Hilo, Hawaii, 11.2 mm (ANSP 85855); C, lectotype of *Cerithium interstriatum* Sowerby, 13 mm (BMNH 109710281119); D, Waikiki, Oahu, Hawaii, 19.5 mm (ANSP 143893); E, Waikiki, Oahu, Hawaii, 19.5 mm (ANSP 143893); F, SEM of protoconch, Honolua Bay, Maui, Hawaii (bar = 75 µm; LACM 69-40); G, Mauritius, 15.5 mm (NMV); H, operculum, Piti Bay, Guam (bar = 0.38 mm; USNM 862330); I, SEM of early whorl sculpture, Piti Bay, Guam (bar = 0.88 mm; USNM 862330); J, Tulear, Madagascar, 16 mm (MNHNP); K, SEM of aperture and body whorl, Piti Bay, Guam (bar = 0.88 mm; USNM 862330); L, Conducia Bay, Mozambique, 14.4 mm (NM H1856); M, Midway Island, 14.4 mm (USNM 79098).

cord, and with thin spiral thread between major spiral cords; 22–28, weak beads on spiral cords forming colabral axial ribs. Varices randomly distributed. Suture moderately impressed. Upper and mid-teleoconch whorls with 27 or 28 strong beads. Body whorl (Figure 64K) long, sculptured with 5 major, weakly papillate, beaded, spirals and smooth interstriae, and large varix opposite outer lip of aperture. Base of body whorl weakly excavated with moderate siphonal constriction and sculptured with fine spiral striae. Aperture round, small, about one-fifth the shell length. Columella strongly concave with distinct callus. Anterior canal short, tubular and sharply reflected upwards and to left of shell axis. Outer lip of aperture thin, strongly convex, and weakly crenulate. Small anal canal present flanked by tiny parietal columellar tooth. Shell color white to cream, rarely brown, with irregular light tan blotches and tiny spiral, tan spots on cords. Aperture white. Measurements (Table 23). Periostracum not evident. Operculum (Figure 64H) thin, tan, corneous, subcircular, multispiral around nearly central nucleus, becoming paucispiral later.

Radula (Figure 65): Type-4 radular ribbon (Figure 3D) short, about one-fourteenth the shell length. Rachidian tooth (Figure 65B) having thin posterior longitudinal ridge and short, median, triangular, posterior extension on flat, rectangular, basal plate; cutting edge with sharp triangular main cusp, flanked with 2 or 3 small denticles. Lateral tooth (Figure 65B) with strong central ridge and long lateral, posterior extension on basal plate. Large, triangular main cusp flanked by one inner denticle and 3 or 4 small, outer denticles. Marginal teeth (Figure 65A,B) with moderately broad central shafts, broad bases and pointed, serrated apices with sharp cusp at tips. Inner marginal tooth with 4 inner flanking denticles and 3 outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Head-foot white-cream color. Snout with pair of brown double bands and white bilobed tip. Long cephalic tentacles pink, striped with tan, each bearing small black eye on tentacular peduncle. Wide mantle edge fringed with small papillae overhanging snout.

Large, wide osphradium. Ctenidium with long, triangular, feather-like filaments. Pair of large, long jaws (0.5 mm in shell 17 mm long) comprised of scale-like elements. Salivary glands comprised of paired, thin, convoluted tubes originating behind and passing through nerve ring, lying mostly anterior to it. Weak esophageal gland present.

Nervous system tightly organized with supraesophageal ganglion close to right pleural ganglion.

SYNONYMIC REMARKS.—*Cerithium interstriatum*, first proposed by Sowerby in 1855, was later described by him (1865) under the name *clavis*. As no locality was given for either taxon, I select Honolulu, Hawaii, as a proper type locality for *C. interstriatum*. The types of both taxa have been examined and are identical. The single, worn type of *C. interstriatum* (Figure 64C) does not match the figured specimen, but is here selected as lectotype. There are two paratypes of *C. clavis*, but neither match the figure in Sowerby (1865). The smaller of the two, which still has color and is not as beachworn as the larger, is herein selected as the lectotype (Figure 64A). Examination of the holotype of *C. thaanumi* Pilsbry and Vanatta (Figure 64B) shows that it is also conspecific with *C. interstriatum*.

TABLE 23.—Shell morphometrics of *Cerithium interstriatum*.

Character	$\bar{x}$ (n = 10)	sd	v	Range
Shell length	14.6	1.8	3.2	12.3–16.6
Shell width	4.6	0.5	0.2	3.8–5.4
Aperture length	2.9	0.4	0.1	2.3–3.6
Aperture width	2.3	0.4	0.2	1.6–3.0
Number whorls	13.2	1.0	1.1	11–14
Number spiral cords	3.1	0.3	0.1	3–4
Number nodes	25.2	2.2	4.8	22–28

ECOLOGY.—*Cerithium interstriatum* does not appear to occur in large populations and is uncommon in most localities. I have observed this species on subtidal, silty sand and coral rubble at Piti lagoon, Guam, and museum records indicate that it has been collected in similar subtidal, muddy-sand habitats throughout its range. At Tulear, Madagascar, *C. interstriatum* is relatively common in coarse sandy bottoms in shallow lagoons

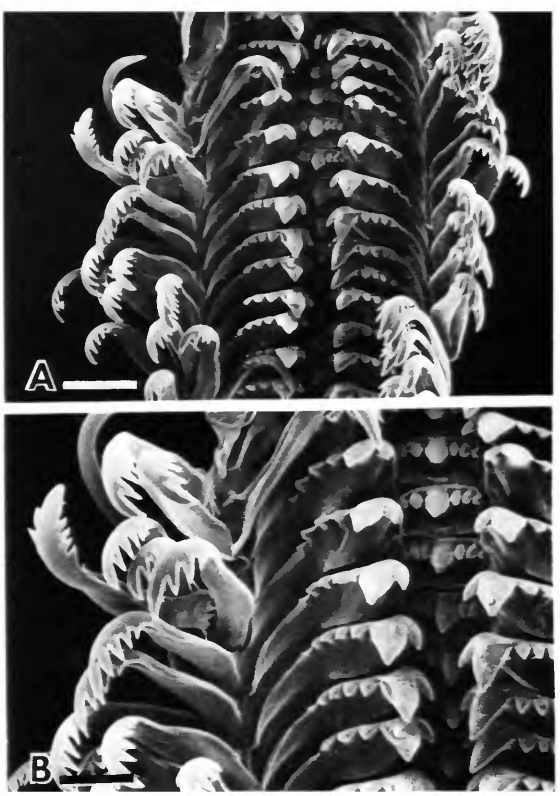

FIGURE 65.—Radula of *Cerithium interstriatum* Sowerby, Mauritius (NMV): A, ribbon with marginals spread open to show dentition (bar = 50 μm); B, half row showing dentition of rachidian, lateral, and marginal teeth (bar = 25 μm).

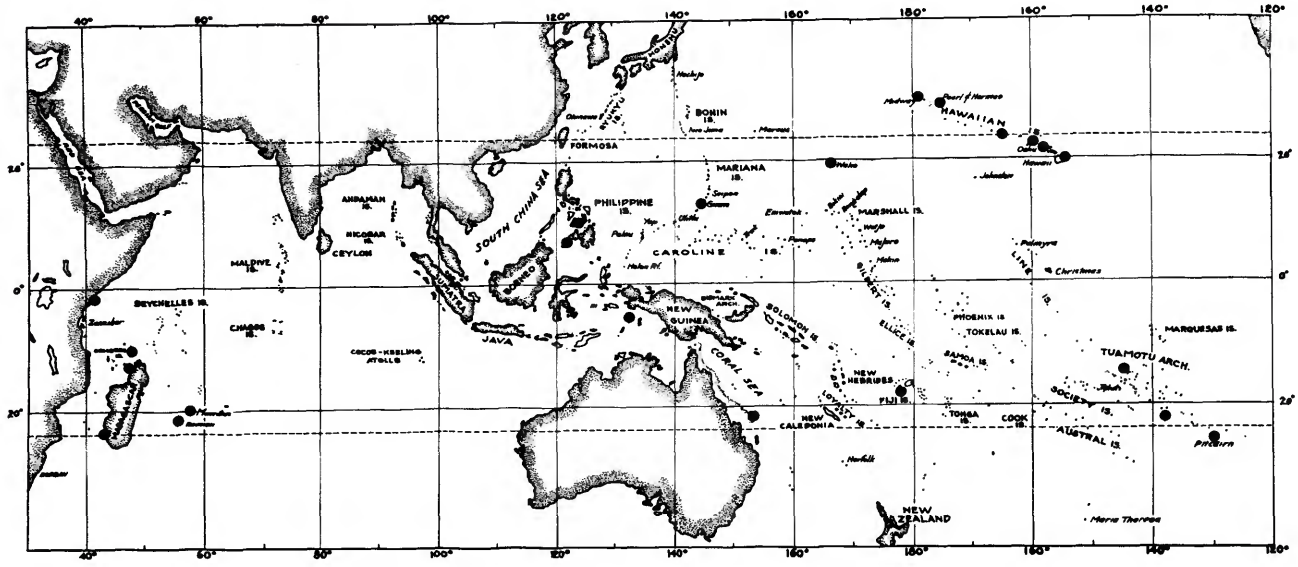

FIGURE 66.—Geographic distribution of *Cerithium interstriatum* Sowerby.

of the Grand Récif (Thomassin, in litt.). The spawn mass is unknown, but Taylor (1975:96) has shown that it has a planktotrophic larval stage. The elaborately sculptured protoconch with deep sinusigeral notch (Figure 64F) confirms a planktonic stage in life history. The veliger has an unpigmented, bilobed, unequal velum, and is found in the plankton around Oahu, Hawaii, from April through August (Taylor, 1975:96). The wide Indo-Pacific range of this species suggests a long pelagic phase in life history.

DISCUSSION.—*Cerithium interstriatum* is distinguished by its small, narrow, elongate shell sculptured with three major beaded spiral cords, and by its small aperture and acutely convex outer lip. This species is not common in museum collections and does not appear to occur in large populations. Although shells from throughout the range are remarkably alike in shell sculpture, there is some intraspecific variation in the relative absence or presence of interstriae: some individuals lack the spiral thread between the papillate spiral cords (Figure 64G,L,M). The largest examples of this species are from the Hawaiian Islands (Figure 64D,E), where *C. interstriatum* grows nearly twice the length of individuals from other areas. Some snails are of an overall brown color rather than white (AMNH 218329).

The only other congener with which this species may be confused is *C. nesioticum* Hedley (Figure 86), which is a larger, wider species. The latter has a similar, but highly variable sculpture, with four major, beaded spiral cords, instead of three. Moreover, *C. nesioticum* is not as narrowly elongate and does not have the extreme convexity of the outer lip seen in *C. interstriatum*.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 66).—*Cerithium interstriatum* has a wide Indo-Pacific distribution from east Africa and Madagascar throughout the Indian Ocean to Indonesia. In the Pacific, it has been recorded from the Philippines, South Coral Sea, Wake Id, and the Marianas eastward to the Hawaiian Islands, where it is very common among all the islands of the Hawaiian arc. In the South Pacific, it occurs from Fiji through the Cook Islands, and eastward through the Tuamotus as far as Pitcairn Id.

SPECIMENS EXAMINED.—EAST AFRICA: Conducia Bay, Mozambique (NM H1856); 0–1.8 m, Chumbe Id, SW Zanzibar (ANSP); N of Vasco da Gama Pt, Malindi, Kenya (ZMA). MADAGASCAR: Tulear (MNHNP); 3–8 m, Grand Récif, Tulear (MNHNP); 0–1.8 m, N end of Nossi Kalakajoro, Îles Radama, SW of Nossi Bé (ANSP); 1.52 m, Nossi N'Tangam, W Nossi Bé (ANSP). INDIAN OCEAN ISLANDS: 250 m, Benthedi Sta DR-8, 11°29′S, 47°18′E, W of Îles Glorieuses (MNHNP); 1.2 m, Benthedi Sta DR-8, NW side of Tamarin Bay, W Mauritius (ANSP); Reunion (MNHNP); "La Rounail," Boucanano, Reunion (MNHNP). AUSTRALIA: 6–13 m, 29°26′S, 159°28′E, Middleton Reef, S Coral Sea (AMS). PHILIPPINES: Punta Engano, Mactan, Cebu (AMNH 218329); 146 m, Mactan Id, Cebu (AMNH 203346); Little Santa Cruz Id, Mindanao (Springsteen coll). INDONESIA: 5°30′S, 132°18′E, NW of Tajandu Id, Kai Ids, Moluccas (WAM). MARIANA ISLANDS: 4.57 m, lagoon, Piti Bay, Guam (USNM 862330); WAKE ISLAND: (LACM HH-4476).

HAWAIIAN ISLANDS: Kure Id (USNM 671156); Eastern Id, Midway Ids (USNM 678006); Midway Id (ANSP, USNM 485528, 634821, 634830, 790908); Pearl and Hermes Reefs (USNM 405183, 467893); Laysan Id (ANSP, USNM 335026);

French Frigate Shoals (ANSP); Haena, Kauai (ANSP); Hanelei, Kauai (ANSP); Paumalu, Oahu (ANSP); Hickam Field Air Station, Pearl Harbor, Oahu (USNM 484457); 45.7–109.7 m off Keehi Lagoon entrance, Oahu (LACM 75-61); reef off Quarantine Id, Honolulu, Oahu (USNM 339354); Honolulu Harbor, Oahu (ANSP); 15.24 m, near reef runway, Honolulu, Oahu (Salisbury Collection); 45.7–91.4 m off Waikiki, Oahu (USNM 339356); 36.6 m, Waikiki, Oahu (ANSP 179832); 15.2 m off Waikiki, Oahu (LACM 75-60); Waikiki Beach, Oahu (ANSP 143893); Diamond Head, Oahu (LACM 38-14); beach near Makupuu Pt, Oahu (LACM 72-202); 1.5–9.1 m, Honolua Bay, Maui (LACM 69-40); Hilo, Hawaii (ANSP); Keokea, Hilo, Hawaii (USNM 339352); Keaukaha, Hilo, Hawaii (USNM 339355); 8 km SW of Kapoho, Hawaii (USNM 409094). TUAMOTU ARCHIPELAGO: Takaroa (USNM 819897); Mururoa (USNM 819772). PITCAIRN ISLANDS: Western Harbor, Pitcairn Id (USNM 789359).

Cerithium koperbergi Schepman, 1907

FIGURES 67, 68

Cerithium koperbergi Schepman, 1907:188–189, pl. 12: fig. 1, 1a [holotype: ZMA 3-06-004, 8.9 mm, one paratype, ZMA; type locality: Kajoe Ragi, Celebes, Indonesia, post-Tertiary].

DESCRIPTION.—Shell (Figure 67): Shell short, squat, with nearly concave, rapidly expanding upper spire, and comprising 11 or 12 inflated adult whorls, reaching 8.7 mm length and 4.5 mm width. Protoconch unknown. Early teleoconch whorls (Figure 67D) straight-sided, sharply indented presuturally,

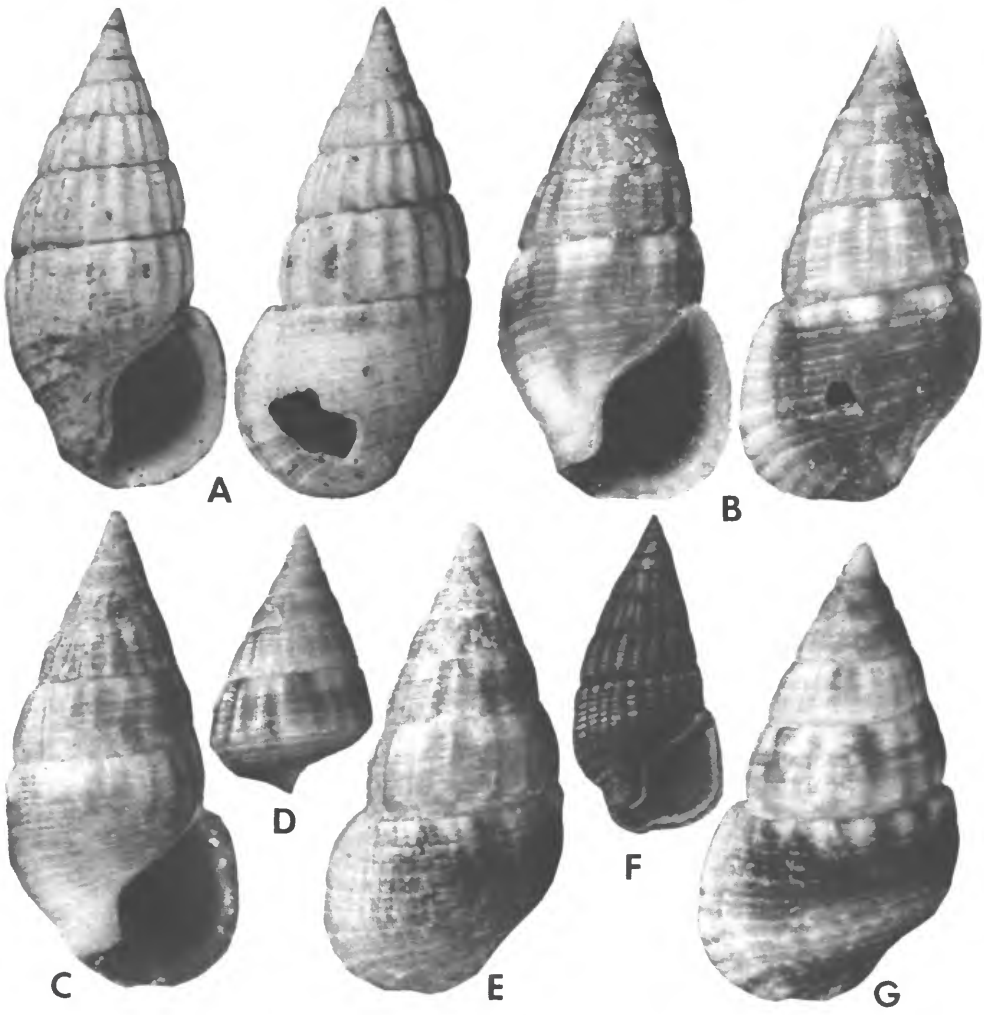

FIGURE 67.—*Cerithium koperbergi* Schepman: A, paratype, Kajoe Ragi, Celebes, Indonesia, post-Tertiary fossil, 8.9 mm (ZMA 306004); B, Dawi Id, E Padaido Islands, West Irian , Indonesian New Guinea, 8.3 mm (ANSP 205333); C,E, same data as B, 8.3 mm; D, immature shell, same data as B, 5.5 mm; F, figure of holotype from Schepman, 1907, pl 12: fig. 1; G, same data as B, 8.8 mm.

TABLE 24.—Shell morphometrics of *Cerithium koperbergi*.

Character	$\bar{x}$ (n = 6)	sd	v	Range
Shell length	8.3	0.3	0.1	7.7–8.7
Shell width	4.2	0.3	0.1	3.7–4.5
Aperture length	2.6	0.3	0.1	2–2.9
Aperture width	1.6	0.1	0	1.4–1.8
Number axial ribs	18.8	0.4	0.1	18–19

sculptured with 3 spiral threads. Adult teleoconch whorls inflated, sculptured with about 15 fine spiral lirae crossed over by 18 or 19 strong axial ribs. Suture strongly impressed. Body whorl large, wide, and with strong varix opposite outer lip of aperture. Base of body whorl rounded, with very slight siphonal constriction. Aperture circular-ovate, about one-third the shell length. Anterior siphonal canal short, shallow, wide, turned to left of shell axis. Anal canal a short spout at posterior of aperture. Columella sharply concave with callus and slight columellar lip. Outer lip of aperture thick, nearly smooth, sometimes with weak crenulation, and slightly pendant below anterior canal. Shell color cream with wide orange and rose spiral bands. Aperture white, tinged with rose. Measurements (Table 24). Operculum unknown.

Radula: Unknown.

Anatomy: Unknown.

SYNONYMIC REMARKS.—This species was described as a fossil from the Celebes ("post-Tertiary strata"), but living specimens (Figure 67B-E,G) conspecific with the fossil type material (Figure 67A,F) have been dredged in western New Guinea, the Moluccas, and off the southern Celebes, Indonesia.

DISCUSSION.—*Cerithium koperbergi* is distinguished by its small, squat, pupate shell, sculptured with strong axial ribs, and by its creamy orange or rose color. It does not have a parietal columellar tooth setting off the anal canal, as do other *Cerithium* species. In overall morphology, it most closely resembles *Clypeomorus* species, which are intertidal cerithiids, but it lacks the beaded sculpture common to them (see Houbrick, 1985). *Cerithium koperbergi* is a very rare and most unusual subtidal, offshore species that appears to be endemic to the eastern part of the Indonesian archipelago. Specimens have all been dredged from moderate depths on sandy or gravel bottoms, and the narrow geographic range suggests direct development. As the ecotope of this species differs greatly from that of *Clypeomorus* species, and the anatomy remains unknown, it is tentatively allocated to *Cerithium*.

FOSSIL RECORDS.—The type material is from the Quaternary strata of Celebes (Schepman, 1907:188–189).

GEOGRAPHIC DISTRIBUTION (Figure 68).—*Cerithium koperbergi* appears to be endemic to eastern Indonesia, from the Celebes, east through the Moluccas to western New Guinea. More dredging in the Indonesian area may enlarge the known range.

SPECIMENS EXAMINED.—INDONESIA: Kajoe Ragi, Celebes (paratype, Quaternary fossil) (ZMA); 72–78 m, 3°16′S, 128°04′E, off Tg Ani, Piru Bay, Ceram (WAM); 36 m, 6°45′S, 118°50′E, Pulu Sarassa, Sabalana Kepulauan (Postillion Ids) (ZMA). NEW GUINEA: 13 m, 1°15′S, 136°30′E, 1.6 km E of Dauwi Id, E Kepulauan Padaido (E Padaido Ids), West Irian (ANSP 205333).

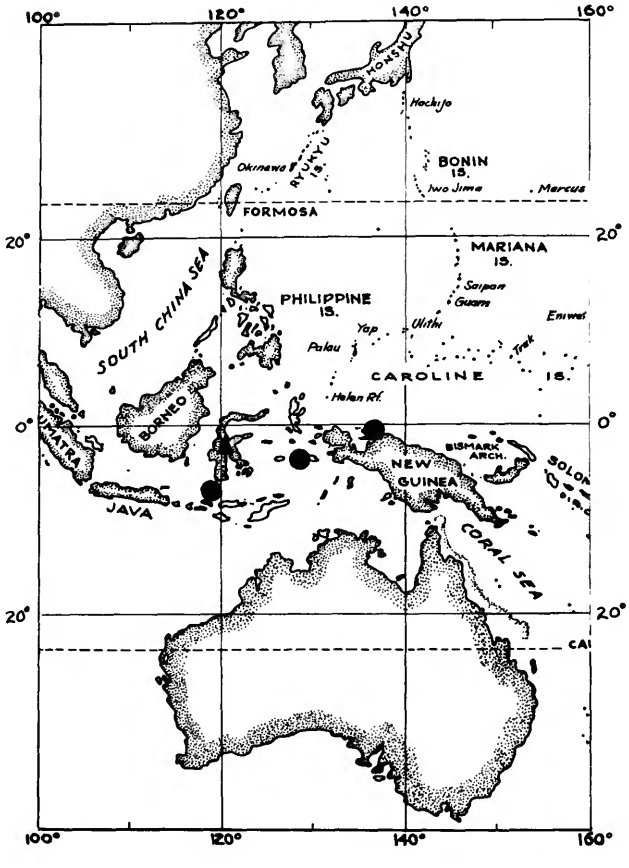

FIGURE 68.—Geographic distribution of *Cerithium koperbergi* Schepman (black triangle = locality where fossil type species was found).

Cerithium leptocharactum Rehder, 1980

FIGURES 69, 70

Cerithium (Thericium) leptocharactum Rehder, 1980:38, pl. 6: figs. 5–7 [holotype: USNM 756335, 18 mm × 8 mm; Paratypes (2): USNM 751613; type locality: Easter Island].

DESCRIPTION.—*Shell* (Figure 69): Shell elongate, turreted, comprising 10 angulate whorls, reaching 18 mm length and 8 mm width. Protoconch unknown. Early teleoconch whorls with about 7 fine spiral threads, largest centrally placed, and with weak, broad axial ribs. Adult teleoconch sculptured with fine, unequal, spiral threads and narrow grooves, and with spiral row of subsutural beads and spiral row of peripheral nodes on last three whorls. Penultimate and previous whorls with about 10

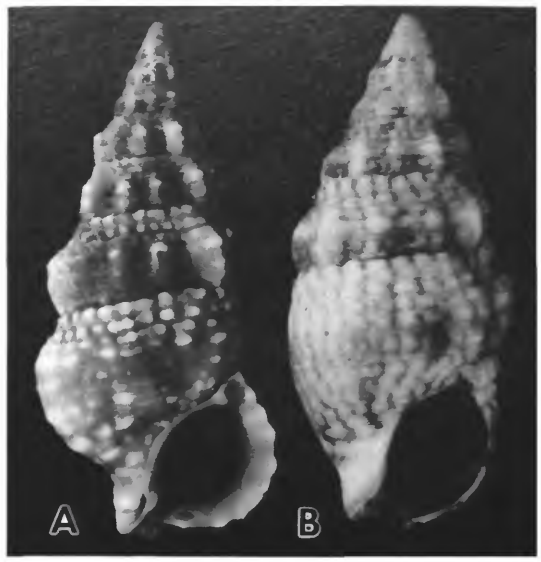

FIGURE 69.—*Cerithium leptocharactum* Rehder: A, holotype, Easter Island, 18 mm (USNM 756335); B, paratype, 11.7 mm (USNM 751613).

broad, angulate, axial ribs, crossed over by thin spiral threads and grooves. Suture distinct, impressed, and slightly sunken into each anterior whorl. Large varices randomly placed. Body whorl elongate, with moderately excavated base and strong siphonal constriction; sculptured with about 9 spiral, beaded threads, numerous fine spiral threads. Large varix opposite outer lip of aperture. Aperture ovate, a little less than one-third the shell length. Columella slightly concave with callus and columellar lip. Anterior siphonal canal of moderate length, slightly turned to left of shell axis. Anal canal distinct, bordered with parietal columellar tooth. Outer lip convex, weakly crenulate; interior with weak spiral denticles. Shell color tan-brown with white beads, varices, and axial ribs on early whorls. Aperture pink. Operculum unknown.

Radula: Unknown.

Anatomy: Unknown.

SYNONYMIC REMARKS.—The original description was based on a mixed lot: of the three type specimens of *C. leptocharactum,* only the holotype (Figure 69A), a fully grown shell, and one paratype (Figure 69B), an immature shell, are conspecific. The other paratype, a fully mature shell, is merely a worn, colorless specimen of *C. egenum* Gould. As the original description was based on a mixture of two species, a new description is presented above.

DISCUSSION.—This poorly known species is represented by only two known specimens, the holotype and paratype. The latter (Figure 69B), which is an immature shell, was assigned to *C. leptocharactum* with hesitation by Rehder (1980:38), who noted that the specimens varied considerably in sculpture and color. If the worn specimen of *C. egenum* is excluded, the remaining two specimens are distinctive in having dense, very fine spiral sculpture and pink apertures. As only 2 specimens

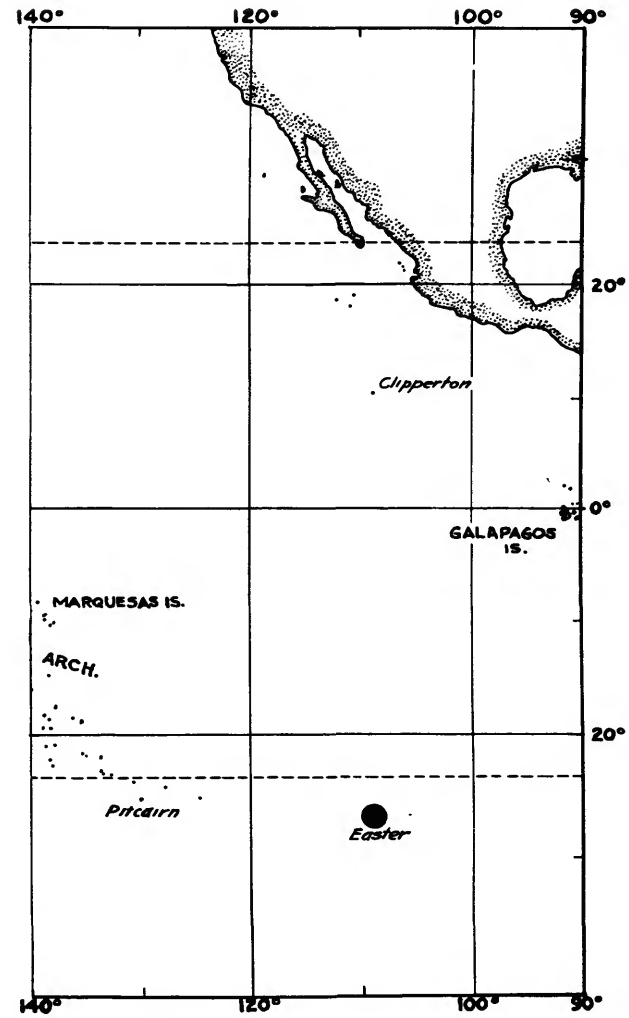

FIGURE 70.—Geographic distribution of *Cerithium leptocharactum* Rehder.

are available, nothing about intraspecific variation may be said.

This species somewhat resembles *C. rehderi,* new species, in overall shape, but is undoubtedly distinct, and as far as is known, endemic to Easter Island.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 70).—Easter Island.

SPECIMENS EXAMINED.—EASTER ISLAND: Te Raa Raa, S side Handa Piko (USNM 756335, holotype); E of Hanga Tee, Vaihu (USNM 751613, paratype).

Cerithium lifuense Melvill and Standen, 1895

FIGURES 71–73

Cerithium armatum Philippi, 1848:22 [lectotype, herein selected MNHNC, no number, 22 mm × 5 mm; type locality not given, herein designated as Marinduque Id, Philippines; not *Cerithium armatum* Goldfuss, 1844]; 1849:16, pl. 1: fig. 5.—Sowerby, 1855:859, pl. 189: fig. 68, pl. 180: fig. 96; 1865, pl. 3: fig. 14.—Tryon, 1887:124, pl. 20: figs. 31, 32; pl. 21: fig.

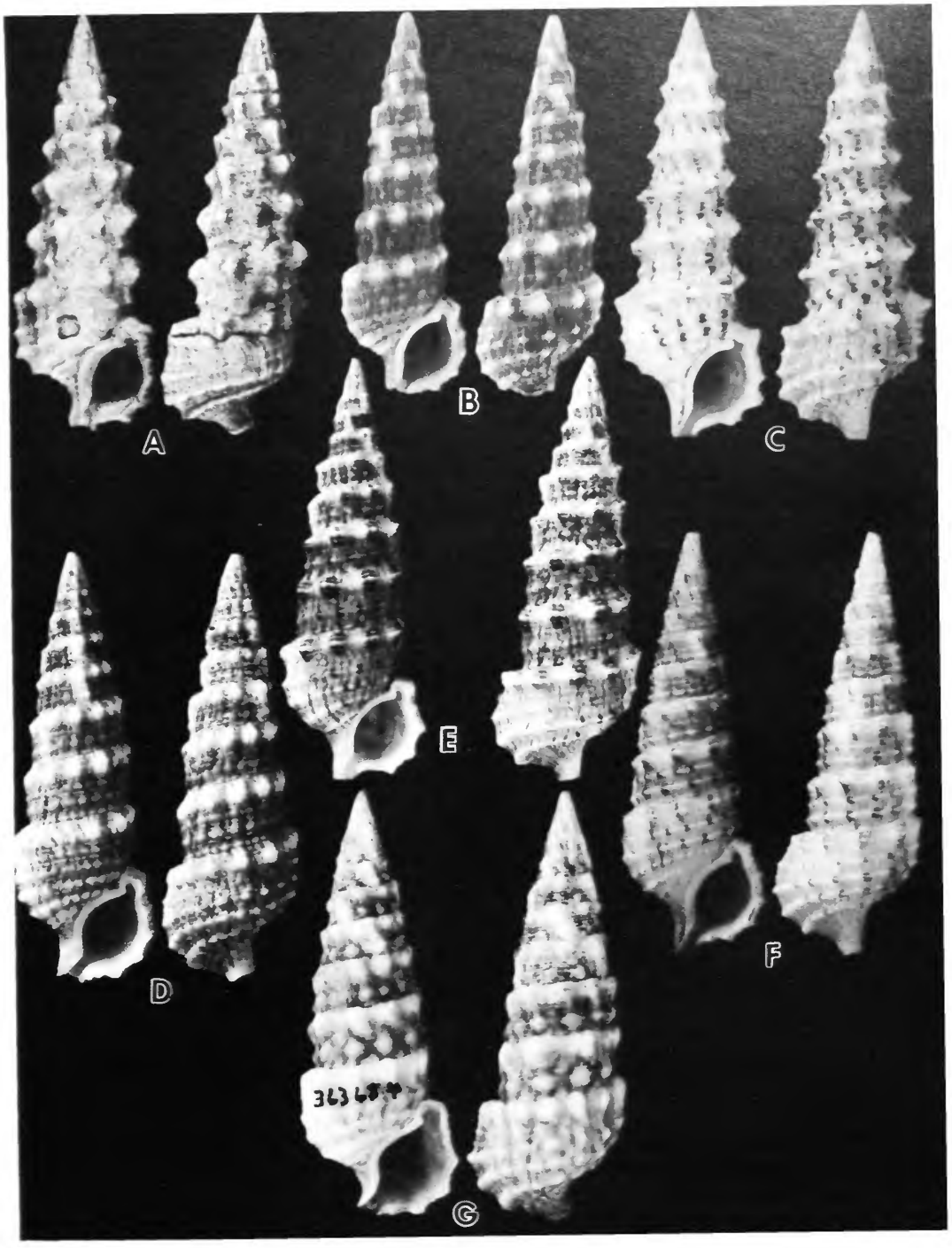

FIGURE 71.—Phenotypic variation in *Cerithium lifuense* Melvill and Standen: A, lectotype of *Cerithium armatum* Philippi, 22 mm (MNHNC); B, holotype of *Cerithium armatum lifuensis* Melvill and Standen, Lifu, Loyalty Islands, 26.5 mm (MM); C, Cebu, Philippines, 25 mm (MCZ 22662); D, Touho, New Caledonia, 31.6 mm (ANSP 270267); E, Bohol Id, Philippines, 30.2 mm (ANSP 230883); F, Anse de Sigave, Futuna, Horn Islands, 26.8 mm (USNM 676620); G, Waki, Satsuma, Japan, 32.8 mm (USNM 363684).

33.—Kobelt, 1895:165, pl. 31: figs. 2–4.

Cerithium armatum Phil. var. *lifuensis* Melvill and Standen, 1895:115, pl. 3: fig. 33 [holotype, 26.5 mm × 8.5 mm, and 8 paratypes: Manchester Museum, EE4780; type locality: Lifu, Loyalty Islands].

Cerithium lifuense murita (Yokoyama).—Habe, 1964:41, pl. 12: fig. 23.

Cerithium lifuense Melvill and Standen.—Cernohorsky, 1972:64, pl. 12: fig. 10.

DESCRIPTION.—*Shell* (Figure 71): Shell tall, tapering, elongate, comprising 14 or 15 concave, spinose, nodular whorls and reaching 32.8 mm length and 10.1 mm width. Protoconch unknown. Early teleoconch (about first 4 whorls) with broad, sloping subsutural ramp and two spiral cords. Adult teleoconch sculptured with fine spiral lirae and with prominent, keel-like spiral of spines or nodes, followed by 1 or 2 weakly beaded, spiral cords; cords with 8–13 beads. Whorls straight-sided or concave below spiny subsutural keel. Suture incised, wavy. Varices randomly distributed. Body whorl narrow, elongate, with slightly excavated base and moderate siphonal constriction; sculptured with spiny or knobby subsutural spiral band and 4 or 5 spiny or beaded spiral cords. Large varix opposite outer lip of aperture. Aperture ovate, about one-fourth the shell length. Columella concave with thick callus and well-defined columellar lip. Anterior siphonal canal moderately elongate, tubular, slightly reflected dorsally and to left of shell axis. Anal canal well defined, bordered by parietal columellar tooth extending into shell aperture. Outer lip of aperture thick, crenulate. Measurements (Table 25). Periostracum thin, tan.

Radula (Figure 72): Type-1 radular ribbon (Figure 3A) short, about one-thirteenth the shell length. Rachidian tooth (Figure 72A) square with rounded edges having pair of very small posterior ridges and broad, median, triangular extension on basal plate; cutting edge with triangular, pointed, main cusp, flanked on each side with two very small denticles. Lateral tooth (Figure 72B) with long, narrow, central column and long, basal-lateral extension on basal plate; cutting edge with large, pointed main cusp, one inner flanking denticle, and 3 or 4 pointed, outer flanking denticles. Marginal teeth (Figure 72A,B) long, with broad shafts, and curved, spoon-like tips with spatulate main cusps. Inner marginal tooth with 3 pointed, inner flanking denticles and 1 or 2 tiny, outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Unknown.

TABLE 25.—Shell morphometrics of *Cerithium lifuense*.

Character	$\bar{x}$ (n = 22)	sd	v	Range
Shell length	26.4	3.4	11.5	18.9–32.8
Shell width	8.5	1.0	0.9	6.7–10.1
Aperture length	6.6	1.0	1.0	4.6–8.7
Aperture width	4.5	0.6	0.4	3.5–5.9
Number whorls	14.8	0.4	0.2	14–15
Number spiral cords	2	0.6	0.3	1–3
Number beads	10	1.4	1.0	8–13

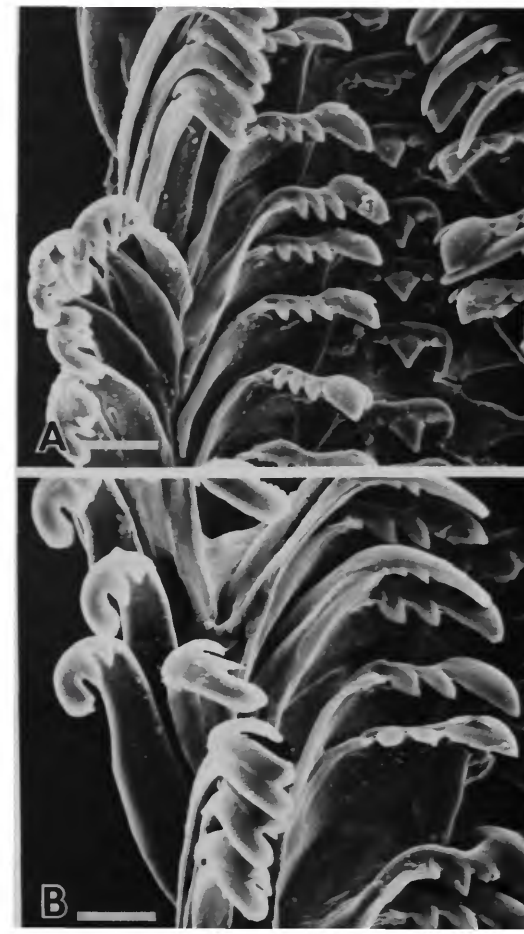

FIGURE 72.—Radula of *Cerithium lifuense* Melvill and Standen, Kranket Id, Madang, Papua New Guinea (AMS C108197): A, half row with marginals spread open (bar = 50 μm); B, detail of lateral and marginal dentition (bar = 50 μm).

SYNONYMIC REMARKS.—This species is not commonly cited in the literature. The name most commonly applied to it has been *Cerithium armatum* Philippi, 1848, but that name is preoccupied. The lectotype of *C. armatum* (Figure 71A) is the common phenotype of this variable species. Melvill and Standen (1895) proposed a varietal name, *lifuensis*, for what they considered to be a form of this species from the Loyalty Islands. Cernohorsky (1972:64) was the first to accord *lifuense* specific status. The holotype (Figure 71B) and 8 beachworn paratypes of *C. armatum lifuensis* are clearly conspecific with *C. armatum* Philippi. *Cerithium nigropunctatum* Sowerby, 1855, suggested by Tryon (1887:124) to be an immature specimen of *C. armatum*, is conspecific with *C. scabridum* Philippi, 1848. Habe (1964:41) considered the potamidid fossil, *Potamides murita* Yokoyama, 1928, to be a subspecies of *C. lifuense* and proposed a new combination, but I do not concur, as the figured holotype of the the former species bears little resemblance to the latter. According to Kosuge (in litt.),

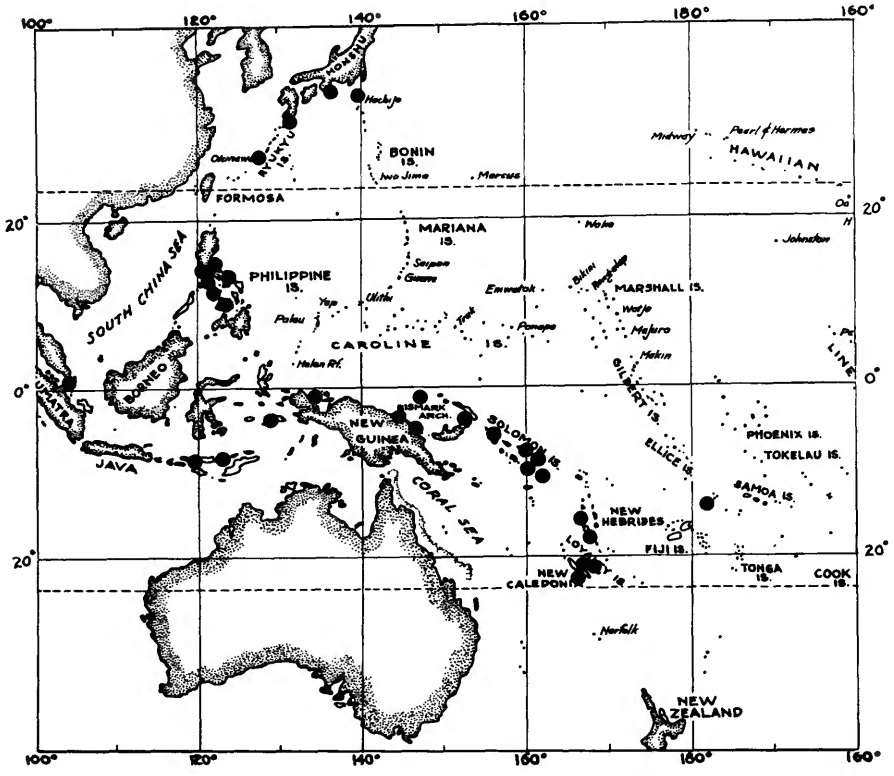

FIGURE 73.—Geographic distribution of *Cerithium lifuense* Melvill and Standen.

the type of *murita* was destroyed or lost during World War II.

ECOLOGY.—*Cerithium lifuense* is a subtidal species found at depths from 1 to 55 m, on sandy, rubble bottoms associated with fringing reefs along continental shores and high islands. Nothing specific is known of its ecology, but it appears to be common offshore in the Philippines where it is frequently collected in tangle nets. Few of the examined specimens had drill holes or cracked apertures. Spawn and larvae are unknown, and as none of the examined shells had intact, uneroded protoconchs, the mode of reproduction can not be inferred.

DISCUSSION.—*Cerithium lifuense* is distinguished by a long slender shell of 15 concave whorls and by a wide spiral row of 8–12 pointed, white, subsutural nodules. Below these are 1 or 2 spirals with smoother nodules. Several prominent former growth varices occur on the shell and the body whorl has a large varix opposite the outer lip. The anal canal is highly developed and 3–5 spiral rows of nodules sometimes occur on the body whorl.

The number and development of spiral nodose cords varies from 1 to 3, and the number of spiny nodules on the dominant spiral of each whorl varies from 8 to 13. Shells from the Philippines tend to have 2 spiral cords and an average of 9 nodules (Figure 71C,E), while those from New Guinea and adjacent archipelagos to the east have 2 or 3 spiral cords and an average of 10 nodules (Figure 71F). Shells from New Caledonia (Figure 71D) frequently have 10–13 large, smooth, axially elongate nodules and one subsutural spiral cord, presenting a smoother aspect.

Cerithium lifuense should be carefully compared with *C. novaehollandiae*, as some phenotypes of both species can be similar. Specimens from Japan (Figure 71G) are morphologically similar to *C. novaehollandiae*, and the highly sculptured phenotypes of the latter species that occur in New Caledonia closely resemble some forms of *C. lifuense*. *Cerithium novaehollandiae*, however, is largely confined to Australasia. It is usually a larger species than *C. lifuense*, and lacks concave whorls, tends to have wide, uninterrupted axial ribs, has smoother nodules, and is sculptured with numerous spiral incised lines on each whorl.

FOSSIL RECORDS.—Fossils of Late Pleistocene or Holocene age from sand quarries at Cap des Pins, Lifu, Loyalty Islands have been examined (AMS C30716).

GEOGRAPHIC DISTRIBUTION (Figure 73).—This species has a western Pacific distribution, but also extends westward into the Indonesian Archipelago and SE Asia. It is confined to continental margins and to large, high islands associated with large archipelagos.

SPECIMENS EXAMINED.—MALAYSIA: Singapore (USNM 770609). JAPAN: Mikake-jima, Izu Ids (Vermeij collection); 1–2 m, Cape Bansho-zaki, near Seto Marine Lab, Wakayama Prefecture, Honshu (LACM 82-19); Washi, near SE point of Kyushu (MCZ); Washi, Kyushu (ANSP 242437, USNM 613738). RYUKYU ISLANDS: Waki, Satsuma (USNM 363684); Osima, Osumi (USNM 343860); Channel, Kadena Yacht Club, Okinawa (USNM 812933, 812996, 821056, 821139, 821166, 852194); 1 km S of Kuwae Hospital, near old yacht club, Okinawa (USNM 838411); Horseshoe Cliffs, Onna Village, Okinawa (USNM 838939). PHILIPPINES: W coast Palaui Id, Luzon (USNM 232920); 27.4–54.8 m, Nasasa Bay, San Antonio, Zambales (AMNH); Eman Pt, Morong, Bataan, Luzon (USNM 774780); Bagac, Bataan, Luzon (USNM 774971); Matabungkay, 115 km SSW of Manila, Luzon (AMS); Batangas, Luzon (USNM 786924); Ligpo Pt, Balayan Bay, Luzon (USNM 243767); 25.6 m, Dapdap, Batan Id, Albay Prov, SE Luzon (LACM 76818); 1.8–7.3 m, Kawilihan Anchorage, Sula Channel, Albay Prov, SE Luzon (LACM 76813); Quezon Prov, Polillo Gp (LACM 76886); Cabaloa, Quezon Prov, Polillo Gp (LACM 76747); Lubang Id (ANSP); Cabra Id, Lubang Gp, Mindoro (USNM 653895); Puerto Galera, Mindoro (AMNH 207497); 18.3–27.4 m, Cape Calavite, Mindoro (LACM 76773, 76855); Calapan, Mindoro (AMNH, MCZ, USNM 634010); 1–6 m, Ata Id, 2 km W of Kawayan, Marinduke (AMS); 3.7–12.8 m, Cambalo Reef, Romblon Prov, Sibuyan Id (LACM 76842); Canlapia Reef, Romblon Prov, Sibuyan Id (LACM 76851); Masbate, Masbate (BMNH); Cataingan Bay, Dumurug Pt, Masbate (USNM 243645, 243832); Cebu, Cebu (ANMH, MCZ 22662); Mactan Id, Punta Enganio, Cebu (USNM 845806); 146 m, Mactan Id, Cebu (AMNH 203273); W side Hadayan Id, NW end Bohol (ANSP 230883); 3–4.5 m, Bulata, Negros (AMS); Guigulugau, Negros (USNM 244053); 9°06′30″N, 122°52′24″E, near Giligaon, N of Maloh, off Negros (USNM 821773).

INDONESIA: Larantoeka, E Flores (ZMA); Komodo Id (FSM 24758); Ambon, Moluccas (MCZ, ZMA); Kg Ihamahu, NE coast of Saparua Id (WAM). NEW GUINEA: Manokwari, West Irian (ANSP 249604, ZMA); 3.2 km W of Wombrisau, Biak Id, Schouten Ids (ANSP 207699); inlet at N end of Kranket Id, Madang (AMS C108197); Panab Id, Madang, Papua (AMS); 3–12 m, Watsons Bay, Madang, Papua (AMS C95242); Finschafen, Papua (AMS); Rabaul (AMS C58347); Nordup, near Rabaul (AMS). ADMIRALTY ISLANDS: Secadar Harbor, Manus Id (MCZ). SOLOMON ISLANDS: Shortland Id, Bougainville Id (ANSP 327661); Ata'a, N Malaita (ZMA); 4–6 m, Auki Harbor, W coast Malaita Id (AMS C95219); Tineti Pt, Florida Id (WAM); Guadalcanal (MCZ); 12 km W of Honiara, Guadalcanal (LACM 781412); off Honiara Market, Honiara, Guadalcanal (BMNH); Kukum, E of Honiara, Guadalcanal (WAM); S end Malapa Id, Marau Sound, Guadalcanal (LACM 786828); Ugi Id (USNM 600405); San Cristobal (BMNH). NEW HEBRIDES: Maekula Id (CAS); Port Havannah, N Efate (USNM 824782); Malapoa Pt, Mele Bay, Efate Id (LACM 77-39). LOYALITY ISLANDS: Lifu (AMS). NEW CALEDONIA: Reef at Île Ain, 4.8 km ENE of Touho (ANSP 270267); SE side of bay, Touho (ANSP 270350); Poindimie (AMS); Nouméa (AMS). HOORN ISLANDS: E side Anse de Sigave, Futuna (USNM 676620).

Cerithium lissum Watson, 1880

FIGURES 74–76

Cerithium (Cerithium) fusiforme Sowerby, 1855.—Springsteen and Leobrera, 1986:62, pl. 13: fig. 18 [not *C. fusiforme* Sowerby, 1855; is *C. lissum* Watson].

Cerithium (Bittium) lissum Watson, 1880:107, species 7 [holotype: BMNH 1887291665; type locality: Levuka, Fiji, 22 m].

Cerithium lissum Watson, 1886:535–536, pl. 15: fig. 4.—Tryon, 1887:130, pl. 23: fig. 92.—Kobelt, 1893:149, pl. 28: figs. 6, 7.—Cernohorsky, 1978:52, pl. 13: fig. 6.

Cerithium veillardi Drivas and Jay, 1990;271–272, pl. 1: fig. 1 [holotype: MNHNP; type locality: off "Souris-Chaude," between La Saline and St. Leu, Réunion].

DESCRIPTION.—*Shell* (Figure 74A-H): Shell elongate, turreted, fusiform, comprising 11–13 moderately inflated or angulate whorls, and reaching 24.7 mm length and 8.7 mm width. Protoconch unknown. Early teleoconch (Figure 74I) white, with broad, sloping, subsutural ramp, and sculptured with two main spiral cords and tiny axial riblets. Subsutural ramp growing weaker and disappearing on final three whorls. Adult teleoconch whorls sculptured with 11–13 axial ribs crossed over by numerous fine spiral threads and striae, and with 3 or 4 major, raised, spiral bands separated from each other by thin, brown, incised spiral lines; crossover points of axial ribs and spiral bands nodular. Prominent spiral, nodulose band at whorl periphery. Large, white varices sometimes present. Suture sunken, weakly defined to distinct. Body whorl elongate, sculptured with 7–9 spiral, nodulose to smooth bands and spiral striae. Base of body whorl weakly excavated with long, tapering siphonal constriction. Aperture narrowly ovate, about 3.5 times the shell length. Columella concave with moderate callus and well-defined columellar lip. Anterior siphonal canal large, long, reflected dorsally and to left of shell axis. Anal canal well defined, bordered with parietal columellar tooth extending into aperture. Outer lip of aperture convex, thickened, crenulate, and angulate at periphery with weak spiral, internal lirations. Shell color tan with 5 brown, thin spiral lines per whorl, white nodules varices, and apex. Aperture white. Outer lip edge white with thin tan lines. Measurements (Table 26). Periostracum light tan.

Radula (Figure 75): Type-2 radular ribbon (Figure 3B). Rachidian tooth (Figure 75B–D) triangular with pair of basal, posterior ridges and long finger-like, central posterior projection on basal plate; anterior face slightly concave; cutting edge with central, large, pointed main cusp, flanked on each side by 2 or 3 small denticles. Lateral tooth (Figure 75B,C) with posterior, lateral extension and central basal buttress with small, median pustule on broad basal plate; cutting edge with

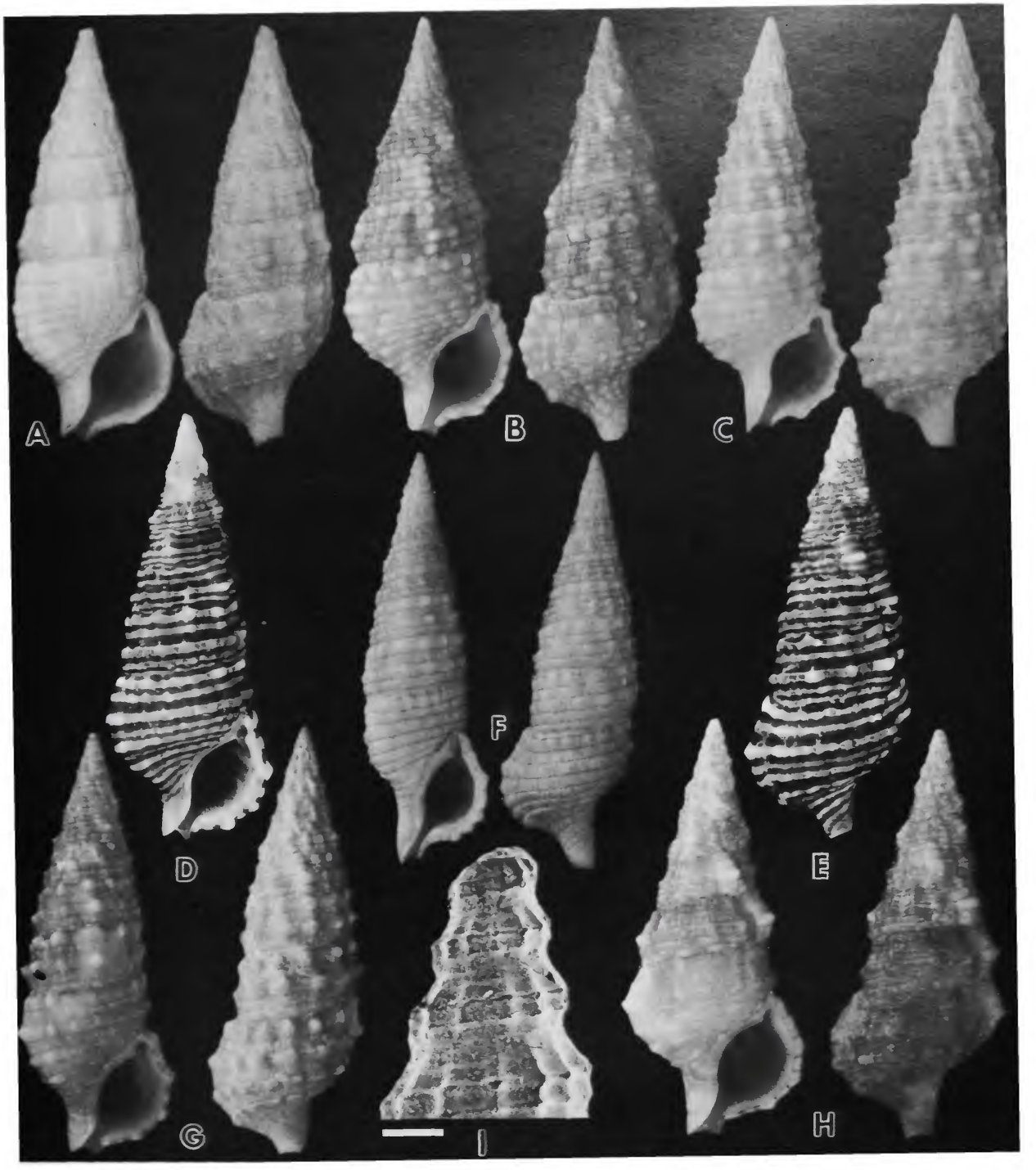

FIGURE 74.—Phenotypic variation in *Cerithium lissum* Watson. A, holotype, Levuka, Fiji, 24 mm (BMNH 1887291665); B, Horseshoe Cliffs, Onna Village, Okinawa, 23.5 mm (USNM 812965); C, Diego Garcia, Chagos Archipelago, 22.6 mm (BMNH); D,E, Réunion, 22.8 mm (MNHNP); F, Diego Garcia, 30.1 mm (BMNH); G, Leven Bank, Îles Glorieuses, 23.3 mm (MNHNP); H, Engano, Mactan Id, Philippines, 19.5 mm (USNM 845801); I, SEM of early whorls, Engano, Mactan Id, Philippines (bar = 0.22 mm; USNM 845801).

TABLE 26.—Shell morphometrics of *Cerithium lissum*.

Character	$\bar{x}$ (n = 12)	sd	v	Range
Shell length	19.6	3.7	14.0	14.1-24.7
Shell width	7.2	1.1	1.2	5.3-8.7
Aperture length	5.2	0.9	0.8	3.8-6.6
Aperture width	3.6	0.5	0.3	2.7-4.5
Number whorls	12.2	0.7	0.5	11-13
Number spiral cords	3.9	0.3	0.1	3-4
Number axial ribs	12.0	0.9	0.7	11-13

broad main cusp, one inner flanking denticle and 2 or 3, small, pointed, outer flanking denticles. Marginal teeth (Figure 75A-C) with thin shafts, narrow bases and curved, hook-like, spatulate tips. Inner marginal tooth with finger-like main cusp, 2 or 3 pointed, inner flanking denticles and one, pointed, outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Unknown.

SYNONYMIC REMARKS.—*Cerithium lissum* was first described as a *Bittium* species by Watson (1880:107), who later (1886:535) placed it in *Cerithium*, mentioning that the attribution to *Bittium* was an error of the press. *Cerithium lissum* rarely has been cited or figured since its original description. Cernohorsky (1978:52) was the first modern writer to mention it. Recently, it has been collected by tangle nets in moderately deep waters around the Philippines, and was figured by Springsteen and Leobrera (1986:62, pl. 13: fig. 18), who with a query, cited it as *C. fusiforme* Sowerby, which is a synonym of *C. columna* Sowerby.

This species was recently described as a new taxon, *C. veillardi* Drivas and Jay, from Réunion, but the depicted type is merely a darkly pigmented, banded morph of *C. lissum*, identical to the specimen figured herein (FIGURE 74D,E).

ECOLOGY.—This species has been collected from depths of 15 to 146 m on rubble, sand, and calcareous substrates. Museum specimen records indicate that it is commonly found on coral boulders in Réunion. Nearly all specimens have been dredged and several individuals were observed to have drill

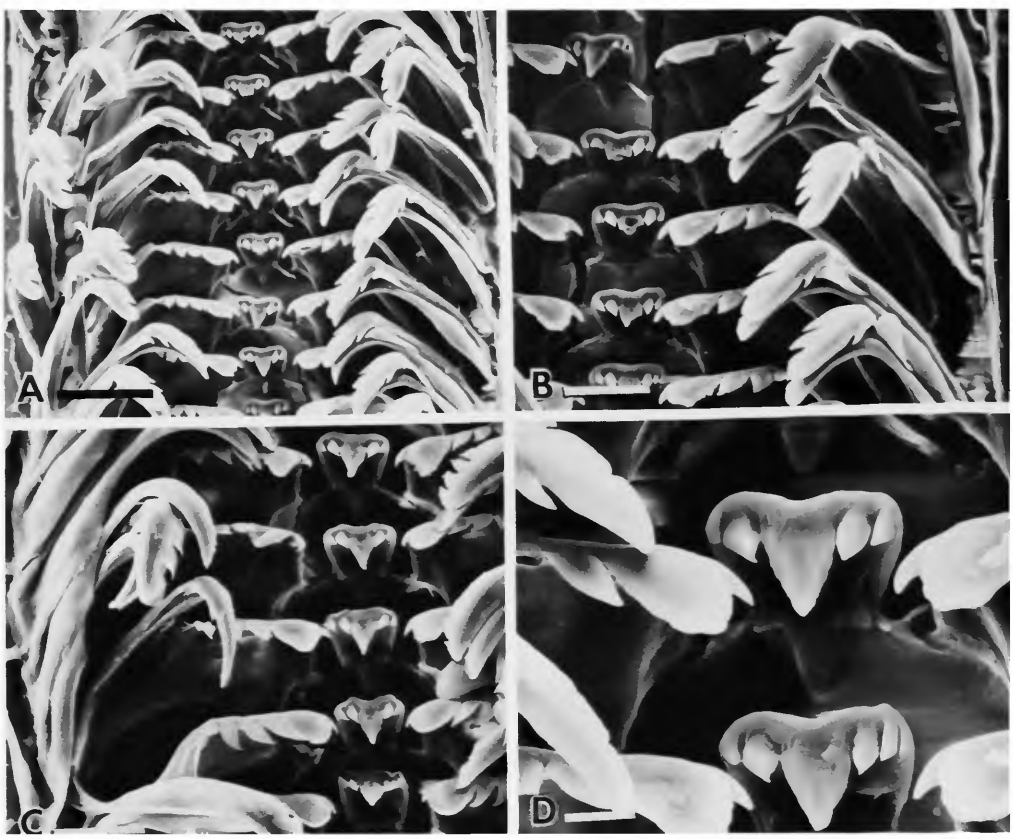

FIGURE 75.—Radula of *Cerithium lissum* Watson, Leven Bank, Îles Glorieuses (MNHNP): A, midsection of radula, (bar = 100 μm); B, half row (bar = 20 μm); C, half row (bar = 50 μm); D, rachidian tooth (bar = 20 μm).

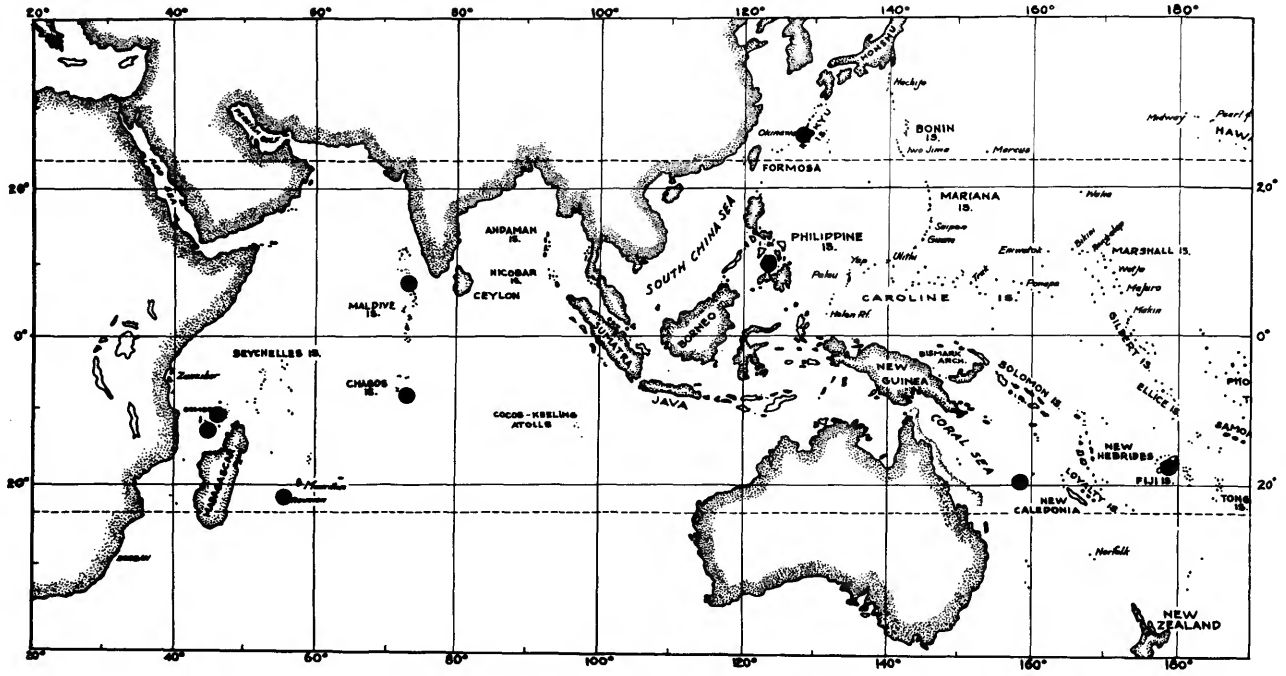

FIGURE 76.—Geographic distribution of *Cerithium lissum* Watson.

holes indicative of naticid predation. Nothing in the literature is recorded about its ecology or reproductive biology. Protoconch, eggs, and larvae remain undescribed.

DISCUSSION.—The distinguishing characters of this species are a fusiform shell with a long siphonal canal, and the sculpture of 4 or 5 wide spiral bands per whorl, each band delineated by a thin, brown, incised spiral line. The subsutural and peripheral bands are nodular.

Cerithium lissum shows wide intraspecific variation in shell form and sculpture. Some phenotypes are very slender, relatively smooth, and fusiform (Figure 74F) while others are more nodular (Figure 74B,C,G), or squatter, with broad, sloping, subsutural ramps, and more angulate outlines (Figure 74H). Some morphs are darkly pigmented with spiral bands (Figure 74D). The largest examined specimens are from Diego Garcia, in the western Indian Ocean (BMNH), and from Okinawa (USNM 841151). Specimens dredged in the Philippines (Figure 74H) tend to be small and have squat, angulate shells (USNM 845801).

Cerithium lissum is geographically sympatric with and most closely resembles *C. phoxum*. Both species have a fusiform, tan colored shell with white varices, and are dredged in moderate depths. *Cerithium phoxum* (Figure 105) is generally a larger, more slender species with narrow spiral cords, and lacks the incised brown spiral lines of *C. lissum*. Some phenotypes of *C. columna* Sowerby have a fusiform shape close to that of *C. lissum* and may be confused with it (Figure 31B,E,I,K,M). Indeed, Springsteen and Leobera (1986:62) figured *C. lissum* under the name *C. fusiforme* Sowerby.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 76).—This rare, relatively deep-water species, is little known in the literature, and has only recently appeared in private and museum collections. First dredged and described from off Fiji, *C. lissum* is now known to have a wide range throughout the Indo-West Pacific, where it appears to be found on deeper reefs around low lying coral islands. It occurs in the Indian Ocean from the Mozambique Channel eastward through the Indian Ocean island groups to the Maldives. In the western Pacific, it is found from the Ryukyu Islands south through the Philippines to the Coral Sea and eastward to Fiji. *Cerithium lissum* undoubtedly occurs in suitable subtidal habitats of moderate depths throughout Indonesia and around other western Pacific island groups.

SPECIMENS EXAMINED.—MOZAMBIQUE CHANNEL: 15 m, 12°45′1″S, 45°17′9″E, N Île Pamanzi, Mayotte (MNHNP); 42 m, 12°34′1″S, 47°40′2″E, Banc du Leven (MNHNP); 35–150 m, 12°32′S, 47°40′2″E, W Banc du Leven (MNHNP). INDIAN OCEAN ISLANDS: 50–80 m, Réunion (MNHNP); 58–70 m, 21°00′S, 55°15′E, Reunion (MNHNP); 42–45.7 m, 5°57′N, 73°24′E, S half of Kendikolu Id, Miladammadulu Atoll, Maldive Islands (ANSP 304460); Diego Garcia (BMNH). RYUKYU ISLANDS: 54.8 m, 26°30′N, 127°54′E, 1 km WNW of Onna Village, Horseshoe Cliffs (USNM 838639, 838846, 841085, 841151).

PHILIPPINES: 146.2 m, Punta Engano, Mactan Id, Cebu

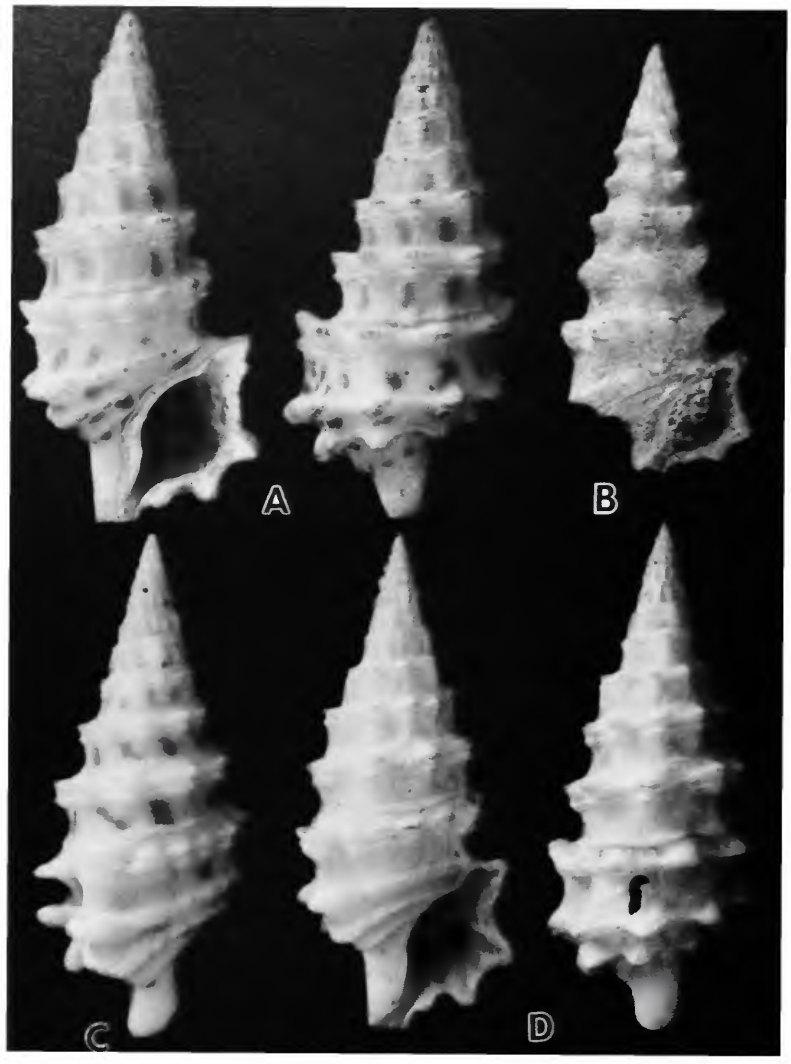

FIGURE 77.—*Cerithium madreporicolum* Jousseaume: A, W Labuan Olendir, Tanimbar, Moluccas, 20.7 mm (USNM 747622); B, paratype of *Cerithium madreporicolum* Jousseaume, Djibouti, French Somaliland, 20.2 mm (MNHNP); C,D, W Labuan Olendir, Tanimbar, Moluccas, 21.1 mm (USNM 747622).

(AMNH 203274, LACM 84-158, 84-159, USNM 845801); off Bohol (USNM 845477). CORAL SEA: 48 m, 19°10′72″S, 158°34′95″E, *Chalcal* 1984 sta D26, Chesterfield-Bellona Plateau (MNHNP). FIJI: 21.9 m, Levuka, Ovalau, Challenger Exp (BMNH 1887291665).

Cerithium madreporicolum Jousseaume, 1930

FIGURES 77, 78

Cerithium madreporicola Jousseaume, 1930:275-277, fig. 3 [holotype: MNHNP, no number, 22.6 mm × 9.8 mm; type locality: Obock, Djibouti].

Cerithium (Serraticerithium) [sic] madreporicola Jousseaume.—Abrard, 1942:59, pl. 6: fig. 22.

Cerithium erythraeonense Lamarck.—Sharabati, 1984, pl. 14: fig. 12a | *erythraeonense* Lamarck, 1822; is *Cerithium madreporicolum* Jousse 1930].

DESCRIPTION.—*Shell* (Figure 77): Shell elongate, tur angulate, comprising 12 or 13 whorls and reaching 22.(length. Protoconch unknown. Early teleoconch whorls (7 with broad, sloping, subsutural ramp, weakly inflated sculptured with two spiral, peripheral threads, many striae, axial ribs, and thick varices. Adult teleoconch w (last 6) strongly concave and having large, subsutural, keel with about 10 spiny nodes; keel sometimes divide

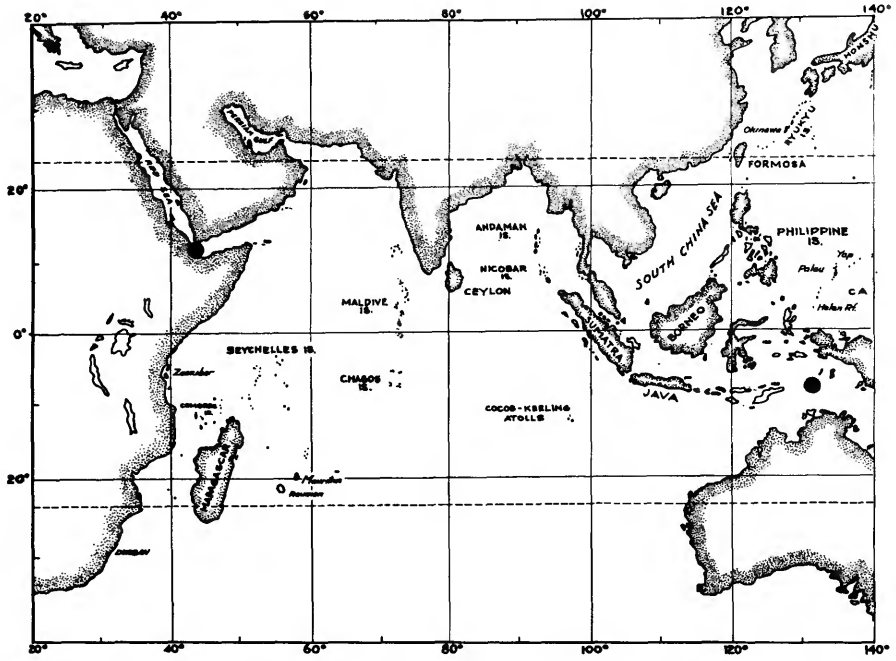

FIGURE 78.—Geographical distribution of *Cerithium madreporicolum* Jousseaume.

sculptured with fine spiral striae, becoming weaker abapically. Suture distinct, wavy. Body whorl elongate, wide, sculptured with fine spiral striae, subsutural keel, and three very spiny spiral cords at whorl periphery. Large varix opposite outer lip of aperture. Base of body whorl acutely excavated, with strong siphonal constriction. Aperture ovate, about three and a half times the shell length. Columella concave with thick callus and lip. Anterior siphonal canal moderately elongate, slightly reflected dorsally and to left of shell axis. Anal canal spout-like, bordered with very weak, parietal columellar tooth. Outer lip of aperture thickened, strongly concave, and with large crenulations forming squarish, angular outline. Shell color white with spiral row of large tan spots at center of each whorl. Operculum unknown.

Radula: Unknown.

Anatomy: Unknown.

SYNONYMIC REMARKS.—*Cerithium madreporicolum* was placed in the subgenus *Serratocerithium* Vignal, 1897, by Abrard (1942:59; misspelled as *Serraticerithium*), who gave no reason for this assignment. *Serratocerithium*, however, is not a cerithiid and although assigned by Wenz (1940:77) to the Campanilidae, is probably better referred to the Potamididae. Sharabati (1984, pl. 4: fig. 12a), in her book on Red Sea shells, figured this species under the name *C. erythraeonense*. This is the only known photograph of this species in recent publications.

ECOLOGY.—The one available record of *Cerithium madreporicolum* cites a subtidal habitat of moderate depth. The specimens were dredged with "mud and sponge."

DISCUSSION.—*Cerithium madreporicolum* was described from fossils or from empty shells of long dead-animals. There are only a few specimens available for examination, and many of these are obviously subfossils (Figure 77B). Although some specimens dredged in the Moluccas also have a chalky, subfossil look, two specimens are fresh with color, and their shiny apertures are indicative of Recent, living snails (Figure 77C,D). Unless these are remarkably preserved fossils, it seems likely that this is a living, albeit rare, species. *Cerithium madreporicolum* may be an extreme variant of *C. munitum* Sowerby, but more specimens need to be examined to resolve this possibility.

FOSSIL RECORDS.—This species was described from empty shells, possibly subfossils, and although Jousseaume (1930:276) mentioned finding one shell on the beach, he hesitated to affirm that it was a living species. Abrard (1942:59) recorded *C. madreporicolum* from the Pleistocene of Obock, near the type locality.

GEOGRAPHIC DISTRIBUTION (Figure 78).—The only putative live-collected specimens of this species are from Tanimbar, Moluccas, Indonesia, but it may have a wider range.

SPECIMENS EXAMINED.—GULF OF ADEN: Djibouti and Obock, French Somaliland (MNHNP, Type material). INDONESIA: 45.7–63.9 m, 8°7′S, 130°51′E, 9.6 km W of Labuan Olendir, Tanimbar, Moluccas (USNM 747622).

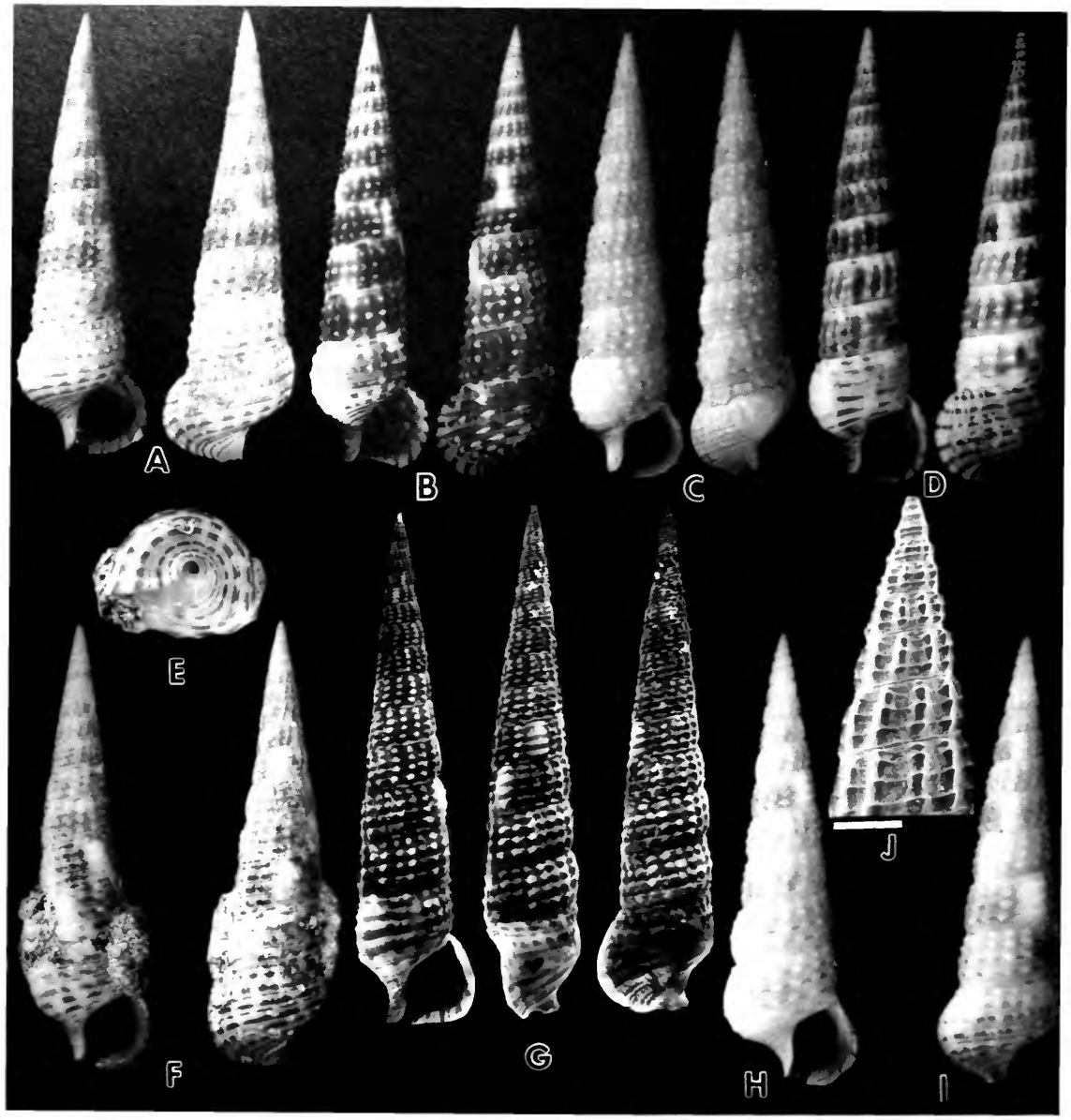

FIGURE 79.—Phenotypic variation in *Cerithium matukense* Watson: A, lectotype of *Cerithium matukense* Watson, Matuke, Fiji, 39.5 mm (BMNH 18872916602); B, 183 m, Bohol, Philippines, 40.1 mm (USNM 862340); C, 335 m, SE Îles Glorieuses, 27.7 mm (MNHNP); D, paratype of *Cerithium matukense* Watson, Matuke, Fiji (BMNH 18872916602); E,F, specimen as recovered from bottom showing apertural, adapaertural, and anterior views with encrusting worm tubes, 440 m, W Îles Glorieuses, 42.4 mm (MNHNP); G, large specimen from 183 m off Bohol, Philippines, 58.1 mm (USNM 862340); H,I, 335 m, SE Îles Glorieuses, 21.3 mm (MNHNP); J, SEM of early whorls, 250 m, Îles Glorieuses (bar = 75 μm; MNHNP).

Cerithium matukense Watson, 1880

FIGURES 79–81

Cerithium matukense Watson, 1880:105–106 [lectotype: BMNH 18872916602, 39.5 mm × 11.0 mm and one paratype; type locality: 310–315 fms off Matuke, Fiji; *Challenger* Expedition, sta 173]; 1886:533–534, pl. 15: fig. 2.—Kay, 1979:122, fig. 45r.

Cerithium (?) *turritellaeforme* [sic] Wissema, 1947:70–71, pl. 3: figs. 82, 83 [holotype: RMGM, no number, 32.9 mm × 8.8 mm, and one paratype; type locality: Onodohalawa Village, Nias, Indonesia; Pliocene-Pleistocene].

Cerithium (Proclava) matukense Watson.—Cernohorsky, 1978:52, pl. 13: fig. 8.—Springsteen and Leobrera, 1986:60, pl. 13: fig. 9.

TABLE 27.—Shell morphometrics of *Cerithium matukense*.

Character	$\bar{x}$ (n = 10)	sd	v	Range
Shell length	42.3	15.8	248.4	21.3-70.5
Shell width	10.5	4.1	16.8	5.9-18.2
Aperture length	8.3	3.1	9.7	4.1-13.9
Aperture width	6.4	2.5	6.0	29-10.6
Number whorls	18.3	2.5	6.2	15-23
Number spiral cords	4.0	-	-	4
Number beads	19.9	2.1	4.5	16-23

DESCRIPTION.—*Shell* (Figure 79): Shell elongate, slender, turreted, comprising 15-23 straight-sided, sometimes weakly inflated whorls with apical angle of 20 degrees, and reaching 70.5 mm length and 18.2 mm width. Protoconch 3.5 whorls with sinusigeral sinus; protoconch 1 smooth; protoconch 2 sculptured with postsutural row of tiny, weak plicae and with two peripheral, spiral threads. First 5 or 6 post-nuclear whorls (Figure 79J) inflated, sculptured with two spiral cords and weak axial ribs becoming stronger as shell becomes larger. Middle whorls each sculptured with 4 narrow, close set, spiral beaded cords. Beads pointing toward shell apex and aligned axially, forming about 16–23 slanting axial riblets per whorl, and presenting overall scaly, rasp-like appearance. Varices thick, randomly distributed. Thin spiral striae present between each spiral cord. Suture weakly compressed, wavy, and bordered with thin presutural cord. Body whorl large, inflated, tumid, with thick varix opposite outer lip of aperture. Body whorl subsuturally constricted, sculptured with six major unbeaded or weakly beaded spiral cords, with weakly plicated, subsutural spiral cord. Base of body whorl moderately excavated and with 4 or 5 thin, spiral cords on siphonal constriction. Aperture large, a little less than one-fifth the shell length and round-ovate with smooth flaring, thin outer lip slightly sinuous in outline. Columella concave with very thin callus and lip. Anterior siphonal canal moderately developed, slightly reflexed and turned to left of shell axis. Anal canal distinct, bordered with parietal columellar plait extending into shell aperture. Shell color white, with large tan or brown blotches and thin, spiral, tan-brown lines, especially at shell base. Beads and varices white; aperture white, with brown, spiral stripes. Measurements (Table 27). Periostracum thin. Operculum oval, corneous, thin, brown and paucispiral with subcentral nucleus.

Radula (Figure 80): Type-3 radular ribbon (Figure 3C) short, about one-thirteenth the shell length. Rachidian tooth (Figure 80B,C) square with tiny, pointed posterior projection at each side of basal plate, and with straight posterior margin, rounded, convex front, and cutting edge with small, blunt main cusp flanked on each side by two very small denticles. Lateral tooth (Figure 80B,C) with long lateral, posterior projection, longitudinal ridge terminating in median, central bulge, and wide central buttress on basal plate; cutting edge with pointed main cusp, one inner, flanking denticle and 3 pointed, outer, flanking denticles. Marginal teeth (Figure 80A,B) with wide, spatulate shafts, narrow bases, and narrow, constricted, hooked tips, terminating in sharp points. Inner marginal tooth with long, pointed, main cusp and 2, pointed, inner flanking denticles, and one very small, outer flanking denticle. Outer marginal tooth same, but without outer flanking denticle.

Animal: Head with short wide snout and long, bilobed tip, short, thick cephalic tentacles, and tiny black eyes. Mantle edge fringed with papillae of moderate length.

Buccal mass of moderate size with pair of jaws composed of microscopic chitinous scales. Stomach large, with style sac and complex sorting areas. Rectum wide.

SYNONYMIC REMARKS.—The only synonym of this species appears to be a Pliocene-Pleistocene fossil from Nias, Indonesia, given the name *C. turritellaeforme* by Wissema (1947:70). His figure of the fossil is clearly conspecific with *C. matukense*.

ECOLOGY.—*Cerithium matukense* has a bathymetric distribution ranging from 18 to 1480 m, but usually occurs at depths of about 500 m. It appears to be a common species on sandy bottoms. Although its long, slender shape and ratchet sculpture (Figure 79J) indicate a burrowing capability, live-collected specimens have sandy worm tubes on their sides and dorsal surfaces (Figure 79E,F), indicating that they live on the sediment surface. This species eats algae and detritus, judging from its stomach contents. The rectum of a live-collected specimen was filled with rod-like fecal pellets of coarse calcareous sand, algal particles, and foraminifera. Empty shells are used by pagurid crabs and sipunculid worms, and frequently bear naticid bore holes.

The eggs and spawn of this species are unknown, but the protoconch (Figure 79J) is typical of species having a planktotrophic larval stage.

DISCUSSION.—This large, distinctive, and poorly known species has only recently been figured in popular shell books (Cernohorsky, 1978, pl. 13: fig. 2; Kay, 1979:122, fig. 45r; Springsteen and Leobrera, 1986:60, pl. 13: fig. 9). An elongate, slender shell colored with brown blotches and thin, brown, spiral threads, straight-sided whorls, and fine, file-like, cancellate sculpture readily characterize it.

Cerithium matukense does not show a great deal of intraspecific variation in shell morphology; specimens from the Philippines (Figure 79B,G) are nearly identical with those from the western Indian Ocean (Figure 79C). Some shells from the Îles Glorieuses have more inflated whorls and differ from typical phenotypes in having a thin spiral thread between each beaded cord (Figure 79H,I). These may comprise another species, but they are best regarded as variants of typical *C. matukense* until more comparative material is available to resolve this problem.

Cerithium matukense should be carefully compared with *Cerithium ophioderma* (Habe) (Figure 100), from which it differs in having four beaded spiral cords per whorl and in lacking the large, lateral, swollen varix on the body whorl (see

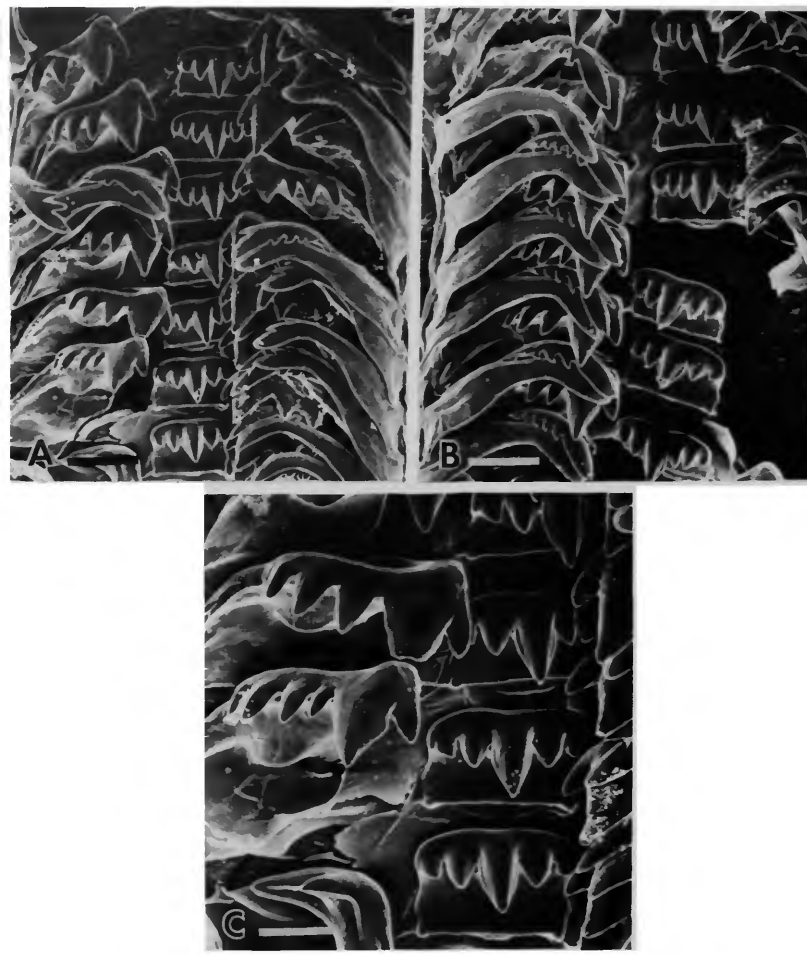

FIGURE 80.—Radula of *Cerithium matukense* Watson, 335–390 m, Îles Glorieuses (MNHNP): A, radula with left marginals folded back (bar = 60 μm); B, marginal teeth folded over lateral and rachidian teeth (bar = 50 μm); C, dentition of rachidian and lateral teeth (bar = 250 μm).

"Remarks" under *Cerithium ophioderma*, p. 141). It also superficially resembles *Cerithium flemischi* Martin (Figure 58), but that species has only two, sometimes three, spiral cords with fewer beads per whorl, and has a deeper, more distinct suture.

Little is known of the anatomy of this species; all live-collected specimens examined were so badly preserved, that the alimentary tract and pallial gonoducts were destroyed.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 81).—Originally described from Fiji, this deep-water species has been found in the western Pacific around the Philippines, Borneo, Guam, Fiji, New Caledonia, and south to the Kermadecs. In the western Indian Ocean, it is common near the Îles Glorieuses and Mayotte. It has also been dredged off Hawaii. Although records are spotty, a generalized Indo-Pacific distribution is indicated.

SPECIMENS EXAMINED.—INDIAN OCEAN ISLANDS: 1300–1480 m, 12°56′S, 45°18′2″E, Benthedi sta 40, E Récif Bandele, Mayotte, Comoro Ids (MNHNP); 275–400 m, 12°53′5″S, 45°16′3″E, Benthedi sta 33, E Passe Longogori, Mayotte, Comoro Ids (MNHNP); 630 m, 12°26′5″S, 46°16′E, Benthedi sta 112, Zelleé Banks (MNHNP); 18–24 m, 12°25′5″S, 46°16′3″E, Benthedi sta 106, Zelleé Banks (MNHNP); 11°32′2″S, 47°16′4″E, Benthedi sta 94, SW Grande Glorieuse (MNHNP); 615–625 m, 11°32′S, 47°23′2″E, Benthedi sta 122, Îles Glorieuses (MNHNP); 700 m, 11°31′8″S, 47°23′5″E, Benthedi sta 123 Îles Glorieuses (MNHNP); 335–390 m, 11°30′S, 47°24′7″E, Benthedi sta 120, Îles Glorieuses (MNHNP); 335-390 m, 1°30′S, 47°24′7″E, Benthedi sta 120DS, Îles Glorieuses (MNHNP); 250 m, 11°29′2″S,

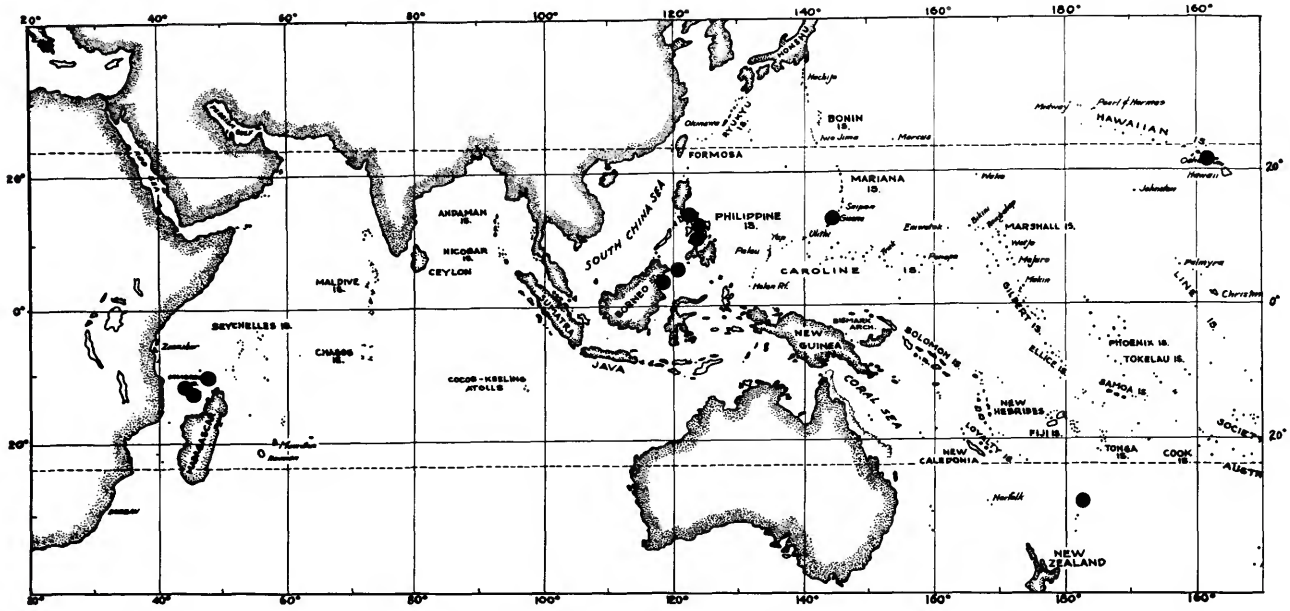

FIGURE 81.—Geographic distribution of *Cerithium matukense* Watson.

47°18′2″E, Benthedi sta 8, Îles Glorieuses (MNHNP); 460-500 m, 11°28′5″S, 47°12′2″E, Benthedi sta 6, Îles Glorieuses (MNHNP); 450 m, 11°28′5″S, 47°17′7″E, Benthedi sta 10, Îles Glorieuses (MNHNP); 440 m, 11°28′5″S, 47°17′7″E, Benthedi sta DS10, Îles Glorieuses (MNHNP); 150–670 m, 11°25′S, 47°22′6″E, Benthedi sta 103, N Île du Lys (MNHNP).

PHILIPPINES: 161 m, USBF sta 5381, Ragay Group, off Arena Pt, Luzon (USNM 284115); 486–551 m, 11°58′N, 122°02′E, "Coriolis," MUSORSTOM, off Panay (MNHNP); Balicsag Ids, Bohol (USNM 862340); 208 m, USBF sta 5398, off Gigantangan Id, NW Leyte (USNM 788812); 603 m, USBF sta 5569, 5570, off Simaluc Id, Tawitawi Ids (USNM 287213 ex 787135); 603 m, USBF 5570, off Simaluc Id, Tawitawi Ids (USNM 287126). INDONESIA: USBF sta 5592, off Silungan Id, Borneo (USNM 774762). NEW CALEDONIA: 460–500 m, 22°40′S, 167°41′E, N.O. *Vauban*, sta DW21 (MNHNP). KERMADEC ISLANDS: 512–549 m, 29°16.5′S, 177°49.5′W, RV *Archeron* sta BS442, SE of Charter Islets, Raoul Id (NMNZ). MARIANA ISLANDS: 219 m, Agana Bay, Guam (UGI 5206); 304.5 m, Agana Bay, Guam (UGI 5342). HAWAIIAN ISLANDS: Off Pearl Harbor, Oahu (BPBM 217694); 366–1280 m, off Waikiki, Oahu (BPBM 222139); 366 m, 0.8 km seaward of explosive area between G and B bouys, Oahu (BPBM 220911).

Cerithium munitum Sowerby, 1855

FIGURES 82–85

Cerithium pyramidatum Hombron and Jacquinot, 1852, pl. 23: figs. 20, 21 [holotype MNHNP, no number, 32.5 mm × 12.8 mm; type locality: Hogoleu; not *Cerithium pyramidatum* Deshayes, 1834]; 1854:100–101.—Tryon, 1887:129.

Cerithium munitum Sowerby, 1855:858–859, pl. 180: fig. 93 [type not found, type locality: Masbate, Philippines; neotype herein designated: AMS C117184, Broadhurst Reef, E of Townsville, Queensland, Australia, 40.3 mm × 16.3 mm]; 1865, pl. 10: fig. 69 [reference to Philippi and citation of Mediterranean in error].—Tryon, 1887:129, pl. 23: figs. 82–84.—Kobelt, 1898:211–212, pl. 37: figs. 10, 11.—Abbott and Dance, 1982:64.

Cerithium proditum Bayle, 1880:249 [new name for *Cerithium pyramidatum* Hombron and Jacquinot, 1852; not *Cerithium proditum* Bayle, 1880, pl. 246, new name for *Cerithium fusiforme* Sowerby, 1855].

Cerithium audouini [sic] Bayle, 1880:354 [new name for *Cerithium pyramidatum* Hombron and Jacquinot, 1852].

Cerithium sucaradjanum Martin, 1899:197–198, pl. 31: fig. 455 [holotype: RMGM St-10256, 33.2 mm × 11.8 mm; type locality: Selatjau, Tji Longan, Sukaradja District, Java; Pliocene].

Cerithium talahabense Martin, 1899:201–202, pl. 31: fig. 462 [holotype: RMGM, no number, 20 mm × 9 mm; type locality: St-10374, Tji Talahab, Djampangtengah, Java; Pliocene].

Cerithium dautzenbergi Vignal, 1902:303–304, pl. 8: figs. 11, 12 [holotype MNHNP, no number, 35.9 mm; type locality: Île des Pins, New Caledonia].

Cerithium Boettgeri [sic] Icke and Martin, 1907:241–242, pl. 16: fig. 26a,b [holotype: RMGM, no number; type locality: Dahana, Nias, Indonesia; Upper Miocene; not *Cerithium boettgeri* Von Koenen, 1882].

Cerithium ickei Vignal, 1908:136 [new name for *Cerithium boettgeri* Icke and Martin, 1907; not *Cerithium ickei* Martin, 1914].—Altena, 1938:208.

Cerithium vandervlerki van der Vlerk, 1931:288 [new name for *Cerithium boettgeri*, Icke and Martin, 1907].

Cerithium (*Thericium*) *ickei* Vignal.—Wissema, 1947:64–65, pl. 3: figs. 70–72.

Cerithium (*Cerithium*) aff. *C. columna* Sowerby.—Ladd, 1979:39, pl. 10: fig. 2.

DESCRIPTION.—*Shell* (Figures 82, 83): Shell elongate, turreted, with wide body whorl, comprising 14 or 15 inflated, angulate whorls, and reaching 39.8 mm length and 16.1 mm

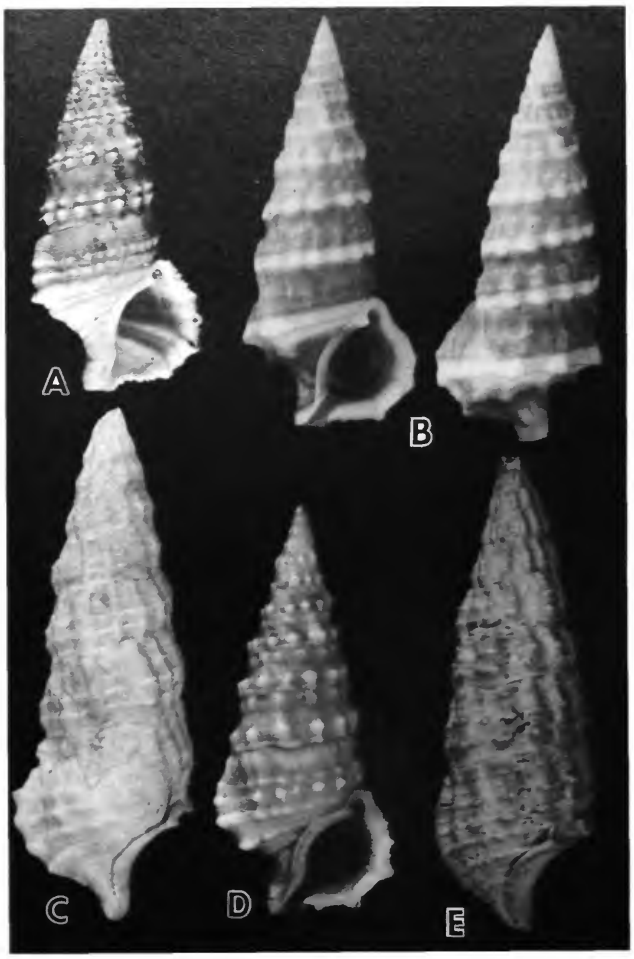

FIGURE 82.—Types of nominal species synonymous with *Cerithium munitum* Sowerby: A, holotype of *Cerithium dautzenbergi* Vignal, Île des Pins, New Caledonia, 35.9 mm (MNHNP); B, neotype of *Cerithium munitum* Sowerby, Broadhurst Reef, E of Townsville, Queensland, Australia, 40.3 mm (AMS C117184); C, holotype of *Cerithium sucaradjanum* Martin, Pliocene of Selatjan, Tji Longan, Sukaradja District, Java, 33.2 mm (RMGM 10356); D, holotype of *Cerithium pyramidatum* Hombron and Jacquinot, Hogoleu, 32.5 mm (MNHNP); E, holotype of *Cerithium talahabense* Martin, Pliocene of Tji Talahab, Djampangtengah, Java, 20 mm (RMGM 10374).

TABLE 28.—Shell morphometrics of *Cerithium munitum*.

Character	$\bar{x}$ (n = 13)	sd	v	Range
Shell length	32.7	4.4	19.4	25.7-39.8
Shell width	13.1	2.1	4.2	10.3-16.1
Aperture length	9.8	1.4	2.1	7.8-11.7
Aperture width	7.7	1.4	2.0	5.6-10.4
Number whorls	14.5	0.5	0.3	14-15
Number spiral cords	2.8	0.6	0.3	2-4
Number nodes	15.0	2.0	3.9	11-19

width. Protoconch unknown. Early teleoconch whorls with broad, sloping, subsutural ramp and sculptured with axial ribs and three spiral cords; first spiral cord on subsutural ramp, and remaining two on whorl periphery. Adult teleoconch whorls with broad, sloping, subsutural ramp, and sculptured with numerous fine spiral striae, spiral row of subsutural plicae, axial ribs, and with one keel-like, nodular spiral cords at whorl periphery. Anti- and penultimate whorls with 11-19 weak to strong, sinuous axial ribs joining nodes to subsutural plicae. Suture wavy, distinct. Body whorl large, very wide, with strongly excavated base, tightly constricted siphonal canal, and sculptured with 2 or 3 spiral, weakly beaded threads and two, keel-like, spiny peripheral cords. Beads and spines usually joined by weak axial ribs. Aperture ovate, about 3.5 times the shell length. Columella moderately concave with strong callus and lip. Anterior siphonal canal well developed, of moderate length, and reflected dorsally to left of shell axis. Anal canal well developed, bordered by parietal columellar tooth extending into aperture. Outer lip convexly flared and crenulated with interior, spiral incised lines. Shell color white to light tan, occasionally brown, sometimes with thick spiral bands of white and tan or with very thin tan spiral threads; nodes and aperture white. Measurements (Table 28). Periostracum thin, tan. Operculum (Fig. 83J) corneous, oval, thin, tan, paucispiral with nucleus close to edge, and covered with fine, microscopic pustules (Figure 84A).

Radula (Figure 84B-D): Type-1 radular ribbon (Figure 3A) short, about one-eleventh the shell length. Rachidian tooth (Figure 84C,D) triangular with rounded edges and concave front, with pair of posterior ridges and short, median triangular extension on cutting edge with large, spade-shaped main cusp flanked by 2 or 3 very small, blunt denticles. Lateral tooth (Figure 84C-I) with long posterior, lateral extension and narrow central buttress bearing small median bump; cutting edge with broad, spade-shaped main cusp, one inner flanking pointed denticle, and 2 or 3 outer flanking, pointed denticles. Marginal teeth (Figure 84B,D) with long narrow shafts, curved, elongate tips and long finger-like apices. Inner marginal tooth with 2 or 3 inner flanking denticles, and 1 or 2 outer flanking denticles. Outer marginal teeth same, but lacking outer flanking denticles.

Anatomy: Animal tan with white blotches and small black dots. Snout with thin dark stripes. Cephalic tentacles thin, elongate, with large peduncles, each with small black eye bordered with yellow. Mantle edge with long, equally spaced papillae, each with transparent edges and opaque, white centers. Underside of mantle at inhalant siphon with short, muscular ridge.

Osphradium black. Ctenidium long, whitish, turning brown anteriorly, comprised of narrow, triangular filaments. Large hypobranchial gland with darkly pigmented, glandular anterior extending from exhalant siphonal edge to ctenidial tip. Wide rectum containing rod-shaped fecal pellets comprised of fine

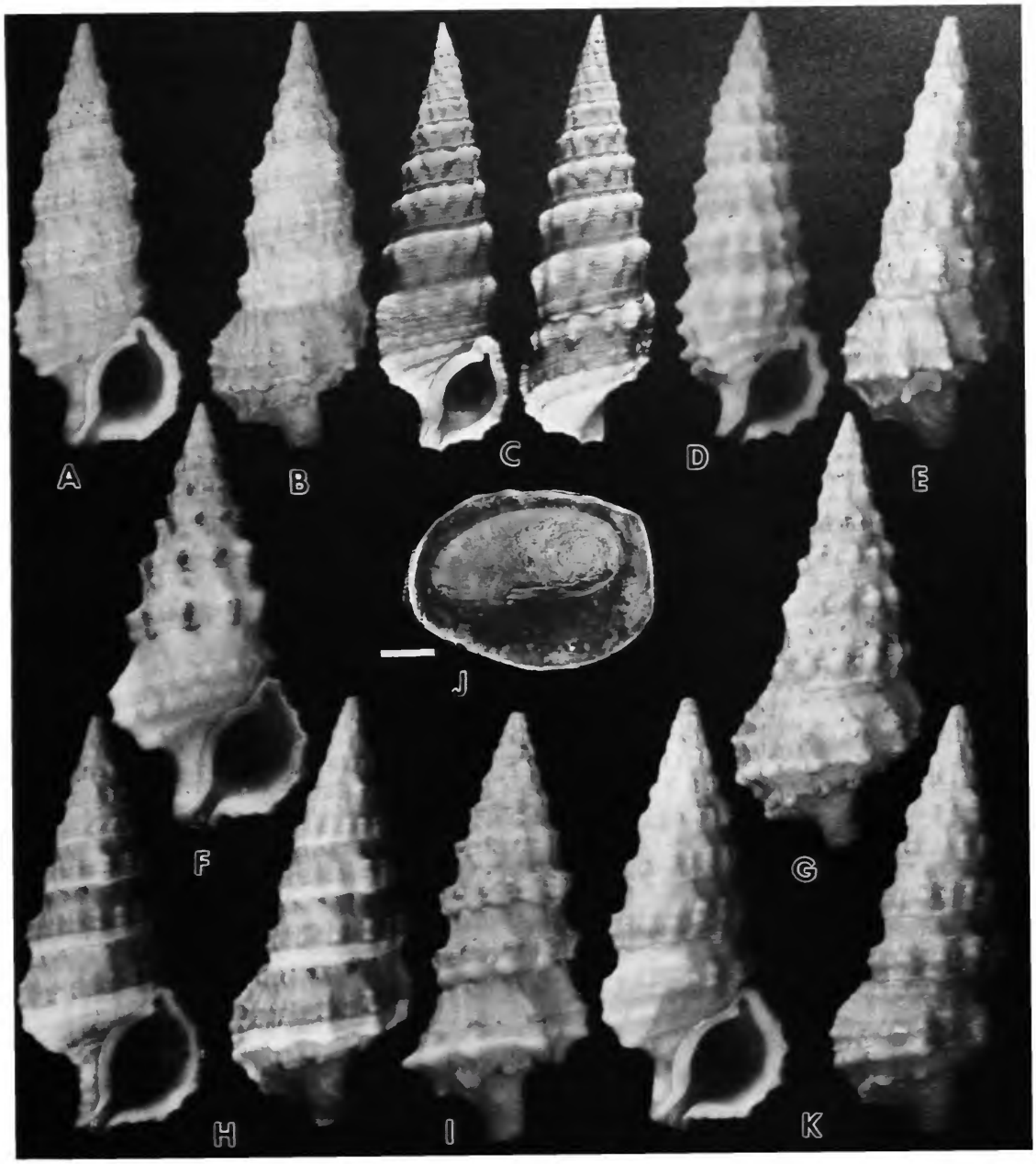

FIGURE 83.—Phenotypic variation of shell shape and sculpture in *Cerithium munitum* Sowerby: A,B, Bikini Atoll, Marshall Islands, 31.7 mm (USNM 584661); C, Broadhurst Reef, off Townsville, Queensland, Australia (AMS); D, Tataan Simalua Island, Tawitawi, Philippines, 29.2 mm (USNM 243704); E, Bikini Atoll, Marshall Islands, 32.8 mm (USNM 585251); F, Bikini Atoll, Marshall Islands, (USNM 585251); G, Ifaluk Atoll, Caroline Islands, 24.1 mm (USNM 616736); H, Enewetak Atoll, Marshall Islands, 28.5 mm (USNM 770576); I, Bikini Atoll, Marshall Islands, 29 mm (USNM 585251); J, obverse of operculum showing attachment scar (bar = 1 mm); K, Kapinga-marangi Atoll, Caroline Islands, 33.8 mm (USNM 611056).

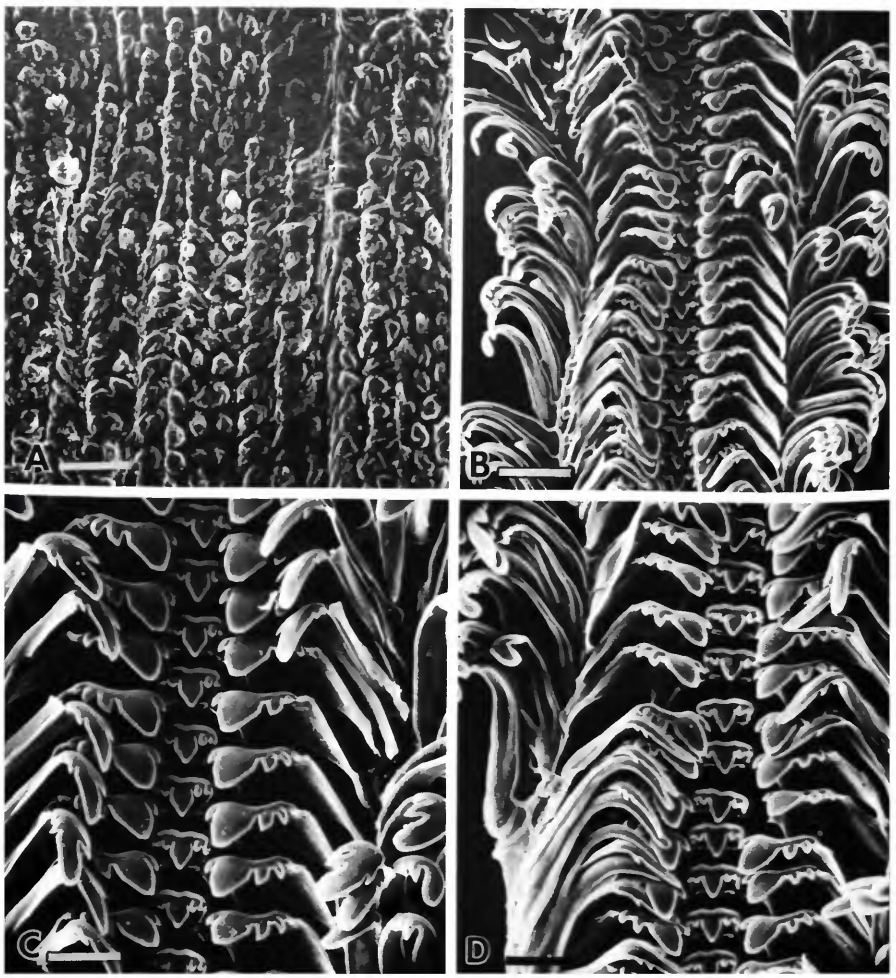

FIGURE 84.—SEM of operculum and radula of *Cerithium munitum* Sowerby: A, opercular surface, Enewetak Atoll, Marshall Islands (bar = 25 μm; USNM 770576); B, radula with marginal teeth spread back, Enewetak Atoll, Marshall Ids (bar = 75 μm; USNM 770576); C, half row, Lizard Id, Queensland, Australia (bar = 75 μm; USNM 795124); D, Enewetak Atoll, Marshall Ids (bar = 60 μm; USNM 770576).

sand grains and detrital particles.

Female pallial oviduct with very short sperm gutter in anterior edge of medial lamina. Male pallial gonoduct with prostate at posterior end.

Buccal mass with pair of jaws comprising many, very small, rectangular, scale-like plates. Pair of tiny salivary glands passing through nerve ring as thin tubes. Esophageal gland present. Stomach large, with style-sac, crystalline style, and gastric shield.

SYNONYMIC REMARKS.—*Cerithium munitum* has been the recipient of ten names, the earliest of which, *C. pyramidatum* Hombron and Jacquinot (Figure 82D), is preoccupied. The earliest available name is *C. munitum* Sowerby. Although Sowerby's type material of *C. munitum* from the Philippines has not been found, his fine illustration of this species serves to unequivocally identify it. As the name *C. munitum* is the one most often used in the past, I regard it as the valid name and herein select a neotype, AMS C117184, Broadhurst Reef, E of Townsville, Queensland, Australia (Figure 82B).

The replacement name proposed by Bayle (1880) for *C. pyramidatum*, *C. proditum*, has an unusual history in that Bayle (1880:249) had previously used it in the same publication as a new name for *Cerithium fusiforme* Sowerby, 1855, thus creating a homonym of one of his own names.

The holotype of *C. dautzenbergi* Vignal, 1902 (Figure 82A) is also here considered conspecific with *C. munitum*.

Examination of the holotypes of the two Pliocene species described by Martin (1899), *C. sucaradjanum* (Figure 82C) and *C. talahabense* (Figure 82E), shows that both fall well within the range of variation observed in Recent *C. munitum* and are morphologically indistinguishable from it. I thus see no reason to accord them specific recognition. It is not uncommon for living *Cerithium* species to occur unchanged in the fossil record as far back as the Miocene (Houbrick, 1974b, 1978b).

Another fossil species described by Icke and Martin (1907), *C. boettgeri*, although dated from the Miocene, seems to be conspecific with *C. munitum*. As the former is a preoccupied name, the two replacement names proposed for *C. boettgeri* also fall into the synonymy of *C. munitum*.

ECOLOGY.—*Cerithium munitum* is not an abundant species, and prefers coral reef lagoons where it lives in sand and dead coral rubble. It is found at moderate, subtidal depths, frequently on "bommies." At Enewetak Atoll, Marshall Islands, it is most commonly seen at night (Scott Johnson, pers. comm.). A population in the lagoon of Lizard Island, Queensland, Australia, lived at 10 m depth on coral rubble (pers. obs.).

Eggs, spawn, larvae, and protoconch are not known, but the wide distribution suggests a planktotrophic larval stage.

DISCUSSION.—This species is easily recognized by a white to light tan shell, distinctively sculptured with tiny spiral incised lines and with two prominent, nodulose, peripheral spiral cords that become more spinose on the body whorl to form a distinctive keel behind the excavated base and siphonal constriction. Nodes are frequently joined to form sinuous axial ribs; the postsutural part of each whorl has a row of spiral plicae and is slightly constricted. The suture is distinctively wavy. The body whorl is wide and the outer lip of the aperture somewhat flaring and crenulated.

Within a population, sculpture varies considerably, particularly in the strength of the axial ribs and presutural spiral cords. Smaller shells tend to have fewer axial ribs. Some specimens are less nodulose (Figure 83A,B) than others, which may have well-developed nodes on virtually all spiral elements (Figures 82D; 83D,E), but these extremes in sculpture are uncommon. Some shells have extreme spiny development of the presutural cords (Figure 83D-I). Although color is normally whitish, shells may be entirely tan (Figure 83C) or brightly banded with white and dark brown (Figures 82B; 83H). The latter color form is sometimes seen in populations from Queensland, Australia, and the Marshall Islands, but is not common.

A phenotype of *C. ruppellii* Philippi, 1849 (Figure 119E,G,H), a species from the Red Sea and East Africa, that has been given the name *C. spathuliferum* Sowerby, 1855, is similar to *C. munitum*, but is geographically allopatric with it. Sowerby (1855:859) figured the "spathuliferum" form of *C. ruppellii* (pl. 180: fig. 94) next to his figure of *C. munitum* (pl. 83: fig. 93), probably indicating he thought there was a close relationship between the two. This similarity, however, is undoubtedly due to convergence, because the two species differ considerably in radular morphology and habitat. Another species with which *C. munitum* may be superficially confused is *C. columna* Sowerby, 1834 (Figure 31), which is sympatric with it. The latter species is easily separated from *C. munitum* by the presence of a central, spinose, spiral cord on each whorl and the absence of a keel on the body whorl. A rare Indian Ocean species, *C. madreporicolum* Jousseaume, 1930 (Figure 77), resembles *C. munitum*, but differs from it in having strongly convex whorls, a large, subsutural, spiny, keel-like cord, and an extremely angulate outer, apertural lip.

FOSSIL RECORDS.—*Cerithium munitum* has been found in Pleistocene-Holocene deposits at Lake Macleod, ENE of Pt Quobba, Western Australia (WAM). I have examined late Tertiary specimens from Kajoe Ragi, Celebes (ZMA). This species has been described under various names (see synonymy above) from Indonesian fossils of Pliocene age. The Holocene fossil from Enewetak Atoll, cited by Ladd (1972:39, pl. 10: fig. 2) as "aff." *C. columna*, is *C. munitum*.

GEOGRAPHIC DISTRIBUTION (Figure 85).—This species has a predominant western Pacific distribution and is common in Melanesia, Micronesia, and parts of western Polynesia. The single record from the Amirantes, in the western Indian Ocean, is questionable, and needs reconfirmation.

SPECIMENS EXAMINED.—INDIAN OCEAN ISLANDS: Alphonse Id, Amirante Islands (BMNH). RYUKYU ISLANDS: Osima, Osumi (AMS, USNM 343861). PHILIPPINES: Subic Bay, Luzon (DMNH); Punta Engano, Mactan Id, Cebu (USNM 845803); off Bohol (USNM 845478); 104.4 m, USBF sta 5478, off Tacbuc Pt, E Leyte (USNM 283106); 180 m, USBF sta 5255, off Dumalag Id, Davao Gp (USNM 237391); Culion, Calamian Gp, Palawan (ANSP 76840); 18 m, USBF sta 5159, off Tinakta Id, Tawitawi, Sulu Archipelago (USNM 274225); 18 m, USBF sta 5159, off Bakun River, Tawitawi, Sulu Archipelago (USNM 236248). INDONESIA: 5°49′S, 132°34′E, N shore of Warbal Id, W of Nuhu Rowa, Kai Ids, Moluccas (WAM).

QUEENSLAND, AUSTRALIA: SE over drop-off to 24 m, Bird Id, Lizard Id (AMS); 7.5 m, Rocky Pt, Lizard Id (AMS, USNM 766737); 9–12 m, SW end of S Id, Lizard Id (AMS); lagoon, Lizard Id (USNM 795124); Bommie No 1, 15 m, Lizard Id (AMS); 4–8 m, 12°24′S, 143°22′E, N end of Eel Reef (AMS); 4–14 m, 13°28′S, 144°02.5′E, NW end of reef S of First Three Id Opening (AMS); 3–6 m, 13°40′S, 144°09′E, NW tip of reef N of No 5 Bank Reef (AMS); 9–15 m, 13°45′S, 144°16′E, S end No 5 Sandbank Reef (AMS); 9–15 m, 14°39′S, 145°58′E, Macgillivray Cay (AMS); 34.5 m, 0.4 km N of North Direction Id (AMS); 36.5 m, 0.8 km W of North Direction Id (AMS); Thetford Reef, E of Cairns (AMS); 9 m, Carter Reef (DMNH); Little Kelso Reef, NE of Townsville (AMS); Wheeler Reef, NE of Townsville (AMS); Centipede Reef, NE of Townsville (AMS); Broadhurst Reef, E of Townsville (AMS); Bowden Reef, E of Ayr (AMS); 48 m, 19°10′72″S, 158°34′95″E, "Charcal," Chesterfield-Bellona Plateau, Coral Sea (MNHNP).

NEW GUINEA: 0.9–9 m, 1.6 km E of Mios Woendi Id,

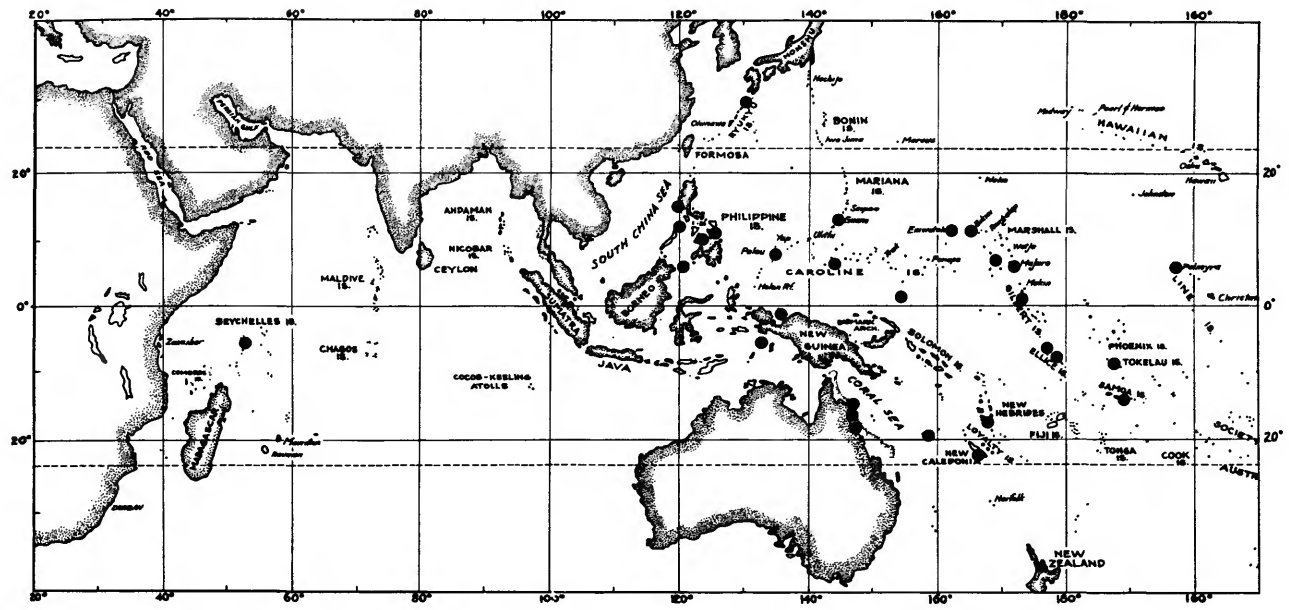

FIGURE 85.—Geographic distribution of *Cerithium munitum* Sowerby.

Padaido Gp, West Irian (ANSP); 36–45 m, 1.6 km NE of Roemwakon Id, Aoeri Id, Geelvink Bay, West Irian (ANSP). NEW HEBRIDES: 7.8 m, 17°32′56.5″S, 16°20′43.5″E, Efate (USNM 788023, 788038). NEW CALEDONIA: 41 m, 18°18′S, 163°02′E, Atoll de Surprise (MNHNP); 70 m, 22°32′S, 166°54′E, Grand Récif Sud (MNHNP); 17 m, 22°38′S, 166°36′E, Île Ouen, Baie du Prony (MNHNP).

MARIANA ISLANDS: 52 m, Tweed's Cave, 0.5 km N Haputo Pt, Guam (USNM 851211, 852113); Apra Harbor, Guam (USNM 852091); E Orote Pt, Gab-Gab Beach, Apra Harbor, Guam (USNM 851034, 851105, 852040, 852169, 852170); Western Shoals, Apra Harbor, Guam (USNM 862338); 1.5 m, Western Shoals, Apra Harbor, Guam (DMNH); Jaeo Shoals, Apra Harbor, Guam (USNM 842625). PALAU: Small id S of Koror (USNM 862337); 3.2 km NE of Gamadaguru on N tip of Gamudoko Id (ANSP); 30.6 m, 3.2 km NE of Gamudoko Id, off Urukthapel Id (ANSP 202899). CAROLINE ISLANDS: Lagoon, Ifaluk Atoll (USNM 616342, 616628, 616733, 616736); Tokoelwwa-ilala, Kapingamarangi Atoll (USNM 622365); lagoon, Werua, Kapingamarangi Atoll (USNM 611056).

MARSHALL ISLANDS: Jieroru Id, Enewetak Atoll (USNM 582302); pinnacle, Sand Id No 2, Enewetak lagoon, Enewetak Id, Enewetak Atoll (USNM 821843); 10–20 m, power plant pinnacle, lagoon, Enewetak Id, Enewetak Atoll (USNM 770576); Bikini Id, Bikini Atoll (USNM 586807, 862339); 54–59.9 m, Bikini lagoon, Bikini Atoll (USNM 584661); 45–54 m, Bikini lagoon, Bikini Atoll (USNM 585251); 45 m, 4.8 km SW of Bikini Id, Bikini Atoll (USNM 586606); Pokak Atoll (USNM 615896); Kwajalein Atoll (CAS); Majuro Atoll (USNM 486659, 862336); 36 m, SE Arno lagoon, Arno Atoll (USNM 604047); lagoon off Imrodi Village, Jaluit Atoll (USNM 659844). GILBERT ISLANDS: Tarawa, Tarawa Atoll (CAS). LINE ISLANDS: Palmyra Id (ANSP, USNM 487406); Fanning Id (ANSP). ELLICE ISLANDS: Windward side of Nanumea Id (USNM 433801); Funafuti Atoll (AMS). TOKELAU: Lagoon, Manihiki Atoll (ANSP). SAMOA: Pagopago Bay, Tutuila (USNM 698991).

Cerithium nesioticum Pilsbry and Vanatta, 1906

FIGURES 86–88

Cerithium lacteum Kiener, 1842:58–59, pl.7: fig. 3, 3a, [holotype: not located; pl. 7: fig. 3 herein selected to represent lectotype; type locality: not cited; not *Cerithium lacteum* Philippi, 1836].—Sowerby, 1855:876, pl. 134: figs. 213, 214; 1865, pl. 13: fig. 85.—Tryon, 1887:143, pl. 27: figs. 29, 30, 33.—Jousseaume, 1930:284.

Cerithium pusillum Nuttal in Jay, 1839:75 [nomen nudum]; 1852:316 [not *Cerithium pusillum* Pfeffer, 1840, nor *Cerithium pusillum* Gould, 1849].

Cerithium papillosum Sowerby, 1855:876, pl. 184: fig. 215 [holotype: BMNH 19071028222, no locality cited, 15 mm × 5.3 mm; not *Cerithium papillosum* Eudes-Deslongchamps, 1842].—Jousseaume, 1930:285.

Lampania lactea (Kiener).—Paetel, 1887:351.

Cerithium spiculum Hedley, 1899:433, fig. 21 [lectotype, herein selected: AMS C5941, smallest of 2 syntypes, 11 mm × 4 mm; type locality: Nuklailai, Funafuti, Ellice Islands; not *Cerithium spiculum* Eudes-Deslongchamps, 1842].

Cerithium (Liocerithium) lacteum Kiener.—Sturany, 1903:53.—Schepman, 1909:163.

Cerithium voyi Pilsbry and Vanatta, 1905:787 fig. 3 [holotype: ANSP 58192; type locality: Flint Island, Line Islands; 17 mm × 6 mm].—Clench and Turner, 1962:159.

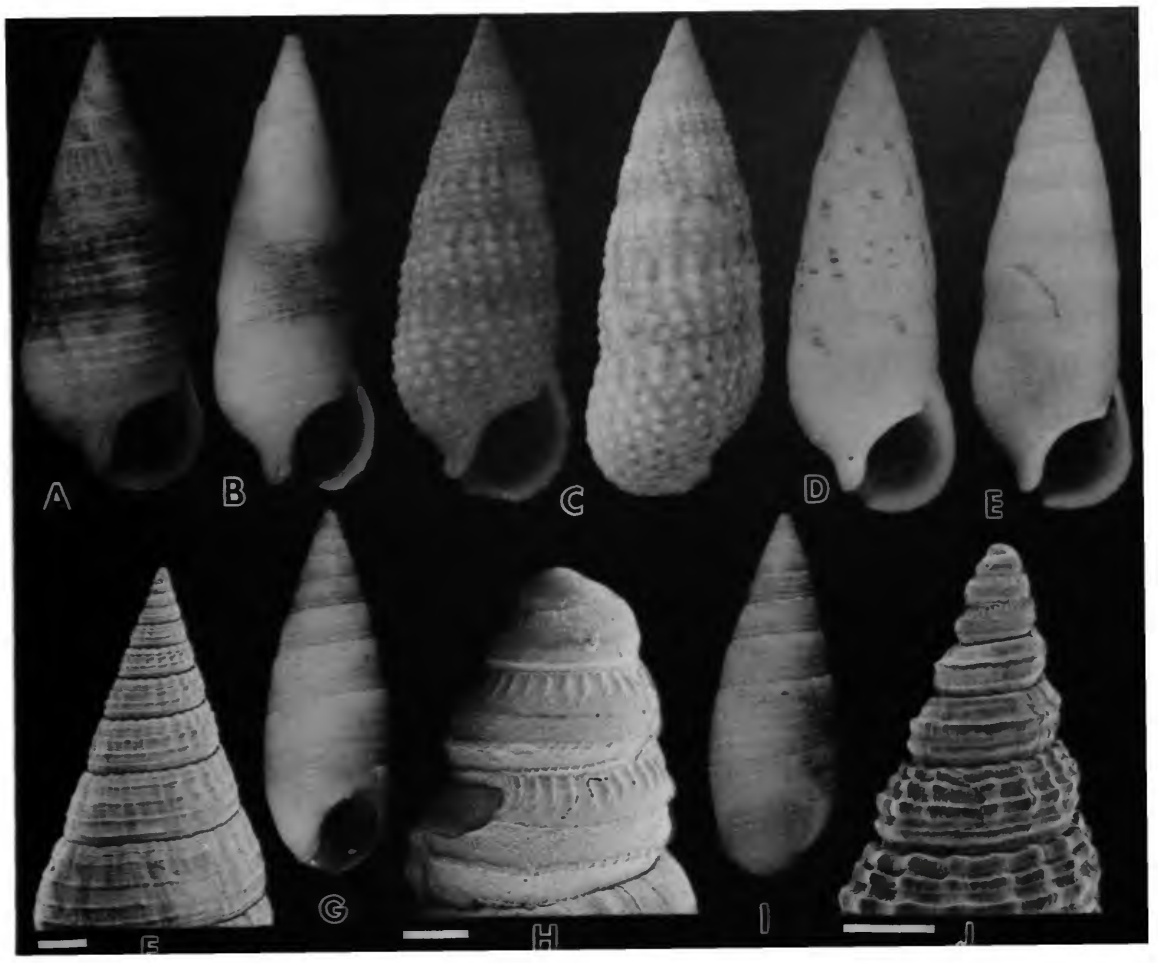

FIGURE 86.—Types of nominal taxa synonymous with *Cerithium nesioticum* Pilsbry and Vanatta and specimens showing phenotypic variability. A, *Cerithium nesioticum* Pilsbry and Vanatta, incorrectly cited as "lectotype" on label, but a non-type specimen, 18 mm (ANSP 17720); B, holotype of *Cerithium voyi* Pilsbry and Vanatta, Caroline Ids, 17.3 mm (ANSP 58192); C, holotype of *Cerithium papillosum* Sowerby, 15 mm (BMNH 19071028222); D, Île Picard, Aldabra, Seychelles, 17.2 mm (USNM 837813); E, Enewetak Atoll, Marshall Ids, 16.5 mm (USNM 770724); F, SEM of early whorls, Tahiti, Society Ids (bar = 0.13 mm; USNM 671594); G,I, lectotype of *Cerithium spiculum* Hedley, Funafuti, Ellice Ids, 11 mm (AMS C5941); H, SEM of protoconch, Tahiti, Society Ids (bar = 50 µm; USNM 671594); J, SEM of early whorls, Tahiti, Society Ids (bar = 1 mm; USNM 671594).

Cerithium nesioticum Pilsbry and Vanatta, 1906:788, fig. 4 [new name for *Cerithium pusillum* Nuttall, 1852, and *C. lacteum* Kiener, 1842].—Dautzenberg, 1929:272; 1932:56.—Clench and Turner, 1962:104 [wrongly attributed to Pilsbry and Lowe].—Kay, 1979:123, fig. 45H.—Mastaller, 1979:47.

Cerithium collacteum Iredale, 1929:278 [new name for *Cerithium lacteum* Kiener, 1841].

Cerithium (Semivertagus) lacteum Kiener.—Thiele, 1929:213.

Cerithium (Liocerithium) nesioticum Pilsbry and Vanatta.—Adam and Leloup, 1938:106, pl. 5: fig. 15.

Cerithium (Semivertagus) nesioticum Pilsbry and Vanatta.—Maes, 1967:114, pl. 6.

DESCRIPTION.—*Shell* (Figure 86): Shell fusiform, elongate, comprising 12–14 inflated, smoothly sculptured whorls, attaining 22 mm length and 6.5 mm width. Protoconch (Figure 86H) comprising 3.5 whorls and with deep sinusigeral notch; protoconch 1 smooth; protoconch 2 with broad, sloping subsutural ramp, and sculptured with 2 spiral cords, and minute, randomly distributed pustules, and subsutural row of axial plaits. Early teleoconch (first two whorls) sculptured with 2 main spiral cords and weak subsutural cord (Figure 86J,F); third to fifth whorls with three main spiral cords crossed by weak axial, colabral riblets. Adult teleoconch sculptured with 4 main spiral cords, beaded or smooth where crossed by weak axial ribs, and with numerous fine spiral striae in interspaces.

TABLE 29.—Shell morphometrics of *Cerithium nesioticum*.

Character	$\bar{x}$ (n = 20)	sd	v	Range
Shell length	16.7	2.4	5.6	13-22
Shell width	5.6	0.6	0.3	4.4-6.5
Aperture length	4.5	0.6	0.3	3.2-5.3
Aperture width	3.1	0.5	0.3	2.2-4.6
Number of whorls	13.5	0.6	0.4	12-14
Number spiral cords	4.1	0.4	0.2	4-6

Suture distinctly impressed. Body whorl elongate with rounded base, very weak basal constriction, and large varix opposite outer lip of aperture; body whorl sculptured with 6–9 spiral cords. Aperture fusiform-ovate, a little less than one-fourth the shell length. Columella concave, with callus and distinct columellar lip. Anterior siphonal canal broad, very short. Anal canal distinct, bordered by weak parietal columellar tooth. Outer lip smooth or weakly crenulate, thick at edge. Shell color creamy white, with porcellaneous spiral cords and spiral rows of faint orange-tan spots. Measurements (Table 29). Periostracum not evident.

Radula (Figure 87): Type-1 radular ribbon (Figure 3A) very small, about one-eleventh the shell length. Rachidian tooth (Figure 87B) rectangular-triangular in outline, having broad base with median posterior projection and pair of basal ridges; anterior front of tooth slightly concave; cutting edge with one large, main, pointed cusp flanked on each side by two pointed denticles. Lateral tooth (Figure 87B) with long, lateral, posterior projection and strong, posteriorly projecting, central buttress with small pustule on broad basal plate; cutting edge with one large, pointed, main cusp, one inner flanking denticle, and 3, sometimes 4 outer flanking, pointed denticles. Marginal teeth (Figure 87) with elongate shafts, curved and serrated at tips. Inner marginal tooth with long, main,pointed cusp, 3 inner flanking, pointed denticles and 2 outer flanking, pointed denticles. Outer marginal tooth same, but without outer-flanking denticles.

Anatomy: Animal whitish-pale green. Head-foot with a few faint, brown flecks. Cephalic tentacles transparent with light, tan patch just over black eye. Mantle edge weakly papillate, bordered with broken black line adjacent to inhalant siphon. Mantle papillae around inhalant siphon, each with yellow spot.

Type-A pallial oviduct (Figure 4A), with long sperm gutter, yellow spermatophore bursa, and cream-colored albumin gland.

SYNONYMIC REMARKS.—This common Indo-Pacific species has been given many names. The earliest name is *Cerithium lacteum* Kiener, 1841, a name previously used by Philippi (1836) for another species. Although the type of *C. lacteum* has not been found, Kiener's illustration (1841, pl. 7: fig. 3) cannot be mistaken for any other *Cerithium* species and as there is no doubt as to its identity, I herein select Kiener's fig. 3 to represent the lectotype of *C. lacteum*. Nuttall in Jay (1852:316), referring to Kiener's figure, renamed this species *C. pusillum*, but that name is also preoccupied. Sowerby (1855) named a beaded phenotype, similar to those found in the western Indian Ocean, *Cerithium papillosum* (Figure 86C), which is likewise a preoccupied name.

FIGURE 87.—Radula of *Cerithium nesioticum* Pilsbry and Vanatta, Enewetak Atoll, Marshall Ids (USNM 821846): A, radula with marginals spread open (bar = 50 μm); B, half row showing dentition of teeth (bar = 25 μm).

Hedley (1899:433) mentioned the close resemblance of *Cerithium spiculum* Hedley, 1899, to *C. lacteum* Kiener, but he considered the former taxon to be distinct. He pointed out the smaller size, narrower outline, and absence of granulations as the distinguishing characters separating the two taxa. The lectotype of *C. spiculum* Hedley (Figure 86G,I) has an undeveloped apertural lip, but is otherwise morphologicaly typical of *nesioticum*. *Cerithium nesioticum* is a replacement name proposed by Pilsbry and Vanatta (1906:788) for *C. pusillum* and *C. lacteum*, and is the name in common use today. A specimen bearing the name *nesioticum* and cited as a type on the label (ANSP 17720) is figured herein (Figure 86A), but is not a type. The replacement name *C. collacteum* Iredale, 1929, is thus not necessary. *Cerithium voyi* Pilsbry and Vanatta, 1905 (Figure 86B), is also considered synonymous with *C. nesioticum*, as there are no salient characters delineating it. Examination of thousands of specimens of the above nominal taxa shows that sculptural variations in size, strength, and development of beading and spiral lines are intergrading

characters among populations throughout a wide geographic range; thus, all the nominal taxa above are considered to be conspecific with *C. nesioticum*.

Cerithium nesioticum has been referred to other higher categories such as *Liocerithium* Tryon, 1887, and *Semivertagus* Cossmann, 1889. There is no reason to accord *Liocerithium* generic status, because it is poorly defined and based solely on shell characters of questionable generic value. *Semivertagus* was proposed by Cossmann (1889) for small Eocene cerithiids that are comparable in general morphology to *C. nesioticum*, but which have a very different, distinctive aperture and columella. It is highly unlikely that there is any close relationship between them and *C. nesioticum*.

ECOLOGY.—There have been no detailed studies on the life history or ecology of this common species. *Cerithium nesioticum* is a shallow-water, littoral species that burrows in sandy substrate in seaward, well-oxygenated, shallow-water habitats such as sandy, rubble-filled pools associated with limestone platforms. It has been found in these kinds of habitats on Fanning Island, Line Islands (Kay, 1971:273), on Tiahura-Moorea, Society Islands (Richard, 1973:310), in boulder tracts of reefs at Tulear, Madagascar (Thomassin and Galenon, 1977:249), in the Gulf of Elat, Israel (Yaron, 1979:234), and in the Sudanese Red Sea where Taylor and Reid (1984:190) recorded it as comprising 31.8 percent of the shallow-water gastropod fauna from sand and rubble habitats at Harvey Reef. Bandel (in litt.) found it to be common in 0.5–1 m depth on off-shore reefs at Port Sudan, Red Sea, where it burrowed in sandy algal mats, probably to escape intense fish predation. I observed a population living in sandy pockets along a seaward limestone bench at Enewetak Atoll, Marshall Islands. The cream colored shells are difficult to see in the sand, and most lie close to rock edges. I have found this species in similar habitats at Lizard Island, Queensland, Australia, and in Kaneohe Bay, Oahu, Hawaii.

Many drilled shells found in the above localities indicate extensive predation by naticid and muricid snails. Taylor and Reid (1984:190) noted that *C. nesioticum* was a prey item of *Cronia (Muricodrupa) funiculus* (Wood) near Port Sudan in the Red Sea.

The egg masses and larvae of this species have not been described, but the sculptured protoconch (Figure 86H) of 3 whorls with a deep sinusigeral notch, and the extensive Indo-Pacific range, indicate a planktotrophic larval stage before settlement.

DISCUSSION.—*Cerithium nesioticum* is not likely to be confused with most other *Cerithium* species. Its relatively small, smooth, pupate, ivory shell with inflated whorls and small aperture (almost one-fourth the shell length) are distinguishing characters. The early whorls are deeply sculptured with spiral cords and axial riblets (Figure 86J), but this sculpture becomes weak as the whorls enlarge and become more inflated (Figure 86F).

Intraspecific sculptural variation is common and may been seen even within a population. Some shells are nearly smooth (Figure 86B), while others may have the four spiral cords more sharply defined and strongly beaded (Figure 86C), or develop subsutural plications. Small spiral striae may be present in some shells. Shells in the Indian Ocean tend to have the four spiral cords on each whorl beaded (Figure 86D), while those from the central Indo-West Pacific are weakly sculptured (Figure 86E). Populations in the eastern part of the range tend to have shells in which the spiral cords are more accentuated. The many-whorled protoconch (Figure 86H) is typical of a shell with planktotrophic development.

Some beaded phenotypes of *C. nesioticum* (Figure 86C) may be mistaken for *C. interstriatum* Sowerby, 1855, a widespread Indo-Pacific species (Figure 64). The latter species has a deeper subtidal habitat and differs in having a more slender shell with only three beaded spiral cords per whorl, a small aperture, and a body whorl with a more constricted, excavated base and longer siphonal canal.

Retention of the genus *Semivertagus* for this species was not supported by anatomical characters.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 88).—*Cerithium nesioticum* has one of the widest geographic ranges of any cerithiid species. It occurs from the Red Sea south to South Africa, throughout the Indian Ocean to SE Asia, Western Australia, and the Indonesian Archipelago. In the Pacific, it is found from Japan south to Norfolk Id, and throughout Melanesia, Micronesia, and Polynesia, as far north as the Hawaiian Islands and east to the Pitcairn Islands. *Cerithium nesioticum* has recently invaded the eastern Mediterranean (Israel) by way of the Suez Canal (Mienis, 1977:45).

SPECIMENS EXAMINED.—EAST AFRICA: Durban, South Africa (NM 1037); NW of Choca, SW Conducia Bay, Mozambique (NM H1903); Porto Amelia, Mozambique (AMS C109458); Zanzibar (USNM 598433); Mogadiscio, Somalia (USNM 673797, 754972). RED SEA: Eilat, Gulf of Aqaba, Israel (USNM 671243, 672280); Aqaba, Gulf of Aqaba, Jordan (USNM 841313); Port Sudan, Sudan (USNM 770721); Green Id, Massawa Bay (AMS C101189); S side Dissei Id, Massawa (AMS). INDIAN OCEAN ISLANDS: Passe Yangue, Île Picard, Aldabra Atoll, Seychelles (USNM 837599, 837742, 837813); Passe Houareau, Île Malabar, Aldabra Atoll, Seychelles (USNM 837560); Mauritius (USNM 90840); Le Gris Gris, Souillac, S Mauritius (AMS C69469); Jerome Pt, 1.6 km SE of Mahebourg, E Mauritius (AMS C68963, MCZ); Réunion (AMNH); Diego Garcia, Chagos Archipelago (USNM 702181); Alor Pinyii, NW side West Id, Cocos Keeling Ids (MCZ); West Id, Cocos Keeling Ids (AMS); reef off SE end West Id and Pulo Maria, Cocos Keeling Ids (USNM 656227); Christmas Id (AMS); Flying Fish Cove, Christmas Id (WAM); Ethyl Beach, Christmas Id (WAM); Greta Beach, Christmas Id (WAM). THAILAND: Phuket (USNM 749190); Goh Sindarar, Nua (Chance Id) (USNM 661275). JAPAN: Susami, Wakayama Pref, Honshu (USNM 666602); Kikai, Osumi (USNM

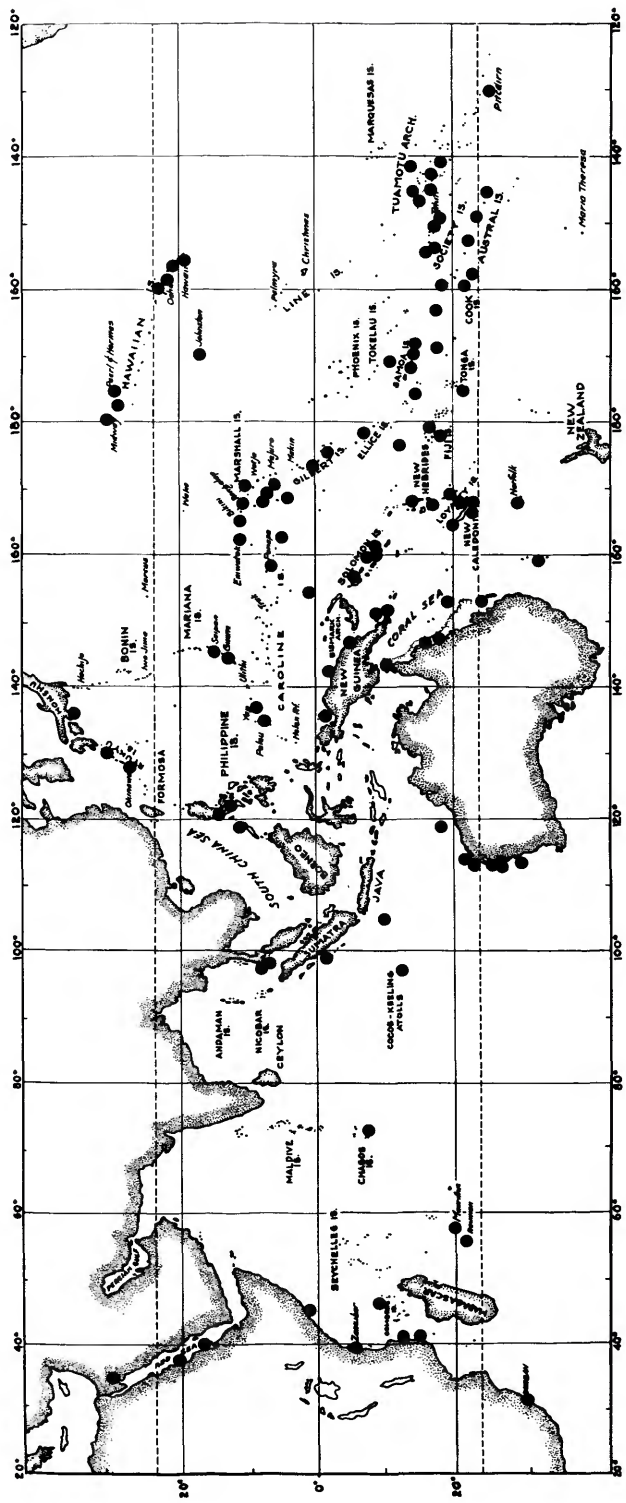

FIGURE 88 (left).—Geographic distribution of *Cerithium nesioticum* Pilsbry and Vanatta.

175585); Oshima, Osumi (MCZ, USNM 273628, 343859, 343871). RYUKYU ISLANDS: Kadena Yacht Club Channel, Kadena, Okinawa (USNM 805583, 821326). PHILIPPINES: Matabungkay, 115 km SSW of Manila, Luzon (AMS); Gaspar Id, Tres Reyes Gp, Marinduque (AMS); Ulugan Bay, NW Palawan (AMNH); Balabac (MCZ). INDONESIA: Pulau Bai Batu Gp, off SW Sumatra (USNM 654523); Puluu Stupa, Mentawai Id, SW of Sumatra (USNM 655114).

WESTERN AUSTRALIA: Eagle Bay, W of Dunsborough (AMS); N of Gun Id, Abrolhos Ids (WAM); N side Beacon Id, Abrolhos Ids (WAM); Surf Pt, Dirk Hartog Id (WAM); Blow Holes, Carnarvon (AMS); W of Pt Cloates (WAM); W of Cloates (WAM); S of wreck of SS *Mildivia*, NW Cape (AMS); SE corner Clerke Reef, Rowley Shoals (WAM); W side Mermaid Bay, Rowley Shoals (WAM). QUEENSLAND, AUSTRALIA: Murray Id, Torres Strait (AMS C29535, MCZ); Yam Id, Torres Strait (AMS); Hope Id, S of Cooktown (AMS); Mackay Reef, NE of Port Douglas (AMS); Low Isles, near Port Douglas (AMS); Euston Reef, NE of Cairns (AMS); Green Id, off Cairns (AMS); N point Lizard Id (AMS); NE Herald Cay, Coral Sea (AMS); Keeper Reef, NE of Townsville (AMS); Wheeler Reef, NE of Townsville (AMS); Marion Reef, Coral Sea (LACM 77-120); North West Id, Capricorn Gp (AMS); Tryon Id, Capricorn Gp (AMS); Lady Musgrave Id (AMS); Caloundra (AMS). NEW GUINEA: Reef E of Noesi Id, Mios Woendi, Padaido Ids, Irian Jaya (AMS, MCZ); Celeo Reef, 8 km off Aitape, Papua (USNM 593918); Megiar Harbor, 115 km N of Madang, Papua (AMS); East Cape, E tip of Papua (AMS); S side Massas Id, Madang, Papua (AMS); Siassi Id, Papua (AMS); Kuia Id, Lusancay Ids, Trobriand Gp, Papua (AMS). SOLOMON ISLANDS: Kieta, Bougainville Id (AMS C44153); Hataheta Id, N side Santa Isabel Id (LACM 78-59.15); 6–12 km off N entrance of Aoki Harbor, W coast Malaita Id (AMS); Laulasi, S of Aoki, Malaita Id (AMS); East Pt, Small Nggela Id, Florida Gp (AMS); Ghavutu Id, Nggela Sule, Florida Ids (LACM 78-66.12).

NEW HEBRIDES: Pakea, Banks Gp (AMS C15618); Pointe d'Arbel, Efate Id (USNM 787516); W side Pango Pt, Mele Bay, Effate Id (LACM 77-40); reef S of Utja, Aneityum (USNM 692129). LOYALTY ISLANDS: Lifu (AMS C4690, USNM 423295, 423298, 423324, 423326, 423375); Île des Pins, Atoll Uvea (USNM 692933). NEW CALEDONIA: Bay S of Wala Village, Île Art (USNM 806112); Poe, Bourail (AMS); Unia, near Yate (USNM 783722); Anse Vata, Nouméa (AMS); Atira Id (USNM 724178); Île des Pins (MCZ). NORFOLK ID: (AMS). LORD HOWE ID: (MCZ); reef at S end of lagoon (AMS C2838, C49863, C59537). FIJI: NW Rambi Id, Vanua Levu (USNM 695296, 695349, 695360, 695386); N side Yandua Tamba Id, Vanua Levu (USNM 694680); W of Ngarataka Id, Vanua Levu (USNM 695123); Nadi Bay, Viti

Levu (AMS); SW of Tulane Harbor, Koro (USNM 695890); Rat Tail Passage, main Suva reef, S Viti Levu (USNM 824834); Lacala Bay, Suva, Viti Levu (USNM 790672); Suva Harbor, Viti Levu (USNM 532249, 845784); Ndravuni, S of Viti Levu (USNM 791050); E of Ndravuni Id, Kandavu (USNM 695999); E of Ono Id, Kandavu (USNM 696067); S of Yauravu Pt, Kandavu (USNM 696686); S of Ngaloa Pass, Kandavu (USNM 696474). MARIANA ISLANDS: N Tipalao Pt, Guam (USNM 842608); Tweed's Cave, Haputo Pt, Guam (USNM 851142, 851234, 851280, 852122); Apra Bay, Guam (USNM 232944); Pago Bay, Guam (USNM 792436); Saipan (USNM 486784). PALAU: Babalthaup (MCZ). CAROLINE ISLANDS: Mutunlik, Kusai Id (USNM 609565); Yap Id (USNM 630813, 630818); Elato Atoll (USNM 590964); Langor Id, Ponape, Ponape Id (LACM 69-1); Mutunlik, Kusai Id (USNM 609565); Tirakaume, Kapingamarangi Atoll (USNM 610883, 610933).

MARSHALL ISLANDS: Rigili Id, Enewetak Atoll (USNM 581600); Aaraanbiru Id, Enewetak Atoll (USNM 582289); Muti Id, Enewetak Atoll (USNM 716386); Enewetak Id, Enewetak Atoll (USNM 580986, 660659, 770481, 770724, 821846); Namu Id, Bikini Atoll (USNM 579951, 580528); Bikini Id, Bikini Atoll (MCZ, USNM 579305, 585181); Bokonfuaaku Id, Bikini Atoll (USNM 586102); Eninman Id, Bikini Atoll (USNM 586896); Burok Id, Rongelap Atoll (USNM 583998); Arbar Id, Rongelap Atoll (USNM 582442); Kabelle Id, Rongelap Atoll (USNM 582108, 582400); Bigonattam Id, Rongerik Atoll (USNM 586330, 586353); Kwajalein Id, Kwajalein Atoll (USNM 587351); Lae Id, Lae Atoll (USNM 614903); Ailuk Id, Ailuk Atoll (USNM 615120); SE side Enybor Id, Jaluit Atoll (USNM 659341); Ebon Id, Ebon Atoll (MCZ). GILBERT ISLANDS: Apamama (USNM 434006). HAWAIIAN ISLANDS: Green Id, Kure Id (USNM 678236); Midway Id (USNM 485532, 542576, 634848); Sand Id, Midway Id (USNM 606714); USBF sta 68, Pearl and Hermes Reef (USNM 428525); Laysan Id (USNM 335026); Kealia, Kauai (USNM 339348); Kaena Pt Oahu (USNM 484775); Mokuleia, Oahu (USNM 485534, 485535); Kahuku, Oahu (AMS); Kahuku Pt, Oahu (USNM 767242); Punaluu, Oahu (USNM 420902); Pearl Harbor, Oahu (USNM 484433, 484440); Honolulu reef, Oahu (USNM 335025); Quarantine Id, Honolulu, Oahu (USNM 339345); Waikiki, Honolulu, Oahu (USNM 343496); Makapuu Pt, Kailua Bay, Oahu (AMS, USNM 484767); Black Pt, Haunama Bay, Oahu (USNM 487819, 809776); S of Lanai Id (USNM 335022); Honokowai, Maui (USNM 339346); Paia Beach, N shore Maui (USNM 343498); Honaunau, Hawaii (USNM 343497); Keei, near Napoopoo, Kona Coast, Hawaii (USNM 420887, 767581); Hookena, Hawaii (USNM 420889); Keokea, Hilo, Hawaii (MCZ, USNM 339344, 346374, 612298); Keaukaha, Hilo, Hawaii (USNM 339347, 346375); Kapoho, Hawaii (USNM 409077, 409078); Kewaihae, Hawaii (USNM 632006); (MCZ).

LINE ISLANDS: Sand Id, Johnston Atoll (USNM 693928). ELLICE ISLANDS: Near village, Vaitupu (USNM 685861, 686090); main id, Nukulailai (USNM 685861). WALLIS AND HOORN ISLANDS: NW of Mua, Alofi (USNM 676759); E coast, Faoia (USNM 676126). SWAINS ISLAND: Beach, NW coast (USNM 768424, 768433); reef near Taulaga Village (USNM 704323). SAMOA: Mataatu Harbor, N coast Savaii (USNM 675748); Apia, Samoa (USNM 573909); Tutuila Id (USNM 589254); Fagaitua Bay, Tutuila (USNM 704710); Ofu, Manua Gp (USNM 381216). TONGA: Ha'Ateiho Reef, S coast of Tonga (USNM 654246). NIUE: Alofi (USNM 685495). COOK ISLANDS: Pukapuka Id (Danger Id) (USNM 819896); Palmerston Id (USNM 685156); Aitutaki (USNM 684873); N tip Akitua, Aitutaki (USNM 684852); Motu Akaiami, Aitutaki (USNM 684989); Black Rock, NW Rarotonga (MCZ); Rarotonga (AMS C57448, C57462); Mangaia (USNM 613445).

AUSTRAL ISLANDS: N shore, Rurutu (USNM 684152); Moerai, Rurutu (USNM 684018, 684109, 684266); Tubuai (USNM 819776); Motu Moturoa, Tubuai (USNM 683666, 683707); E coast Motu Motihia, Tubuai (USNM 705528); Motu Veiamanu, Raevavae (USNM 676826). SOCIETY ISLANDS: W side, ocean reef, Bellinghausen (USNM 705229); E side, ocean reef, Scilly (USNM 705301); NE end Ocean Reef, Mopelia (USNM 705146); Motu Ahi, Maupiti (USNM 706326); Motu Tuanae, Maupiti (USNM 751470); Motu Toahotu, Tahaa (USNM 674157); Tetaro Id, Uteroa, Raiatea (USNM 652641); Motu Iriru, Raiatea (USNM 675543); Motu Tipaemau, Raiatea (USNM 675301); Motu Taiahu, Huahine (USNM 675118); Motu Rimatuu, Tetiaroa (USNM 705972, 705973); Motu Tiaranunu, Tetiaroa (USNM 705808, 705862); Toatane Reef, W of Avaroa, Moorea (USNM 652765); W of Pt Hauru, Moorea (USNM 630519); NW Motu Fareone, Moorea (USNM 753691); Tahiti, numerous localities throughout (USNM 668444, 668459, 668580, 668778, 669017, 669554, 671694, 671700, 672650, 672832, 672850, 673716, 674429, 674461, 791360, 797263, 804436).

TUAMOTU ARCHIPELAGO: N of Temao Helo, Makatea (USNM 629818); reef, W end Manihi (USNM 790237); Manihi (USNM 790237); Matiti Id, Tikahau (USNM 629360); Tikahau (USNM 629296); W side Avatoru Pass, Rangiroa (USNM 782824); Anaa (USNM 775894, 788980, 791379, 819777); Takaroa (USNM 790049); Raroia (numerous localities throughout, USNM 698513, 698592, 711915, 720440, 720511, 720588, 721183, 721245, 722898, 723038, 723061, 723179, 723250, 723329, 723343, 723376, 723390, 723441); NE side Tepukamaruia Id, Takume (USNM 723666, 723727); near Hikitake Id, Amanu (USNM 671796); Vahi Tahi (USNM 613185). PITCAIRN ISLANDS: W side Oeno Id, Pitcairn Id (USNM 789590). NIUAFOU: (USNM 383785, 383798, 383821, 468483, 519039, 519072).

Cerithium nodulosum Bruguière, 1792

FIGURES 89–96

Cerithium Le Cérite Adanson, 1757:155, pl. 10: fig.2 [non-binomial, is *Cerithium erythraeonense* Lamarck, 1822, fide Fischer-Piette, 1942:250, pl.

8: fig. 16a,b].—Deshayes, 1843:311-312.
Murex aluco Born, 1780:321-322 [in part; not *Murex aluco* Linné, 1758].
Cerithium nodulosum Bruguière, 1792:478, pl. 442: fig. 3 [lectotype, herein selected: MHNG 1907/13; type locality: "mer Rouge; l'Ocean Asiatique; Îsle d'Amboine," herein restricted to Ambon Island, Indonesia; 103 mm × 41 mm; not *Cerithium nodulosum* Philippi, 1836, nor Hall, 1845, nor Moore, 1867].—Quoy and Gaimard, 1834:112-113, pl. 54: figs. 5, 6.—Kiener, 1841:4-5, pl. 3: fig. 4.—Deshayes, 1843:287.—Sowerby, 1855:854, pl. 78: fig. 42; 1865, pl. 1: fig. 3.—Kobelt, 1880:76-77, pl. 15: fig. 1.—Tryon, 1887:122, pl. 19: figs. 13, 14; pl. 20: fig. 15.
Cerithium adansonii Bruguière, 1792:479 [Le Cérite Adanson, 1757, cited in synonymy; holotype: MNHNP, no number, type locality: 55.5 mm].
Cerithium curvirostra Perry, 1811, pl. 35: fig. 2 [type not located, Perry's figure selected to represent lectotype; type locality: "Eastern Seas and Persian Gulf"].
Murex tuberosus Dillwyn, 1817:749-750 [type not located; type locality: Amboina; in part].
Murex nodulosus Wood, 1818:131, no. 147; 1825:131, no. 147, pl. 27: fig. 147.
Cerithium erythraeonense Lamarck, 1822:70 [holotype: MHNG 1097/19; type locality: Red Sea, 60 mm].—Tryon, 1887:123, pl. 20: fig. 16.—Kobelt, 1890:77-78, pl. 15: figs. 2, 3.—Vignal, 1923:18.—Jousseaume, 1930:273.—Lamy, 1938:64.—Fischer-Piette, 1942:250-253, pl. 8: fig. 16a,b.—Sharabati, 1984, pl. 4: fig.a 12.
Cerithium tuberosum Sowerby, 1855:855, pl. 178: fig. 49 [not *Cerithium tuberosum* Grateloup, 1847].—Sowerby, 1865, pl. 1: fig. 5.
Cerithium omissum Bayle, 1880:250 [new name for *Cerithium tuberosum* Sowerby, 1855, not *Cerithium tuberosum* Grateloup, 1847].
Matilda eurytima Melvill and Standen, 1896:310-311, pl. 11: fig. 73.—Tomlin, 1936:150 [Paralectotype: NMW 1955.158.207, 6.6 mm; syntype: MM].—Trew, 1987:40.
Contumax decollata Hedley, 1899:437-438, fig. 25 [lectotype, herein selected: AMS C5949, 17.4 mm].—Viader, 1951:147, pl. 4: fig. 15.
Contumax nodulosus Bruguière.—Cotton, 1952:1.
Cerithium (Contumax) nodulosum Bruguière.—Kaicher, 1956, pl. 3: fig. 6.
Cerithium nodulosum erythraeonense Lamarck.—Bosch and Bosch, 1982:49.
Cerithium (Cerithium) nodulosum (Bruguière) [sic].—Springsteen and Leobrera, 1986:59, pl. 13: fig. 2.

DESCRIPTION.—*Shell* (Figures 89A-C,E,F,H-J; 90): Shell very large, solid, elongate, angular, comprising 15-18 angulate whorls, and reaching 114 mm length and 50 mm width. Shell sculpture varying with ontogenetic shell stage: (1) protoconch (Figure 89I) comprising 2 whorls with well-developed sinusigeral sinus; protoconch 1 smooth; protoconch 2 sculptured with fine spiral striae, pustules, and thin subsutural axial plicae; (2) juvenile shells (Figure 89B,E) with inflated whorls and fine cancellate sculpture formed by 4 or 5 fine spiral cords crossed by numerous axial riblets; (3) subadults (Figure 89H) with cancellate sculpture on early whorls; second spiral cord gradually enlarging, with nodulose carina developing large nodes on later whorls. Broad subsutural ramp on later whorls; (4) adult shells (Figure 89A,C,F,J) usually lacking early sculpture due to erosion. Teleoconch whorls with 7-14 prominent, pointed nodes forming strong, angulate keel. Smooth, narrow spiral cords (about 10 on penultimate whorl) crossing numerous axial riblets, creating weak cancellate appearance; spiral sculpture dominating. Well-defined, nodulose, subsutural, spiral cord defining distinct, wavy suture. Body whorl very large, with strong siphonal constriction, and strongly excavated base sculptured with 5 spiral, nodulose cords crossed by wavy axial ribs. Aperture large, about one-third shell length and with well-developed, narrow, anterior siphonal canal slightly reflexed to left of shell axis. Anal canal flanked by strong parietal columellar plait extending well within aperture. Outer lip thick, flaring, strongly crenulate, forming short, distinct posterior spout at anal canal and having claw-like anterior extension crossing over anterior siphonal canal; interior of outer lip with deep spiral grooves. Columella white, strongly concave, and with narrow, thick callus and well-defined lip. Shell color white with fine brown-gray spiral lines or spots, and irregularly shaped, brown-gray blotches. Aperture white. Measurements (Table 30). Periostracum thin and tan. Operculum (Figure 89D,G) thick, corneous, dark brown, ovate, paucispiral, and with eccentric nucleus.

Radula (Figures 91A-C; 92): Type-1 radular ribbon (Figure 3A) robust, short, about one-tenth shell length, and with about 8 or 9 rows of teeth per mm. Rachidian tooth (Figures 91B,C; 95B) having square basal plate with short central posterior projection flanked by small ridge on each side; anterior edge straight to convex; cutting edge comprising large, spade-shaped, central cusp flanked on each side by 1 or 2 small, blunt denticles. Lateral tooth (Figures 91A,B; 95B) rhomboidal, with long lateral extension and strong, central-lateral, posterior projection on basal plate; cutting edge with very long, triangular, central cusp flanked on inner side with two small cusps and on outer side by 2 or 3 small cusps. Marginal teeth (Figures 91B,C; 95B) spatulate with rounded, curved, spoon-like, tips. Inner marginal tooth with 3 or 4 small, inner denticles and 1 or 2 small, outer denticles; outer marginal tooth same, but with no outer denticles (Figure 91C).

Anatomy (Figures 92-94): Animal large, with 5 or 6 whorls comprising digestive gland and gonad, stomach, kidney, mantle cavity and head-foot, respectively. Head-foot dusky grayish yellow overlain with black blotches and tiny white dots. Muscular foot with warty, crescent-shaped propodium, and with broad, whitish sole. Deep propodial mucus gland at leading edge of sole. Right side of foot with ciliated groove emerging from exhalant siphon and terminating in pad-like, glandular ovipositor near edge of sole in females. Metapodium with large, black operculum. Head large, muscular, having massive, broad, shovel-shaped snout with bilobed tip. Pair of long cephalic tentacles each with large black, yellow-ringed eye on wide peduncular base. Mantle edge thick, comprising double row of long, dark papillae (Figure 92A). Mantle edge thick and elongate at orange pigmented inhalant siphon and at exhalant siphon.

Yellow osphradium a long, tall, narrow, bipectinate ridge comprising oval filaments (Figure 92B,C), lying closely adjacent to ctenidium (Figure 92B). Osphradium extending full length of ctenidium but deviating from it anteriorly at inhalant siphon. White, well-developed ctenidium nearly the length of the mantle cavity, relatively narrow and composed of large, elongate, triangular filaments (Figure 92B), each with supporting rod along leading edge. Thick hypobranchial gland adjacent

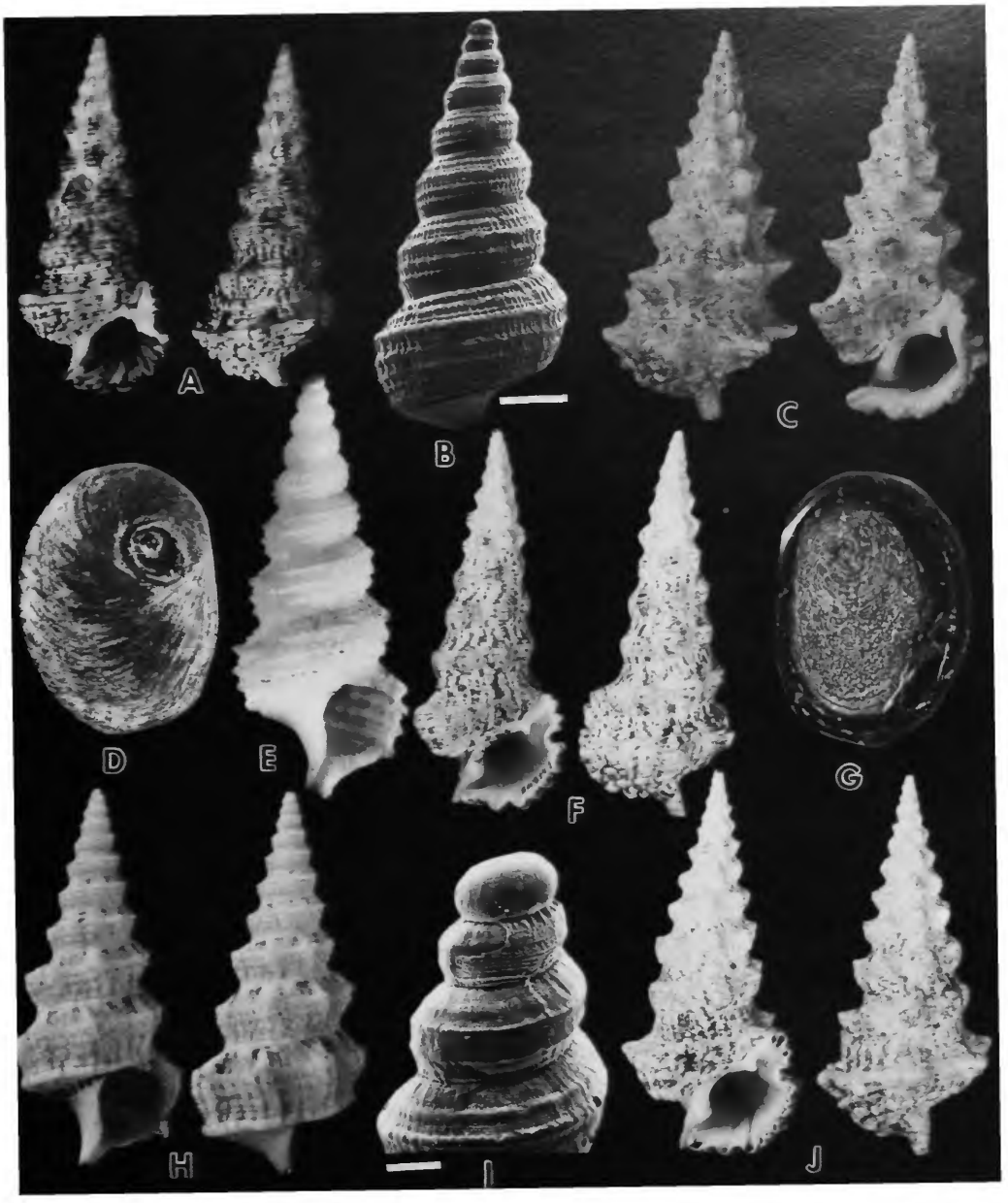

FIGURE 89.—*Cerithium nodulosum* Bruguière operculum: A, lectotype of *Cerithium nodulosum* Bruguière, Ambon Id, 103 mm (MHNG 190713); B, SEM of early whorls (bar = 0.5 mm; USNM 594654); C, Enewetak Atoll, Marshall Ids, 101 mm (USNM 582026); D,G, operculum, showing free (A) and attached (B) sides, Enewetak Atoll, Marshall Ids, 12 mm (USNM 582026); E, paralectotype of *Matilda eurytima* Melvill and Standen, 6.6 mm (NMW 1955158207); F, Ryukyu Ids, Japan, 104 mm (USNM 563747); H, subadult shell, Kapingamarangi Atoll, Caroline Ids, 23 mm (USNM 611104); I, SEM of protoconch and early whorls (bar = 101 μm; USNM 594654); J, Uvea, Loyalty Ids, 98.5 mm (USNM 692665).

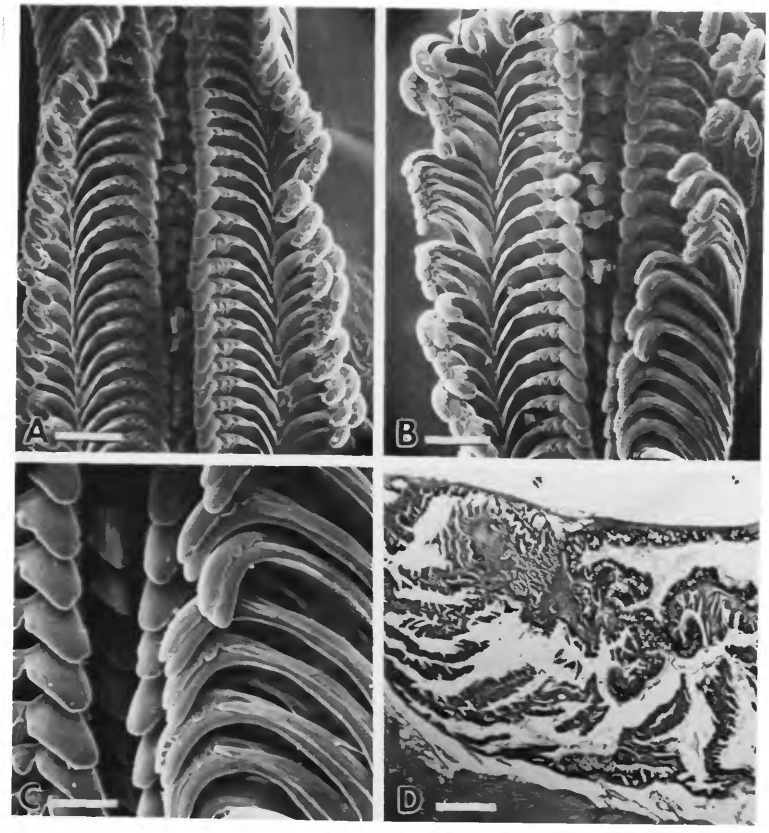

FIGURE 90.—*Cerithium nodulosum* Bruguière: A, Gulf of Suez, 65.6 mm (USNM 771358); B,C, holotype of *Cerithium erythraeonense* Lamarck, 60 mm (MHNG 109719); D, Gulf of Aqaba, Israel, 68 mm (USNM 671273); E, holotype of *Cerithium adansonii* Bruguière, and of the *Cerithium* "Le Cerite" of Adanson, 55.5 mm (MNHNP).

to and about three times as wide as ctenidium, and folded transversely to form shallow, thick ridges secreting great amounts of mucus. Large, wide, convoluted rectum highly ciliated externally, with anus just behind mantle edge. Interior of rectum filled with transversely stacked oval fecal pellets. Pallial gonoducts open, slit tubes comprising lateral (attached) and medial (free) laminae connected to mantle floor along their dorsal margins. Female pallial oviduct (Figure 93) thick; male duct thinner, less glandular.

TABLE 30.—Shell morphometrics of *Cerithium nodulosum*.

Character	$\bar{x}$ (n = 20)	sd	v	Range
Shell length	70.1	19.7	386.6	52.1–114
Shell width	31.0	8.8	76.6	21.4–50
Aperture length	24.9	6.4	40.8	14.4–34.7
Aperture width	15.9	3.2	10.4	10.6–21.7
Length last two whorls	42.4	9.0	81.2	29.4–59.4
Number nodes	9.4	2.0	4.0	7–14

Large buccal mass within broad snout with robust radular ribbon about one-tenth shell length. Pair of large, semicircular jaws with outer covering of microscopic, scale-like plates lying at mouth opening. Pair of small salivary glands comprising thin, loosely coiled tubes running through nerve ring, and emptying in anterior dorsal surface of buccal cavity. Mid-esophagus very wide with interior walls folded into many thin, glandular lamellae comprising esophageal gland (Figure 91D). Stomach large, massive, comprising 1.5–2 whorls, and typically cerithioid in layout with large, posterior, ciliated sorting area, single opening to the digestive gland, large, unciliated, raised central pad, cuticularized gastric shield, and short style sac with thick, short, crystalline style.

Aphallate males with bright orange testes producing typical (eupyrene) and atypical (apyrene) sperm. Apyrene sperm with six flagellae. Vas deferens a thin tube on inner side of visceral

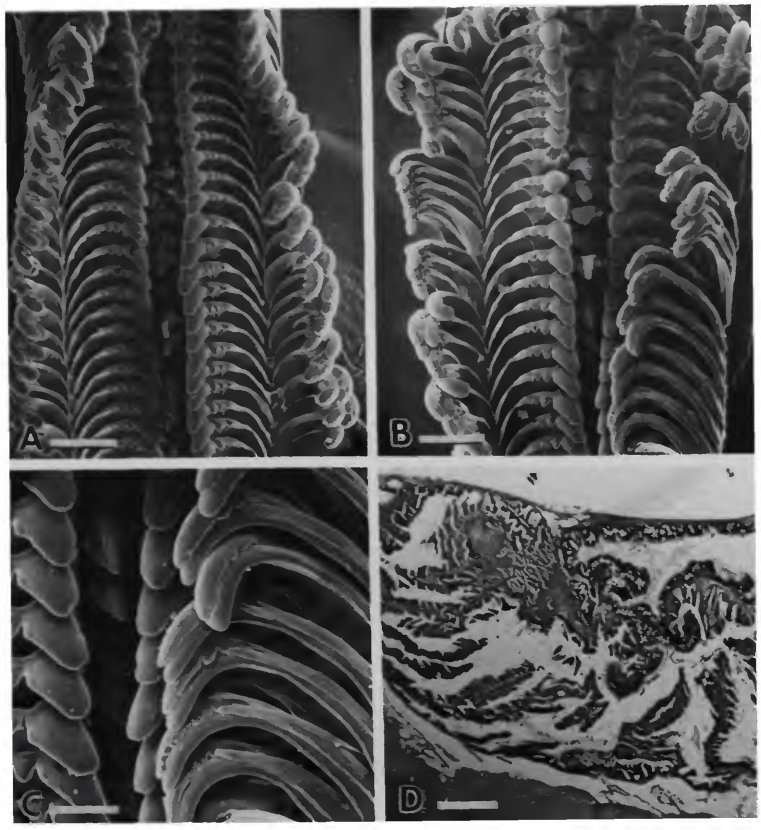

FIGURE 91.—SEM of radula of *Cerithium nodulosum* Bruguière, and section through esophagus; Enewetak Atoll, Marshall Ids (USNM 582026): A, radula with marginals spread open (bar = 30 μm); B, marginals partly folded on right side (bar = 30 μm); C, dentition of marginals (bar = 0.15 mm); D, section through mid-esophagus showing esophageal gland (bar = 0.27 mm).

coils, packed with both kinds of sperm in ripe males. Male pallial gonoduct an open tube of two thin laminae with thicker glandular posterior part comprising spermatophore organ. Females with cream-yellow ovary. Coelomic oviduct (Figure 93, od) a wide tube on inner surface of visceral whorls discharging into posterior pallial oviductal groove (Figure 93, odg). Type-A pallial oviduct (Figure 4A). Non-glandular part of medial lamina (Figure 93, ml) with short sperm gutter (Figure 93, sg) along anterior edge, opening into long ciliated tube and enlarging to form large spermatophore bursa (Figure 93, sb) in posterior of medial lamina. Interior epithelial lining of mid-posterior spermatophore bursa (Figure 94C,D, sb) highly folded and heavily ciliated, but folds absent in posterior bursa (Figure 94E,H, sb). Posterior seminal receptacle (Figure 93, psr) on inner side of posterior part of non-glandular medial lamina (Figure 93, ml), adjacent to spermatophore bursa. Posterior seminal (Figure 93, psr; Figure 94E,F, sr) receptacle small, bright orange, spherical, opening by tiny duct (Figure 94E,F, sr) to lumen of oviductal groove (Figure 94F, odg). In section, posterior seminal receptacle (Figure 94E,F, sr) folded, forming many small pouches lined with epithelial tissue (Figure 94F, sr). Within posterior seminal receptacle, heads of oriented eupyrene sperm embedded in epithelium (Figure 94D). Thick, white, glandular, posterior part of oviduct comprises albumen gland (Figure 93, ag; Figure 94C, ag); middle of oviduct yellow, and anterior white, both probably comprising capsule gland. Long tubular anterior seminal receptacle (Figure 93, asr; Figure 94C,D,G, sr) about 16 mm long and 3 mm wide, with opening (Figure 93, oasr; Figure 94B, oasr) in anterior non-glandular lateral lamina (Figure 93, ll), opposite sperm gutter (Figure 93, sg) of medial lamina. Opening of anterior seminal receptacle (Figure 93, osr) in lateral lamina adjacent to opening of spermatophore bursa (Figure 93, osb) in medial lamina. Anterior seminal receptacle filled with oriented sperm with

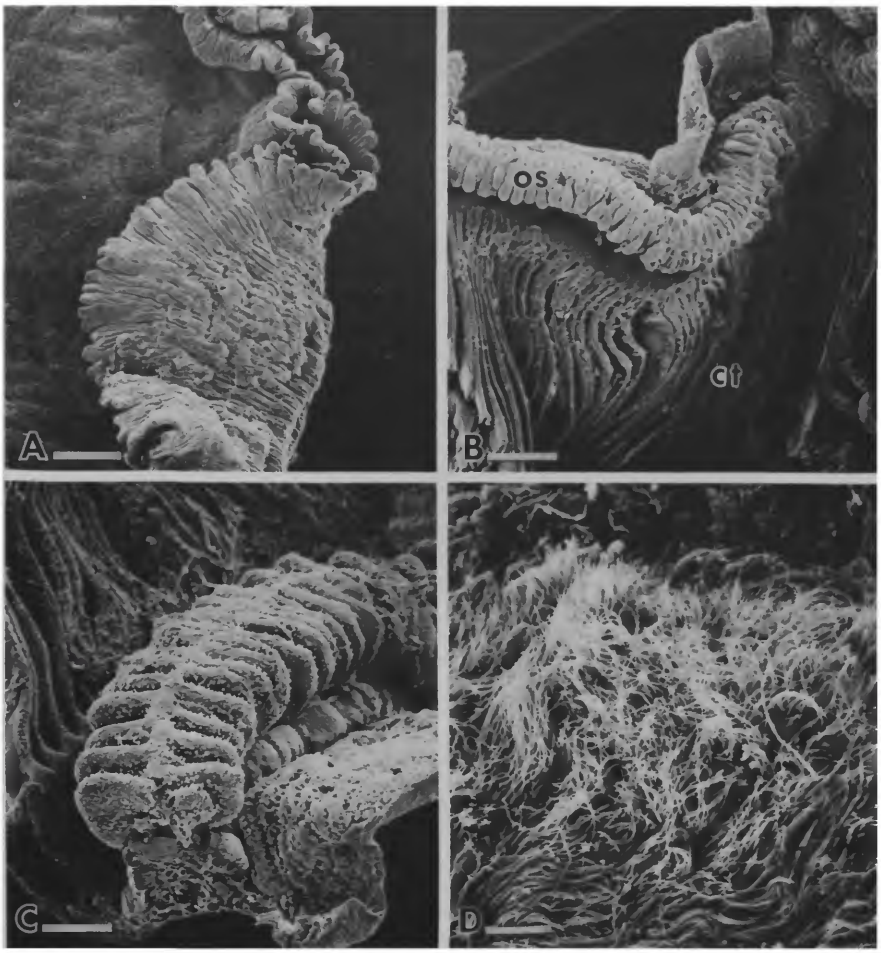

FIGURE 92.—SEM micrographs of critical point dried anatomical features of *Cerithium nodulosum* Bruguière: A, bifurcate mantle edge (bar = 0.38 mm); B, relationship of osphradium (os) to ctenidium (ct) (bar = 0.43 mm); C, detail of osphradium showing staggered arrangement of bipectinate osphradial filaments (bar = 0.14 mm); D, flagellae of oriented sperm in wall of anterior seminal receptacle (bar = 15 μm).

heads embedded in inner epithelial lining (Figure 94G) of lateral lamina.

Spawn mass comprising large, crescent-shaped cluster of many coiled jelly strings and thick, ribbon-like, axial base attaching to substrate. Jelly strings filled with eggs, 4 or 5 eggs deep. Individual eggs enclosed in hyaline capsule of 0.28 μm diameter. Planktotrophic veliger larvae with well-defined velum and compound cilia, hatching 3 or 4 days after deposition of egg mass. Embryonic shells light brown and slightly pitted (see Houbrick, 1971, for more complete description and figures of spawn and larvae).

SYNONYMIC REMARKS.—The first name given this species was the non-binomial *Cerithium* "Le Cérite" of Adanson (1757). Bruguière (1792) later gave Adanson's species a binomial name, *Cerithium adansonii*, citing "Le Cérite" Adanson as a synonym. The holotype of *C. adansonii* (Figure 90E), although eroded, is clearly conspecific with the holotype of *C. erythraeonense* Lamarck (Figure 90B,C), which is a Red Sea phenotype of *C. nodulosum* Bruguière, the earliest valid name for this species, as it preceeds *C. adansonii* by one page. As *adansonii* is a valid taxon, shown to be synonymous with *C. erythraeonense* Lamarck, 1822 (Fischer-Piette, 1942:250–253), it is the available name should subspecific or specific status be conferred on the Red Sea phenotype. Two putative types of *C. nodulosum*, in the Lamarck collection at the Geneva Museum, are probably from the original type-lot in Bruguière's

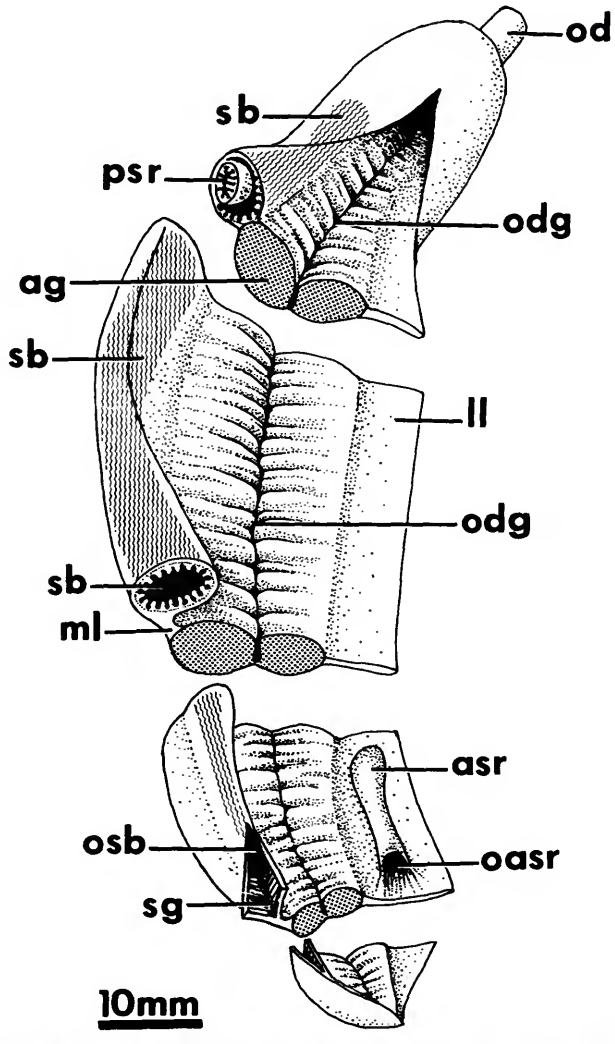

FIGURE 93.—Diagrammatic representation of pallial oviduct of *Cerithium nodulosum* (anterior at bottom). (Abbreviations: *ag* = albumin gland; *asr* = anterior seminal receptacle; *ll* = lateral lamina; *ml* = medial lamina; *oasr* = opening to anterior seminal receptacle; *od* = coelomic oviduct; *odg* = oviductal groove; *osb* = opening to spermatophore bursa; *psr* = posterior seminal receptacle; *sb* = spermatophore bursa; *sg* = sperm gutter.)

collection, as many of his shells were passed on to Lamarck. The larger, 102 mm, has an underdeveloped aperture and outer lip, while the smaller, 100 mm, has a better developed lip. Neither shell appears to be the same as the shell figured by Bruguière (1791, planches, 442/3), but the smaller one closely matches Kiener's (1841, pl. 2: fig. 1) figure of *C. nodulosum*. The smaller shell is herein selected as the lectotype of *C. nodulosum* Bruguière (Figure 89A).

Although Perry's type of *C. curvirostra* has not been found, his illustration of it leaves no doubt that it is conspecific with *C. nodulosum*. The type of *Murex tuberosus* Dillwyn is lost, but was based on a mixed concept of *Pseudovertagus aluco* and *C. nodulosum*, as may been seen by consulting his figure references, and is best regarded as a nomen dubium. The paralectotype of *Matilda eurytima* Melvill and Standen (Figure 89E) is clearly a juvenile of *C. nodulosum*. Sowerby's figures of *Cerithium tuberosum* (1855, pl. 178: fig. 49) and his subsequent figure (1865, pl. 1: fig. 5) are both clearly representations of the Red Sea phenotypes of *Cerithium nodulosum*. Bayle (1880:250), noting that *tuberosum* was preoccupied, proposed the replacement name *Cerithium omissum* for *C. tuberosum* Sowerby.

Some authors have referred Bruguière's (1792) name, *nodulosum*, to the genus *Contumax* Hedley, 1899, but the type species of that genus, *Contumax decollata*, as later noted by Hedley (1914:738), is conspecific with *Cerithium nodulosum*, and *Contumax* thus becomes a synonym of *Cerithium*.

ECOLOGY.—This species is commonly found just shoreward of reef edges, on intertidal and subtidal rocky shelves, having veneered sand and shallow, sandy depressions. Museum records indicate that this kind of habitat is consistent throughout the geographical range of *C. nodulosum*. I have observed populations in similar habitats at Enewetak Atoll, Marshall Islands; Pago Bay, Guam; New Caledonia; Fiji; and Lizard Island, Queensland, Australia. Yaron (1979:233) recorded that large populations of Red Sea *erythraeonense* phenotypes live in shallow, subtidal, sandy patches in a lagoon behind the reef at Ras Bourka, Gulf of Aqaba. More detailed discussions of the habitat of this species are presented in Houbrick (1971:560) and Yamaguchi (1977:249–251).

Cerithium nodulosum attaches its crescent-shaped egg mass, containing huge numbers of embryos, on rocky substrate, and these undergo partial development and are released at the veliger stage into the plankton. Reproductive biology, spawn, and larvae have been treated in detail elsewhere (Houbrick, 1971). Yamaguchi (1977) has investigated the growth and mortality rates of a population on Guam and found that the adult stage, characterized by formation of the distinctive aperture and outer lip, was reached within three years of settlement. This determinate growth did not result in the same size for adults, as there was considerable variation in shell length of non-growing adults (Yamaguchi, 1977:259). The Guam population showed irregular or semi-annual recruitment. Young snails were predominant in the inner reef flat, but migrated to the middle reef flat as they approached the adult stage.

Predation has not been observed on adults of *C. nodulosum*, but the species is used as bait by man in some regions (Yamaguchi, 1977:262). Although Yamaguchi (1977:262) found high mortality rates of 15–20 percent per month for growing juveniles, it is doubtful that many predators can break the heavily armored, adult shell of *C. nodulosum*.

DISCUSSION.—The major distinguishing characters of *C. nodulosum* are its great size and the large, spirally arranged nodes on each whorl; no other living *Cerithium* species

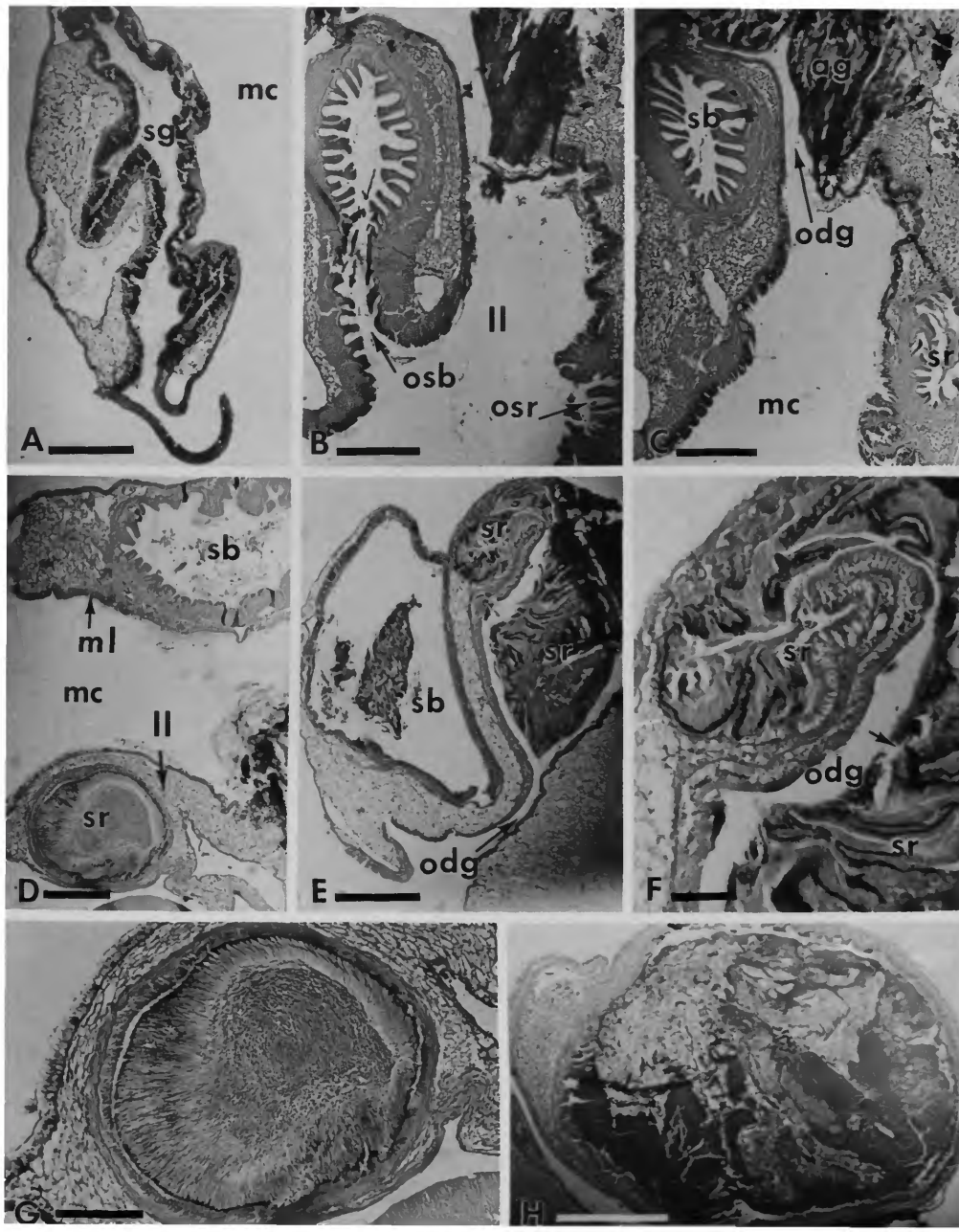

FIGURE 94.—Sections of pallial oviduct of *Cerithium nodulosum* Bruguière: A, anterior section showing sperm groove (sg) and mantle cavity (mc) (bar = 0.5 mm); B, openings to spermatophore bursa (osb) in medial lamina (ml) and to anterior seminal receptacle (osr) in lateral lamina (ll) (bar = 0.5 mm); C, anterior section through spermatophore bursa (sb) and anterior seminal receptacle (sr) showing oviductal groove (odg) and albumin gland (ag) (bar = 0.5 mm); D, medial section showing mantle cavity (mc), anterior seminal receptacle (sr) with oriented sperm in lateral lamina (ll), and spermatophore bursa (sb) in medial lamina (ml) (bar = 0.4 mm); E, posterior section through medial lamina showing oviductal groove (odg), spermatophore bursa (sb) with disintegrating sperm in center, and posterior seminal receptacle (sr) of medial lamina (bar = 0.5 mm); F, detail of opening of posterior seminal receptacle (sr) of medial lamina to oviductal groove (odg) (bar = 0.15 mm); G, anterior seminal receptacle with oriented sperm (bar = 0.2 mm); H, spermatophore bursa of medial lamina containing disintegrating spermatophore (bar = 0.63 mm).

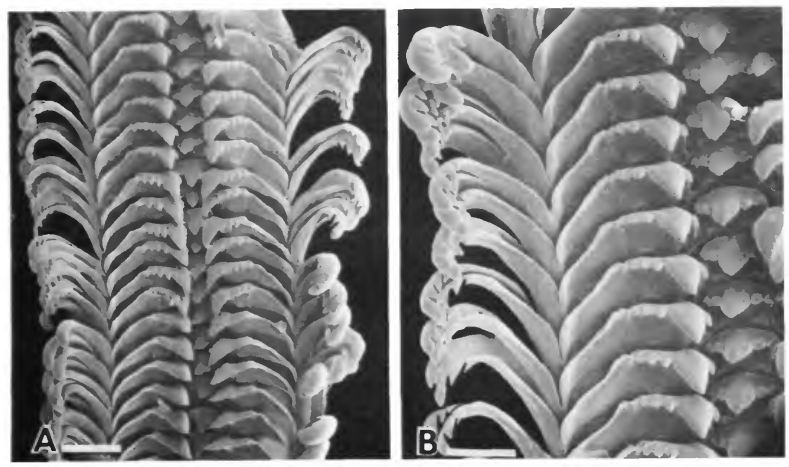

FIGURE 95.—Radula of *Cerithium nodulosum* Bruguière, Suez, Egypt, USNM 23145): A, radula with marginals spread open (bar = 0.22 mm); B, half row showing dentition of rachidian, lateral, and marginal teeth (bar = 160 μm).

approaches it in size or shape. The hook-like lower lip of the aperture extending over the anterior siphonal canal, and the marked difference in sculpture between immature and adult shells are other unique features. *Cerithium nodulosum* has determinate growth and is not likely to be confused with any of its congeners. The only species approaching it in size is *C. echinatum* Lamarck, which has much different sculpture. Some large *Pseudovertagus* species may possibly be confused with *C. nodulosum*, but none of these has wide body whorls, similar apertures, or comparable nodulose sculpture. They do, however, share the unusual cancellate sculpture of the early whorls of *C. nodulosum*, and immature individuals of both species are difficult to distinguish. This may indicate a phyletic link between *Cerithium* and *Pseudovertagus*, but more comparative anatomy is needed to pursue this. Surprisingly, the large potamidid, *Pyrazus ebininus*, (Bruguière) closely resembles *C. nodulosum* in size and overall morphology, but differs in having a strongly flared outer lip and a well-developed, wide anal canal. *Pyrazus* is not likely to be found with *C. nodulosum*, as it is restricted to muddy estuarine environments in a limited area of Australia.

There is little intraspecific variation in *Cerithium nodulosum*. Shell and radular morphologies of populations from the central Pacific closely resemble those from eastern Africa. An allopatric variety exists in the Red Sea that has been given the name *C. erythraeonense* (Figure 90). Sowerby (1865, species 5) pointed out that individuals from Red Sea populations (cited as *C. erythraeonense* Lamarck) have a smaller, less heavy, more lightly pigmented shell, with a longer canal, a more angulate and sharply notched outer lip, and more delicate, sharp shell sculpture than those in other parts of the Indo-Pacific. Jousseaume (1930:273) remarked that considering the intraspecific variation commonly seen in *Cerithium* species, the Red Sea forms are best considered as a race or local variety, and I concur with this judgement. Aside from the smaller size and lighter color of individuals from Red Sea populations, there appear to be no statistical differences in shells from other populations. Moreover, there are no radular differences between the Red Sea populations (Figure 95) and other allopatric morphs (Figure 90A-C). Although the *erythraeonense* morphs are confined to the Red Sea and thus satisfy one criterion for subspecific status, other evidence supporting this hypothesis is lacking, and until detailed anatomical and biochemical studies are made between these populations, it is premature to confer formal taxonomic status to Red Sea *erythraeonense* phenotypes.

FOSSIL RECORDS.—*Cerithium nodulosum* has been recorded from the late Miocene of Bikini Atoll, Marshall Islands, from the Neogene of Palau, from the Pliocene-Pleistocene of Guam, and from the early Miocene of Fiji (Ladd, 1972:39). A large, undescribed, Pleistocene species from Santo Domingo (Caribbean) looks very much like *C. nodulosum*, (Houbrick, per. obsr.) and may be a Tethyian relation.

GEOGRAPHIC DISTRIBUTION (Figure 96).—This species has an Indo-West Pacific distribution. It occurs in suitable habitats along tropical continental shores and among island groups throughout the Red Sea and Indian Ocean, although no records exist for India. It is found throughout SE Asia, Indonesia, and the tropical parts of Australia. In the Pacific, it ranges from the Ryukyus south throughout Melanesia, Micronesia, Tokelau, and Samoa. Barash and Danin (1972:307) recorded that although this species is common in the Suez Canal, only one worn shell has been found on the Mediterranean coast of Israel.

SPECIMENS EXAMINED.—EAST AFRICA: NE Nacala Bay,

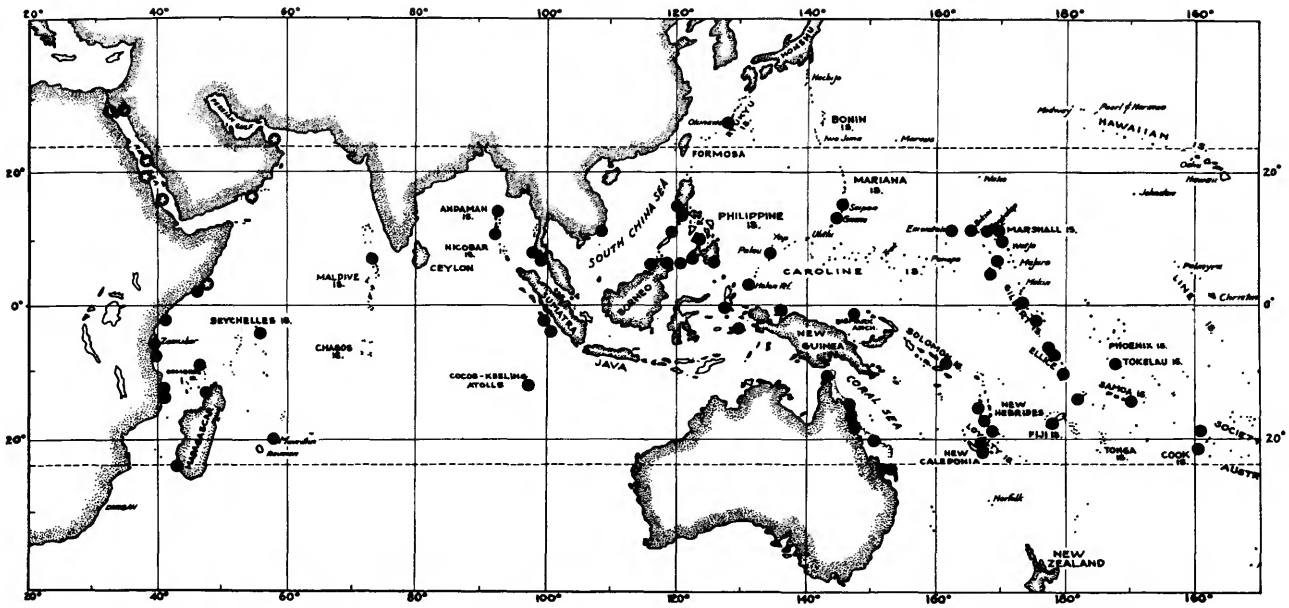

FIGURE 96.—Geographic distribution of *Cerithium nodulosum* Bruguière (solid circles) and *erythraeonense* morphs (stars).

(Porto Belmore), Mozambique (NM H1910); SE Lunga Bay, off Colajido, Mozambique (NM H1913); Wimbe Beach, Port Amelia, Mozambique (NM G3518); Oyster Bay, 6.4 km N of Dar es Salaam, Tanzania (MCZ); Chumbe Id, SW Zanzibar (ANSP); Bweju, SE Zanzibar (USNM 604465); Mnazi Moja, Zanzibar City, Zanzibar (USNM 604416); Bawe Id, Zanzibar (MCZ, USNM 597146); Chango Id, W Zanzibar (MCZ); Shimona, Kenya (AMNH); Likoni, Mombassa, Kenya (BMNH); Malindi, 121.6 km N of Mombassa, Kenya (USNM 595052); Mogadiscio, Somalia (AMNH).

RED SEA: Suez, Egypt (MCZ, USNM 23145, 31726, 77358); 64 km S of Suez, W shore, Gulf of Suez, Egypt (USNM 789910); Ras Matamura Cape, Gulf of Suez, Egypt (RMNH); Ras Sukheir, Gulf of Suez, Egypt (RMNH); El Belahim, Gulf of Suez, Egypt (RMNH); Dahab, Gulf of Aqaba, Egypt (USNM 794181); Ras Abu Galum, Gulf of Aqaba, Egypt (USNM 794175); Ophir Bay, Gulf of Elat, Israel (USNM 769993); Nuweiba, Sinai, Israel (AMS); El Hibek, E Sinai, Israel (AMS); Eilat, Israel (AMNH, MCZ); Aqaba, Gulf of Aqaba, Israel (MCZ, USNM 671273); Aqaba, Jordan (USNM 841309, 841312); Jubal Straits, Egypt (ANSP); El Korathaba District, Egypt (AMNH); Port Sudan, Sudan (USNM 770716); Massawa, Ethiopia (ANSP); 0.6–1.5 m, E side of Taulud Id, Massawa, Ethiopia (AMNH); 15°48′N, 40°05′E, Dahlac Kebir Id, Dahlac Archipelago (USNM 702528); 0.6 m, Sharm Ubhur, 1 km from sea, 35 km N of Jiddah, Saudi Arabia (AMNH); Jiddah Harbor, Jiddah, Saudi Arabia (USNM 637001); near Jiddah, Saudi Arabia (USNM 852268); Entedebir, Somalia (USNM 672278); Mogadiscio, Somalia (USNM 673804). ARABIAN SEA: Muscat, Oman (USNM 798212); Salalah, S coast of Oman (AMNH).

MADAGASCAR: Nossi Sakatia, W Nossi Bé (MCZ); Ambatoloaka Beach, Pt Tafondro, Nossi Bé (USNM 719567); Ambatomboka, Nossi Bé (USNM 713407); W Mahatsinjo, S Nossi Bé (USNM 633343); reef off Tulear (USNM 718360); Grande Récif, Tulear (MCZ); NW side of Nossi Ve Id, 32 km SSW of Tulear (MCZ); Point Louis (MCZ). INDIAN OCEAN ISLANDS: Île Malabar, Passe Houareau, Aldabra Atoll, Seychelles (USNM 836574); Passe Yangue, Île Picard, Aldabra Atoll, Seychelles (USNM 837565); Passe Dubois, Île Picard, Aldabra Atoll, Seychelles (USNM 837905, 837932); Anse Royale, Seychelles (ANSP); Mahé, Seychelles (BMNH); Mauritius (MCZ); S half of Kendikolu Id, Miladummadu Atoll, Maldive Ids (ANSP); Nend Ongu Id, N Malosmadulu Atoll, Maldive Ids (ANSP); North Andaman Ids (BMNH); Port Blair, Andaman Ids (BMNH, USNM 173052); Alor Pinyu, NW side of West Id, Cocos Keeling Ids (USNM 656436); lagoon, N of N Lagoon, West Id, Cocos Keeling Ids (MCZ, USNM 589218).

THAILAND: Goh Sindarar Nua (Chance Id), (USNM 661286); Goh Huyong, Similan Ids (USNM 661213, 661462); Pulau Tanga, Butang Gp (USNM 661651). MALAYSIA: Gaya and Manukum Ids, Jesselton, Sabah (AMNH, USNM 658315); W Marudu Bay, N Borneo (USNM 632185); Karakid, S Banggi, N Borneo (USNM 632186); Sandakan, N Borneo (USNM 658103); Bohaydulong Id, N Borneo (USNM 657483); Mandi Barrah Id, Sabah (AMNH). VIET NAM: Nha

Trang Harbor, S Viet Nam (MCZ). RYUKYU ISLANDS: Okinawa (USNM 67096); reef off Ogimi, Okinawa (USNM 488130); Itoman Reef, Okinawa (AMNH). PHILIPPINES: Gubat, Sorsogon Prov, Luzon (ANSP, MCZ, USNM 631632); E coast Polillo Id (USNM 311119); Lubang Id (MCZ); Baliquias, Lubang Id (USNM 472972); Tilig Reef, Lubang Id (USNM 244062); Iling Id, Mindoro (MCZ); Gasan, Marinduque (USNM 303921); Conception Beach, Conception Id, Panay (USNM 845809); Cebu, Cebu (ANSP); Mantacao Id, off W Bohol (USNM 244001); Santa Cruz Id, off Zamboanga, Mindanao (USNM 243959); Samai Id, Davao Bay, Mindanao (MCZ); Palawan (MCZ); Cuyo Id, Cuyo Ids, Palawan (USNM 801557) Siasi, Sulu Archipelago (MCZ); Sitanki, Sitanki Id, Tawitawi Gp (USNM 243640); between Siasi and Bongao Ids, Sulu Archipelago (USNM 313966). INDONESIA: Pulau Bai, Batu Gp, off Sumatra (USNM 654610); Pulau Melila, off Sumatra (USNM 654436); Mega Mentawai Ids, SW of Sumatra (USNM 655059); Pulau Stupai, Mentawai Ids, SW of Sumatra (USNM 655234); SW tip Sanding Id, Mentawai Ids, off Sumatra (USNM 655235); Pulau Siburu, N of Sipora, SW of Sumatra (USNM 654729); W shore Veeckens Bay, S Pagi Id, SW of Sumatra (USNM 655010); Pulau Penju, S of Sumatra (USNM 661876); Kasiroeta Id, Moluccas (MCZ); Oong Bay, Mandidi Id, Moluccas (MCZ); Ceram, Moluccas (MCZ); Sorido Village, Biak Id, Schouten Ids, West Irian (USNM 600503).

QUEENSLAND, AUSTRALIA: Reef N of Terry Beach, W side of Price of Wales Id, Torres Strait (AMS C109728); Murray Id, Torres Strait (MCZ); Yam Id, Torres Strait (AMS C105852); Undine Reef, near Port Douglas (MCZ); Rudder Reef, NE of Port Douglas (AMS C114931); Low Islands (ANSP); Holmes Reef, off Cairns (AMS C93058); Double Id, near Cairns (MCZ); NE Herald Cay, Coral Sea (AMS); Porpoise Cay, Wreck Reef (AMS C142895); off Pebbly Beach, Lizard Id (AMS C108946, USNM 766735); Watt Reef, Townsville (AMS C67653); Hayman Id, 0.8 km NW of Hook Id, Whitsunday Passage (MCZ); Langford Reef, Whitsunday Gp (AMS C114932); Whitsunday Id, Whitsunday Gp (AMS C93061); Fairfax Id (USNM 666530); Fairfax Id, Bunker Gp, off Gladstone (AMS C69053); Bushy Cay (AMNH); Green Id (AMS C80247); Hope Id (AMS C28006). BISMARCK ARCHIPELAGO: Marop Reef, Manus Id, Admiralty Islands (AMNH). SOLOMON ISLANDS: Ataa, N Malaita Id (AMNH, MCZ). NEW HEBRIDES: Palikulo Bay, Espiritu Santo (USNM 686261); SE coast Santos Id (USNM 793711); Pointe d'Arbel, Efate Id (USNM 787540, 787815); reef near Ijipthav, Aneityum (USNM 692347).

LOYALITY ISLANDS: Île Beautemps-Beaupre, Atoll Beautemps-Beaupre (USNM 693148, 693165); Île des Pins, Atoll Uvea (USNM 692842, 692878, 692896); Îlots Deguala, Atoll Uvea (USNM 692985); outer reef, E of Île Longue, Atoll Uvea (USNM 692718); inner reef W of Îlot Styx, Atoll Uvea (USNM 692729); SE end Îlot Guetie, Atoll Uvea (USNM 692650); tip of Cape Lekin, Atoll Uvea (USNM 692793); SE side Îles Jumeaux, Atoll Uvea (USNM 693108); NW end Bandal Bay, Lifu (USNM 692603); SW end Bandal Bay, Lifu (USNM 692596, 692615); Baie de Gaitena, Lifu (USNM 782244). NEW CALEDONIA: (MCZ); bay S of village, Île Art (USNM 806131); Sand Cay, N of Kuea Bay, central N side of Id (USNM 693346); Bogota Reefs, central N side of Id (USNM 693381); SE side of entrance to Lavaissiere Bay (USNM 693454); Nani Id, central N side of Id (USNM 693482, 693528); reef off Nenou Id, central N side of Id (USNM 693588); E side Kuakue Bay, SE end of Id (USNM 693709); 8 km S of Touaourou (USNM 795361); W side Kouebuni Id (USNM 693841); Redika Id (USNM 724162); outer reef, opposite Nouméa (USNM 725178); Lighthouse opposite Nouméa (USNM 724398). FIJI: Off Oinafa, NE coast Rotuma (USNM 686185, 686192); Bega Id (MCZ); E end of Thakau Tanau Reef, Viti Levu (MCZ); Yanuca Id (ANSP).

MARIANA ISLANDS: Maug Id (USNM 486721); Saipan (MCZ, USNM 602459); lagoon, SW Tinian (MCZ); Tumon Bay, Guam (USNM 592825); Piti Bay, Guam (MCZ); bomb holes, Piti Bay, Guam (USNM 842630); Apra Harbor, Guam (USNM 243627, 243735); Talofofo Bay, Guam (MCZ); Cocos Id, SW Guam (ANSP). PALAU ISLANDS: Kayangel Id (MCZ, USNM 489013, 621125); reef, W Babelthuap Id (USNM 620928); Malakal Harbor, Malakal (MCZ); Ngaremediu Pt, SE side of Urukthapel Id (USNM 596162); Eil Malk (MCZ); Garakayo Id (MCZ, USNM 621121); reef, N of Gorokotau Id (USNM 621143). CAROLINE ISLANDS: Malakal Harbor, Upolu Id (USNM 621038); Round Rock, Helen Channel, Helen Rock (MCZ). MARSHALL ISLANDS: Rigili Id, Enewetak Atoll (USNM 581240, 581301, 581982); Teiteiripucchi Id, Enewetak Atoll (USNM 582026); Engebi Id, Enewetak Atoll (USNM 587622); Billee Id, Enewetak Atoll (USNM 587522); Rijoru Id, Enewetak Atoll (MCZ, USNM 584697); Aranit Id, Enewetak Atoll (USNM 587456); Aaraanbiru Id, Enewetak Atoll (USNM 582279, 582573, 582582); Muit Id, Enewetak Atoll (USNM 655686); Enewetak Id, Enewetak Atoll (USNM 801418); W side Bokororyuru Id, Bikini Atoll (USNM 584762); W central part Namu Id, Bikini Atoll (USNM 580517); ocean side Bikini Id, Bikini Atoll (USNM 579217, 579730, 579738, 584804, 585103); Yomyaran Id, Bikini Atoll (USNM 580461, 580508); Enyu Id, Bikini Atoll (USNM 580954); Naen Id, Rongelap Atoll (USNM 585355); Lomuilal Id, Rongelap Atoll (USNM 584808, 585007); Kieshiechi Id, Rongelap Atoll (USNM 585418); Kabelle Id, Rongelap Atoll (USNM 582399); Bigonattam Id, Rongerik Atoll (USNM 586339); Rongerik Atoll (MCZ); N end Bock Id, Rongerik Atoll (USNM 594654); Wotho Id, Wotho Atoll (USNM 614218); Kwajalein Atoll (USNM 486100); Bikar Atoll (USNM 615739); Utirik Id, Utirik Atoll (USNM 615636); NW corner Taka Islet, Taka Atoll (USNM 615429, 615506, 615551); Aikluk Id, Ailkuk Atoll (USNM 615091); between Nedo and Likiep Ids, Likiep Atoll (USNM 615305); Likiep Atoll (USNM 596142); lagoon side Uliga Id, Majuro Atoll (USNM 607560); N end Lijeron Id, Jaluit Atoll

(USNM 660038); E side Pinglap Id, Jaluit Atoll (USNM 659807); Ebon Atoll (MCZ).

GILBERT ISLANDS: W of Aiaka Maneaba, Onotoa Atoll (USNM 607618); between Rakai Ati and Rake Maneku, Onotoa Atoll (USNM 607674); S end Rakai Ati, Onotoa Atoll (USNM 607595, 607631); Abiang Id (MCZ); Apamama (USNM 433999); Kingsmills Id (MCZ). ELLICE ISLANDS: Near village, Vaitupu (USNM 686073); Funafuti Atoll (MCZ); lagoon shore near village, Funafuti Atoll (USNM 768900); N motu, reef flat, Nukulailai (USNM 685762); W side, Main Id, Nukulailai (USNM 685668, 685828). WALLIS AND HOORN ISLANDS: Passage to N Anse de Sagave, Futuna (USNM 676700); E side Anse de Sigave, Futuna (USNM 676480); N and S sides, Nukuhifala (USNM 676264); E of Nukuhifala (USNM 676351); NW of Mua, Alofi (USNM 676708, 676751); W shore, Faioa (USNM 676075, 676098). TOKELAU ISLANDS: S side Fenua Fala (USNM 768142); lagoon, N side Fenua Loa, S point, Fakaofu (USNM 768204); W point Mulifenua, Fakaofu (USNM 768280). SAMOA: W side of Apia Harbor, Upolu Id (MCZ); Tutuila (MCZ); Pago Pago, Tutuila Id (AMNH). COOK ISLANDS: 0.4 km N of Nikaupara Village, W Aitutaki (MCZ); S Rapoka Id, SE of Aitutaki (ANSP); 0.4 km N of Matavera, NE Rarotonga (MCZ).

Cerithium novaehollandiae A. Adams, 1855

FIGURES 97–99

Cerithium *Novae-Hollandine* [sic] A. Adams in Sowerby, 1855:864, pl. 178: fig. 54. [lectotype, one of 3 syntypes, herein selected: BMNH, 19861741, 3 paralectotypes 19861742–4; type locality: New Holland (Australia), herein restricted to Darwin, Northern Territory.]

Cerithium Novae-Hollandiae A. Adams.—Sowerby, 1865, pl. 5: fig. 30.—Watson, 1886:532.—Tryon, 1887:124, pl. 21: fig. 34.—Kobelt, 1893:123, pl. 23: fig. 8.—Cernohorsky, 1972:64, pl. 13: fig. 11.—Hinton, 1972, pl. 7: fig. 22, 22a.

Cerithium vignali Sowerby, 1912:237–238, fig. 1 [holotype: BMNH 1912816197; type locality: New Caledonia, herein restricted to Nouméa, New Caledonia].

DESCRIPTION.—*Shell* (Figure 97): Shell long, slender, turreted, reaching 49 mm length and 14.4 mm width, with 15–17 straight-sided to slightly convex whorls. Protoconch unknown. Early whorls sculptured with 3 spiral threads, second one being widest. Nodes and axial ribs beginning at fifth and sixth whorls. Adult whorls sculptured with 2–5 major spiral cords and numerous fine spiral striae crossed by 9 or 10 low, broad, slightly slanted axial ribs. Penultimate whorl with 10–16 axial ribs. Axial ribs sometimes nodular and nodes aligned with spiral cords. Subsutural spiral cord strongest. Axial sculpture normally predominant, but spiral sculpture sometimes strong and nodulose presenting overall granular appearance. Suture wavy. Aperture a little over one-third the shell length, oval to fusiform with concave columella, thick columellar callus, and distinct columellar lip. Outer lip of aperture moderately crenulate, thick. Anal canal well developed, flanked by small parietal columellar plait and pinched extension of outer lip forming slight anal canal. Anterior siphonal canal well developed, slightly reflected to left. Body whorl sculptured with 5 or 6 spiral, beaded cords and with large varix opposite outer lip of aperture; siphonal constriction forming strong concave base. Shell color white with presutural, broad, brown-tan spiral band on each whorl. Measurements (Table 31). Periostracum light tan.

Radula (Figure 98): Type-1 radula (Figure 3A). Rachidian tooth (Figure 98B,D) with triangular basal plate having central posterior projection flanked on each side by small pustule. Dorsal cutting edge of rachidian tooth rounded anteriorly and with central, arrow-shaped, pointed cusp flanked on each side by two sharp denticles. Lateral tooth (Figure 98B,D) trapezoid, with long lateral projection and thick, pillar-like, central buttress projecting posteriorly on basal plate; dorsal cutting edge with single inner denticle, large, sharply pointed cusp, and 3 or 4 smaller, sharp, outer denticles. Marginal teeth (Figure 98C,D) long, curved, with leaf-like ends having rounded denticles and tips. Inner marginal tooth with 3 or 4 inner denticles and 2 outer denticles. Outer marginal tooth same, but lacking outer denticles.

Anatomy: Animal brightly pigmented; head-foot yellowish, flecked with black. Head-foot with small pink pustules. Top of mantle with longitudinal brown stripes. Mantle edge papillate, having many longitudinal folds, and thickened at inhalant siphon. Interior of inhalant siphon with crescent-shaped, raised, pink, papillate ridge surrounding bright orange spot.

Ctenidium narrow, brown, becoming black anteriorly. Ctenidial filaments long, tapering. Hypobranchial gland large, wide, secreting considerable mucus. Rectum wide, longer than pallial oviduct.

Pallial oviduct long with long sperm gutter at anterior of medial lamina. Spermatophore bursa yellow, long, and narrow. Seminal receptacle not seen. Pallial oviduct type unclear.

SYNONYMIC REMARKS.—This poorly known species is aptly named, as it is essentially endemic to Australiasia. The lectotype (Figure 97A) is the common phenotype. I consider *Cerithium vignali* Sowerby, 1912 (Figure 97F), from New Caledonia, to be conspecific with *Cerithium novaehollandiae* (see "Discussion" below).

ECOLOGY.—*Cerithium novaehollandiae* lives in low, intertidal to shallow subtidal, sand-rubble habitats associated with fringing reefs. I observed a population at Magnetic Island, Queensland, Australia, in which individuals partially burrowed in the substrate, but were not infaunal. As the spawn mass, larvae, and the protoconch are unknown, it is not possible to infer the mode of development. The rectum of live-collected individuals is filled with sand grains and organic matter.

DISCUSSION.—The major characters defining this species are a relatively large, slender shell pigmented with a wide, brown, presutural band and sculpture of 11–16 low, broad, axial ribs

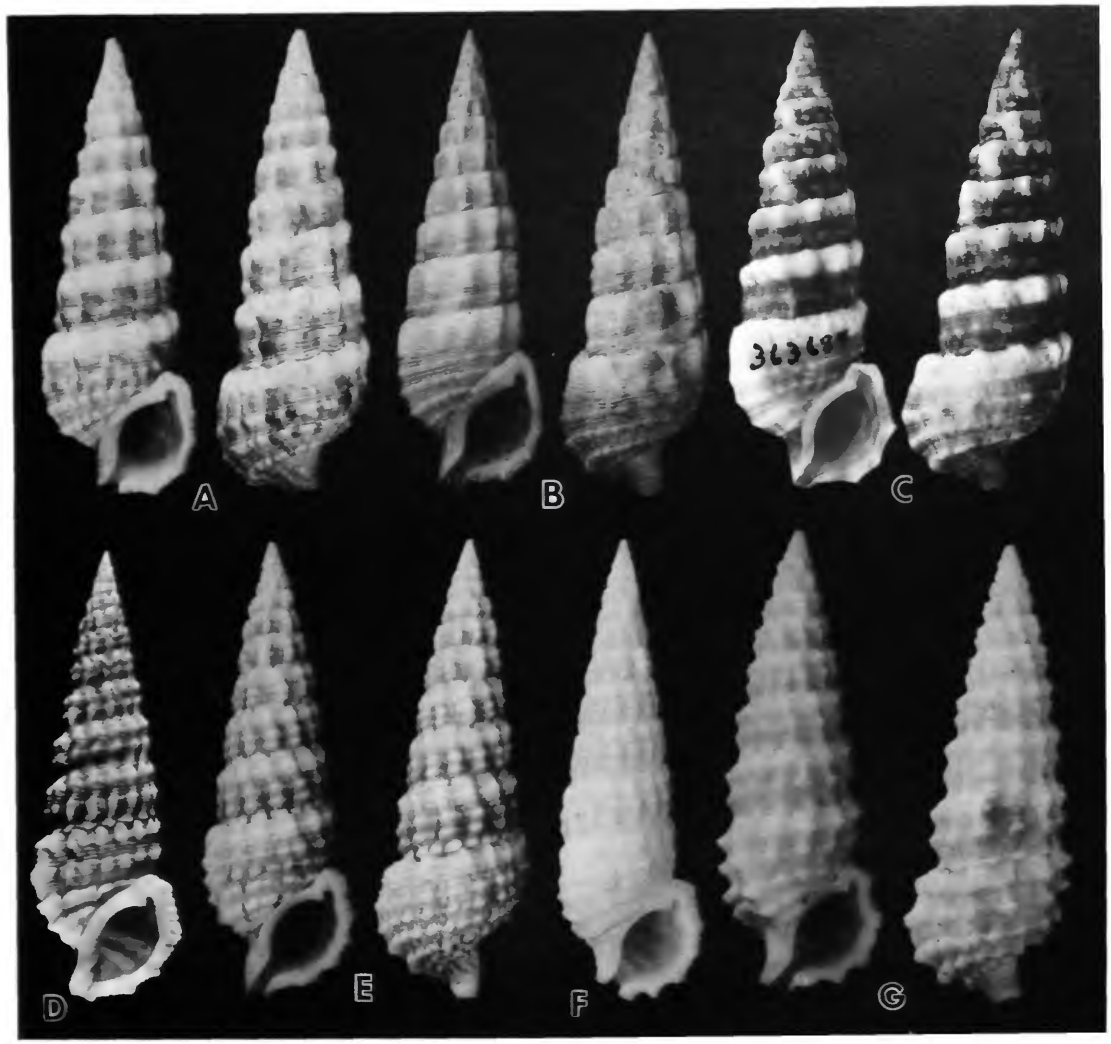

FIGURE 97.—Types of *Cerithium novaehollandiae* A. Adams showing phenotypic variation: A, lectotype of *Cerithium novaehollandiae*, 38.7 mm (BMNH 19861741); B, Augustus Id, Western Australia, 41.5 mm (MCZ); C, Waki, Satsuma, Japan, 35 mm (USNM 363684); D, Michaelmas Cay, NE of Cairns, Queensland, Australia, 43.8 mm (AMS); E, Baie de Citron, Nouméa, New Caledonia, 36.5 mm (ANSP 270970); F, holotype of *Cerithium vignali* Sowerby, New Caledonia, 35.9 mm (BMNH 1912816197); G, Tataan, Simalac Ids, Tawitawi, Philippines, 21.9 mm (USNM 243704).

TABLE 31.—Shell morphometrics of *Cerithium novaehollandiae*.

Character	$\bar{x}$ (n = 22)	sd	v	Range
Shell length	38.3	6.8	46.9	24.5–49
Shell width	11.4	2.7	7.3	8.6–14.4
Aperture length	10.1	1.4	1.9	8.3–12.2
Aperture width	6.8	1.1	1.1	5–8.9
Number whorls	16.2	0.7	0.5	15–17
Number axial ribs	11.9	1.8	3.2	10–16
Number nodes per rib	1.5	0.6	0.3	1–3

and numerous, tiny, incised, spiral lines. The axial ribs tend to be slanted and medially constricted, sometimes becoming nodular and aligning to form 2 or 3 spiral cords.

Cerithium novaehollandiae, especially phenotypes from Japan (Figure 97C), may be confused with the sympatric *Cerithium lifuense* Melvill and Standen, 1895, but the latter species lacks incised spiral lines and tends to have spinose nodules (Figure 71A–G). Shells of these two species should be carefully compared (see p. 103 under *C. lifuense*).

Cerithium novaehollandiae displays considerable intraspeci-

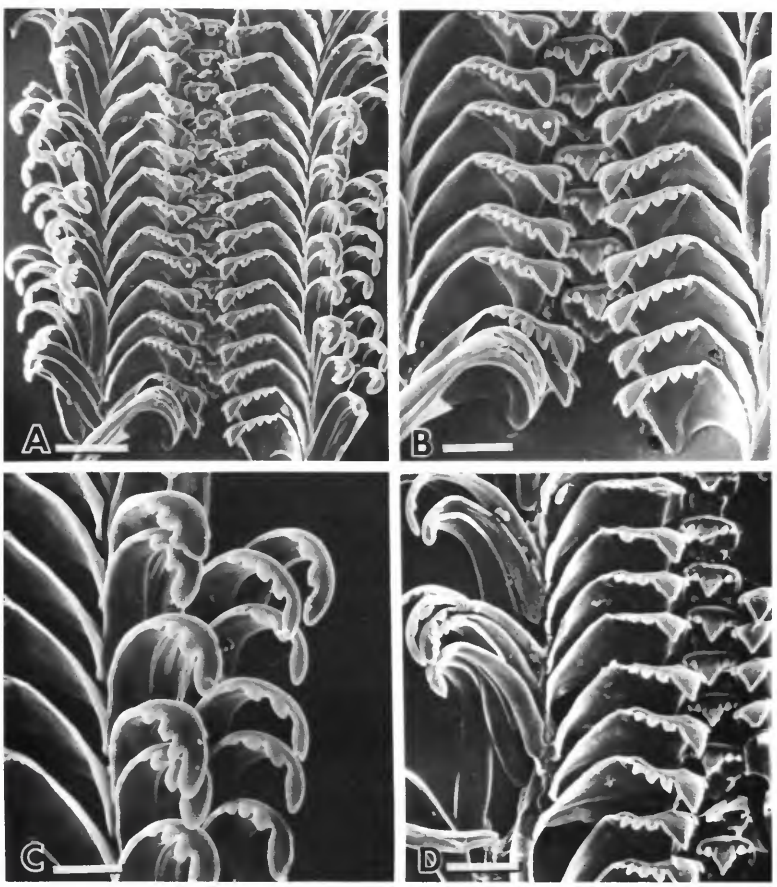

FIGURE 98.—Radula of *Cerithium novaehollandiae* A. Adams: A, radula with marginals spread open, E Port Darwin, Western Australia (bar = 160 μm; MCZ); B, detail of rachidian and lateral teeth, same data as A (bar = 68 μm); C, detail of marginal teeth, same data as A (bar = 43 μm); D, half row, Broome, Western Australia (bar = 84 μm; ANSP 232999).

fic variation in shell sculpture. The largest individuals examined are from northern Australia. Individual populations show only minor variation in shell sculpture, and the basic phenotype in each population appears to be correlated with the local environment. For instance, western and northern Australian populations from intertidal, low energy, silty, sand habitats comprise individuals with shells with or without weak nodules on their axial ribs and with ribs extending across the entire length of the whorl (Figure 97A,B). In contrast, shells from off-shore, low, sandy cays associated with extensive reefs tend to lose the brown bands and are whiter and extremely nodulose, with the nodules lining up to form two spiral cords (Figure 97D,G). Some of these forms have convergent shell sculpture and live in microsympatry with *Cerithium columna* Sowerby and *Rhinoclavis aspera* (Linné). Shells from New Caledonia and the Loyalty Islands have more axial ribs (16), which are broken into three nodes (Figure 97E,F). These forms were given the name *Cerithium vignali* Sowerby, 1912 (Figure 97F), but are identical with off-shore, sandy cay phenotypes from Australia and New Guinea (USNM 862512, ANSP 205036). Given the range of variation in the species and the lack of geographic segregation among phenotypes, these minor sculptural differences do not warrant specific or subspecific recognition.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 99).—From New Guinea and New Britain south to Western Australia, Northern Territory, and Queensland, Australia, and to New Caledonia and the Loyality Islands. The one record from the Sulu Archipelago, Philippines needs reconfirmation.

SPECIMENS EXAMINED.—PHILIPPINES: Tataan, Simaluc Islandas, Tawitawi (USNM 243704). WESTERN AUSTRALIA: Perth (AMS C30446); N of islet SW of Gun Island, Houtman Abrolhos islands (WAM); W of Gun Island,

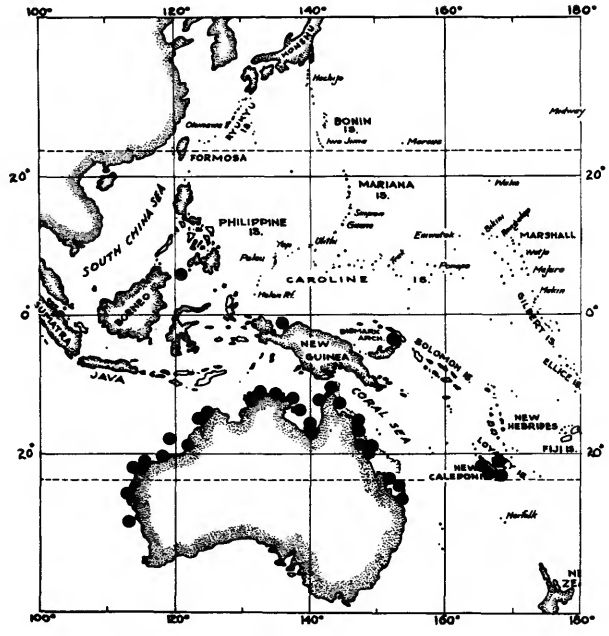

FIGURE 99.—Geographic distribution of *Cerithium novaehollandiae* A. Adams.

Houtman Abrolhos islands (WAM); N side of Gun Island, Houtman Abrolhos islands (WAM); Beacon Island, Goss Passage, Houtman Abrolhos islands (WAM); W side of White Bank, N Rat Island, Houtman Abrolhos islands (WAM); 3.7 m, Good Friday Bay, Houtman Abrolhos islands (LACM 66-217); Geraldton (AMS C51375); SE of Dirk Hartog Island (WAM); Carnarvon (AMS); Mangrove Bay area, North West Cape (WAM); Learmouth, Exmouth Gulf (WAM); 16 km S of Exmouth town, Exmouth Gulf (WAM); 27.2 km S of Exmouth town, Exmouth Gulf (AMS C69351); near Charles-Knife Road, Exmouth Gulf (WAM); Wapet Beach and Jetty, Exmouth Gulf (WAM); near old cannery jetty, Exmouth Gulf (WAM); Bay of Rest, Exmouth Gulf (WAM); Onslow (AMS C90848); W of Flat Island, near Long Island, off Onslow (WAM); W of Flat Island, near Onslow (WAM); Thevenard Island, off Onslow (WAM); W of Rat Island, near Big Island, off Onslow (WAM); Weld Island (AMS); NE side of Sholl Island, Passage islands (WAM); E of Cape Poivre, Barrow Island (USNM 691753); Barrow Island (WAM); Bandicoot Bay, Barrow Island (USNM 694074); North West Island, Montebello islands (WAM); Eaglehawk Island, Dampier Archipelago (WAM); SW of W Point, Kendrew Island, Dampier Archipelago (WAM); Boat Bay, Kendrew Island, Dampier Archipelago (WAM); E side of Kendrew Island, Dampier Archipelago (WAM); NE end of Rosemary Island, Dampier Archipelago (WAM); Delambre Island, Dampier Archipelago (WAM); off Legendre Island, Dampier Archipelago (WAM); Back Beach, Dampier (WAM); boat passage between Dampier Peninsula and Dolphin Island (WAM); W of Long Island, Passage islands (WAM); Port Headland (USNM 824805); Emu Creek, W end of Sinclair Bay (USNM 631194); Cape Bossut (WAM); Roebuck Bay (AMNH); Broome (AMS C51010, ANSP 232999, MCZ, UF); entrance point, Broome (ANSP); N of Cable Beach, Broome (WAM); 1.6 km NE of Gantheaume Pt, Broome (ANSP); Clerke Reef, Bedwell Island, Rowley Shoals (WAM); Augustus Island (MCZ); Coronation Island, Bonaparte Archipelago (WAM 456-76); Walsh Point, Admiralty Gulf (WAM); Corneille Island, Institut islands (WAM); Port Sampson (WAM).

NORTHERN TERRITORY, AUSTRALIA: Port Darwin (ANSP, MCZ, WAM); Fanny Bay, Darwin (AMNH, AMS C99779); E arm of Darwin Harbor (AMS); E Port Darwin (AMS); Smith Pt, Port Essington, Coburg Peninsula (AMS C73621, C122916); Black Pt, Port Essington (AMS); Vashon Head, Port Essington, Coburg Peninsula (AMS); Berkeley Bay, E side of Port Essington, Coburg Peninsula (AMS); Sandy Island, Coburg Peninsula (WAM); Crocker Island, near Coburg Peninsula (AMS C77615); Goulbourn Island, near Coburg Peninsula (AMS C92647); Malay Bay (AMS C77154); Crocodile Island, NE of Boucaut Bay (AMS C90470); Elcho Island, Wessel islands (AMS C101943); SW Bay, Groote Eylandt, Gulf of Carpentaria (AMS C61438); Yirrkala Mission (AMS C74880, C92805).

QUEENSLAND, AUSTRALIA: Forsyth Island, Gulf of Carpentaria (AMS C14799); Mornington Island, Gulf of Carpentaria (AMS); Bountiful Island, Gulf of Carpentaria (AMS); Mapoon Mission, Gulf of Carpentaria (AMS C14284); Terry Beach, W side of Prince of Wales Island, Torres Strait (AMS); 16.5 m, Prince of Wales Channel (BMNH *Alert*); lee of Turtle Island, Cape York (AMS); 5.5–21.9 m, off Albany Island, Cape York, Torres Strait (BMNH); Stover Bay, Somerset, Cape York Peninsula (AMS); Portland Roads (MCZ); Lizard Island (AMS, USNM 766740, 766951); Cape Flattery (AMS C41326); Low islands, near Port Douglas (AMS); Low Isles (AMS); Four Mile Beach, Port Douglas (AMS); Michaelmas Cay, N of Cairns (AMS); Buchans Pt, N of Cairns (AMS); Cairns (AMS); Kurramine Beach, S of Innisfail (AMS); Dunk Island, S of Innisfail (AMS); Eclipse Island, Palm islands (AMS); Little Broadhurst Reef, E of Townsville (AMS); Geoffrey Bay, Magnetic Island, off Townsville (AMS, USNM 836908); Picnic Bay, Magnetic Island, off Townsville (AMS); Bowen (AMS); Dingo Beach, SE of Bowen (AMS); Edgecumbe Bay (AMS C98737); Langford Reef, Hook Island (AMNH); Hook Island (AMS C84481); Cid Harbor, Whitsunday islands (AMNH); South Molle Island (USNM 845783); Lupton Island, Cumberland Gp (MCZ); Long Island, Whitsunday Gp (AMS); Hamilton Island, Whitsunday Passage (AMS); Lindeman Island, Cumberland Gp (AMS, ANSP 138535); Brampton Reef, near Bowen (AMNH); Mackay (AMS C76996); Seaforth, near Mackay (AMS C98739); Flat Top Island, near Mackay (AMNH,

USNM 622984); N Keppel Island (AMS C67772); Keppel Bay (AMNH, USNM 824773); 21 m, Wistari Reef, Capricorn Gp (AMS); Pt Vernon (AMS); Pialba Beach, Hervey Bay (AMS); Peel Island, Moreton Bay (AMS); Carter Reef (DMNH 31481, USNM 862512).

NEW GUINEA: Reef E of Noesi Isle, Mios Woendi Atoll, Padaido islands, Irian Jaya (ANSP 205036). BISMARCK ARCHIPELAGO: Duke of York Island, New Britain (AMS). LOYALITY ISLANDS: Lifu (AMS, MNHNP); Île de Pins, Atoll Uvea (USNM 692864, 692929). NEW CALEDONIA: Numerous stations from western side of island (MNHNP); 2.1 m, N side of Baie de Citron, Nouméa (ANSP 270970); 0.6–1.5 m, Île Ain, 4.8 km ENE of Touho (ANSP 270267); 1.2–2.1 m, SE side of bay, Touho (ANSP 270350); Touaourou (USNM 784154).

Cerithium ophioderma (Habe, 1968), new combination

FIGURES 100–102

Proclava ophioderma Habe, 1968:27(3); 87(88), fig. 1 [holotype: NSMT 38666; paratype: USNM 766591; type locality: Okinoshima, near Cape Ashizuri, Shikoku, Japan].—Okutani, 1972:82, fig. 18; 1975:189, pl. 10: fig. 23.—Inaba and Oyama, 1977:90–91.

DESCRIPTION.—*Shell* (Figure 100): Shell elongate, turreted, reaching 51 mm length, comprising 16–20 straight-sided whorls, and having apical angle of 20 degrees. Protoconch unknown. Earliest teleoconch whorls inflated, sculptured with three spiral cords and broad axial ribs. Adult teleoconch whorls sculptured with three spiral cords, lower two wide, weakly nodulose or plicate; subsutural spiral cord thin and most plicate, separated from lower two cords by thin, spirally constricted thread. Thin spiral thread below suture. Plications with weak nodes closely adpressed and pointing toward shell apex, forming scaly, file-like appearance. Nodes aligned axially. Varices randomly distributed. Suture indistinct, slightly wavy. Body whorl large, much inflated, with about 10 or 11 spiral cords. Subsutural spiral cord plicate. Very large, thick varix on body whorl opposite outer lip. Body whorl with sharp siphonal constriction. Aperture round-ovate, about one-fifth shell length. Anterior siphonal canal moderately long, thin, directed anteriorly, but turned slight to left of shell axis and reflected dorsally. Anal canal distinct with parietal columellar plication extending into shell aperture. Columella concave with narrow parietal callus and thickened parietal lip. Outer lip semicircular, thin, flaring, slightly crenulate. Shell color white with tan blotches and numerous, tan, axial lines broken by spiral ridges, presenting overall spotted appearance. Measurements (Table 32). Operculum thin, light tan.

Radula (Figure 101): Type-3 radular ribbon, short, small. Rachidian tooth (Figure 101B) rectangular, with small, central, posterior projection, and pair of lateral posterior ridges and projections on basal plate; anterior front concave having cutting edge of central, long-pointed cusp, grooved on each side, and flanked on each side by two denticles. Basal plate of lateral tooth (Figure 101B) broad, flat, with wide central buttress projecting downward, ending in ridge, and with short lateral projection; cutting edge with large main cusp, one inner denticle, and 2 or 3 outer denticles. Marginal teeth (Figure 101) with broad spatulate bases and hooked serrated tips; inner marginal tooth tip with long main cusp, three inner cusps, and one outer cusp; outer marginal same, but lacking outer cusps.

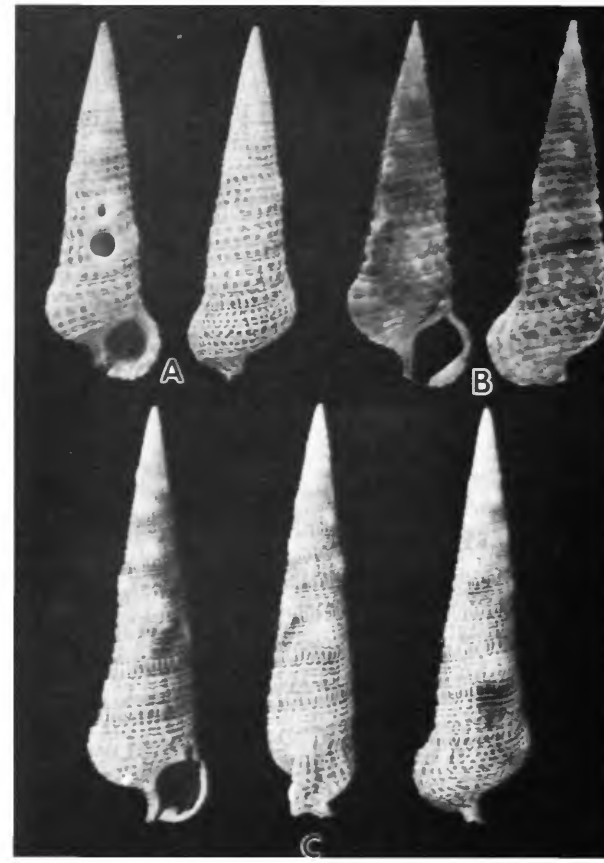

FIGURE 100.—*Cerithium ophioderma* (Habe): A, holotype, Okinoshima, Kachi Pref., Shikoku, Japan, 36.5 mm (NSMT 38666); B, South China Sea, 29.5 mm (NSMT 57137); C, large specimen from Mactan Id, Bohol Strait, Philippines, 50.8 mm (USNM 862958).

Anatomy: Eyes present in dried specimen.

SYNONYMIC REMARKS.—In the original description, this species was assigned by Habe (1968:90) to the genus *Proclava* Thiele, 1929, but the latter taxon has been shown to be a subgenus of *Rhinoclavis* Swainson (Houbrick, 1978b:69). Members of *Proclava* are characterized by a distinct mid-columellar plait, a heavy parietal callus, and long, reflected, anterior canal, all of which are lacking in the holotype of *Cerithium ophioderma* (Figure 100A). Habe (1968:91) noted a

TABLE 32.—Shell morphometrics of *Cerithium ophioderma*.

Character	$\bar{x}$ (n = 5)	sd	v	Range
Shell length	37.8	8.0	63.3	29.5–51
Shell width	11.0	1.7	3.0	9.5–13.9
Aperture length	7.7	1.3	1.7	6.6–9.7
Aperture width	5.6	1.0	0.9	4.9–7.3
Number whorls	17.6	1.5	2.3	16–20
Number spiral cords	3.0	–	–	3

superficial resemblance between *Cerithium ophioderma* and *Rhinoclavis articulata* (Adams and Reeve, 1850; cited as *Cerithium attenuatum* Philippi, 1848). While it is true that both species have dominant plicae on the subsutural spiral cord and share a common morphology and color pattern, *R. articulata* has a columellar plait, a long, reflected, anterior canal, and a strong parietal callus, all clearly *Rhinoclavis* characters. *Proclava ophioderma* is herein transferred to *Cerithium*.

DISCUSSION.—This species most closely resembles *Cerithium matukense* Watson (Figure 79), but differs from it in having only three spiral, plicate, major cords per whorl, the most dominant one being subsutural. The body whorl varix is prominent and laterally placed in contrast to the lateral-ventral varix in *Cerithium matukense*. The plications on *Cerithium ophioderma* are placed closely together and do not line up in straight axial lines.

Because only a single specimen with a dried animal was available, anatomical data were not obtained. Eyes were present and the snout appeared to be short.

ECOLOGY.—Only nine lots of this species, several with poor bathymetric and locality data, were examined. Specific bathymetric information given with the original description (Habe, 1968), stated that collections were made by coral fishing nets at 50–100 m depth. Okutani (1975:185) recorded specimens from 200 m on an isolated submarine bank off Hachijo Island, separated from other banks by depressions of more than 1000 m. He noted that this bank is entirely in the

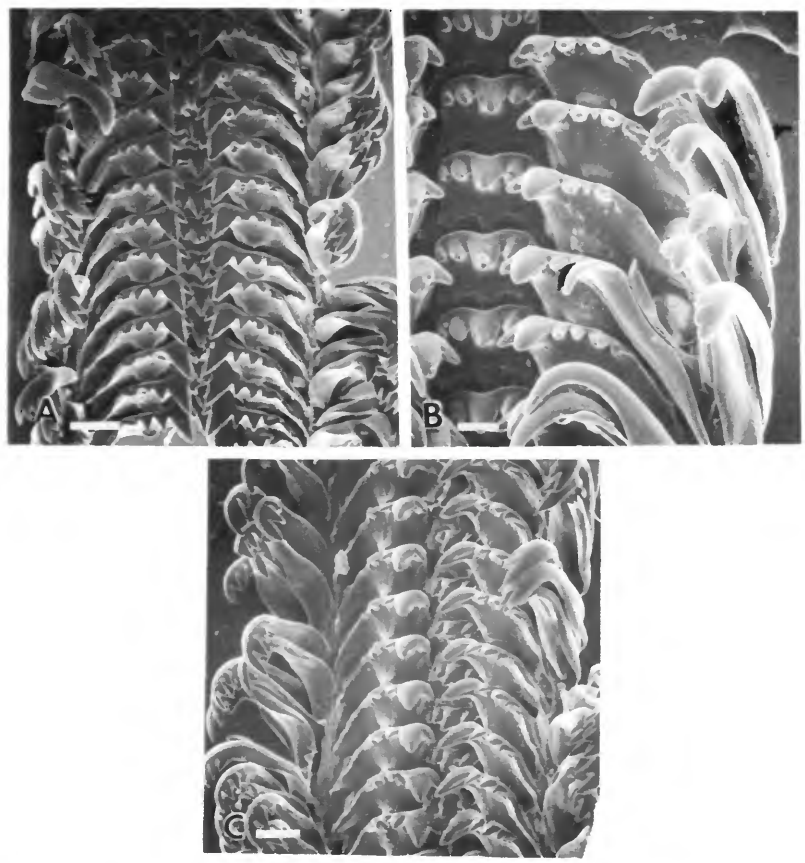

FIGURE 101.—Radula of *Cerithium ophioderma* (Habe) from Île des Pins, New Caledonia (MNHNP): A, radular ribbon with marginal teeth folded back (bar = 33 μm); B, detail of rachidian and lateral teeth (bar = 57 μm); C, lateral view of ribbon showing buttress on lateral teeth and details of marginal teeth (bar = 67 μm).

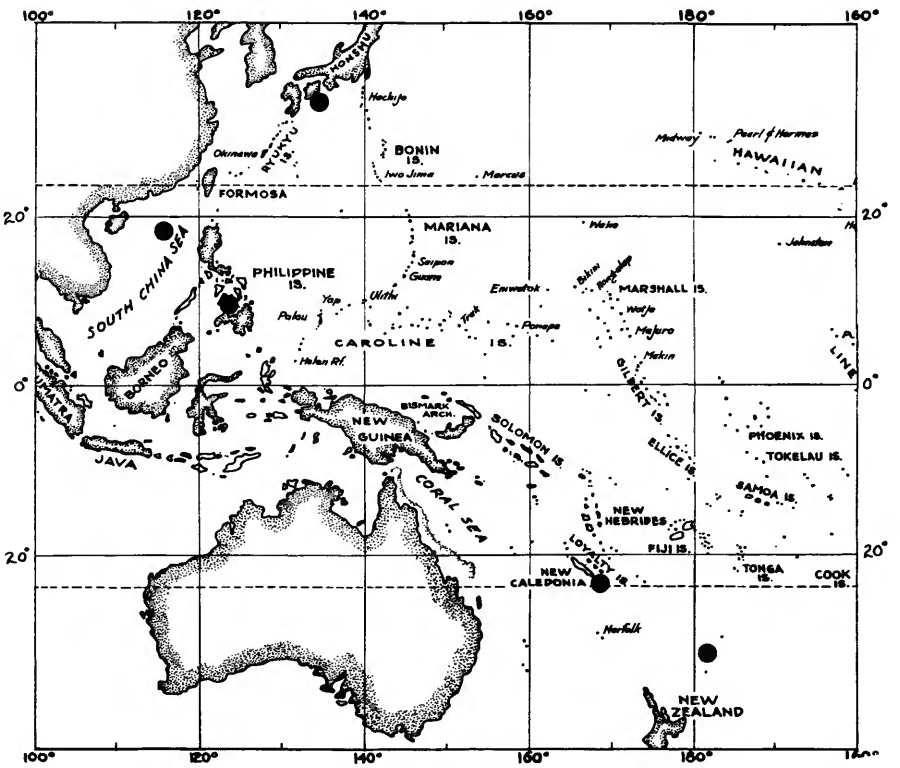

FIGURE 102.—Geographic distribution of *Cerithium ophioderma* (Habe).

Kuroshio current, which never lowers below 15° C at the depth of 200 m. The deepest depths recorded, 245–275 m, are from off New Caledonia. Specimens have recently been taken in the Philippines in tangle nets (Figure 100c). The elongate shell shape and sculpture indicate an infaunal, sandy habitat.

FOSSIL HISTORY.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 102).—The few records available indicate a restricted range in depths ranging from 50 to 275 m including southern Japan, the South China Sea, the Philippines, New Caledonia, and Kermadec Islands. *Cerithium ophioderma* was recorded by Okutani (1972:82) from 145 m, Zenisu Banks, off Izu-Shichito Ids, Honshu, but I have not seen the specimens.

SPECIMENS EXAMINED.—JAPAN: Shikoku (USNM 766591; paratype); Okinoshima, near Cape Ashizuri, Shikoku (NSMT 38666); Okinoshima, Kochi Pref, Shikoku (NSMT, USNM 862513). PHILIPPINES: Off Punta Engano, Mactan Id (USNM 845476, 862958). SOUTH CHINA SEA (NSMT 57137). NEW CALEDONIA: 233 m, N.O. *Vauban*, 24°45′S, 168°08′E and 24°42′S, 168°07′E, S of Île des Pins (MNHNP); 245–275 m, N.O. *Jean-Charcot* 24°48′S, 168°08′E, S of Île des Pins (MNHNP); 170 m, N.O. *Coriolis*, 23°24′S, 168° 07′E, S of Île des Pins (MNHNP). KERMADEC ISLANDS: 82–100 m, R.V. *Archeron*, 29°18.9′S, 177°56.4′W, SE of Smith Bluff, Raoul Id (NMNZ).

Cerithium pacificum, new species

FIGURES 103, 104

Clypeomorus traillii (Sowerby).—Springsteen and Leobrera, 1986:60, pl. 13: fig. 11 [not *Cerithium traillii* Sowerby, 1855; is *Cerithium pacificum*, new species].

DESCRIPTION (Figure 103).—*Shell:* Shell shiny, elongate, pupate, with convex apex, and comprising about 14 moderately convex adult whorls, reaching 27.1 mm length and 10.1 mm width. Protoconch unknown. Early teleoconch whorls with large axial ribs and having presutural cord divided into two weaker spiral cords forming presutural carinae. Axial ribs weaker and minor spiral cords appearing on successive whorls. Adult teleoconch whorls with very weak axial sculpture and with 3 spiral, weakly beaded cords. Subsutural beads axially elongate. Penultimate whorl sometimes with 4 spiral cords each having 14–35 small beads. Suture weakly defined, straight. Body whorl thin, moderately inflated, but narrowly constricted subsuturally, and sculptured with strong subsutural plications;

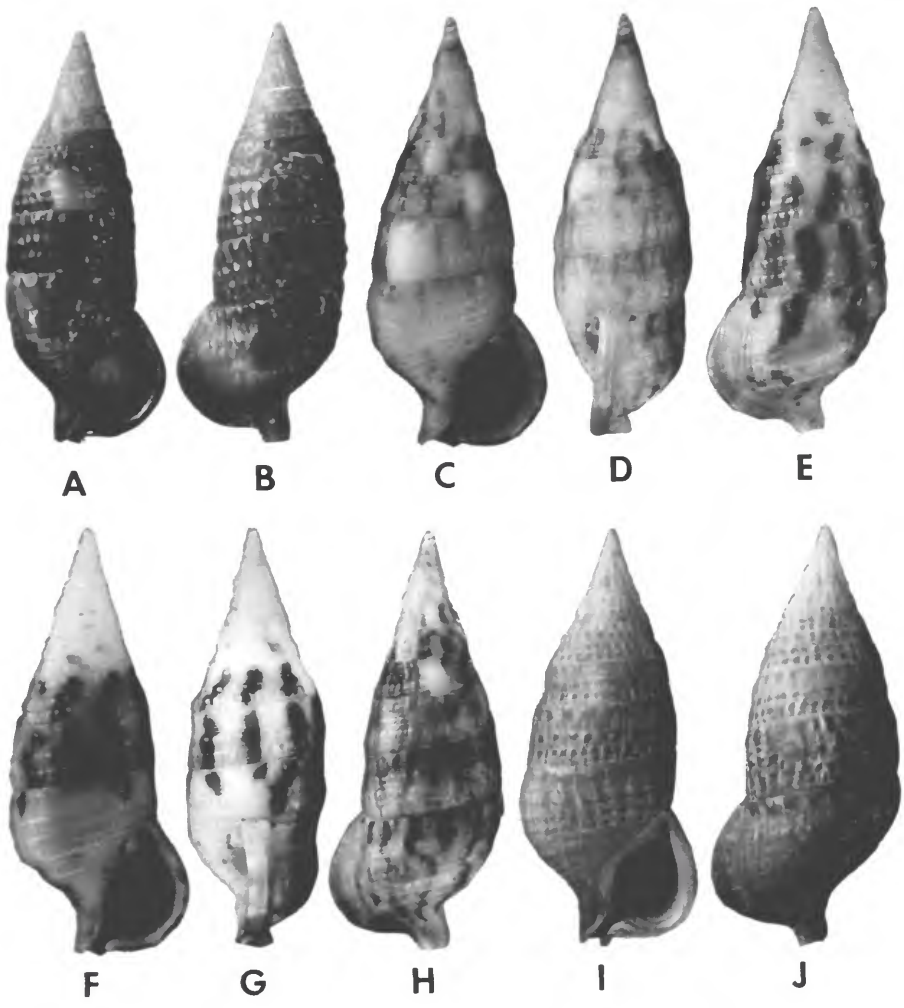

FIGURE 103.—*Cerithium pacificum*, new species, showing variability in color and sculpture: A,B, holotype, Bikini Atoll, Marshall Ids, 24 mm (USNM 584662); C-H, apertural, lateral, and adapertural views of two specimens from Punta Engano, Mactan Id, Cebu, Philippines, 18 mm and 16 mm, respectively (USNM 845803); IJ, 10 m, Enewetak Atoll, Marshall Ids, 24 mm (USNM 821845).

TABLE 33.—Shell morphometrics of *Cerithium pacificum*.

Character	$\bar{x}$ (n = 7)	sd	v	Range
Shell length	22.7	2.7	7.1	18.1-27.1
Shell width	8.6	0.9	0.9	7.0-10.1
Aperture length	6.0	0.7	0.4	5.3-7.1
Aperture width	3.7	0.6	0.3	3.3-4.7
Number whorls	14.1	0.4	0.1	14-15
Number spiral cords	3	-	-	3
Number beads	22.0	6.8	46.3	18-35

body whorl nearly smooth elsewhere except for weak spiral striae and large, broad varix opposite outer lip of aperture. Base of body whorl with slight basal excavation and moderately elongate, strongly constricted, anterior siphonal canal dorsally reflected to left of shell axis. Aperture narrowly ovate, about one-fourth the shell length. Columella concave with moderate callus and slight columellar lip. Anal canal well defined by parietal columellar tooth extending into aperture. Outer lip smooth, thickened, weakly flaired, and pendant. Shell color a shiny cream to tan; early whorls white. Some specimens cream with tan axial flammules. Measurements (Table 33). Periostracum thin, tan. Operculum unknown.

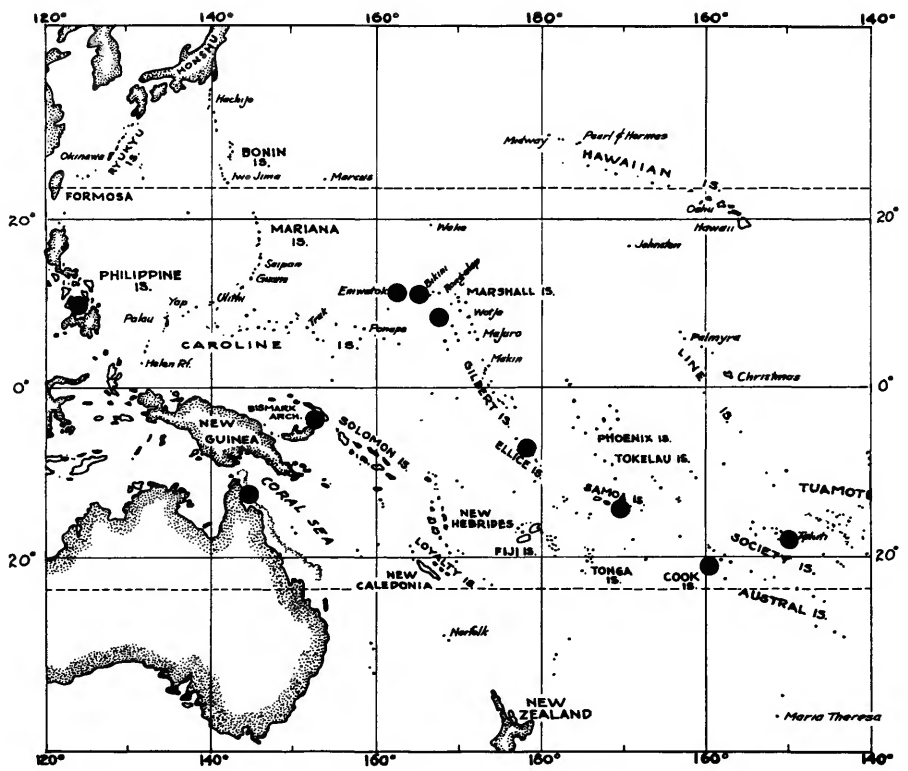

FIGURE 104.—Geographic distribution of *Cerithium pacificum*, new species.

Radula: Unknown.

Animal: Unknown.

HOLOTYPE.—USNM 584662; 23.4 mm length, 8.4 mm width (Figure 103A,B).

PARATYPES.—USNM 862491, 4 specimens.

TYPE LOCALITY.—Bikini lagoon, Bikini Atoll, Marshall islands, 55–61 m.

ETYMOLOGY.—Named after the Pacific Ocean.

SYNONYMIC REMARKS.—This new species was recently figured by Springsteen and Leobrera (1986, pl. 13: fig. 11) under the name, *Clypeomorus traillii* (Sowerby).

ECOLOGY.—*Cerithium pacificum*, new species, lives at moderate depths in lagoons associated with coral reef habitats. Most specimens have been collected by dredging or SCUBA. It is evidently not a common species, and is not known to occur in large populations. At Enewetak Atoll, this species has been found occasionally in the lagoon on pinnacles among coral rubble (Scott Johnson, pers. comm.; USNM 821845). In Rarotonga, Cook Islands, it has been found in the stomach of the fish, *Coris aygula* (USNM 732245). As the protoconch is undescribed, the mode of development remains unknown.

DISCUSSION.—*Cerithium pacificum*, new species, is easily distinguished by its tan, shiny, pupate shell with concave-sided apex and smooth, weakly beaded sculpture. The overall shape of the shell is close to that of *Clypeomorus purpurastoma* Houbrick, 1985 (see Houbrick, 1985:84, fig. 38), but *Cerithium pacificum* has a much longer anterior canal, tan color, and a smoother shape. *Cerithium claviforme*, Schepman, 1907 (Figure 28), also resembles *C. pacificum*, but differs from it in having strong nodes and only two spiral cords per whorl.

There does not appear to be a great deal of intraspecific variation in this species. The very small beads are slightly more strongly developed on some specimens (Figure 103C-H) than on others. Shell color is usually tan (Figure 103A,B,I,J), but some shells from the Philippines are pigmented with narrow axial flammules and spiral spots (Figure 103C-H). Freshly collected specimens usually have a shiny, porcelaneous texture.

This uncommon, subtidal species, rarely seen in museum or private collections, has recently been collected by tangle nets in the Philippines.

FOSSIL RECORDS.—Holocene subfossils of this species have been found in Eacho, Lifu, Loyality Islands (MNHNP). A

Miocene species from Enewetak and Bikini Atolls, Marshall Islands, described by Ladd (1972:36–37, pl. 9) as *Rhinoclavis floraensis*, resembles and may be related to *C. pacificum*, new species. *Rhinoclavis floraensis*, however, differs from *C. pacificum* in having a median spiral row of pointed nodes on each whorl. Ladd (1972:37) also recorded *R. floraensis* from the Pliocene and Pleistocene of the Marianas.

GEOGRAPHIC DISTRIBUTION (Figure 104).—From the Philippines south through New Guinea to northeastern Australia and throughout Micronesia as far east to the Cook Islands and the Tuamotus.

SPECIMENS EXAMINED.—PHILIPPINES: Punta Engano, Mactan Id, Cebu (USNM 845803). QUEENSLAND, AUSTRALIA: 3–35 m, 12°40′S, 143°51′E, Log Reef (AMS). BISMARCK ARCHIPELAGO: Duke of York Id (AMS). MARSHALL ISLANDS: 10 m, lagoon off Enewetak Id, Enewetak Atoll (USNM 821845); 54.8–60.9 m, Bikini Lagoon, Bikini Atoll (USNM 584662, holotype); 45.7–54.8 m, Bikini Lagoon, Bikini Atoll (USNM 585256); Kwajalein, Kwajalein Atoll (DMNH 95095, 95253, 175575). ELLICE ISLANDS: Funafuti Lagoon, Funafuti (USNM 433840). SAMOA: 12.1 m, Fagatele Bay, Tutuila, American Samoa (UGI 5341). COOK ISLANDS: 27.4 m, S coast, Rarotonga (USNM 7322415). SOCIETY ISLANDS: Moorea (coll Busson); filled area, Patutoa, Tahiti (USNM 669582).

Cerithium phoxum Watson, 1880

FIGURES 105–107

Cerithium phoxum Watson, 1880:106 [holotype and one paratype: BMNH 18872916634; type locality: Levuka, Fiji, 22 m]; 1886:534–535, pl. 40: fig. 3.—Kobelt, 1893:143, pl. 28: figs. 4, 5.

Cerithium (Vertagus) phoxum Watson.—Tryon, 1887:148, pl. 28: fig. 59.

Cerithium balteatum Philippi.—Cernohorsky, 1972:65, pl. 14: fig. 5 [not *C. balteatum* Philippi, 1848; is *C. phoxum* Watson].

DESCRIPTION.—*Shell* (Figure 105A,G,I-L): Shell elongate, tapering and slender, comprising 13–15 nearly straight-sided whorls, and reaching 31.1 mm length and 9.2 mm width. Protoconch unknown. Early teleoconch whorls white, sculptured with two thin spiral lirae, and having broad subsutural ramp. Adult shell sculpture highly variable, consisting of weakly beaded spiral cords, spiral striae, 13–18 axial folds, and many wide varices. Teleoconch usually with 3 or 4 primary, weakly beaded, spiral cords per whorl, one thin spiral lira (sometimes several) in interspaces between dominant spirals, numerous fine spiral striae crossing 13–15 broad, colabral axial ribs, and with randomly distributed, large white varices. Axial ribs wavy where crossing spirals and forming fine cancellate pattern, especially on early teleoconch whorls. Beads usually weak and variable in number; sometimes nodular and pointed, especially on middle spirals, but sometimes absent. Suture deeply impressed, slightly wavy, and overhung by each successive whorl. Body whorl narrow, sculptured with 5 or 6 occasionally weakly beaded, primary spiral cords, a thin spiral thread in each interspace, and with strong varix opposite outer lip of aperture. Two dominant cords at periphery of body whorl. Base of body whorl moderately excavated, sculptured with fine spiral striae; anterior siphonal canal moderately constricted. Aperture ovate, narrow, about one-fourth the shell length. Columella concave, thin, with distinct columellar lip. Anterior siphonal canal well developed, of moderate length, tubular, slightly twisted dorsally and to left of shell axis. Anal canal well developed, defined by strong parietal columellar tooth. Outer lip thickened, moderately crenulated having fine interior spiral striae. Shell color light tan, occasionally with faint brown blotches and spots on spiral bands. Spiral cords darker tan. Varices and aperture white. Measurements (Table 34). Periostracum thin, tan. Operculum (Figure 105H) brown, paucispiral, and with eccentric nucleus.

Radula (Figure 106): Type-1 radular ribbon (Figure 3A) short, about one-tenth the shell length. Rachidian tooth (Figure 106D) small, triangular, having narrow basal plate, and with central posterior projection flanked by narrow ridge on each side. Dorsal edge of rachidian tooth slightly concave; cutting edge with central, arrow-shaped cusp flanked on each side by two small denticles. Lateral tooth (Figure 106C,D) with long lateral basal projection and thick, posteriorly projecting, central buttress on basal plate; cutting edge with single inner denticle, large, pointed main cusp, and 2 or 3 small, pointed, outer denticles. Marginal teeth (Figure 106B–D) long curved, with hook-like tips serrated with small, rounded denticles. Inner marginal tooth with 3 inner denticles and 2 or 3 outer denticles. Outer marginal tooth same, but lacking outer denticles.

Anatomy (known only from single, dried specimen): Head-foot tan with black stripes and blotches across snout and sides of foot. Mantle edge papillate. Buccal mass large with well-developed jaws. Rectum filled with cylindrical fecal pellets consisting of coarse sand.

SYNONYMIC REMARKS.—This is a poorly known taxon that has not been mentioned in the recent literature. The types (Figure 105A,B) represent the common phenotype. Cernohorsky (1972:64, pl. 14: fig. 5) figured *C. phoxum* under the name *C. balteatum* Philippi, which is a distinct species.

ECOLOGY.—*Cerithium phoxum* occurs subtidally from shallow intertidal depths to 124 m, on soft to coarse sandy rubble bottoms around reef areas. Most Australian specimens have been dredged offshore, while most of those from Fiji have been taken in shallower waters. Empty shells frequently have drilled holes indicative of naticid predation, or broken apertures characteristic of crab attacks. The egg mass and type of development are unknown.

DISCUSSION.—*Cerithium phoxum* is an extremely variable species, difficult to characterize without making many exceptions. Characterized by a tall, turreted, cream to light tan shell with large white varices, it is sculptured with four primary spiral cords overlain by axial ribs, and has a slightly excavated body whorl base, and a moderately long, constricted siphonal

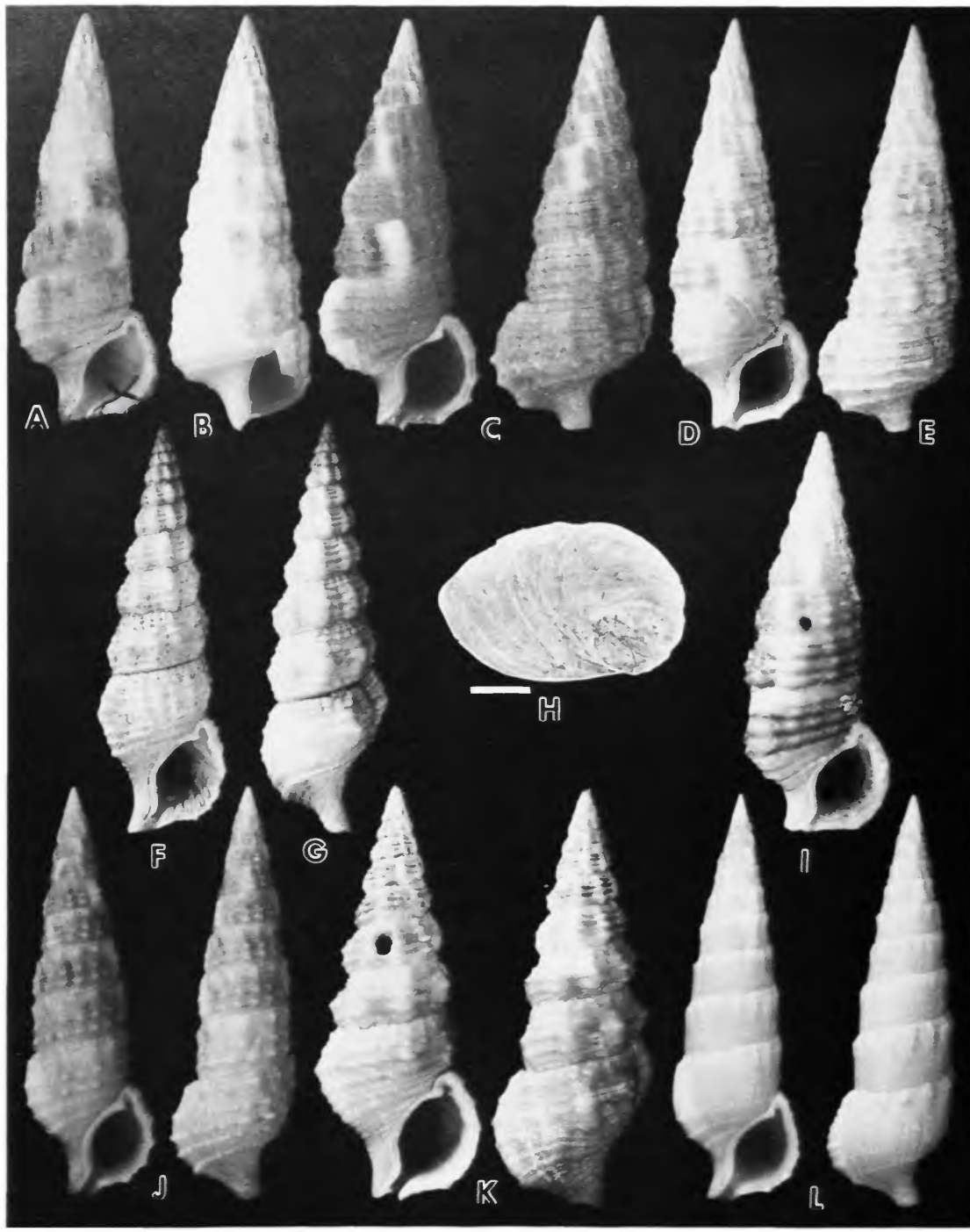

FIGURE 105.—Phenotypic variation in *Cerithium phoxum* Watson. A, holotype of *Cerithium phoxum* Watson, 11.9 m, Levuka, Fiji, mm (BMNH 18872916634); B, paratype of *Cerithium phoxum*, same data as A, 20.5 mm (BMNH 18872916635); C, 37–46 m, Roemwakon, Aoeri Id, Geelvink Bay, Irian Jaya, 19.3 mm (ANSP 205585); D,E, Matas Id, Aoeri Id, Geelvink Bay, Irian Jaya, 22.7 mm (ANSP 208934); F,G, Cebu, Philippines, 30.1 mm (AMS C33570); H, operculum, Rambi Id, Vanua Levu, Fiji, 0.4 mm (USNM 695390); I, Matas Id, Aoeri Ids, Geelvink Bay, Irian Jaya, 20.7 mm (ANSP 208934); J, Rambi Id, Vanua Levu, Fiji (bar = 26.4 mm; USNM 695390); K, Tabaco, Albay Prov, Luzon, Philippines, 20.6 mm (ANSP 230832); L, Georgia Cove, Rambi Id, Vanua Levu, Fiji, 31.1 mm (USNM 695390).

TABLE 34.— Shell morphometrics of *Cerithium phoxum*.

Character	$\bar{x}$ (n = 11)	sd	v	Range
Shell length	25.8	3.3	10.8	19.6-31.1
Shell width	7.8	1.0	1.0	6.1-9.2
Aperture length	6.0	0.9	0.9	4.6-7.5
Aperture width	4.1	0.6	0.4	3.2-5.1
Number whorls	14.1	0.7	0.5	13-15
Number axial folds	12.5	2.0	3.9	10-14

canal. Many specimens lack the spiral cords. The impressed suture is set into each successive whorl. An overall fine cancellate sculpture is overlain by sutural axial plications that do not extend the length of the whorl, and with large white varices.

Although this species is not common in museums or private collections, a sufficient number of specimens was examined to suggest a wide range of variation. Some specimens are less cancellate than others, and have fewer axial ribs on the penultimate whorl (Figure 105J) or may completely lack them (Figure 105L). Beads are pointed and nodular on some specimens (Figure 105F,G,K). Shells from Fiji tend to be large, elongate, and weakly sculptured or nearly smooth (Figure 105J,L). Specimens from the western parts of the range tend to have smaller shells with more cancellate sculpture, and are less elongate (Figure 105D-G,K). Initially, I considered these phenotypes to be a distinct species, but there are so many intergrades that the whole complex is best regarded as conspecific until more material is available. A population from the Philippines (USNM 286012) comprised dwarfed individuals under 15 mm length.

Cerithium phoxum is similar in overall morphology to *C. lissum* Watson (Figure 74), but differs from it in having a strongly excavated shell base and in lacking the large beads and dark, spiral, incised lines so distinctive of the latter species. *Cerithium phoxum* may be confused with *C. dialeucum*

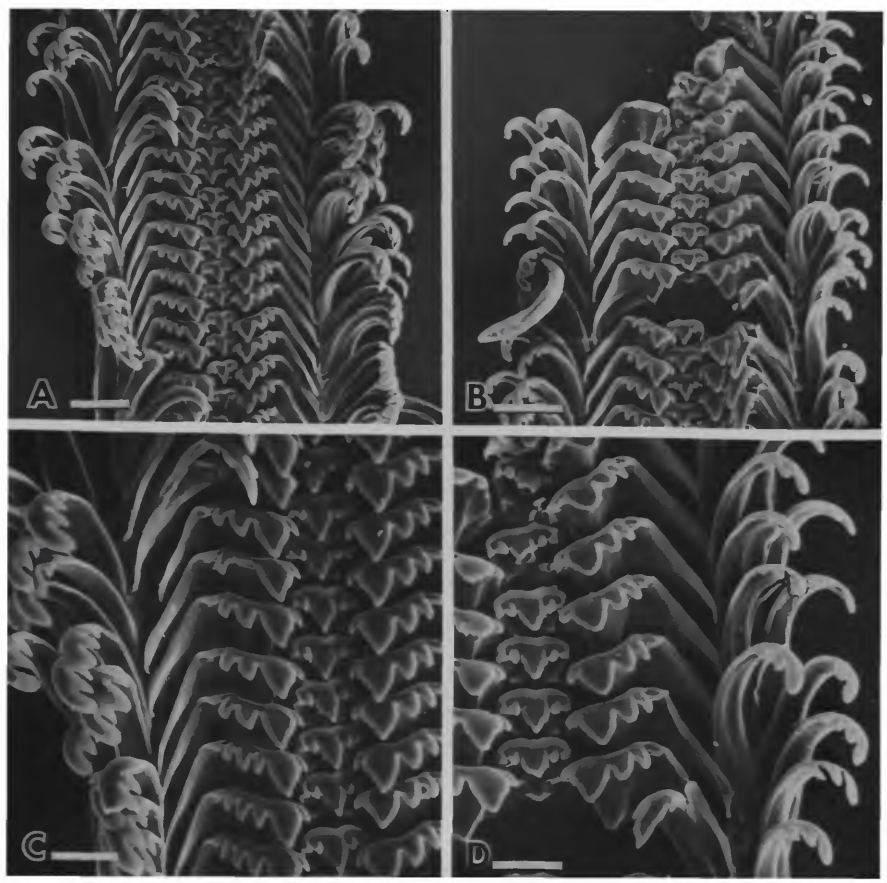

FIGURE 106.—Radula of *Cerithium phoxum* Watson, Rambi Id, Vanua Levu, Fiji (USNM 695390): A, radula with marginals spread open (bar = 75 μm); B, same (bar = 87 μm); C, half row showing dentition of teeth (bar = 43 μm); D, half row (bar = 43 μm).

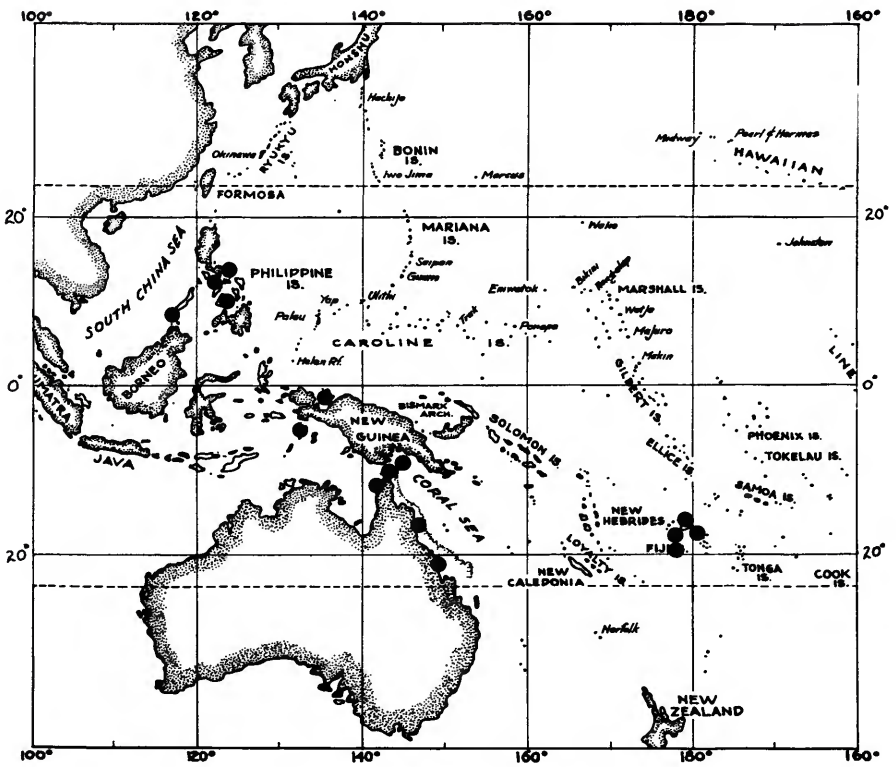

FIGURE 107.—Geographic distribution of *Cerithium phoxum* Watson.

Philippi (Figure 45), with which it is geographically sympatric, but the former is narrower, less angular in profile, and lacks the wide subsutural cord distinguishing the latter species. Some phenotypes of *C. balteatum* Philippi (Figure 17) also resemble *C. phoxum* in sculpture, but the latter species is much smaller, and has a deeply impressed suture, a presutural ramp, and a deeply excavated shell base bordered by a strong spiral cord.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 107).—This species is restricted to the western Pacific, being confined to the Philippines, Australasia and nearby island groups, and Fiji.

SPECIMENS EXAMINED.—PHILIPPINES: 36.6 m, USBF sta 5218, Ragay Gulf, off N Burias (USNM 255244, 278782); Tabaco, Albay Prov, E side of Luzon (ANSP 230832); Cebu Id (AMS C33570); 68.6 m, USBF sta 5179, off NE Tablas (USNM 236610, 236766); 124.3 m, USBF sta 5357, NE of Balabac Id, Palawan (USNM 286012); 45.7–51.2 m, 12.8–14.4 km W of Cape Melville lighthouse, Balabac Id, Palawan (WAM 1022-84). INDONESIA: 32.9–36.6 m, 5°32′S, 132°41′E, N of Du Rowa, N of Nuhu Rowa, Kai Ids, Moluccas (WAM 1027-84); 54.8–56.7 m, 5°32′S, 133°E, E side of Mitduan Reef, W coast of Nuhu Tjut, Kai Ids, Moluccas (WAM 1029-84). QUEENSLAND, AUSTRALIA: Mapoon, Gulf of Carpentaria (AMS C14283); Albany Passage, Torres Strait (AMS C142388); 0.8 km N of Eagle Id, N Queensland (AMS C142370); 18 m, 15°44′S, 145°27.1′E, N Queensland (AMS C142365, C142379); 16–22 m, Low Isles, near Port Douglas (AMS C142363); 55 m, 16°33′48″S, 146°09′36″E, NE of Cairns (AMS C142376); Lindeman Id, Cumberland Ids, N of Mackay, N Queensland (AMS C109474).

NEW GUINEA: 32.9–36.6 m, 3.2 km N of Matas, Aoeri Ids, Geelvink Bay, Irian Jaya (ANSP 208934); 36.6–45.7 m, 1.6 km NE of Roemwakon, Aoeri Id, Geelvink Bay, Irian Jaya (ANSP 205585, 334636); 22–33 m, 2.4 km SW of Yule, Papua New Guinea (AMS C74807). BISMARCK ARCHIPELAGO: 15–40 m, 4°12′S, 152°13′E, Nodup, Rabaul, New Britain (AMS C142378). FIJI: W side of Mali Pass, N coast of Vanua Levu (USNM 694878); N side of Verevere Id, N coast of Vanua Levu (USNM 694961, 694969); NW Rambi Id, Albert Cove, W coast of Vanua Levu (USNM 695246, 695292); Georgia Cove, Rambi Id, Vanua Levu (USNM 695390); off Naseleseli Pt, N end of Taveuni (USNM 695485); Manna Id, N of Viti Levu (USNM 824826); Viti Levu (LACM 67-93); Malolo Reef, NW side of Viti Levu (LACM 74-45); Komave, S coast Viti Levu (AMS); barrier reef W of entrance to Suva Harbor, Viti Levu (USNM 532248); 1.2–1.5 m, inside Suva

Reef, Suva, Viti Levu (USNM 773887); S side of Waya Id, Kandavu (USNM 696316); Yauravu Pt, S tip of Kandavu (USNM 697072).

Cerithium punctatum Bruguière, 1792

FIGURES 108–111

Cerithium punctatum Bruguière, 1792:498 [lectotype, larger of 2 syntypes, herein selected: MHNG 109743; type locality: Senegal; 11.8 mm; not *Cerithium punctatum* (Linné), Philippi, 1848; nor *Cerithium punctatum* Woodward, 1833].—Lamarck, 1822:76.—Kiener, 1842:48–49, pl. 16: fig. 4.

Cerithium punctatum (Trochus) [sic] Linné .—Philippi, 1848:18, pl. 1: fig. 16 [not *Cerithium punctatum* Bruguière 1792].

Cerithium alveolus Hombron and Jacquinot, 1852, pl. 24: figs. 28, 29 [holotype: MNHNP, no number; type locality: Samoa; 14.8 mm × 3.1 mm]; 1854:105–106.—Salvat and Rives, 1975:270, fig. 66.

Cerithium piperitum Sowerby, 1855:867, pl. 181: figs. 136–137 [new name for *Cerithium punctatum* Bruguière, 1792]; 1865, pl. 12: fig. 81.—Martens and Langkavel, 1871:36.—Tryon, 1887:144, pl. 27: figs. 31, 32.—Kobelt, 1898:117–118, pl. 22: figs. 12, 13.—Adam and Leloup, 1938:106–107, pl. 5: fig. 16a,b.

Cerithium (Liocerithium) piperitum Sowerby.— Tryon, 1887:144, pl. 27: figs. 31, 32.

Lampania piperita (Sowerby).—Paetel, 1887:351.

Cerithium (Semivertagus) piperitum Sowerby.—Maes; 1967:114, pl. 6: fig. 1.

Cerithium (Semivertagus) alveolus (Hombron and Jacquinot).—Cernohorsky, 1972:68–69, pl. 15: fig. 8.

Cerithium (Thericium) alveolus (Hombron and Jacquinot).—Ladd, 1972:37, pl. 9: figs. 7, 8.

DESCRIPTION.—*Shell* (Figure 108A–J): Shell small, conic-ovate, comprising 8–10 slightly convex to straight-sided whorls, and reaching 17.3 mm length and 7.4 mm width. Protoconch of 3 whorls; protoconch 1 smooth; protoconch 2 sculptured with subsutural plaits and 2 spiral threads. Early teleoconch whorls (Figure 108C) sculptured with fine spiral incised lines, 3 primary spiral cords, and fine spiral striae. Adult teleoconch whorls sculptured with 2–4 dominant spiral cords, several smaller, spiral threads, and many microscopic spiral striae per whorl. Whorls angulate centrally. Dominant central spiral cord with as many as 10–14 weak beads, but sometimes smooth. Thick varices randomly distributed on teleoconch. Suture weak, closely adpressed, wavy. Body whorl wide, convexly angulate, with moderately constricted base. Body whorl sculptured with 10–12 spiral cords, 4 or 5 posterior to constriction of shell base. Varix on body whorl opposite outer lip of aperture. Aperture ovate, about one-third the shell length. Columella concave with slight columellar callus and lip. Anterior siphonal canal very short, tubular, directed about 45° to left of shell axis. Anal canal weakly developed, bordered with small columellar plait. Outer lip of aperture convex, thick and smooth. Shell color white, irregularly spotted with blackish brown and with spiral rows of spots on spiral cords. Columella purple. Edge of outer lip with small dark spots. Measurements (Table 35). Periostracum thin, tan.

Radula (Figure 109): Type-1 radular ribbon (Figure 3A) a little more than one-fifth the shell length. Rachidian tooth (Figure 109B-D) squarish with central posterior projection and pair of small, posterior, lateral ridges on basal plate; anterior front convex centrally having cutting edge with central, spade-shaped, main cusp flanked on each side with 2 or 3 small denticles. Basal plate of lateral tooth (Figure 109B,C) with wide, strong central buttress projecting posteriorly, with small central pustule and short lateral, posterior extension; cutting edge of lateral tooth with large, wide main cusp, one inner denticle and 4 or 5 pointed, outer denticles. Marginal teeth (Figure 109C,D) long, spatulate with wide central portions, narrow, curved serrated tips, and narrow bases. Inner marginal tooth tip with long narrow main cusp, 3 pointed inner denticles, and 2 outer pointed denticles. Outer marginal tooth same, but lacking outer denticles.

Anatomy: Pattern of pigmentation closely matching that of shell. Head-foot yellowish white with large, dark brown to black spots and blotches overlain with yellow and white papillae. Cephalic tentacles with dense black dots and with larger spots on snout, head, and foot (Figure 110). Large black spot on metapodium and two large spots on sides of foot, one beneath each eye and the other centrally placed. Mantle edge bordered with black and white papillae. Papillae at inhalant siphon yellow. Body comprising about 4 coils with white ovary and orange testes. Snout short, broad, and bilobed.

Osphradium orange, high and wide in relation to ctenidium. Ctenidium orange-brown, comprised of long narrow filaments. Hypobranchial gland white, thick, folded transversely, and papillate where covering rectum.

Buccal mass large, robust. Massive salivary glands tightly coiled distally, passing through nerve ring as winding, thick tubes and empting into buccal mass. Type-A pallial oviduct (Figure 4A). Anterior sperm gutter short. Spermatophore bursa orange, extending length of medial lamina. Posterior seminal receptacle dark orange. Orange ciliated tract leads into anterior seminal receptacle of lateral lamina.

SYNONYMIC REMARKS.—This species is commonly known as *C. alveolus* in the literature, but it is clear from the above synonymy that *C. punctatum* Bruguière is an earlier available name. Examination of the types (Figure 108A,F,I) leaves no doubt that the two taxa are conspecific. The synonymic history of this species is complicated by the confusion of authors as to the identity of homonymous taxa, particularly *Trochus punctatus* Linné, 1758. Dodge (1958:213–215) discussed the status of *Trochus punctatus* Linné, and did not believe that it was a *Cerithium* species nor synonymous with *C. punctatum* Bruguière. Hanley (1855:324) was unable to find *Trochus punctatus* in the Linnaean collection in London but referred to Philippi's (1848:23) citation of it under *Cerithium*, and indicated that he tentatively accepted this assignment. Dance (1967:22) cited *Trochus punctatus* in his list of Linnaean species not represented by specimens in the Linnaean collection. As the type is lost, it is best to regard the Linnaean species

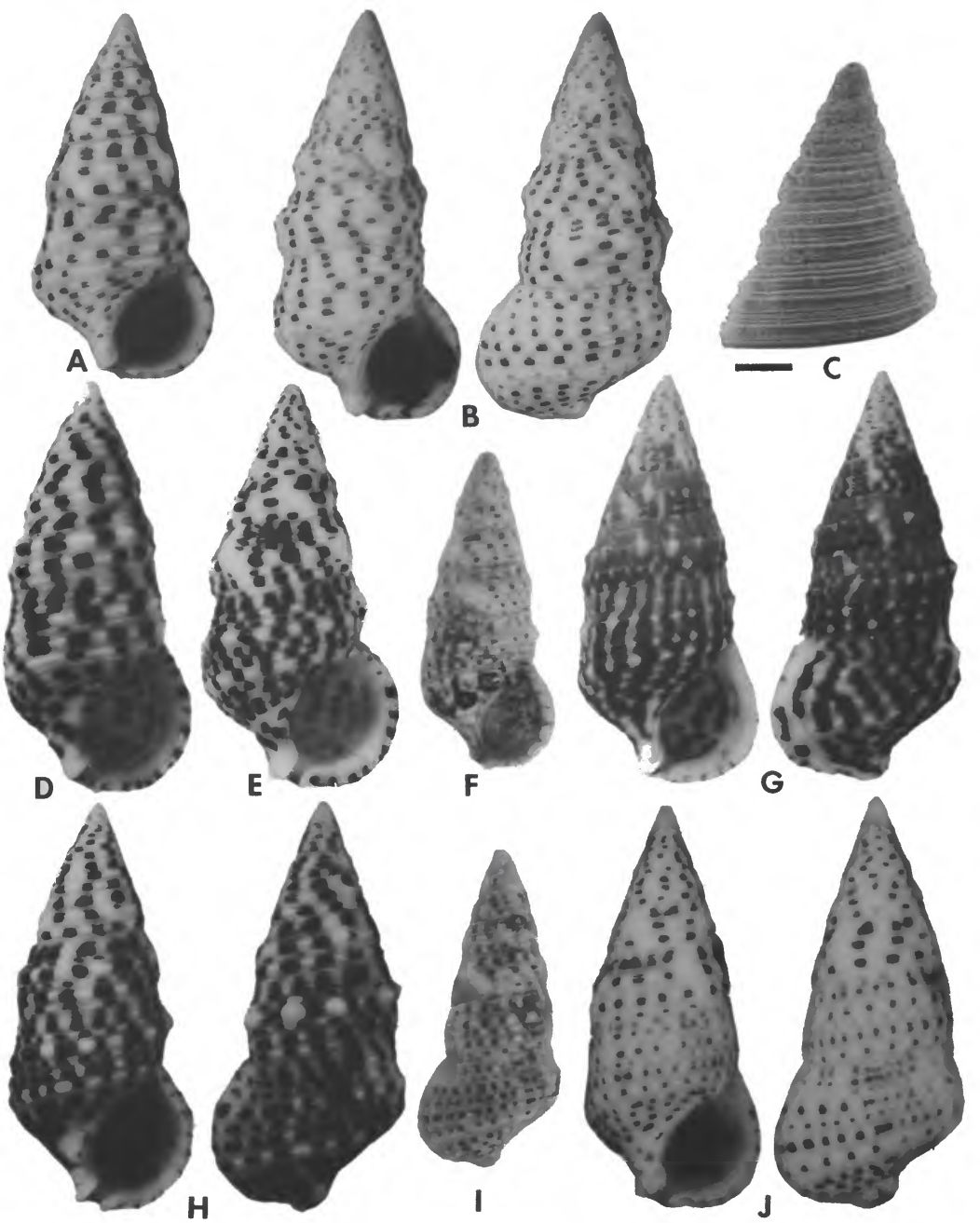

FIGURE 108.—Types of nominal taxa synonymous with *Cerithium punctatum* Bruguière and specimens demonstrating phenotypic variation: A, holotype of *Cerithium alveolus* Hombron and Jacquinot, Samoa, 14.8 mm (MNHNP); B, figured specimen of *Cerithium piperitum* Sowerby (1855, pl. 181: fig. 136), 19 mm (BMNH); C, SEM of early whorls with fine spiral sculpture, Heron Id, Queensland, Australia (bar = 0.5 mm; AMS); D, Pulau Melila, Sumatra, 13.9 mm (USNM 654421); E, Niuafou, Tonga, 14.5 mm (USNM 383835); F,I, lectotype of *Cerithium punctatum* Bruguière, "Senegal," 11.8 mm (MHNG 109743); G, Butang Gp, Thailand, 13.2 mm (USNM 661608); H, Pulau Melila, Sumatra, 13.8 mm (USNM 654421); J, Bikini Atoll, Marshall Ids, 9.5 mm (USNM 579310).

TABLE 35.—Shell morphometrics of *Cerithium punctatum*.

Character	$\bar{x}$ (n = 16)	sd	v	Range
Shell length	12.9	2.8	8.0	8–17.3
Shell width	5.8	1.1	1.3	3.6–7.4
Aperture length	4.2	0.9	0.9	2.5–5.6
Aperture width	3.1	0.6	0.4	2–4
Number whorls	9.1	0.7	0.5	8–10
Number spiral cords	2.9	0.6	0.4	2–4
Number nodes	8.9	5.1	26.3	0–14

as a nomen dubium. *Trochus punctatus* Linné was allocated to *Cerithium* by Philippi (1848:23) after *Cerithium punctatum* Bruguière, 1792, had been described; thus, *Cerithium punctatum* (Linné) becomes a secondary homonym of *C. punctatum* Bruguière. *Cerithium piperitum* Sowerby, 1855, was proposed as a replacement name for *C. punctatum* and a specimen figured by Sowerby (1855, pl. 181: fig. 136) and depicted herein (Figure 108B), is clearly conspecific with the lectotype of *C. punctatum* (Figure 108F,I). The lectotype and paralectotype of *C. punctatum* Bruguière are conspecific with the holotype of *C. alveolus* Hombron and Jacquinot (Figure 108A). The locality given by Bruguière (1792:498), Senegal, is incorrect, as *C. punctatum* is an Indo-Pacific species. Neither Philippi's (1849, pl. 1: fig. 16) nor Sowerby's (1855, pl. 184: fig. 240) illustrations of Linné's *Cerithium punctatum* (Linné) look like the lectotype of *C. punctatum* Bruguière (Figure 108F,I), but appear to represent a *Cerithiopsis* species. Kobelt (1898:117) was apparently unclear as to the identity of Bruguière's species and thought that Sowerby had mixed *C. punctatum* Bruguière with *C. piperitum* Sowerby and had copied Kiener's (1842:48) diagnosis.

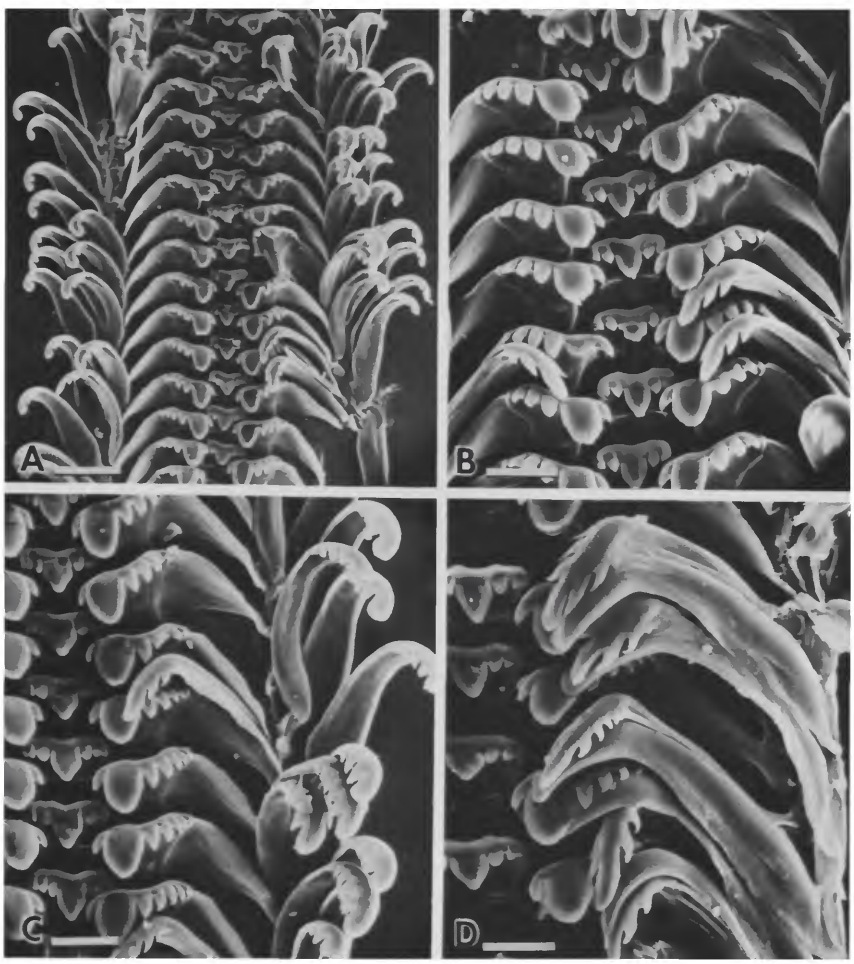

FIGURE 109.—Radula of *Cerithium punctatum* Bruguière: A, radula with marginals spread open, Paje, Zanzibar (bar = 86 μm; ANSP 213353); B, rachidian and marginal teeth, Pago Bay, Guam (bar = 40 μm; USNM 774771); C, half row, same data as B (bar = 40 μm); D, marginal teeth folded over ribbon, same data as B (bar = 50 μm).

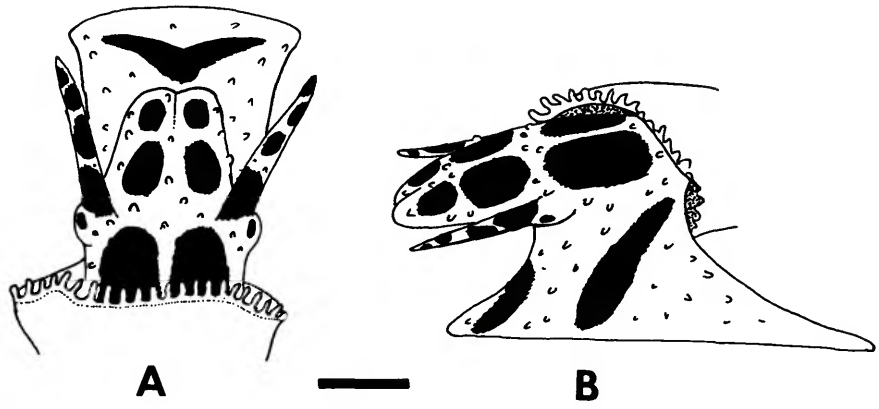

FIGURE 110.—Headfoot of *Cerithium punctatum* showing characteristic patterns of dark pigment: A, dorsal view; B, left lateral view (bar = 1 mm).

Cerithium punctatum has been allocated to several subgenera, the most unusual being *Lampania* Gray, 1847, a potamidid genus. Tryon (1887:144) placed this species in the subgenus *Liocerithium* Tryon, 1887, while Maes (1967:114) and Cernohorsky (1972:68) both referred it to *Semivertagus* Cossmann, 1889. Most recently, it was placed in *Thericium* Monterosato, 1890, by Ladd (1972:37).

ECOLOGY.—*Cerithium punctatum* lives on algal mats associated with seaward, mid-intertidal, limestone benches, platforms, and reef flats adjacent to fringing coral reefs. It is not a burrowing species and is rarely found on sand patches. It is thus subject to the wave action and incoming tides. On Guam and at Enewetak Atoll, it frequently is found entangled in filaments comprising algal mats on seaward benches (pers. obsr.). It has been recorded in similar habitats in the Tuamotus (Richard and Salvat, 1972:1548; Poli and Salvat, 1976; Richard, 1973), the Marshall Islands (Demond, 1957:291, cited as *C. alveolus*), and Cocos-Keeling Islands (Maes, 1967:114). *Cerithium punctatum* comprises up to 14 percent of the fringing reef mollusks in Moorea (Richard, 1973:310–311; Richard and Salvat, 1972:1548, cited as *C. piperitum*). Salvat and Rives (1975:270) and Richard and Salvat (1972:1548) both noted that it was commonly associated with algae, especially *Halimeda*. In Guam and Enewetak, *C. punctatum* lives seaward of *Clypeomorus nympha*, which burrows in sandy patches in the rocky, high intertidal zone. *Cerithium punctatum* has a robust radula and large buccal mass and probably grazes the microalgae associated with the algal mats on which it lives.

The spawn mass, eggs, and larvae are unknown, but the wide Indo-Pacific distribution and protoconch (Figure 108C) indicate a planktotrophic phase in life history.

DISCUSSION.—This common species is identified by its small conical shape and spiral pattern of brownish black dots on a white background. The peripheral angulate whorls and sculpture of many fine spiral cords (Figure 108C) are also distinctive characters.

Cerithium punctatum may be confused with *Clypeomorus nympha* Houbrick, 1985 (better known as *Cerithium sejunctum* Iredale, 1929), which is also small and with a somewhat similar color pattern, and with which it is sympatric. Both species, of similar sizes and color patterns, occur together on seaward benches on hard substrates. *Cerithium punctatum*, however, does not have the pupate shell of *C. nympha* and is not beaded. Another species that occurs in similar habitats with *C. punctatum* is *Bittium zebrum* (Kiener), but it is a slender, very tiny species with many different color morphs.

Cerithium punctatum does not exhibit a great deal of intraspecific variation in shell characters. Populations in the Philippines, Indonesia, and SE Asia appear to have more individuals with strong nodulose central spiral cords (Figure 108D,G,H) than those from other parts of the range. The largest individuals observed were from the Philippines, Indonesia, Fiji, and the Tuamotus. Populations from Micronesian atolls frequently comprise small individuals. Some individuals are darkly pigmented (Figure 108G), but this is not common; others may have very small spots on a white background (Figure 108B,J).

FOSSIL RECORDS.—This species, cited as *C. alveolus*, has been recorded from the Pleistocene of Saipan and other Mariana Islands, and from the Holocene of Enewetak Atoll, Marshall Islands (Ladd, 1972:37, pl. 9: figs. 7, 8). Ladd's figure of this taxon is that of a badly eroded specimen that only vaguely resembles the living species. Holocene fossils of this species, found at Turtle Beach, NW Cape, Western Australia, are in the Western Australian Museum.

GEOGRAPHIC DISTRIBUTION (Figure 111).—*Cerithium punctatum* has a very wide Indo-Pacific distribution, from eastern African shores in the Indian Ocean to the Tuamotus in the Pacific. In the Indian Ocean, it does not seem to have penetrated the Red Sea or Persian Gulf, but extends southward

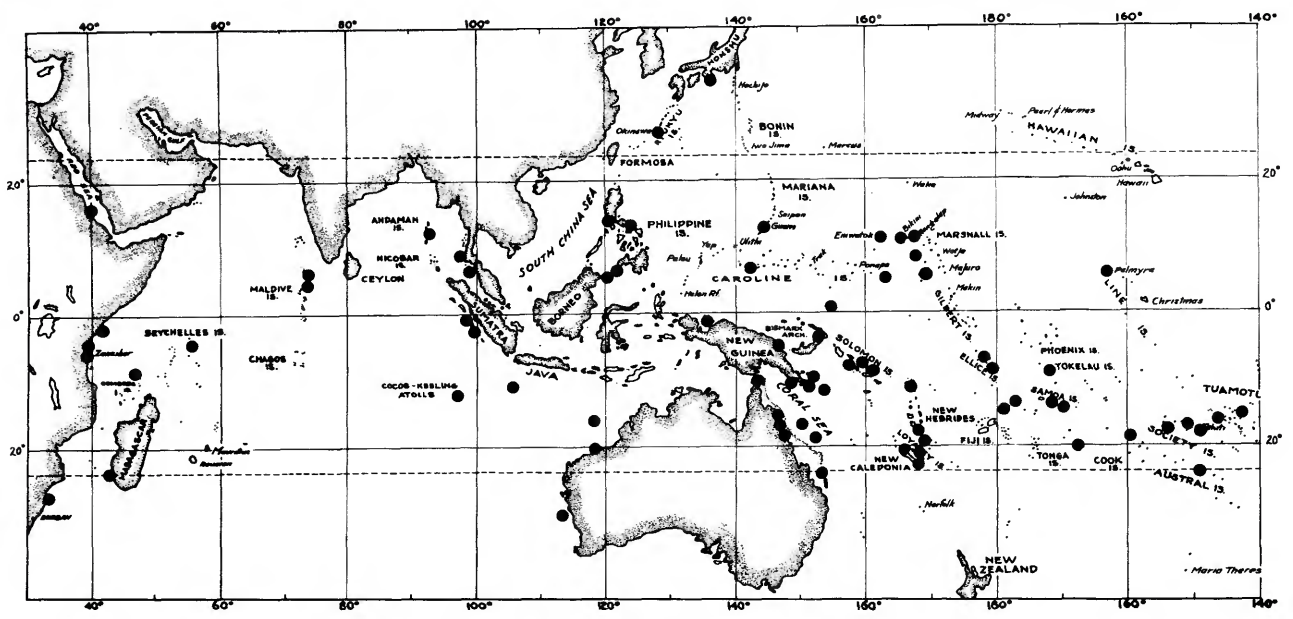

FIGURE 111.—Geographic distribution of *Cerithium punctatum* Bruguière.

to southern Madagascar. It ranges from southern Japan south to new Caledonia and the Austral Islands in the Pacific.

SPECIMENS EXAMINED.—EAST AFRICA: Emboti, Pondoland, South Africa (NM A1862); Inner Sinda Id, Tanzania (USNM 604318); SW end of Mdudya Id, 15 km N of Dar es Salaam, Tanzania (AMS); Mbweni, Zanzibar (AMNH); Mnazi Moja, W Zanzibar (ANSP); Paje, SE Zanzibar (ANSP); 8 km N of Chnaka, E Zanzibar (ANSP); 5.4 km SE of Gedi, Kilifi Dist, Kenya (AMNH). RED SEA: E end of Dessie Id, 40 km off Massawa, Ethiopia (ANSP). MADAGASCAR: Tulear (USNM 718404, 718418); N end of Nossi Kalakajoro, Îles Radama (ANSP).

INDIAN OCEAN ISLANDS: Passe Houareau, Île Malabar, Aldabra, Seychelles (USNM 837440); Seychelles (USNM 634728); N end Ongu Id, N Malosmadulu Atoll, Maldive Ids (ANSP); between Maro and Mafilefuri Atolls, Maldive Ids (ANSP); Imma Id, SE side of N Male Atoll, Maldive Ids (ANSP); Fadiffolu Atoll, Maldive Ids (ANSP); N end of Bangtau Bay, W side of Phuket Id, Andaman Ids (ANSP); S end, Direction Id, Cocos Keeling Ids (USNM 656272); N end of Pulo Siput, SE Cocos Keeling Ids (ANSP); Flying Fish Cove, Christmas Id (WAM).

THAILAND: Pulau Tanga, Butang Gp (USNM 661608); Goh Sindarar Nua (Chance Id) (USNM 661270, 661313).

JAPAN: Osima, Osumi Peninsula, Kagoshima (MCZ, USNM 3438720, 563900). RYUKYU ISLANDS: Okinawa (USNM 617540, 666634, 671094); 1 km NNW of Oku, Okinawa (LACM 7761); Itoman Reef, Okinawa (LACM 27343).

PHILIPPINES: Sabtang Id, Batanes Gp (USNM 243922, 775149); Looc Bay, Bagac, Bataan, Luzon (USNM 774888); Maricaban Id, Luzon (USNM 232940); Maculabo Id, Luzon (USNM 240249); Barrio Rizal, near Gubat, Sorsogon Prov, Luzon (ANSP); Cebu (USNM 48009); Magallanes Bay, N end of Mactan Id, Cebu (ANSP); Gavilan Pt, near Campo Id, Mindanao (USNM 619912, 619914); Pangapuyan Id, Mindanao (USNM 619923); Panubigen Ids, Mindanao (USNM 619824); Silino Id, Mindanao (USNM 821666); Little Santa Cruz Id, Mindanao (USNM 244882, 786919); Big Santa Cruz Id, Mindanao (USNM 812473); Toburan, Basilian Id, Mindanao (USNM 619982); Bagabagon, near Basilian Id, Mindanao (USNM 619996); Tengolan Id, Basilian Id, Mindanao (USNM 619797); Kilay Id, near Langas Id, Basilian Id, Mindanao (USNM 619763); Balukbaluk Id, Basilian Id, Mindanao (USNM 620028); Atong Atong, Basilian Id, Mindanao (USNM 775142); Pohusito, Basilian Id, Mindanao (USNM 619776, 775137); Kapago, Basilian Id, Mindanao (USNM 775140); Sangig, Basilian Id, Mindanao (USNM 620073); Tanusa, S end Basilian Id, Mindanao (USNM 619787); Bulibali, near Nangal Pt, Basilian Id, Mindanao (USNM 619748); Kauluan Id, Basilian Id, Mindanao (USNM 619756); Boboh, near Matanol Pt, Basilian Id, Mindanao (USNM 620042); Cabaluay, Sulu Sea (USNM 619625); Manicaan, Sulu Sea (USNM 775135); Babag, near Taluksangay, Sulu Sea (USNM 775126); Calarian, Sulu Sea (USNM 619634); Sangboy Id, Sulu Sea (USNM 619612); Bubuan Id, Jolo (USNM 243658); Tara Id (USNM 233032, 243776); Papatag Id, Tawitawi (USNM 244023); Beti Siasi and Bongao

Ids, Sulu Archipelago (USNM 313964); Bolong, near Sangali, Sulu Sea (USNM 775139). INDONESIA: Pulau Bai, Batu Gp, off Sumatra (USNM 654556, 654623); Pulau Siburu, N of Sipora, SW of Sumatra (USNM 654847); Sanding Id, Mentawai Ids, Sumatra (USNM 655244, 655312); Mega, Mentawai Ids, Sumatra (USNM 655063); Pulau Stupai, Mentawai Ids, Sumatra (USNM 655106, 655156); Pulau Melila, off Sumatra (USNM 654421).

WESTERN AUSTRALIA: SW Beacon Id, Wallabi Gp, Abrolhos Ids (WAM); Kendrew Id, Dampier Archipelago (WAM); Clerke Reef, Rowley Shoals (WAM). QUEENSLAND, AUSTRALIA: Bramble Cay, NE of Torres Strait (AMS); Yorke Id, Torres Strait (AMS); Murray Id, Torres Strait (AMS, USNM 273848); S end, Blue Lagoon, Lizard Id (AMS, USNM 766772, 766878, 766966, 783645); Green Id (AMS); Bird Id (USNM 101399); Hope Id, SE of Cooktown (AMS); Endeavour Reef (ANSP); Low Isles, near Port Douglas (AMS); Michaelmas Cay, near Cairns (AMS); Buchan's Pt, N of Cairns (AMS); NE Cay, Herald Gp (AMS); Lihou Reef (AMS C108561); King Reef, off Kurramine Beach, S of Innesfield (AMS); Palm Id, N of Townsville (AMS); Hook Id (AMS); Gillett Cay, Swain Reefs (AMS); Tryon Id, Capricorn Gp (AMS); E end of Heron Id (AMS); West Cay, Diamond Banks (AMS); W of Wilson Id, Capricorn Gp (AMS); Kepple Bay (AMS); NW Ids, Capricorn Gp (AMS); Lady Musgrave Id, Bunker Gp, E of Gladstone (AMS); Wreck Reef (AMS); Lady Elliot Id (AMS). NEW GUINEA: Abroeki Id, Maransabadi Id, Aoeri Ids, Geelvink Bay, Irian Jaya (ANSP); Mios Woendi, Schouten Ids, Irian Jaya (USNM 542687); Madang, Papua (AMS); inlet, W end of Kranket Id, Madang, Papua (AMS); Duke of York Id, Papua (AMS); off Kaibala Village, N end of Kiriwina Village, Trobriand Gp, Papua (AMS); near Okaibolma Village, E coast of Kiriwina, Trobriand Gp, Papua (AMS); Milne Bay, Papua (AMS); East Cape, E tip of Papua (AMS); E tip of Gum Id, Conflict Gp, Louisiade Archipelago, Papua (AMS); Idlers Beach, 28 km W of Port Moresby, Papua (AMS); reef near Basilisk Passage, Port Moresby, Papua (AMS); Kapa Kapa, about 72 km N of Port Moresby, Papua (AMS).

SOLOMON ISLANDS: Hetaheta Id, N side of Santa Isable, Central Dist (LACM 785994); entrance to Aoki Harbor, W coast of Malaita Id (AMS); Loulasi Id, S of Aoki, W coast of Malaita Id (AMS); S side of Roncador Reef, Malaita Id (LACM 78556); Pavuvu Id, Russell Gp (USNM 488342); Ata (AMS). SANTA CRUZ ISLANDS: Vanikoro (AMS); Reef Ids (AMS). NEW HEBRIDES: Point Ardel, Port Vila, Efate Id (AMS); Vila Harbor, Efate Id (USNM 787506, 787895); Aneiteum (MCZ); ESE of Inyeug Id, Aneiteum (USNM 692231). LOYALTY ISLANDS: W of Îlot du Styx, Atoll Uvea (USNM 692755); Lifu (AMS C3850, C4691, USNM 423296); Chateaubriand Bay, Relais de We, Lifu (CAS); Gadja, Baie du Sud, Lifu (AMS C36103). NEW CALEDONIA: E of Nani Id, central N side (USNM 693554); Unea, near Yate, Touaourou (USNM 783721); S of Yate, Touaourou (USNM 784392, 806085). FIJI: W side Mali Pass, Vanua Levu (USNM 694851); NW Rambi Id, Albert Cove, Vanua Levu (USNM 695222); SW side Ovatea, Vanua Levu (USNM 694763); Mana Id, Mamanutha Gp (USNM 790964); Vunda Pt, S of Lautoka, Viti Levu (AMS); off Nadi, Viti Levu (USNM 638500); Mbenga Id, Viti Levu (MCZ); Bega Id (ANSP, USNM 613634); N side, Nananu-i-ra Id, Viti Levu (USNM 694593); Suva Bay, Viti Levu (AMS, USNM 532109, 532234, 773891); Laucala Bay, Suva, Viti Levu (USNM 790674); Caboni Beach, NE Viti Levu (USNM 824812); Thakau Mai, off Viti Levu (USNM 694333); S of Yauravu Pt, Kandavu (USNM 696680); E of Korolevu Bay, Kandavu (USNM 696178); Ndravuni Id, Kandavu (USNM 695948).

MARIANA ISLANDS: Neye Id Channel, Guam (USNM 842621); Pago Bay, Guam (USNM 774771, 847274). CAROLINE ISLANDS: Yap (USNM 591139); NW end Falarik Id, Ifaluk Atoll (USNM 616607, 616620); Elato Atoll (USNM 590967); Kapingamarangi (USNM 610814); 1.6 km W of Torongahai, Kapingamarangi (USNM 611070); reef at Mutunlik, Kusaie Id (USNM 609470, 609475). MARSHALL ISLANDS: Enewetak Atoll (USNM numerous localities throughout); Bikini Atoll (USNM numerous localities throughout); Piganiyaroyaro Id, Rongelap Atoll (USNM 585580); Kabelle Id, Rongelap Atoll (USNM 582109, 582418); Tufa Id, Rongelap Atoll (USNM 584183); Arbar Id, Rongelap Atoll (USNM 582441); Rongelap Id, Rongelap Atoll (USNM 585525); Latobach Id, Rongerik Atoll (USNM 582921, 585730); Ailuk Id, Ailuk Atoll (USNM 615107, 615143); Wotho Id, Wotho Atoll (USNM 614418, 614421); Likiep Id, Likiep Atoll (USNM 596137, 615317); Ebbetyu Id, Ujae Atoll (USNM 607426); Kwajalein, Kwajalein Atoll (USNM 486059, 486102, 587353); Ine Village, Arno Atoll (USNM 635421); Lijeron Id, Jaluit Atoll (USNM 660086); Mejatto Id, Jaluit Atoll (USNM 660101); Imrodj Id, Jaluit Atoll (USNM 660232); Kabbenbock Id, Jaluit Atoll (USNM 659093); Enybor Id, Jaluit Atoll (USNM 659511). LINE ISLANDS: Palmyra Id (USNM 348473). ELLICE ISLANDS: Main id, Vaitupu (USNM 685976); Funafuti (AMS C5764).

WALLIS ISLANDS: Faoia (USNM 676133). TOKELAU: Tokelau Islet, NE Nukunono (USNM 768621); Fenua Loa, Fakaofu (USNM 768171). SAMOA: Mataatu Harbor, N coast Savaii (USNM 675749); Asau Harbor, N coast Savaii (USNM 675909); Felialupo Road, W side Savaii (USNM 675978); Apia (USNM 335021, 573851, 774540); NE Apia Harbor, Apia (USNM 675625); N end Mulinuu Pt, Upolu (USNM 675675); E side Manono Id, Upolu (USNM 620992); Mulifanua, NW of Upolu (USNM 675678); Matautu, Lefaga Bay, Upolu (USNM 675606); Ofu (LACM 22541, MCZ); Ofu, Manu'a Gp (USNM 381189, 381220, 699450); Pago Pago Harbor, Tutuila (AMS C5764); Pagopago Bay, Tutuila (USNM 698966); Faga Togo, Tutuila (MCZ); Faga-alu, Tutuila (USNM 699031, 699107); Fagaitua Bay, Tutuila (USNM 704699); Nuuuli, Tutuila (USNM 699961); Poloa Bay, Tutuila (USNM 699544); Leone Bay, Tutuila (USNM 699332).

TONGA: Niuafou Id (USNM 383835). COOK ISLANDS: Tom's Id, Palmerston (USNM 685239); Akitua, NE Aitutaki (AMS). AUSTRAL ISLANDS: Motu, N coast of Tubuai (USNM 732314).

SOCIETY ISLANDS: W side, ocean reef, Bellinghausen (USNM 705230); N end large motu, Mopelia (USNM 705174); Motu Ahi, N side Maupiti (USNM 706261, 706328); lagoon shore, Maupiti (USNM 706105); Motu Tuanae, Maupiti (USNM 751437); S Farepiti Pt, Bora Bora (USNM 629925); Fanui Bay, Bora Bora (USNM 629902); Bora Bora (USNM 617593); Motu "I Atara," Tahaa (USNM 674293); S tip of Motu "I Tehotu," Tahaa (USNM 674324); near "Hipu," Tahaa (USNM 674302); Motu Iriru, Raiatea (USNM 675392, 675509); Motu Tipaemau (USNM 675173); Port du Bourayne, Huahine (USNM 630292, 652713, 652733); Toatane Reef, W of Avaroa Pass, Huahine (USNM 652769); Motu Onetahi, Tetiaroa (USNM 705680, 705899); Motu Tiaraunu, Tetiaroa (USNM 705864); Patutoa, Tahiti (USNM 669589); Fare Ute Pt, Papeete, Tahiti (USNM 668942); E side of Taunoa Pass, Tahiti (USNM 668799); reef flat, Arue, Tahiti (USNM 672782, 791363); Tiarei, Tahiti (USNM 363367); 35 km NE Mahaena, Papeete, Tahiti (USNM 672705); 1 km S of Faaone River, Faaone, Tahiti (USNM 669224); near mouth of Nahoata River, Pirao, Tahiti (USNM 668375); Taone, Tahiti (USNM 673457). TUAMOTUS: Matiti Id, Tikahau (USNM 629306, 629312, 629332, 629389, 629652); Maiai Id, Tikahau (USNM 652516); Temao Harbor, Makatea (USNM 629777); Avatoru Pass, Rangiroa (USNM 782743); Manihi (USNM 790243); Havana Id, Raroia (USNM 720647); Garumaoa Id, Raroia (USNM 723362); Vahitahi (USNM 613293); lagoon near village, Tatakoto (USNM 782704).

Cerithium rehderi, new species

FIGURES 112, 113

DESCRIPTION.—*Shell* (Figure 112): Shell tall, turreted, slender, comprising about 13–15 straight-sided or weakly inflated whorls and reaching 21.1 mm length and 7 mm width. Protoconch unknown. Early teleoconch whorls (Figure 112F) with broad, sloping, subsutural ramp and sculptured with 3 weak spiral threads crossing over strong axial riblets. Adult teleoconch sculptured with 2 or 3 beaded, major, spiral cords, numerous fine spiral threads, and irregular, weak, axial ribs and randomly placed varices. Subsutural cord tightly beaded and cincture-like. Two strongest beaded cords beneath whorl center. Penultimate whorl sometimes with weak anterior major spiral cords and 12–15 axial ribs. Suture indistinct, fine and wavy. Body whorl sculptured with four major, beaded, spiral cords; excavated base set off by anterior-most beaded spiral cord. Large varix opposite outer lip of aperture. Aperture ovate, about one-fourth the shell length. Anterior siphonal canal tightly constricted, of moderate length, reflected dorsally, and slightly to left of shell axis. Anal canal well developed, set off by parietal columellar plait. Columella concave with moderately thick callus and weak columellar lip. Outer lip thickened at edge, strongly crenulate, and convex. Shell color tan-brown with spiral subsutural row of white beads; other beads and varices sometimes white. Aperture white. Measurements (Table 36). Periostracum not evident. Operculum not known.

TABLE 36.—Shell morphometrics of *Cerithium rehderi*.

Character	$\bar{x}$ n = 000	sd	v	Range
Shell length	16.4	3.2	10.1	12.9–21.1
Shell width	5.5	1.1	1.2	4.2–7
Aperture length	4.1	0.7	0.5	3.2–5.1
Aperture width	2.7	0.5	0.3	2.2–3.5
Number whorls	13.7	0.8	0.6	13–15
Number spiral cords	3	–	–	3
Number axial ribs	13	0.9	0.9	12–15

Radula: Unknown.

Anatomy: Unknown.

HOLOTYPE.—USNM 859954, 15.4 mm × 5.4 mm (Figure 112A).

PARATYPES (5).—USNM 798574.

TYPE LOCALITY.—Haava Straits, between Tahuata and Hiva Oa, Marquesas, 56–72 m.

ETYMOLOGY.—Named in honor of Dr. Harald Rehder, for his work on Polynesian fauna.

ECOLOGY.—This rare species appears to live in moderate depths around the Marquesas where all specimens have been dredged in depths of 38 to 73 m on rubble or coarse sandy bottoms. The developmental biology of *C. rehderi* is unknown.

DISCUSSION.—The slender, tapering, light tan shell with white beads, sculptured with three main spirally beaded cords, and a strongly excavated shell base readily identify this species. As only five lots have been examined, intaspecific variation is not fully understood, but there appears to be much sculptural plasticity.

Cerithium rehderi, new species, differs greatly from all other sympatric French Polynesian *Cerithium* species. The light tan shell color with white subsutural beads and general fusiform shape is similar to that of *C. lissum* Watson (Figure 74) and, to a lesser degree, that of *C. phoxum* Watson (Figure 105), which are both widely allopatric to it (the eastward range of these two species ends at Fiji). *Cerithium rehderi* does not have the spiral incised, brown lines seen in *C. lissum*, and differs in having a strongly excavated shell base. *Cerithium phoxum* lacks the beaded sculpture seen in *C. rehderi*. Some specimens of *C. rehderi* have sculptural patterns similar to those of *C. leptocharactum* Rehder (Figure 69), but as only a few

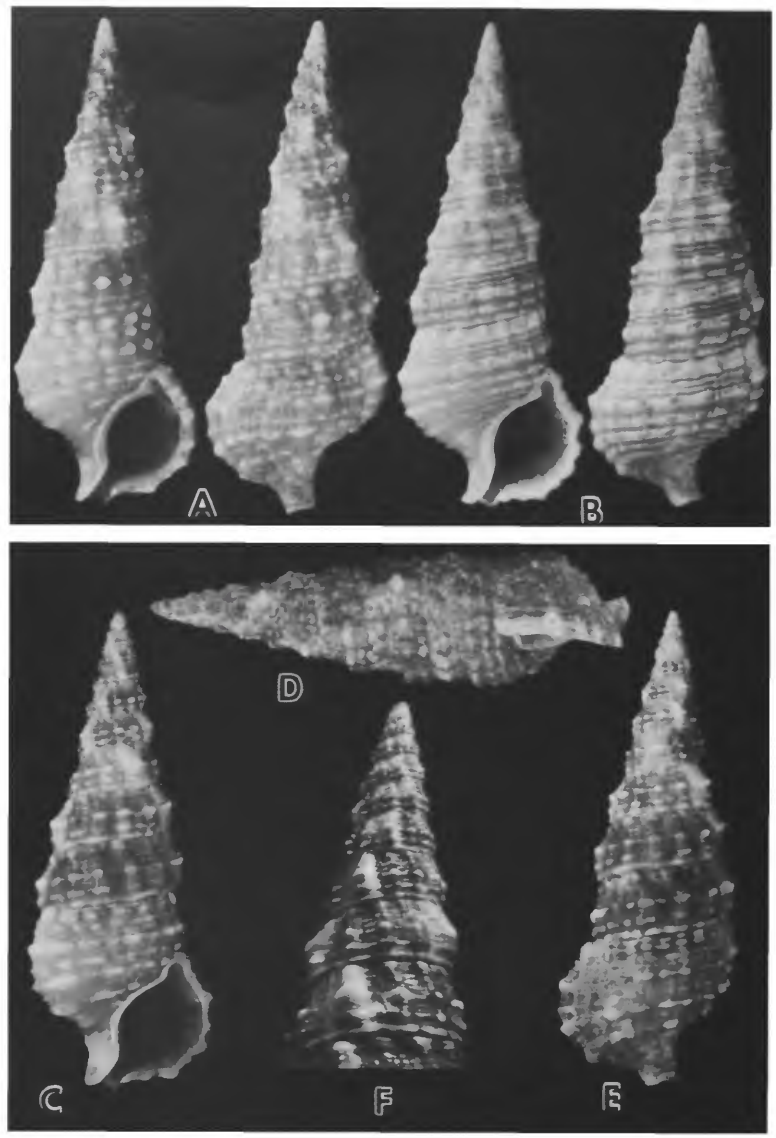

FIGURE 112.—*Cerithium rehderi*, new species: A, holotype, 57–73 m off Tahuata, Marquesas, 15.4 mm (USNM 859954); B, 66–82 m off SW coast Tahuata, Marquesas, 18.5 mm (USNM 790728); C–F, paratype showing early whorls (F), same locality data as A, 21.1 mm (USNM 867227).

specimens of the latter are known, it is premature to speculate on their relationship to each other. When more material of both taxa is available, they may prove to be closely related.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 113).—*Cerithium rehderi* appears to be endemic to the Marquesas.

SPECIMENS EXAMINED.—MARQUESAS ISLANDS: 60.3 m, 0.8 km off NW Point, Hatutu (USNM 790148); 38.4–58.4 m, outside entrance Baie Anaho, Nukuhiva (USNM 790431); 47.5–58.5 m, Baie Hatuatua, Nukuhiva (USNM 799888); 56.7–73.1 m, Haava Straits, between Tahuata and Hiva Oa (USNM 859954 holotype, 798574 paratypes); 65.8–82.3 m, off SW coast Tahuata (USNM 790728); 67.6–73.1 m, W side central Fatu Hiva (USNM 798574).

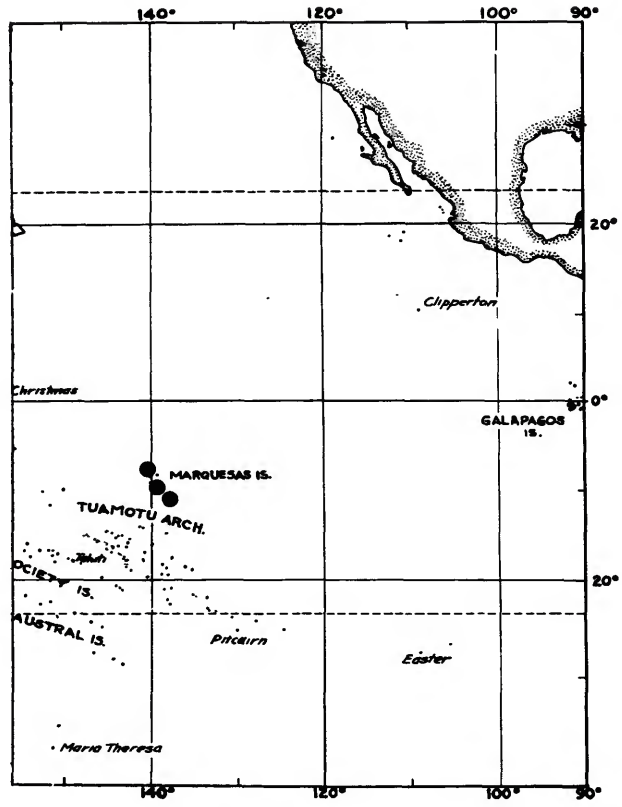

FIGURE 113.—Geographic distribution of *Cerithium rehderi*, new species.

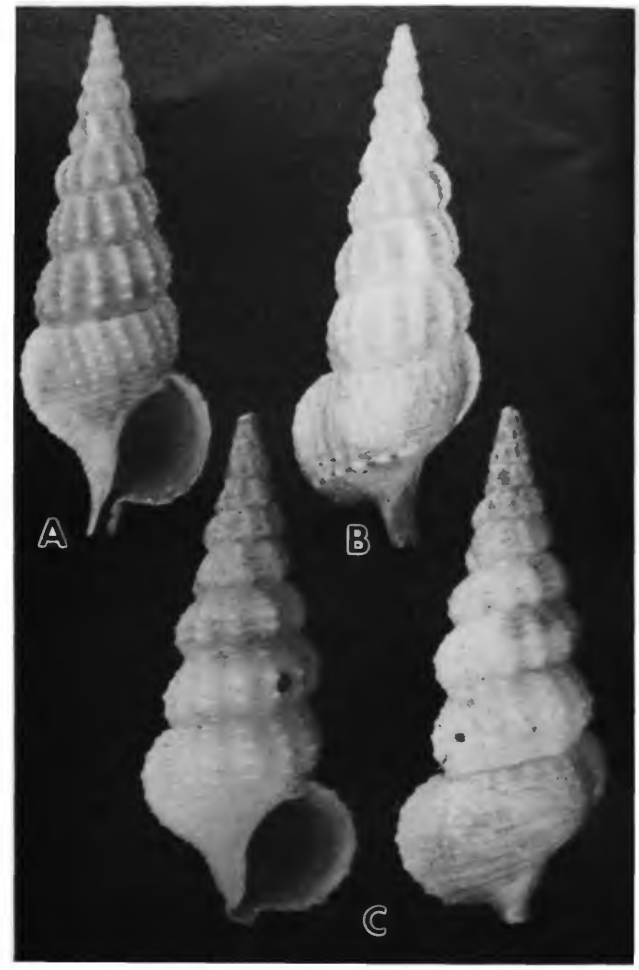

FIGURE 114.—Types of *Cerithium rostratum* Sowerby: A,B, lectotype of *Cerithium rostratum* Sowerby, Philippines, 18.1 mm (BMNH 19861741); C, lectotype of *Cerithium gracile* Pease, Hawaii, 12 mm (BMNH 1961173).

Cerithium rostratum Sowerby, 1855

FIGURES 114–117

?Cerithium ravidum Philippi, 1849:3, pl. 1: fig. 8 [type not found, no locality given; nomen dubium].

Cerithium rostratum Sowerby, 1855:861, pl. 158: fig. 104 [lectotype: BMNH 19861741, 3 paralectotypes, BMNH 198617424; type locality: Philippines, herein restricted to Cebu; 18.1 mm × 6.18 mm]; 1865, pl. 14: fig. 95.—Tryon, 1887:130, pl. 23: figs. 90, 91.—Kobelt, 1898:211, pl. 37: figs. 8, 9.—Hedley, 1899:430.—Schepman, 1909:159.

Cerithium gracile Pease, 1861:432 [lectotype: BMNH 1961173 and 3 paralectotypes, BMNH 19661174; type locality: Sandwich Islands, 12.0 mm × 4.8 mm; not *Cerithium gracile* Lamarck, 1804].—Tryon, 1887:173, pl. 36: figs. 50, 51.—Kay, 1965:45, pl. 5: figs. 5, 6.

Cerithium amabile Bayle, 1880:246 [new name for *Cerithium gracile* Pease, 1861; incorrectly attributed to Sowerby by Bayle].

Cerithium albovaricosum E.A. Smith, 1884:501 [new name for *Cerithium gracile* Pease, 1861].

Colina (Ischnocerithium) rostrata (Sowerby).—Thiele, 1929:212.—Wenz, 1940:758, fig. 2199.—Ladd, 1972:32, pl. 4: fig. 17.

Cerithium (Ptychocerithium) rostratum Sowerby.—Abrard, 1942:60, pl. 6: fig. 27.

Cerithium (Ischnocerithium) rostratum (Sowerby).—Cernohorsky, 1972:66, pl. 14: fig. 6.

DESCRIPTION.—*Shell* (Figures 114, 115): Shell thin, elongate, slender, fusiform, comprising 12–16 angulate whorls and reaching 22.9 mm length and 7.8 mm width. Protoconch 3 whorls (Figure 115F): protoconch 1 smooth, 0.5 whorls; protoconch 2, 3 whorls, elaborately sculptured with two centrally placed spiral threads and strong pre- and subsutural, colabral, axial ribs; interspace between spiral threads with tiny chevron-like ribs. Deep sinusigeral sinus at protoconch lip. Early teleoconch (Figure 115K) with broad, sloping subsutural ramp and sculptured with 2 or 3 spiral cords. Adult teleoconch whorls acutely angulate to moderately inflated, sculptured with wide to slender axial ribs crossed by numerous small spiral threads sometimes forming tiny beads at cross-over points. Varices randomly placed. Penultimate whorl with 0–25 axial ribs and 5–9 thin, spiral cords. Suture deeply impressed, straight. Body whorl elongate, weakly excavated at base, sloping into elongate, tightly constricted, straight, anterior siphonal canal. Body whorl sculptured with large varix

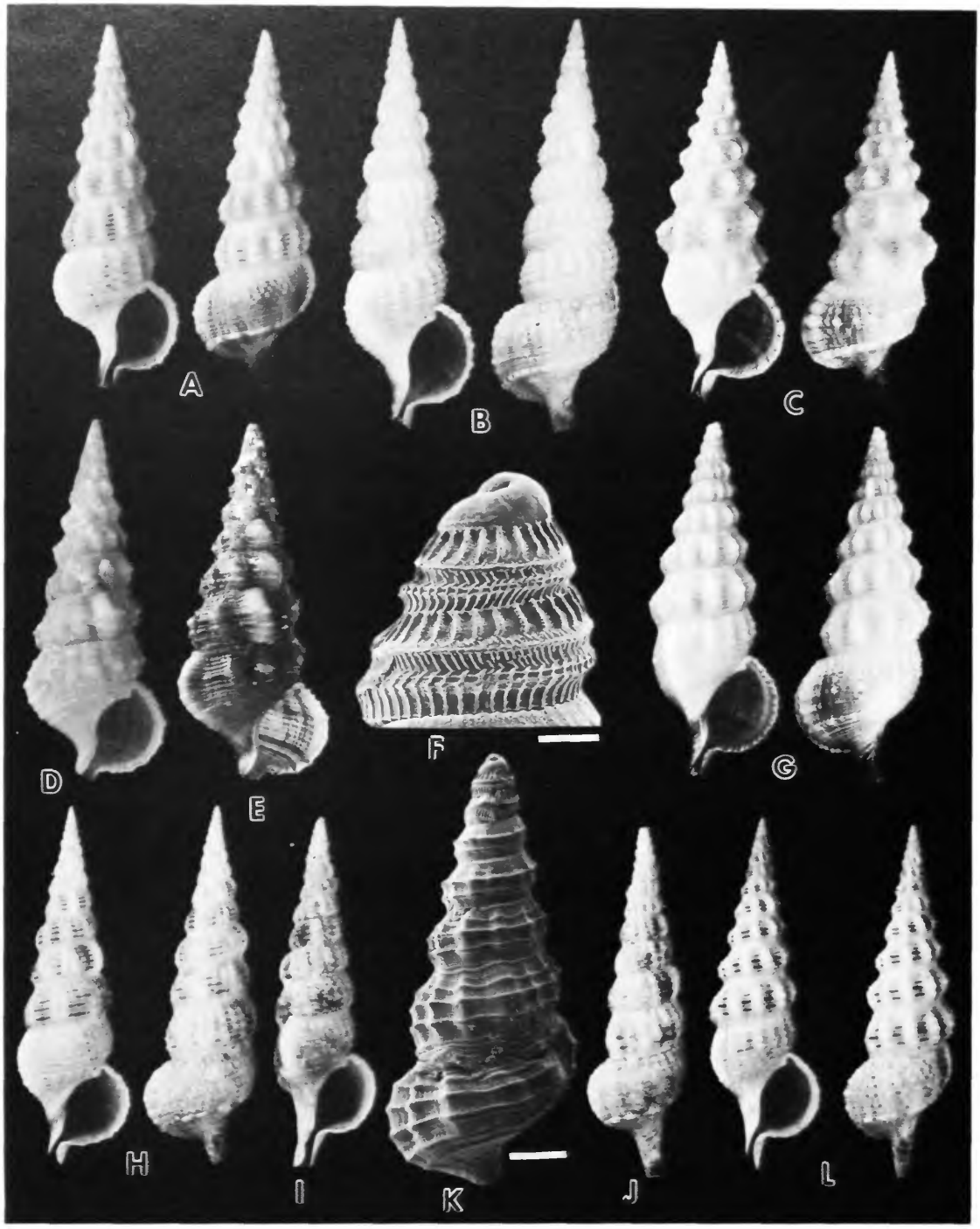

FIGURE 115.—Phenotypic variation in *Cerithium rostratum* Sowerby: A, Falarick Id, Ifaluk Atoll, Caroline Ids, 18 mm (USNM 616424); B, finely beaded morph, Port Blair, Andaman Ids, 21.9 mm (BMNH 1838 Winkworth); C, nodulose morph, Suva, Fiji, 20 mm (USNM 794739); D, Bikini Atoll, Marshall Ids, 12.7 mm (USNM 580514); E, melanistic specimen, same locality as D, 10.6 mm (USNM 580514); F, SEM of protoconch, Gulf of Aqaba, Israel (bar = 60 µm; USNM 671235); G, Suva, Fiji, 17.4 mm (USNM 794739); H, Bikini Atoll, Marshall Ids, 16.9 mm (USNM 586808); I,J, Bikini Atoll, Marshall Ids, 15.6 mm (USNM 586808); K, SEM of early whorls, Gulf of Aqaba, Israel (bar = 0.3 mm; USNM 580514); L, Port Matalvi, Luzon, Philippines, 26.7 mm (USNM 240132).

TABLE 37.—Shell morphometrics of *Cerithium rostratum*.

Character	$\bar{x}$ (n = 22)	sd	v	Range
Shell length	16.5	3.8	14.3	8.6–22.9
Shell width	5.5	1.1	1.1	3.6–7.8
Aperture length	4.2	0.9	0.9	2.3–6.2
Aperture width	3.0	0.7	0.5	1.7–4.5
Number whorls	13.8	1.1	1.2	12–16
Number spiral cords	6.7	1.3	1.6	5–9
Number axial ribs	14	3.5	11.9	10–25

opposite outer lip of aperture, numerous fine spiral threads and striae, sometimes beaded, and with main spiral cord at edge of long, sloping, basal excavation; axial ribs usually absent. Aperture ovate, about one-fourth the shell length. Columella concave with thin columellar callus. Anal canal weak, bordered by small, parietal, columellar plait. Outer lip strongly convex, thin, weakly crenulate, closely adpressed anteriorly to form siphonal tube. Shell color white, with thin tan-brown spiral lines interrupted by white axial ribs. Light brown blotches sometimes present and shells occasionally melanistic. Anterior of siphon dark brown to purple. Measurements (Table 37). Periostracum not apparent.

Radula (Figure 116A–D): Type-1 radular ribbon (Figure 3A) very small, about one-tenth the shell length. Rachidian tooth (Figure 116A,B) triangular, with large, central, posterior projection, and pair of basal ridges on elongate basal plate; anterior front slightly concave at center, with cutting edge having one main, arrow-shaped, pointed cusp flanked on each side by 2 pointed denticles. Lateral tooth (Figure 116B,C) with broad basal plate having long, lateral, posterior projection and wide, elongate, central, posterior buttress bearing central pustule; cutting edge of lateral tooth with wide, main cusp, one inner flanking, pointed denticle, and 3 or 4 outer flanking, pointed denticles. Marginal teeth (Figure 116A,C) long, narrow, widely spatulate at bases, and with curved, foliated, serrated

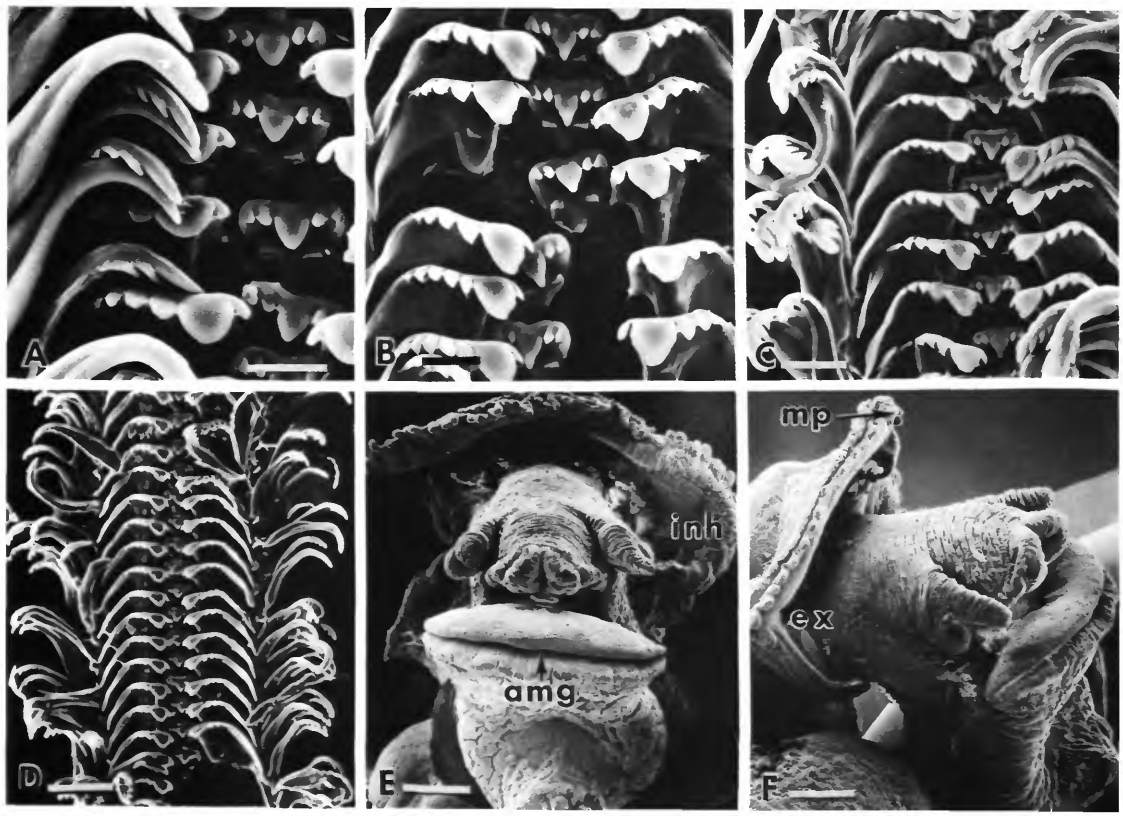

FIGURE 116.—Radula and critical point dried specimens of *Cerithium rostratum* Sowerby: A, half row with marginal teeth folded over ribbon, Dar es Salaam, Tanzania (bar = 25 μm; USNM 703858); B, rachidian and marginal teeth, same locality as A (bar = 25 μm; USNM 703858); C, half row, same locality as A (bar = 50 μm; USNM 703858); D, radula with marginals folded back, same locality as A (bar = 100 μm; USNM 703858); E, SEM of headfoot, anterior view, showing inhalant siphon (inh) and deep anterior mucus gland (amg) at foot edge (bar = 0.38 mm; USNM 847630); F, SEM of right side anterior headfoot showing papillae (mp) on bifurcate mantle edge and exhalant siphon (ex); note bilobed snout tip (bar = 0.38 mm; USNM 847267).

tips. Inner marginal tooth with long, central major cusp, 3 or 4 pointed denticles, and 2 or 3 outer pointed denticles. Outer marginal tooth same, but without outer denticles.

Anatomy (Figure 116E,F): Animal long, slender, comprising 5 or 6 whorls. Females with cream-colored ovary; males with orange testis. Head foot greenish pink, and covered with fine white papillae presenting warty appearance. Sole of foot very narrow, propodium wide, crescent-shaped, with deep, anterior, pedal mucus gland (Figure 116F, amg). Right side of foot in females without ciliated groove and ovipositor. Snout long, narrow, with tiny bilobed tip (Figure 116E,F). Cephalic tentacles long, slender, each with eye surrounded by black and bright orange pigment. Mantle edge bifurcate, fringed with white papillae (Figure 116E,F, mp), each protruding between scallops forming edge of shell aperture lip. Inhalant siphon widely projecting beyond mantle edge (Figure 116E, inh), blackish green within, and fringed with orange papillae. Exhalant siphon (Figure 116F, ex) producted by fold in mantle edge. Top of mantle green.

Mantle cavity deep. Osphradium high, brown, becoming lighter tan posteriorly. Ctenidium long, slender, white, comprising long, finger-like filaments. Hypobranchial gland, pale green, thin, with transverse ridges, and relatively narrow.

Buccal mass small, with very short radula. Salivary glands thin, white, coiled tubes originating behind large nerve ring and passing through, becoming loosely coiled on buccal mass. Esophageal gland of moderate size, tan and flattened dorsal-ventrally. Large stomach with complex sorting areas and large posterior raised pad, short style sac, and gastric shield.

Type-A pallial oviduct (Figure 4A) with posterior albumen gland, white, central capsule gland, and short sperm gutter at anterior edge of medial lamina. Spermatophore bursa narrow anteriorly, becoming large, swollen, at posterior and divided partially by interior longitudinal ridge. Interior of spermatophore bursa finely papillate. Posterior seminal receptacle of medial lamina tiny, pink. Anterior seminal receptacle of lateral lamina with small opening leading into thin, slender tube extending posteriorly to central lateral lamina.

SYNONYMIC REMARKS.—This species is usually named *C. rostratum* in the literature, but an earlier name may be *Cerithium ravidum* Philippi. Although the figure presented by Philippi (1849, pl. 1: fig. 8) looks somewhat like *Cerithium rostratum* Sowerby, it is not a clear representation. As the type of *C. ravidum* has not been found, and no type locality was given in the original description, *C. ravidum* is considered a nomen dubium. *Cerithium rostratum* Sowerby is the earliest available name for this species, and a lectotype (BMNH 19861741, Figure 114A,B) is here selected. The lectotype (Figure 114C) and paralectotypes of *C. gracile* Pease are clearly conspecific with *C. rostratum* Sowerby. As the former taxon is preoccupied, two replacement names were proposed for it, *Cerithium amabile* Bayle, 1880, and *Cerithium albovaricosum* E.A. Smith, 1884. Apparently Bayle and Smith were unaware that *C. gracile* was conspecific with *C. rostratum*.

Thiele (1929:212) allocated *C. rostratum* to the genus *Colina* H. and A. Adams, 1854, proposing the subgenus *Ischnocerithium* Thiele, 1929, and designating *C. rostratum* as the type. *Colina* species have elongate, constricted body whorls and distinctive radulas. Thiele (1929), noting the long, attenuated siphonal canal of *C. rostratum*, a feature shared by *Colina* species, may have assigned it to *Ischnocerithium* on that basis. Thiele's (1929) concept of *Colina* also embraced *Ataxocerithium* Tate, 1894, which belongs in the TRIPHOROIDEA (Houbrick, 1987b, cited as CERITHIOPSACEA). It is clear that neither *Ataxocerithium* nor *C. rostratum* should be assigned to *Colina*. Cernohorsky (1972:66) considered *Ischnocerithium* to be a subgenus of *Cerithium*, but there are no anatomical reasons for according this taxon higher category status, and the shell characters defining the genus *Ischnocerithium* are, at best, equivocal.

ECOLOGY.—This species is commonly found on marine angiosperm grass beds in quiet, sandy lagoons, usually in large populations. I have observed it in Laucala Bay, Viti Levu, Fiji, in shallow water on *Enhalus* grass beds, crawling on grass blades and on associated algae and sand. At Pago Bay, Guam, it is common on intertidal and subtidal grass beds on *Enhalus* grass blades. Shells are normally overgrown with epiphytes and are frequently eroded at their apices. Many specimens have peeled apertures suggesting heavy crab predation. *Cerithium rostratum* is abundant on the sandflats of One Tree Id, Queensland, Australia, where it appears to have some association with the alga *Laurencia* (G. Skilleter, in litt). It is rarely found in sediment samples, suggesting that it does not commonly burrow. This species is frequently dredged in similar, deeper habitats throughout its range, and has been taken in depths of up to 35 meters. It occupies much the same habitat that *Cerithium muscarum* (Say) does in the western Atlantic (Houbrick, 1974a:18–19).

Although its reproductive biology has not been studied, and the egg mass is unknown, *C. rostratum* has the largest, most elaborately sculptured protoconch of any known *Cerithium* species (Figure 115F); this, along with its wide geographic range, and very small egg size, indicate a long planktotrophic stage.

DISCUSSION.—*Cerithium rostratum* is easily recognized by a slender, elongate shell, comprised of broadly inflated, angulate whorls, sculptured with wide axial ribs, and by a long, attenuated, anterior siphonal canal with purple tip. The elaborately sculptured protoconch (Figure 115F) of *C. rostratum* clearly distinguishes it from other species.

This species displays a great deal of intraspecific variation in shell size and sculpture. Some populations have adult shells ranging from large to very small sizes. Other populations are comprised totally of dwarfed shells. The length of the siphonal canal may also vary between populations but this is apparently related to habitat; shells from protected grass beds in sheltered bays and lagoons have long canals (Figure 115A–C,G,I,J,L) while those from more atypical, less protected substrates are

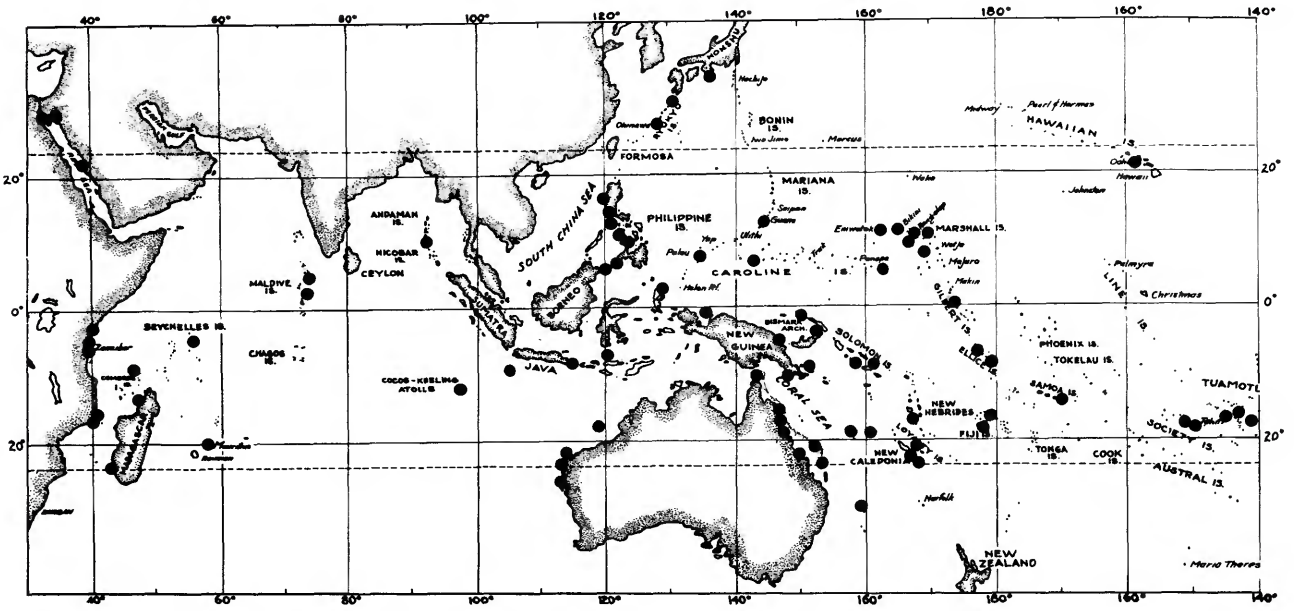

FIGURE 117.—Geographic distribution of *Cerithium rostratum* Sowerby.

usually smaller and have shorter canals (Figure 115D,E). The number and intensity of axial ribs vary considerably within populations. Some individuals show very strong axial rib development (Figure 115A,C,G,L) while in others ribs are weak or nearly absent (Figure 115B,H). This may be due to pauses in growth rate because axial ribs are colabral and appear to be laid down during growth stages. Some shells have large, randomly distributed varices (Figure 115B,D,E). This may be a response to predation pressures, shells with thicker varices being more prone to resist peeling by crab predators.

The shell of *C. rostratum* is not easily confused with those of other *Cerithium* species except when immature (Figure 115K) or if missing the siphonal canal: it may then look similar to *Cerithium dialeucum* Philippi (Figure 47A-G) or *Cerithium torresi* E.A. Smith (Figure 135A-J). *Cerithium citrinum* Sowerby (Figure 25A-I) is the species most similar to *C. rostratum*, but the former has a much larger, solid, bright yellow shell sculptured with many fine spiral striae, and has a much wider body whorl than does *C. rostratum*. The anterior siphonal canal of *C. citrinum*, is also much longer that that of *C. rostratum* and is directed to the left of the shell axis by a 45 degree angle.

FOSSIL RECORDS.—*Cerithium rostratum* has been recorded from the Pleistocene of French Somalia (Khor Anghar) by Abrard (1942:60, pl. 6: fig. 27). Ladd (1972:32) cited it (as *Colina rostrata*) from Late Miocene, Pleistocene, and Holocene drill holes on Enewetak Atoll, and from Pliocene to Holocene drill holes on Bikini Atoll, Marshall Islands.

GEOGRAPHIC DISTRIBUTION (Figure 117).—This species is found throughout the Red Sea and Indian Ocean eastward throughout Indonesia and tropical Australasia. In the western Pacific, it occurs from southern Japan south throughout Micronesia and Melanesia to Lord Howe Island. It is common throughout the central Pacific as far east as the Tuamotus and north to Hawaii, where it is not common.

SPECIMENS EXAMINED.—EAST AFRICA: Mozambique (USNM 629037); 20–21 m, Nocela, Mozambique (ANSP); Mboa Magi, 14.4 km S Dar es Salaam, Tanzania (USNM 604575); entrance to Dar es Salaam Harbor, Tanzania (AMS); 3–5 m, between Makatumbe Id and Dar es Salaam, Tanzania (AMS); Ras Chokir, Dar es Salaam, Tanzania (USNM 703858); 3–4 m, NW corner of Mbudya Id, 16 km N of Dar es Salaam, Tanzania (AMS); Mnazi, Moja, W Zanzibar (MCZ); 1.6 km N of Paje, SE Zanzibar (ANSP); Mnemba Id, NE Zanzibar (ANSP); Twiga, 19.2 km S of Mombassa, Kenya (ANSP); Waitarii Beach, near Malindi, Kenya (ZMA). RED SEA: Gulf of Suez (USNM 23117); 14.6–53 m off Mersat Abu Samra, Israel (ZMTA); Eilat, Gulf of Aqaba, Israel (USNM 671235, 672279); Nuweiba, Sinai, Israel (AMS); Gulf of Aqaba, Jordan (USNM 841317); Jidda Harbor, Saudi Arabia (USNM 637026).

GULF OF ADEN: Aden, Saudia Arabia (AMS). MADAGASCAR: Anakao, 32.8 km S of Tulear (MCZ); Tulear (USNM 718361); between Ambatoloaka and Madirokely, SW Nossi Bé (AMS); SW Ambariotelo, SE of Nossi Bé (MCZ); N of Nossi Ambariotelo, SE of Nossi Bé (AMS); W of Pt Mahatsinjo, S Nossi Bé (ANSP); E side of Pt Lokobe, S Nossi Bé (MCZ); Nossi Bé (USNM 720153); Ilampy, 4.16 km NE of

Ambodi Fotora, Île St Marie (MCZ).

INDIAN OCEAN ISLANDS: Île Picard, Aldabra, Seychelles (USNM 837414, 837499, 837739, 837821, 837887); Passe Houareau, Île Malabar, Aldabra Atoll, Seychelles (USNM 837439, 837457); Port Glaud, W Mahé, Seychelles (ANSP); Point La Rue, E Mahé, Seychelles (ANSP); Seychelles (AMS); Mauritius (USNM 91071); 0.4 km SW of Cap Malheureux, N Mauritius (ANSP); 20°5′S, 57°30′E, NW tip, Arsenal Bay, Mauritius (USNM 716567); 0.4 km N of Black River Bay, W Mauritius (ANSP); Le Gris-Gris, Sovillac, S Mauritius (AMS); between Mafilefuri and Muro Ids, Fadiffolu Atoll, Maldives (ANSP); SE side of W Male Atoll, Maldives (ANSP); 3.6–5.4 m, SE of Possession Pt, Hornsburh Id, Cocos Keeling Ids (ANSP, USNM 656323); 1.2–1.8 m, 0.4 km W of Pulo Bras and Pulo Gangsa, Cocos Keeling Ids (MCZ); lagoon side S tip of Home Id, Cocos Keeling Ids (ANSP); 1.6 km N of Tonjong Puji, West Id, Cocos Keeling Ids (USNM 656358); West Island, Cocos Keeling Ids (AMS, USNM 656195); 0.4 km N of Pula Maria, Cocos Keeling Ids (USNM 656364); 43.2 km off NE Pt, Christmas Id (AMS). ANDAMAN ISLANDS: Port Blair (BMNH).

JAPAN: Susami, Wakayama Pref, Kyushu (USNM 666609). RYUKYU ISLANDS: Osima, Osumi (USNM 343870); Amami Ids (ANSP); Ada Village, Kunugami Prov, Okinawa (ANSP); Ogimi, Okinawa (USNM 488052); Nago, Okinawa (USNM 363722); Shioya, Shanawan Bay, Okinawa (USNM 489147); Okinawa (USNM 671101). PHILIPPINES: 100 Ids, Lingayen Gulf, Pangasinam Prov, NW Luzon (LACM 88791); Port Matalvi, Luzon (USNM 240132); Zambales, Luzon (MCZ); 5.5–16.5 m, Port Real, Quezon, Luzon (LACM 76857); Talaga, Bataan, Luzon (AMS); West Tip, Corregidor, Luzon (ANSP); Matabungkai, SSW of Manila, Luzon (AMS); Tilic Bay, Lubang Id (MCZ); Little Balateros Cove, Puerto Galera, Mindoro (AMS); 1–6 m, Ata Id, 2 km W of Kawayan, Marinduque (AMS); Cataingan Id, Dumurung Pt, Masbate (USNM 239988); Bantayan Beach, Dumaguete City, Negros (USNM 812613); Guijulugan, Negros (USNM 244050); Cebu, Cebu (AMS); Salpa Id, 2 km S of Olango Id, E Cebu (ANSP); Banacon Id, Danajon Bank, NW of Bohol (AMS); 3.6–7.2 m, E side of Jagoliao Id, NW end of Bohol (ANSP); E side Jagbolaran Strait, Bohol (USNM 233082); Zamboanga, Mindanao (USNM 233164); Sinonog Id, Mindanao (USNM 619858); near Bolong, Gavilan Id, Mindanao (USNM 619913); Mariqui, Mindanao (USNM 619843); Badlak Id, Mindanao (USNM 619956); Sibakel Id, Mindanao (USNM 620080); Basilan Id, Mindanao (USNM 619749, 619778, 619883, 619901, 620002, 620023, 620041, 620090, 620106); Landang, Sulu Sea (USNM 619677); Manicaan, Sulu Sea (USNM 619710); Babag, near Taluksangay, Sulu Sea (USNM 619667); off Muobo Beach, Jolo Id, Sulu Archipelago (ANSP); Isle, 0.4 km W of Tara Id (USNM 243769); 0.9–6 m, SE side of Lapac Ids, Siasi Id, Sulu Archipelago (ANSP). INDONESIA: Batoe Id (ZMA); beach, Bali Beach Hotel, Bali (ANSP); Morotas, Halmahera Gp (USNM 542518).

WESTERN AUSTRALIA: Turtle Bay, North West Cape (WAM); off Mangrove Id, North West Cape (WAM); Carnarvon (WAM); Point Cloates (WAM); Clerk Reef, Rowley Shoals (WAM). QUEENSLAND, AUSTRALIA: Murray Id, Torres Strait (AMS, MCZ); Somerset, Cape York Peninsula (AMS); 0.4 km N of North Direction Id (AMS); Two Islands, N of Cooktown (AMS); Rocky Id, N of Cooktown (AMS); Hope Id, SE of Cooktown (AMS); Palfrey Id, off Lizard Id (AMS); Watson's Bay, Lizard Id (AMS); Casuarina Beach, Lizard Id (USNM 766808); 20 m, off East Face, Lizard Id (AMS); Low Isles, near Port Douglas (AMS, USNM 623131); Michaelmas Cay, off Cairns (AMS); Green Id, off Cairns (AMS, MCZ); NE Cay, Herald Gp, Coral Sea (AMS); Ellis Reef, near Kurramine (AMS); Eclipse Id, Palm Ids, off Townsville (AMS); Palm Id, off Townsville (AMS); Magnetic Id, off Townsville (AMS); Bowen (AMS); Hamilton Id, Whitsunday Passage (AMS); Lindeman Id, Cumberland Gp, N of Mackay (AMS); Swain Reefs (AMS); N Keppel Id, Keppel Bay (AMS); E end of Heron Id (AMS); North West Id, Capricorn Gp (AMS); Lady Musgrave Id, Bunker Gp (AMS); Dundowran, Hervey Bay (AMS); Caloundra (AMS); Morris Id (AMS); Flinders Id (AMS); Wreck Bay, Coral Sea (AMS); 38–50 m, 19°11′90″S, 158°55′80″E, RV *Chacal*, Chesterfield-Bellona Plateau, Coral Sea (MNHNP). NEW GUINEA: 1–10 m, E Mios Woendi Id, Padaido Ids, Irian Jaya (AMS); Mios Woendi Id, Biak Id, Irian Jaya (MCZ, USNM 542701); 45.7–51.2 m, lagoon 1.6 km E Dawvi Wamsoi Id, E Padaido Ids, Irian Jaya (ANSP); N shore of Maroepi Id, Ambai, Japen Id, Irian Jaya (MCZ); 0.8 km SW Seroei Village, Japen Id, Irian Jaya (ANSP); inlet, N end of Kranket Id, Madang, Papua (AMS); N tip of Buriwadi Id, Lusancay Ids, Trobriand Gp (AMS); Fisherman Id, near Port Moresby, Papua (AMS).

BISMARCK ARCHIPELAGO: New Hanover (AMS); Rabaul, New Britain (AMS). SOLOMON ISLANDS: Ataa, Malaita Id (AMS, ANSP); Pavuvu Id, Russell Gp (USNM 488386). NEW HEBRIDES: Point Ardol, Port Vila, Efate (AMS); Vate (AMS). LOYALTY ISLANDS: Lifu (AMS, USNM 423276, 423306, 423308). NEW CALEDONIA: Belep Id (AMS); Oubatche (AMS); N Gatope Id, Voh (ANSP); Plage de Pol, Bourail (ANSP); Île Cesar, Anse Vata, Nouméa (AMS); Ricaudy Reef, Nouméa (ANSP); Île des Pins (MCZ). LORD HOWE ISLAND: 44 m, 31°38′S, 159°03′E (AMS); HMAS Kimbla, 44 m off Lord Howe Id (AMS). FIJI: Albert Cove, NW Rambi Id, Vanua Levu (USNM 695231); N side Verevere Id, Vanua Levu (USNM 694972); Sali Sali, Viti Levu (USNM 694514); Viti Levu Bay, Viti Levu (USNM 824804); 9–35 m, Nadi Bay, Viti Levu (AMS); off Nadi, Viti Levu (USNM 638560); Yakuilau Id, off Nadi Bay, Viti Levu (USNM 658797); 18–24 m, Momi Bay, W Viti Levu (ANSP); Suva reef, Viti Levu (USNM 845793); Laucala Bay, Viti Levu (USNM 794739); Komave, Coral Coast, Viti Levu (AMS); Sauvi Bay, SE coast of Viti Levu (AMS); E of Korolevu Bay, Kandavu (USNM 696108).

MARIANA ISLANDS: Guam (USNM 620401); Tumon

Bay, Guam (USNM 592817); USO Beach, Guam (USNM 842611); Apra Bay, Guam (USNM 233153, 243741, 853085); Pago Bay, Guam (USNM 847267); Nimitz Beach, Guam (USNM 852050). PALAU: (USNM 636541, 636557); 5–15 m, Kayangel Lagoon (ANSP); N side of West Pass, Babelthuap Id (ANSP); Ngadarak Reef, Malakal Harbor (ANSP). CAROLINE ISLANDS: Falarik Id, Ifaluk Atoll (USNM 616377, 616424, 616521, 616707, 616712); Elangalap Ids, Ifaluk Atoll (USNM 616700); reef at Mutunlik, Kusaie Id (USNM 609564). MARSHALL ISLANDS: Wotho Id, Wotho Atoll (USNM 614448); Enewetak Atoll, numerous localities throughout, (USNM 432421, 542752, 542753, 542799, 581227, 581478, 581544, 581549, 581602, 582277, 587180, 587201, 587211, 587222, 587274, 587301, 821848); Bikini Atoll (numerous localities throughout, USNM 580345, 580514, 582436, 582766, 582857, 583026, 583662, 584934, 584940, 585183, 586083, 586685); Lomuilal Id, Rongelap Atoll (USNM 585798); Kabelle Id, Rongelap Atoll (USNM 582401); Rongelap lagoon, Rongelap Atoll (USNM 584292); Rochi Id, Rongelap Atoll (USNM 584162); Burch Id, Rongelap Atoll (USNM 583465); Bock Id, Rongerik Atoll (USNM 584661, 584934, 594940); Kevai Dock, Kwajalein Atoll (AMNH); Kwajalein Id, Kwajalein Atoll (USNM 486072, 622819); Ailuk Atoll (USNM 615138, 615139); Taka Id, Taka Atoll (USNM 615455). GILBERT ISLANDS: Abamama Id (USNM 434001).

HAWAIIAN ISLANDS: Honolulu Harbor, Oahu (BPBM 63079). ELLICE ISLANDS: Lagoon side, Nui (USNM 685877); main id, Vaitupu (USNM 685940). SAMOA: Samoa (USNM 91053, 91162); Tutuila (ANSP). SOCIETY ISLANDS: W of Pt Tiva, Huahini (USNM 675545); Opunohu Bay, Moorea (USNM 630654); near Blue Lagoon, Pirae, Tahiti (USNM 668679, 668701); Mataiea, Tahiti (USNM 791364); Taone, Tahiti (USNM 673448). TUAMOTU ARCHIPELAGO: Avatoru Pass, Rangiroa Atoll (USNM 789640, 789690, 790933); between Garumaoa Id and Ohave, Raroia Atoll (USNM 722231); Montufano Id, Raroia Atoll (USNM 721247); Tahuna Riri Id, Raroia Atoll (USNM 720595); lagoon side, Oneroa Id, Raroia Atoll (USNM 721330); Anaa Atoll (USNM 791380); Tauere Atoll (USNM 671880); near Hikitake Id, Amanu Atoll (USNM 671792); Vahitahi Atoll (USNM 613294).

Cerithium ruppelli Philippi, 1848

FIGURES 118–121

Cerithium Ruppelli [sic] Philippi, 1848:22 [type not located; neotype, herein selected MNHNP, no number, 47.2 mm × 16.8 mm; type locality: Suez, Egypt]; 1849:13, pl. 1: fig. 1.

Cerithium Rupellii [sic] Philippi.—Sowerby, 1855:859, pl. 79: fig. 65.

Cerithium spathuliferum Sowerby, 1855:859, pl. 180: fig. 94 [type not located; Sowerby's figure 94 herein selected to represent lectotype; no type locality given, herein restricted to Red Sea]; 1865, pl. 8: fig. 50.

Cerithium erythraeonense var. Lam.—Vaillant, 1865:107, no. 16 [in part].

Cerithium Ruppellii [sic] Philippi.—Sowerby, 1865, pl. 1: fig. 6.—Tryon, 1887:124, pl. 20: figs. 28, 29.

Cerithium Savignyi [sic] P. Fischer, 1865:244 [name based on Savigny figure, 1817, "atlas" *Egypte*, pl. 4: fig. 29; holotype: MNHNP no number; type locality: Suez, Red Sea; 39.5 mm].—Bouchet and Danrigal, 1982:15, fig. 39.

Cerithium Ruppeli [sic] Philippi.—Kobelt, 1893:107–108, pl. 21: figs. 5–7.

Cerithium (Thericium) Ruppelli [sic] Philippi.—Moazzo, 1939:172–173.

DESCRIPTION.—*Shell* (Figures 118, 119): Shell elongate, turreted, large, comprising about 15 angulate whorls, and reaching 47 mm in length and 16.8 mm width. Protoconch unknown. Early teleoconch whorls sculptured with 4 spiral threads and strong axial ribs. Adult teleoconch sculptured with 1–4 main spiral, nodulose cords: first two cords weak; third cord largest, on whorl periphery; fourth cord presutural, usually strong; central cord rarely present. Smaller spiral cords and incised lines usually present. Nodes weak or strong and spinose, aligned forming 13–16 axial ribs. Strong varices randomly placed. Suture weak to indistinct, wavy. Body whorl sculptured with 4 or 5 nodulose or spiny, spiral cords of varying intensity, and with many fine spiral striae and threads. Two cords before siphonal constriction strongest, usually very spinose. Large, thick varix opposite outer lip of aperture. Base of body whorl excavated, and with strong siphonal constriction. Aperture ovate, fusiform, well over one-third to one-fourth the shell length. Anterior siphonal canal tubular, of moderate length, strongly reflected dorsally and to left of shell axis. Anal canal strong, deeply incised, and defined by strong parietal columellar tooth. Columella concave with heavy callus and thick columellar lip. Outer lip of aperture concave, thickened, strongly crenulate, and internally incised with deep spiral

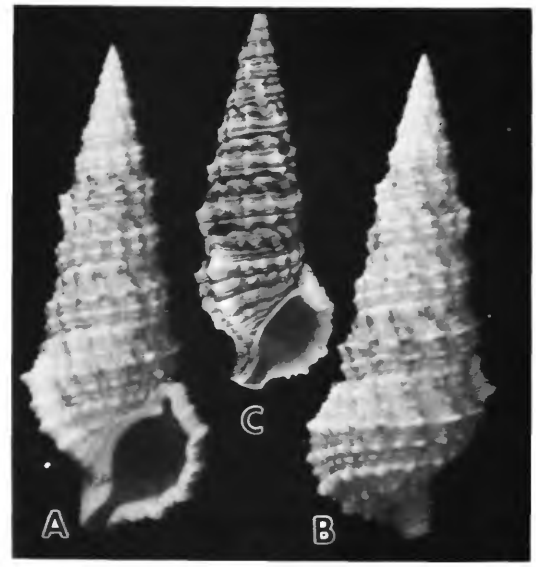

FIGURE 118.—*Cerithium ruppelli* Philippi: A,B, neotype of *Cerithium ruppelli*, Suez, Egypt, 47.2 mm (MNHNP); C, holotype of *Cerithium savignyi* Fischer, Suez, Egypt, 39.5 mm (MNHNP).

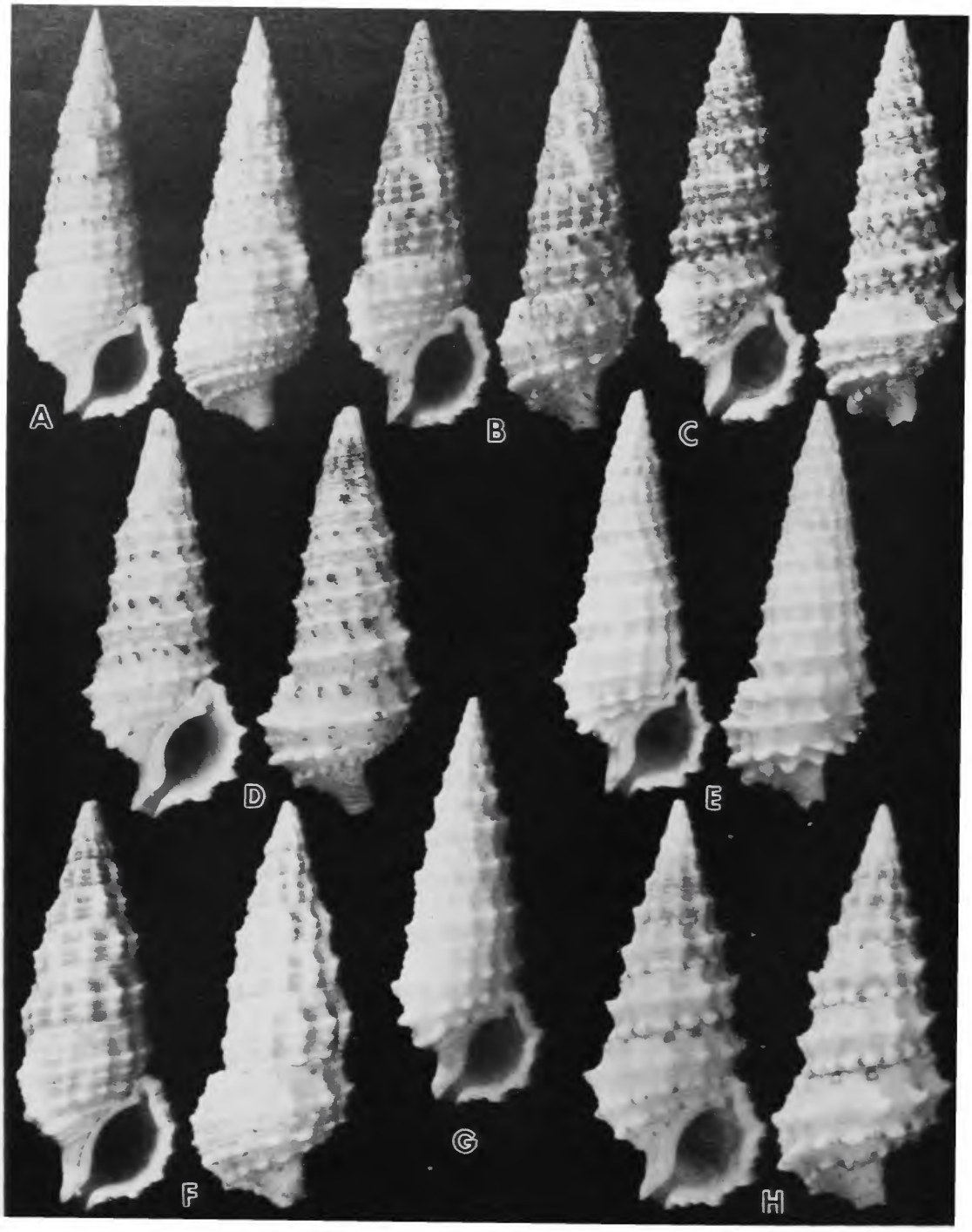

FIGURE 119.—Phenotypic variation between populations of *Cerithium ruppelli* Philippi. A, Aden, 29 mm (MNHNP); B, Port Sudan, Sudan, 37.3 mm (USNM 770718); C, Suez, Egypt, 43.4 mm (MNHNP); D, intermediate *spathuliferum* morph, Ras Abu Galum, Aqaba, Egypt, 39 mm (USNM 798124); E, *spathuliferum* morph, Eilat, Aqaba, Israel, 39.2 mm (USNM 671248); F, intermediate *spathuliferum* morph, Aden, 21.6 mm (MNHNP); G, *spathuliferum* morph, Eilat, Aqaba, Israel, 36 mm (USNM 671248); H, *spathuliferum* morph, Eilat, Aqaba, Israel, 25.9 mm (USNM 671248).

TABLE 38.—Shell morphometrics of *Cerithium ruppelli*.

Character	$\bar{x}$ (n = 10)	sd	v	Range
Shell length	38.1	5.8	33.0	28–47
Shell width	13.3	1.8	3.4	9.6–16.8
Aperture length	10.4	1.7	2.9	7.2–13.2
Aperture width	6.5	1.2	1.5	4.6–9.2
Number of whorls	14.9	0.7	0.5	14–16
Number spiral cords	2.8	1.5	2.2	1–4
Number of nodes	14.1	1.0	1.1	13–16

grooves. Shell color white to light tan or darker brown; subsutural spiral bands of chestnut spots sometimes present. Measurements (Table 38). Periostracum not evident.

Radula (Figure 120): Type-1 radular ribbon (Figure 3A) small, about one and one-half of the shell length. Rachidian tooth (Figure 120B) triangular, with rounded anterior edge and small basal plate having long, central, triangular, posterior extension and pair of weak, posterior, lunate ridges; cutting edge with spade-shaped main cusp flanked on each side by 2 weak denticles. Lateral tooth (Figure 120C) with long posterior-lateral extension, and with thick, central, posterior-projecting buttress bearing small central pustule on large basal plate; cutting edge with large, rounded main cusp, one pointed inner flanking denticle and 2 or 3 outer pointed flanking denticles. Marginal teeth (Figure 120C,D) long, thin, spatulate at bases, with curved, foliated tips. Inner marginal tooth with 3 inner denticles and 1 or 2 outer denticles. Outer marginal tooth same, but without outer denticle.

Anatomy: Unknown.

SYNONYMIC REMARKS.—The original spelling of this name was with only one "i." The type material is lost, but Philippi's (1849, pl. 1: fig. 1) illustration of the taxon is in close agreement with *C. ruppelli* of subsequent authors and can not be confused with any other *Cerithium* species from the Red Sea area; consequently, a neotype (Figure 119A,B) that closely matches his figure is herein selected. Vaillant's (1865:107) variety of *C. erythraeonense* was regarded by Moazzo

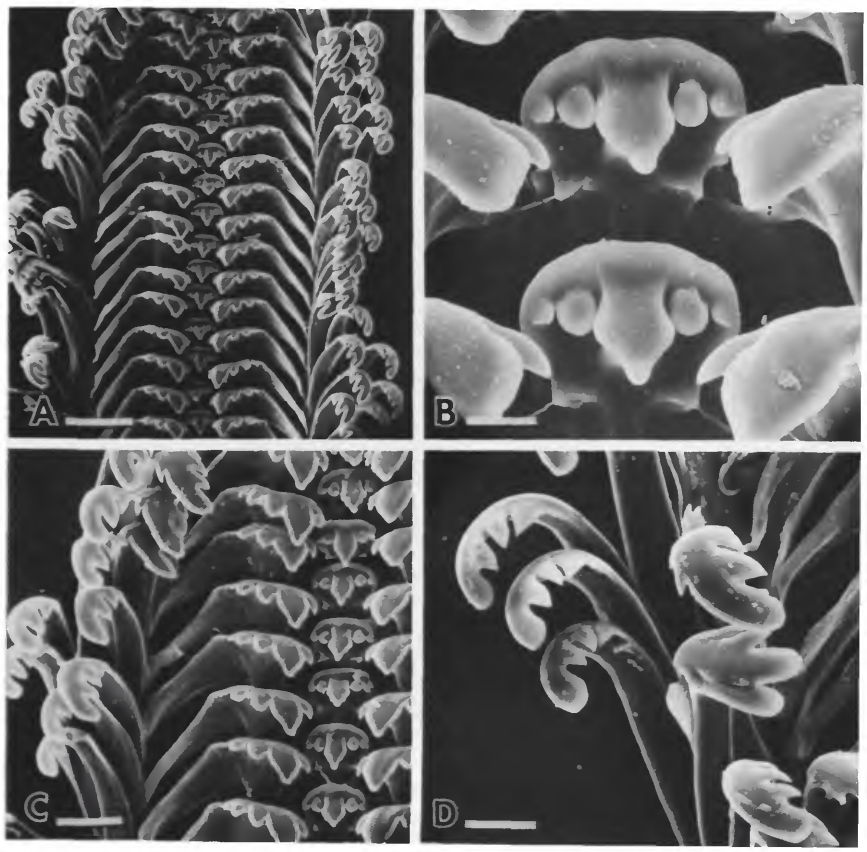

FIGURE 120.—SEM of radula of *Cerithium ruppelli* Philippi, Ras Abu Galum, Aqaba, Egypt (USNM 798124). A, radula with marginals folded open (bar = 125 μm); B, rachidian tooth (bar = 19 μm); C, half row showing dentition of lateral and marginal teeth (bar = 60 μm); D, marginal teeth (bar = 38 μm).

(1939:173) as a synonym of *C. ruppelli*. The holotype of *C. savignyi* Fischer (Figure 118C) is also conspecific with *C. ruppelli*. *Cerithium spathuliferum* Sowerby, which represents a phenotypic extreme of *C. ruppelli*, has a strong keel of spiral nodes on the body whorl and siphonal constriction. As demonstrated below, there are many intergrades between it and the more common phenotype of *C. ruppelli*. Although Sowerby's (1855) type material has not been found, his illustration of *C. spathuliferum* cannot be confused with any other *Cerithium* species from the Red Sea, and undoubtedly represents the keeled, nodulose phenotype of *C. ruppelli*. *Cerithium spathuliferum* is here regarded as a synonym of *C. ruppelli*.

ECOLOGY.—Aside from habitat descriptions not much is known about this species. It appears to live on shallow, soft, subtidal substrates associated with coral reefs. Specimens from the Gulf of Aqaba occur on sloping shores around reefs at depths of 5–10 m. Bandel (in litt.) found this species at 2 m depth among *Halimeda* beds in soft substrates of the fringing reefs and fiords of coastal Aqaba. Yaron (1979:235) recorded *C. ruppelli* from sandy lagoons near coral islets in the Gulf of Aqaba, while Ayal and Safriel (1981:64, 68) recorded it (cited as *C. spathuliferum*) from algal mats and other soft substrates in upper subtidal levels along Sinai shores. Eggs, spawn mass, larvae, and life history are unknown. As the protoconch has not been observed, the developmental mode of this species cannot be inferred.

DISCUSSION.—*Cerithium ruppelli*, while apparently a common species (Jousseaume, 1930:277) in the Red Sea, is poorly represented in museum collections. It is distinguished by its angulate whorls, keel-like central spiral cord, nodulose whorl, and by the two strong, spiral, spinose cords at the shell base posterior to the siphonal constriction.

As noted by Jousseaume (1930:277), this species has a wide range of variation in shell sculpture. There are two common phenotypes that are quite distinct: one phenotype has 4 spiral nodulose cords per whorl, an overall beaded appearance, and is usually tan or brown in color (Figure 119A–C); the other phenotype, *C. spathuliferum* (Figure 119E,G,H), is usually pure white, frequently lacks the smaller spiral threads and lines, has only a single, peripheral spiral cord that is spinose rather than beaded, and has two, very spinose cords before the siphonal constriction. These two phenotypes have been given separate names (see "Synonymic Remarks" above), but it is clear that they are merely two ends of a wider spectrum of shell sculpture. There are many intergrades joining the two phenotypic extremes (Figure 119C,D,F), and no radular differences have been detected. The *spathuliferum* forms were suggested to be varieties of *C. ruppelli* by Jousseaume (1930:278) but are here regarded as conspecific with it.

Cerithium ruppelli, especially the *spathuliferum* phenotype, somewhat resembles *C. munitum* Sowerby (Figure 82), with which it is geographically allopatric. The 4 spiral cords per whorl separate *C. ruppelli* from the latter species. In *spathuliferum* morphs (Figure 119E,G,H), there is only a single spiral, peripheral cord, whereas in *C. munitum*, there are 2 peripheral spiral cords (see "Discussion" under *C. munitum*, p. 120). The other species with which *C. ruppelli* may be confused is *C. columna* Sowerby (Figure 32A–N), but the latter species usually has a squatter, less elongate shell and a wider, longer, anterior siphonal canal. *Cerithium columna*, although geographically sympatric with the former species, differs from it sufficiently so that there is no real problem in separating the two species, but careful comparisons should be made (see *C. columna*, p. 49).

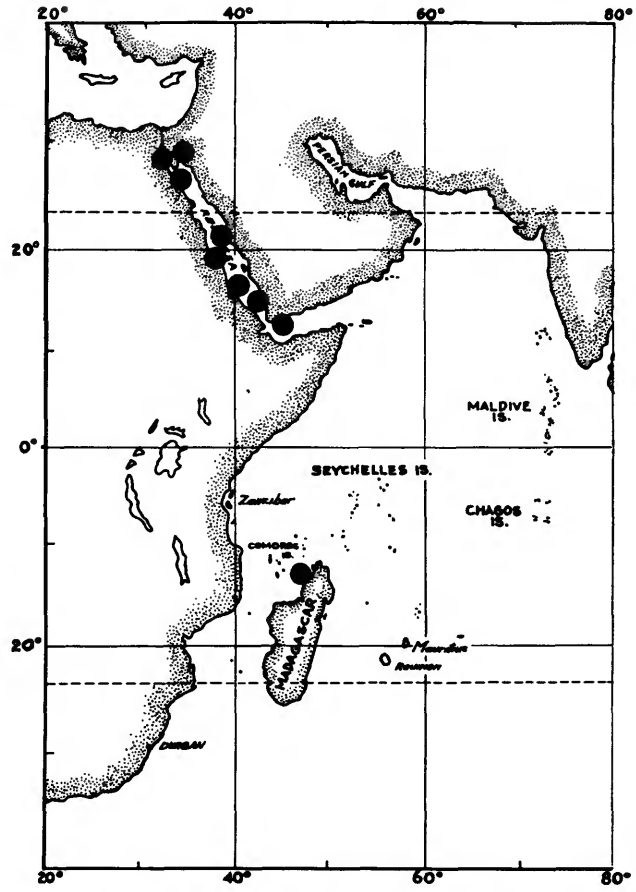

FIGURE 121.—Geographic distribution of *Cerithium ruppelli* Philippi.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 121).—*Cerithium ruppelli* has been thought to be endemic to the Red Sea but I have examined two unequivocal specimens of this species taken in Madagascar. It probably occurs in other suitable habitats in East Africa.

SPECIMENS EXAMINED.—RED SEA: Gulf of Suez (BMNH, MCZ, MNHNP, USNM 23207, 77356); Wadi Feiran, Sinai, Gulf of Suez (RNHL); El Belayim, Gulf of Suez (RNHL);

Ophir Bay, Gulf of Eilat, Israel (USNM 769994); Fara'um Id, Gulf of Eilat, Israel (USNM 780007); Eilat, Gulf of Aqaba, Israel (MCZ 273355, NM G4713, G4716, USNM 671248, ZMA); 10 km S of Aqaba, Israel (AMS); Ras Abu Galum, Gulf of Aqaba, Israel (USNM 798124); Aqaba, Gulf of Aqaba, Jordan (USNM 841306); Hurghada (RNHL); El Korathaba Dist, Egypt (LACM 26117); Port Sudan, Sudan (BMNH, MCZ, USNM 770718, ZMA); Jiddah, Saudi Arabia (DMNH, USNM 852283); Dahlak Archipelago, Ethiopia (NM G4706); Massawa, Ethiopia (ANSP); 0.6–3.0 m, E side Taulud Id, SW of Green Id, Massawa, Ethiopia (AMNH); 4–5 m, S side of Dessel Id, 25 km off Massana, Ethiopia (AMS). GULF OF ADEN: Aden (MNHNP); Gold Mohur, W Aden (RNHL). MADAGASCAR: Nossi Bé (BMNH); Ankifi, S of Nossi Komba (AMS).

Cerithium salebrosum Sowerby, 1855

FIGURES 122–124

Cerithium salebrosum Sowerby, 1855:862, pl. 181: figs. 114, 115 [lectotype, herein selected: BMNH 19861781, 25 mm × 7.5 mm; 10 paralectotypes: BMNH 19861782-11; type locality: Lord Hood's Island, Queensland, Australia]; 1865, pl. 10: fig. 65.—Watson, 1886:532.—Tryon, 1887:131, pl.

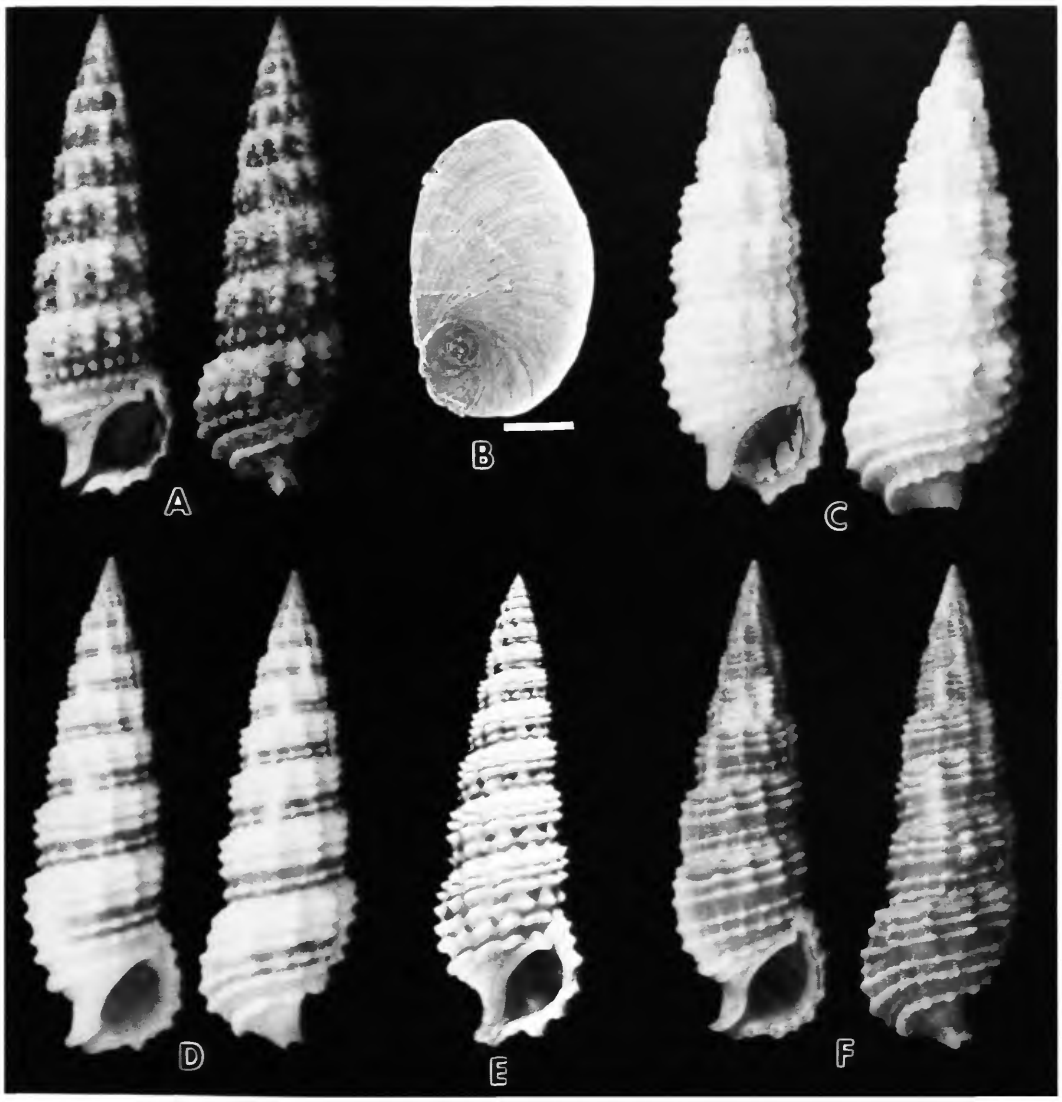

FIGURE 122.—*Cerithium salebrosum* Sowerby. A, lectotype of *Cerithium salebrosum* Sowerby, Hood's Id, Queensland, Australia, 25 mm (BMNH 19861781); B, operculum, Enewetak Atoll, Marshall Ids (bar = 0.75 mm; USNM 770726); C, paralectotype of *Cerithium salebrosum* Sowerby, 23 mm (BMNH 1986178/2-11); D, Motu Patiare, Huahine, Society Ids, 24.8 mm (USNM 674900); E, 1345S, 14416E, N Queensland, Australia, 31.3 mm (WAM); F, Motu Patiare, Huahine, Society Ids, 24.2 mm (USNM 674900).

23: figs. 100–101.—Kobelt, 1895:194–195, pl. 35: fig. 10.—Cernohorsky, 1972:65, pl. 14: fig. 9.—Salvat and Rives, 1975:269, fig. 65.—Abbott and Dance, 1982:65.

DESCRIPTION.—*Shell* (Figure 122A,C-F): Shell slender, fusiform, elongate, comprising 11–15 straight-sided whorls, reaching 31.4 mm length and 9.5 mm width. Protoconch unknown. Early teleoconch whorls moderately inflated, having broad, sloping, subsutural ramp and sculpture of 2 peripheral, spiral threads, 1 or 2 weak spiral lirae, and weak axial riblets. Adult teleoconch sculptured with 4 or 5 spiral cords crossed by 10–14 axial ribs, and becoming nodulose or spinose upon the spiral cords, presenting overall raspy, cancellate pattern. First 3 subsutural spiral cords largest, separated from weaker fourth cord by broad interspace. Interspaces between spiral cords with many microscopic incised lines producing silky, smooth appearance. Whorls flat-sided to slightly angulate with strong but narrow subsutural ramp. Large varices common, randomly distributed. Suture impressed. Body whorl elongate, sculptured with 6 major spiral cords, several weaker spiral striae, and weak, subsutural axial ribs, not extending whorl length. Shell base strongly excavated, demarcated by strong, nodose spiral cord, and with tightly constricted, short, dorsally reflected, anterior siphonal canal. Aperture narrowly ovate, a little less than one-third the shell length. Columella concave with strong columellar callus and distinct columellar lip. Anal canal deep, well defined by parietal columellar tooth. Outer lip convex, strongly crenulate, and with interior, incised, spiral lines. Shell color white, sometimes with light tan spiral bands between white spiral cords and white varices. Protoconch pink to dark purple. Aperture white. Measurements (Table 39). Periostracum not evident. Operculum (Figure 122B) thin, ovate, light tan and paucispiral, with eccentric nucleus, and covered with microscopic granules (Figure 123F).

Radula (Figure 123A-E): Type-2 radular ribbon (Figure 3B) very small, about one-fifteenth the shell length. Rachidian tooth (Figure 123E) with triangular base having long, median, posterior extension and pair of basal ridges; anterior front with concave depression and cutting edge with large, central, pointed, main cusp flanked on each side by 2 denticles. Lateral tooth (Figure 123B,C,E) with long, lateral, posterior extension of basal plate, broad central buttress with weak pustule, and long posterior extension; cutting edge of lateral tooth with broad, pointed main cusp; small, pointed, inner denticles; and three medium-sized, pointed, outer denticles. Marginal teeth (Figure 123C) long, slender, with sharply curved foliated tips, narrow shafts, and tapering bases. Inner marginal tooth with 4 or 5 long, pointed, inner denticles, long main cusp, and 2 or 3 long, pointed, outer denticles. Outer marginal tooth same, but lacking outer denticles.

Anatomy: Head-foot cream-yellow, flecked with brown. Snout with one narrow and two wide brown bands comprised of finer brown lines. Eyes black, surrounded by orange. Mantle edge with moderately long papillae. Single brown spot between each pair of mantle edge papillae on inhalant siphon; mantle edge papillae orange, adjacent to inhalant siphon. Large orange spot on interior inhalant siphon.

TABLE 39.—Shell morphometrics of *Cerithium salebrosum*.

Character	$\bar{x}$ (n = 12)	sd	v	Range
Shell length	21.3	4.9	24.2	12.7–31.4
Shell width	6.6	1.2	1.5	4.7–9.5
Aperture length	4.9	1.2	1.4	3.1–7.2
Aperture width	3.3	0.8	0.6	2–4.8
Number whorls	12.5	1.3	1.8	11–15
Number spiral cords	4.3	0.5	0.2	4–5
Number axial ribs	11.9	1.1	1.3	10–14

SYNONYMIC REMARKS.—This species bears the distinction of having no names other than the original one. A lectotype (Figure 122A) is herein selected from the large type-lot (BMNH 19861781).

ECOLOGY.—This species is a subtidal burrower in clean, sandy substrates of sheltered lagoons associated with low-lying coral atolls and barrier reefs. Demond (1957:292–293) recorded that it lives on sandy lagoon slopes and floors at depths of 1.5–153 m. It occurs to 30 m depth in some atoll lagoons of French Polynesia (Salvat and Rives, 1975:269). *Cerithium salebrosum* is very common in the sandy lagoons of atolls in the Tuamotus. It comprises 15.4 percent of the molluscan fauna in the lagoon of Reao Atoll where it occurs in densities up to 156 individuals per square meter in very fine sediments, at depths of 1–10 m (Salvat, 1972:87–88, 94; Salvat, 1973). At Tiahura, Moorea, it comprises 13 percent of the mollusks of the barrier zone of the lagoon (Richard and Salvat, 1972:1549; Richard, 1973:310–311). In these sandy habitats, *Cerithium salebrosum* is frequently the prey of naticid snails, as evidenced by many drilled shells in museum collections. I have observed *Cerithium salebrosum* in the lagoon of Enewetak Atoll, Marshall Islands, where large populations live in clean white sand, in microsympatry with other infaunal cerithiids, such as *Cerithium tenellum*, Sowerby, 1855, *Rhinoclavis aspera* (Linné, 1758), and *Rhinoclavis fasciata* (Bruguière, 1792). In the aquarium, *C. salebrosum* burrows with ease in sand-filled petri dishes, and is an active crawler, frequently climbing out of dishes.

Eggs, larvae, and mode of reproduction are unknown.

DISCUSSION.—*Cerithium salebrosum* is a highly distinctive species, having a slender, elongate, raspy or prickly shell due to an overall ratchet sculpture of spiny spiral cords crossed by axial riblets. Distinguishing shell features are an elongate, spinose shape, straight-sided whorls, acute subsutural ramp, sculpture of 3 subsutural, major, spiral cords, and a weaker presutural spiral cord separated from the 3 major cords by a wide interspace. The deeply excavated shell base and short, tightly closed, anterior siphon are also distinctive.

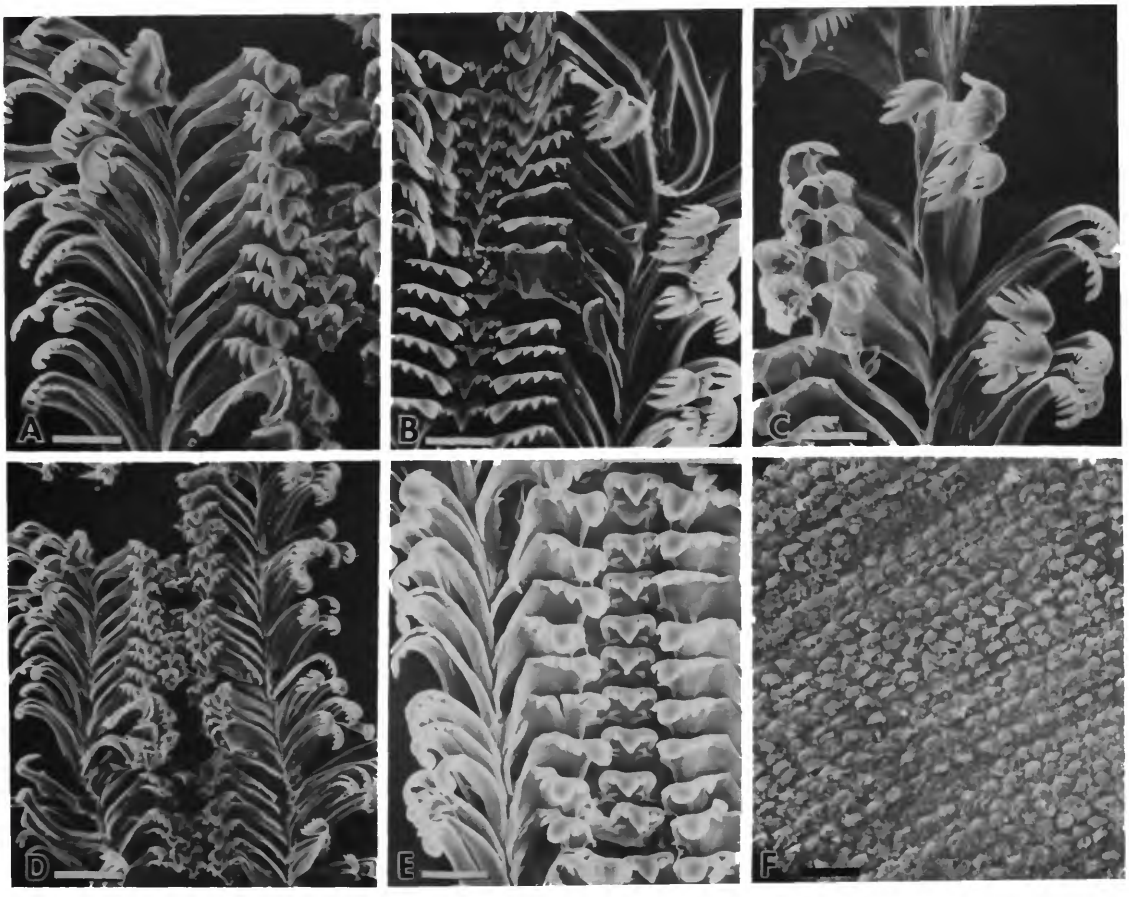

FIGURE 123.—SEM of radula and operculum of *Cerithium salebrosum* Sowerby, Enewetak Atoll, Marshall Ids (USNM 770726). A,B, half row (bar = 50 μm); C, dentition of marginal teeth (bar = 50 μm); D, radula with marginals folded back (bar = 100 μm); E, half row showing rachidian and lateral teeth (bar = 50 μm); F, detail of opercular surface (bar = 40 μm).

Within a population, there is not much sculptural variation but color polymorphism may occur. While most shells are white (Figure 122C), some are melanistic with weak tan stripes (Figure 122A,F). Some populations, such as from North Queensland, Australia (Figure 122E), have more rugose, spiny shells with few former growth varices, while populations from central Pacific atolls, although less spinose, frequently have numerous, well-defined, former growth varices (Figure 122D,F).

The small white shell of *C. salebrosum* most closely resembles that of *C. scobiniforme*, new species (Figure 129), but differs from it in having a finer sculpture of four spiral cords per whorl, instead of three, and in lacking the darkly pigmented anterior siphonal canal. *Cerithium salebrosum* also resembles *Rhinoclavis aspera* (Linné, 1758), with which it is sometimes found in microsympatry, but the former is much smaller and lacks the median columellar plait and long, recurved siphonal canal of rhinoclavid snails.

FOSSIL RECORDS.—This species has been found in Pleistocene reef limestone near Wambeni, Kenya (BMNH). Fossils of Holocene-late Pliocene age also occur at Cap des Pins, Lifu, Society Islands (AMS).

GEOGRAPHIC DISTRIBUTION (Figure 124).—Although *Cerithium salebrosum* has a very broad geographic range, it is best known from the tropical western Pacific, where it occurs from the Philippines south to Australia and throughout Melanesia, Micronesia, and French Polynesia, as far east as the Tuamotus. It does not seem to be as common in the Indian Ocean, but there are reliable records from western Indian Ocean islands and Madagascar. The geographic distribution of *Cerithium salebrosum* appears to be contingent upon the presence of low-lying coral atolls, and the sandy lagoon habitats associated with them.

SPECIMENS EXAMINED.—MADAGASCAR: 29.2 m, 3.2-

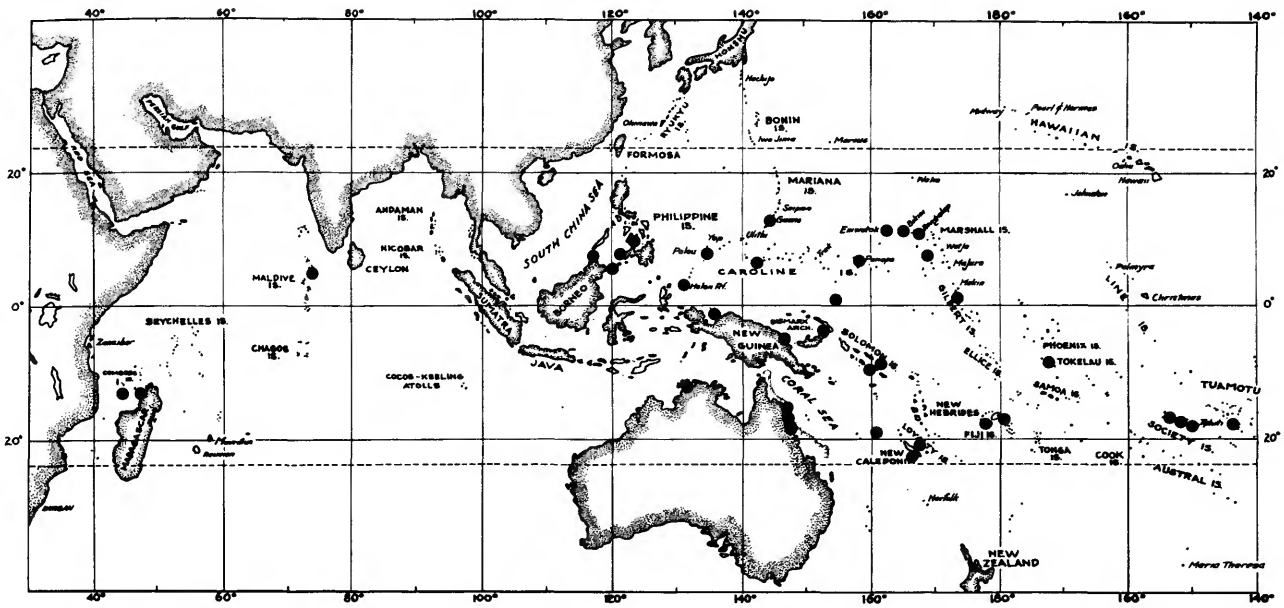

FIGURE 124.—Geographic distribution of *Cerithium salebrosum* Sowerby.

4.8 km S of Nossi Iranja, 51.2 km SW of Nossi Bé (ANSP). INDIAN OCEAN ISLANDS: Sandy Id, Mayotte, Comoros islands (NM G3636); 36.5-45.7 m, lagoon NW of Gan, Addu Atoll, Maldives (ANSP). MALAYSIA: Town Beach, Kudat, North Borneo (USNM 632705). PHILIPPINES: Paluan Bay, Occidental Mindoro (MCZ); Punta Engano, Mactan Id, Bohol (USNM 845808); W side Hadayan Id, NW end Bohol (ANSP); E side Jagoliao Id, NW Bohol (ANSP); off Tinakya Id, Tawitawi, Sulu Archipelago (USNM 274226, 281575). NORTHERN TERRITORY, AUSTRALIA: Milikee Bay, 8 km W of Pt Charles, Darwin (AMS). QUEENSLAND, AUSTRALIA: S end of No 5 Sandbank Reef (AMS); 12°01′S, 143°55′E, reef N of Single Rock Entrance (AMS); off East Face, Lizard Id (AMS); Spur Reef, N of Cairns (AMS); Michaelmas Cay, NE of Cairns (AMS); Little Broadhurst Reef, E of Townsville (AMS). 40 m, 19°11′90″S, 158°55′80″E Chesterfield-Bellona Plateau, Coral Sea (MNHNP). NEW GUINEA: 1.6 km NE of Roemwakon Id, Aoeri Ids, Irian Jaya (ANSP); W of Kranket Id, Madang, Papua (AMS). BISMARCK ARCHIPELAGO: New Britain (AMS). SOLOMON ISLANDS: Aoki Harbor, W coast Malaita Id (AMS); Mbonche, Guadalcanal (LACM 78-76.3); 161°58′E, 10°15′S, S of lagoon entrance, Malaupaina Id (WAM). LOYALTY ISLANDS: Lifu (AMS C30719). NEW CALEDONIA: 40 m, 18°00′S, 165°55′E, Atoll de Huon (MNHNP); 41 m, 18°18′S, 163°E, Atoll de Surprise (MNHNP); Nassadiou, Bourail (ANSP); 12 m, 21°55′S, 165°48′E, Baie de St Vincent (MNHNP); 10 m, 22°19′S, 165°48″E, off Nouméa (MNHNP); 4 km N Dumbea Pass, off Nouméa (ANSP); 15 m, 22°36′S, 166°32′E, Île Ouen, Baie du Prony (MNHNP); 27 m, 22°40′S, 166°48′E, Grande Récif Sud (MNHNP).

FIJI: Off Naselesele Pt, N end Tavenui (USNM 695496); Viti Levu Bay, Viti Levu (USNM 824829); Nadi, Viti Levu (AMS); N Korolevu, Viti Levu (WAM). MARIANA ISLANDS: N Tipilao Bay, Guam (USNM 842609). PALAU: Reef W of Malakal Harbor, Malakal (ANSP); SE shore of Aura Pusnekarj Id, Malakal Harbor, Koror Id (ANSP); Palau (USNM 636243); E lagoon off Melekejok, E Babelthuap (ANSP); N side, Kossol Passage (ANSP); Ngaruangl Id (ANSP). CAROLINE ISLANDS: Lagoon, Ifaluk Atoll (USNM 614197, 616329, 616734); Langar Id, near Ponape Id (LACM 69-1); Round Rock, Helen Channel, Helen Reef (ANSP); Sokoro, Kapingamarangi (USNM 610954). MARSHALL ISLANDS: Jieroru Id, Enewetak Atoll (USNM 582503); Muti Id, Enewetak Atoll (USNM 716385); lagoon, Enewetak Id, Enewetak Atoll (USNM 660640, 770726); Bikini Atoll, numerous localities throughout (USNM 582778, 582861, 582985, 583113, 583181, 583592, 583661, 583921, 584349, 586805); Rongelap Id, Rongelap Atoll (USNM 585494); Kwajalein Atoll (USNM 486074). GILBERT ISLANDS: Teirio, N end of lagoon, Abaiang (AMS). TOKELAU: Tokelau Islet, NE Nukunono (USNM 768611); near Vinil Inlet, Fakaofu (USNM 768342); lagoon, Fenua Loa, S point of Fakaofu (USNM 768243); Swains Id (USNM 704305).

SOCIETY ISLANDS: W side lagoon, Bellinghausen Id (USNM 705247, 705252); Teveiroa Id, Bora Bora (USNM

630031); N side Fauni Pt, Bora Bora (USNM 630011); Motu Tapu, Bora Bora (USNM 630068); Motu Toahotu, Tahaa (USNM 674152, 674177); NE of Patio, Tahaa (USNM 674315); Vaiore Bay, Tahaa (USNM 674109); Uturoa, Raiatea (USNM 630145, 630242, 769016); Motu Tipaemau, Raiatea (USNM 675239); SE side, Motu Iriru, Raiatea (USNM 675344, 675512); near Pt Teffaao, Huahine (USNM 674772, 674868); S tip Motu Pahare, Huahine (USNM 674900); SW tip Motu Vavara, Huahine (USNM 675087); S side Avapaihi Pass, Huahine (USNM 674654); W side Pt Tiva, Huahine (USNM 674615); Mopelia (USNM 705175); Motu Rimatuu, Tetiaroa (USNM 705976, 705993); Opunohu Bay, Moorea (USNM 630608); Patutoa, Tahiti (USNM 669553); E side Taunoa Pass, Tahiti (USNM 668776); Arue, Tahiti (USNM 668448, 672784, 672849); Fare Ute, Tahiti (USNM 673717); 44 km SE Papeete, Tahiti (USNM 674353); Punaavia, 17 km SE Papeete, Tahiti (USNM 672652); Mitirapa, Vairao, Tahiti (USNM 671472); Papara, Tahiti (USNM 791359, 804438, 804440); Mataiea, Tahiti (USNM 671393); Pt Ovauaara, Tautira, Tahiti (USNM 674505). TUAMOTUS: Île Toahotu, Anaa (ANSP); Anaa (USNM 775563).

Cerithium scabridum Philippi, 1848

FIGURES 125–128

Cerithium scabridum Philippi, 1848:23 [type material: not found; type locality: Red Sea; neotype herein designated, USNM 862606, 19.3 mm × 6.7 mm; type locality restricted to Aden, Yemen]; 1849: *Cerithium*, pl. 5: fig. 12.—Sowerby, 1865, pl. 8: fig. 52 [not *C. scabridum* Philippi; is *C. columna* Sowerby].—Cooke, 1885:43.—Tryon, 1887:124.—Kobelt, 1898:210, pl. 37: fig. 6 [not *C. scabridum* Philippi; is *C. columna* Sowerby].

Cerithium nigropunctatum Sowerby, 1855:860, pl. 180: fig. 97 [lectotype, herein selected: BMNH 19071237; other paralectotypes in Metcalfe Collection, not seen; no locality given].

Cerithium adenense Sowerby, 1865, pl. 12: fig 89; [holotype: BMNH 1987039, 16.6 mm × 5.5 mm; type locality: Aden]; 1866, pl. 12 [supplementary]: fig. 316.—Tryon, 1887:124, pl. 20: fig. 30.—Kobelt, 1895:196, pl. 35: fig.12.—H. Fischer, 1901:109.—Abrard, 1942:59, pl. 6: fig. 23.

Cerithium yerburyi E.A. Smith, 1891:417, pl. 33: fig. 4 [lectotype, herein selected: BMNH 188849276; type locality: Aden].—H. Fischer, 1901:110.

Cerithium carnaticum Melvill and Standen, 1898:31, pl. 1: fig. 1 [holotype: MM, EE4779; 13.6 mm × 4.4 mm; type locality: Madras, India; not *C. carnaticum* Stoliczka, 1867].

Cerithium yerburyi var. *djiboutiensis* H. Fischer and Vignal in Fischer, 1901:110, pl. 14: fig. 9 [holotype: MNHNP, no number; type locality: Djibouti].—H. Fischer, 1901:110.

Cerithium scabridum albida Dautzenberg and Bouge, 1933:313 [type not found; no figure; nomen nudum].

Cerithium (Bakka) scabridum var. *hispida* Pallary, 1938:34–35, pl. 1: figs. 16–18 [holotype: not found; type locality: Île Saida, Syria].

Cerithium (Thericium) yerburyi E.A. Smith.—Moazzo, 1939:174.

Cerithium (Thericium) scabridum Philippi.—Moazzo, 1939:173–174.—Abrard, 1942:60, pl. 6: fig. 25.—Barash and Danin, 1972:309–310, fig. 6.

Gourmya (Gladiocerithium) argutum barashi Nordsieck, 1974:234, fig. 24 [holotype not seen; Nordsieck collection; type locality: Shiqmona, Israel].

DESCRIPTION.—*Shell* (Figures 125, 126): Shell slender, turreted, comprising 11–14 convexly angulate whorls, and reaching 27.2 mm length and 9.5 mm width. Protoconch (Figure 126D) 2.5 whorls, smooth, with moderate sinusigeral notch. Early teleoconch whorls with broad, sloping, subsutural ramp, and sculptured with two spiral cords. Adult teleoconch whorls sculptured with 12–16 axial ribs crossed by 2, sometimes 3, major, spiral, nodulose cords, with single minor subsutural beaded, spiral cord and one minor presutural beaded cord varying in size; many, fine, spiral lirae on interspaces. Large, angulate varices randomly distributed. Two major spiral cords at whorl periphery, frequently nodulose and angulate. Suture distinct, slightly wavy. Body whorl sculptured with 5 beaded or nodulose spiral cords, and with moderately excavated base sculptured with 5–7 weaker spiral beaded cords extending down anterior siphonal canal. Large varix on body whorl opposite outer lip of aperture. Aperture ovate, a little more than one-third the shell length. Anterior siphonal canal short, wide, well defined. Anal canal distinct, with strong parietal columellar tooth. Columella concave with strong callus and moderate columellar lip. Outer lip thickened at edge, strongly crenulate. Shell color white, sometimes tan, with brown spiral spots on nodes and beads, and with fine tan specks. Aperture and columella white. Measurements (Table 40). Periostracum thin tan. Operculum, thin, tan, paucispiral with eccentric nucleus.

Radula (Figure 127): Radular ribbon Type-1 (Figure 3A) small about one-tenth the shell length. Rachidian tooth (Figure 127B,C) with triangular shaped basal plate with long posterior projection and pair of basal ridges; anterior front lightly concave; cutting edge with large, triangular, central, main cusp flanked on each side by two very small denticles. Lateral tooth (Figure 127B,C) having long, lateral, posterior projection with long median buttress and small pustule, on broad basal plate; cutting edge of lateral tooth with one broad, main cusp, one inner denticle, and 2 or 3 outer, pointed denticles. Marginal teeth (Figure 127A-C) elongate, narrow, with tapered bases, and curved and serrated at tips. Inner marginal tooth with spatulate major cusp at tip and with 3 inner denticles and 2 outer denticles. Outer marginal tooth same, but lacking outer denticles.

Anatomy: Unknown.

SYNONYMIC REMARKS.—A search for the type material of *C. scabridum* Philippi, 1848, was unsuccessful; however, Philippi's (1849, pl. 1: fig. 12) subsequent illustration of this species is an excellent representation, consistent with the *C. scabridum* of later authors. Both Cooke (1885:43) and Tryon (1887:125) remarked that *C. scabridum* of Philippi was different from *C. scabridum* depicted by Sowerby (1865, pl. 8: fig. 52), and I concur with their judgement; Sowerby's figure resembles typical *C. columna* Sowerby. However, I do not agree with Cooke (1885), who believed that Philippi's fig. 12 represented an immature *C. ruppelli* Philippi, as *C. ruppelli* has 4 main, spirally beaded cords per whorl, whereas *C. scabridum* and Philippi's figure have only two. Philippi (1848:23) noted that *C. scabridum* was similar to the western Atlantic species,

FIGURE 125.—Types of nominal species synonymous with *Cerithium scabridum* Philippi. A-C, neotype of *Cerithium scabridum* Sowerby, Aden, Yemen, 19.3 mm (USNM 862606); D, holotype of *Cerithium adenense* Sowerby, Aden, 16.6 mm (BMNH 1987039); E, holotype of *Cerithium carnaticum* Melvill and Standen, Madras, India, 13.6 mm (MM); F, lectotype of *Cerithium yerburyi* Smith, Aden, 18.3 mm (BMNH 188849276); G, lectotype of *Cerithium nigropunctatum* Sowerby, 9.6 mm (BMNH 19071237); H, holotype of *Cerithium yerburyi* var. *djiboutiensis* Fischer and Vignal, Djibouti, 12.5 mm (MNHNP).

TABLE 40.—Shell morphometrics of *Cerithium scabridum*.

Character	$\bar{x}$ (n = 12)	sd	v	Range
Shell length	17.7	4.9	24.1	12.7-27.2
Shell width	6.6	1.6	2.6	4.5-9.5
Aperture length	5.1	1.2	1.5	3.8-7.5
Aperture width	3.3	1.2	1.4	2.3-5.3
Number of whorls	11.4	3.0	9.1	11-14
Number spiral cords	2.3	0.5	0.2	2-3
Number axial ribs	13.3	1.6	2.6	12-16

C. muscarum Say, but this resemblance is mainly in color. Because there seems to be no problem with the identity of Philippi's taxon and no confusion with other *Cerithium* species from the Red Sea area, and because this taxon has long been recognized as part of the Red Sea and Persian Gulf molluscan fauna, *C. scabridum* is regarded as a valid species. To promote taxonomic stability, I herein designate USNM 862606, from Aden as the neotype of *Cerithium scabridum* Philippi, 1848 (Figure 125A-C).

There are many synonyms of *C. scabridum*. The lectotype of

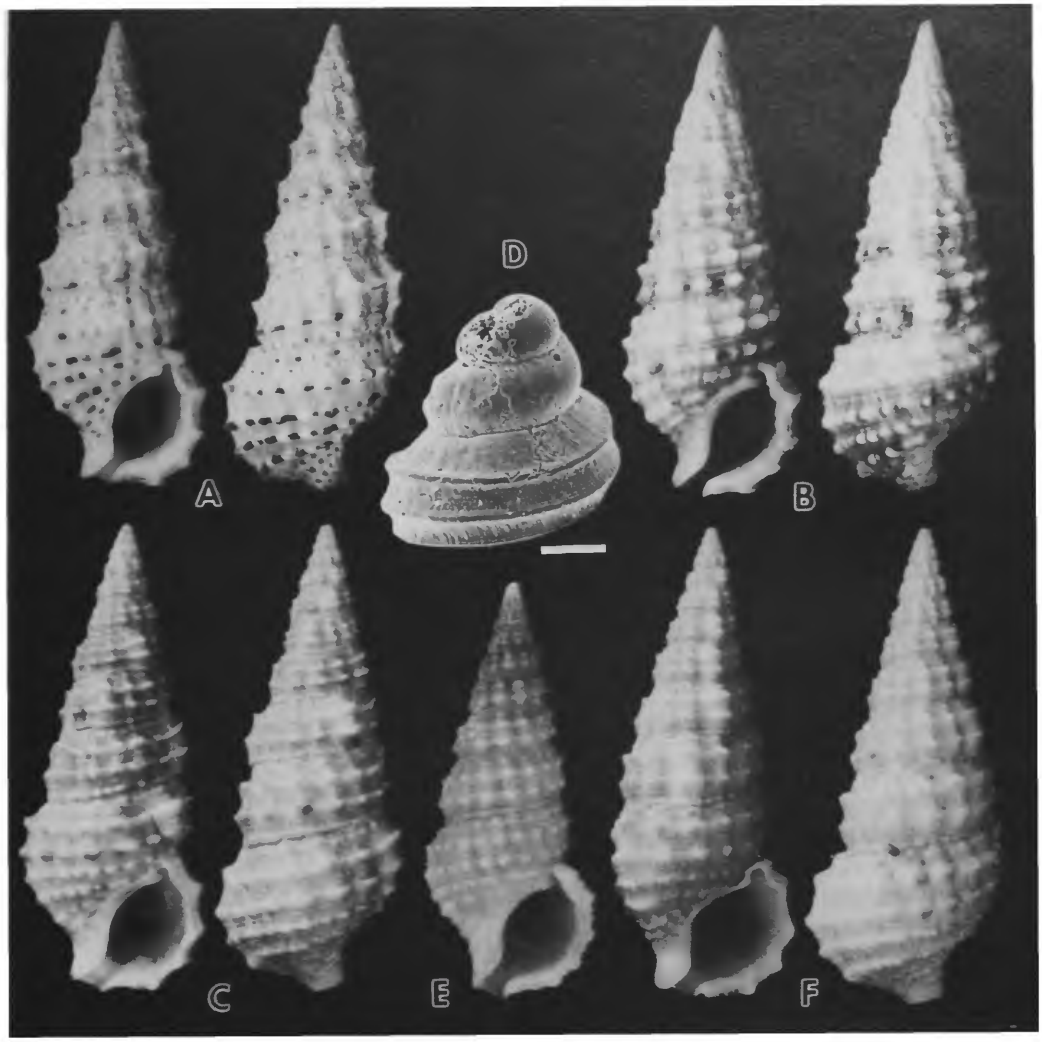

FIGURE 126.—Phenotypic variation in *Cerithium scabridum* Philippi. A, very large specimen, Red Sea, 26.9 mm (MNHNP); B, Aden, 21.3 mm (MNHNP); C, Mediterranean specimen, Haifa Harbor, Israel, 15 mm (ZMTA); D, SEM of protoconch, Gulf of Suez, Egypt (bar = 68 μm; USNM 794186); E, Persian Gulf specimen, 2445N, 504610E, 13.1 mm (RNHL); F, Mediterranean specimen, Haifa Harbor, Israel, 13.5 mm (ZMTA).

C. nigropunctatum Sowerby, 1855 (Figure 125G), and holotype of *C. adenense* Sowerby, 1866 (Figure 125D), are both conspecific with *C. scabridum* Philippi. I do not agree with Tryon (1887:124), Kobelt (1895:196), or Jousseaume (1930:280), who suggested that *C. adenense* was a synonym of *C. ruppelli* Philippi; *C. ruppelli* is a much larger species with a completely different habitat. Cooke (1885:43) stated that *C. adenense* Sowerby was a variety of *Cerithium morus* Linné (= *Clypeomorus bifasciata* Sowerby, 1855), but the latter is clearly different (see "Discussion" below). *Cerithium carnaticum* Melvill and Standen, 1898, is placed into the synonymy of *C. scabridum* with some hesitance: the holotype of *C. carnaticum* (Figure 125E), is a weakly sculptured shell without the usual spotted pigmentation of the latter species. While not a typical phenotype of *C. scabridum*, it is from Madras, India, the edge of the range of that species, which may explain its unusual form. Similar weakly sculptured specimens occur in collections from Yemen (USNM 716308). There are no other *Cerithium* species similar to *C. carnaticum*, and because Melvill and Standen (1898:31) noted its relationship with *C. adenense*, it is herein considered to be an unusual phenotype of *C. scabridum*. The nominal species *C. yerberyi* E.A. Smith, 1891 (Figure 125F), from Aden, is also conspecific with *C. scabridum*, as noted earlier by Tomlin (1927:295). A variety of

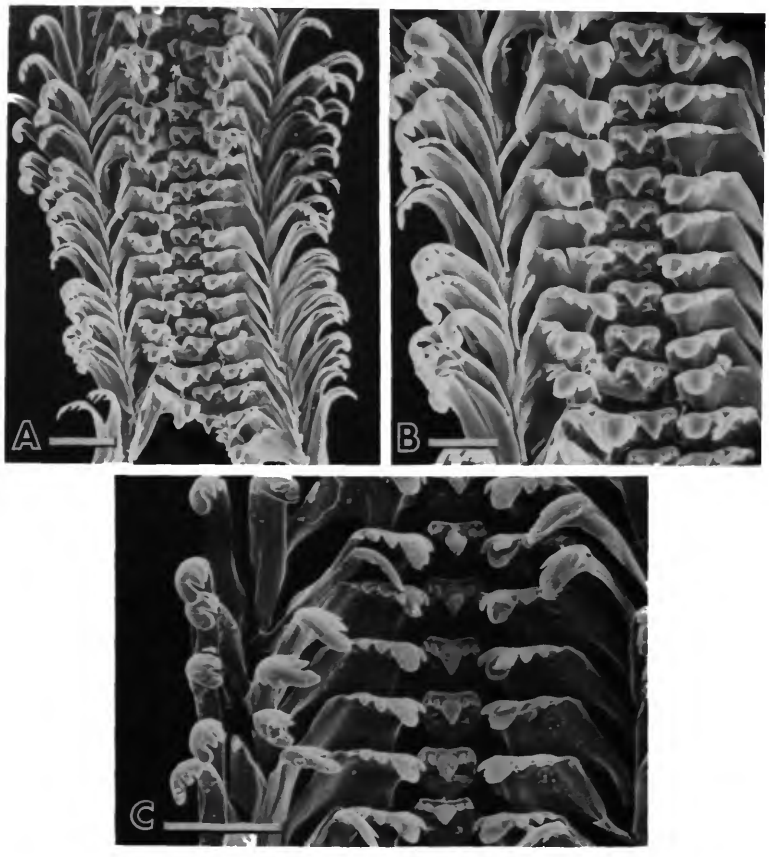

FIGURE 127.—SEM of radula of *Cerithium scabridum* Philippi. A, radula with marginals spread open (bar = 107 μm, Aden; USNM 128594); B, half row, Aden (bar = 60 μm; USNM 128594); C, detail of rachidian, lateral and marginal teeth, Gulf of Suez, Egypt (bar = 100 μm; USNM 794186).

the nominal species *C. yerburyi* was described from a beach-worn specimen of *C. scabridum* and given the name *djiboutiensis* Fischer and Vignal, 1901 (Figure 125H). The type of the varietal form of *C. scabridum* from the Mediterranean, given the name *hispida* by Pallary (1938:34–35), has not been found, but Pallary's illustration of it shows no major differences from typical *scabridum* phenotypes. Pallary also introduced a new subgeneric taxon, *Bacca*, to accommodate this variety. It is obvious that this taxon should not be seriously considered if the nominal species upon which it is based is a synonym of *C. scabridum*, a typical *Cerithium* species. Both Mienis (1974:43–44) and Yaron (1975:34) have shown that *Gourmya (Gladiocerithium) argutum barashi* Nordseick, 1972, is a synonym of *C. scabridum*, and not at all related to *Thericium argutum* Monterosato, as suggested by Nordsieck (1972). Jousseaume (1930:279) listed *Cerithium gemma* Sowerby, 1855, as a variety of *C. scabridum*, but the former taxon is a synonym of *C. zonatum* Wood, 1828.

ECOLOGY.—*Cerithium scabridum* has been the subject of several ecological and pollution studies. Along the Sinai coast, it inhabits protected, mid-littoral, rocky shore habitats where it occurs in large populations in solution basins and tide pools among pebbles, rocks, and algae (Ayal and Safriel, 1981:68). In these habitats it is active during ebbs, and hides in algae or sediment during flows. This species is sensitive to desiccation and is highly vulnerable to fish predation (Ayal and Safriel, 1982a:308, 314). Taylor and Reid (1984:190) recorded *C. scabridum* as a prey item of the gastropod *Cronia (Muricodrupa) funiculus* (Wood), along the Sudan coast.

Ayal (1978) has shown *C. scabridum* to be an *r*-selected species. The egg masses of *C. scabridum*, described by Barash and Danin (1972:309) and Barash and Zenziper (1980:301, fig. 1), are deposited in the habitat of adults, on intertidal rocks and stones. Barash and Zenziper (1980:301) recorded that the egg mass is made of opaque, irregularly coiled strings, 4 mm in diameter, in which egg capsules are embedded in a gelatinous matrix. Each capsule contains one egg of 120–130 μm diameter and egg masses may contain from 5000 to 20000 egg

capsules. Free-swimming veliger larvae hatch from the eggs mass within 4 to 6 days of deposition (Ayal and Safriel, 1982b:399). This species was reported to have a planktotrophic stage by Ayal and Safriel (1977:258), who later showed that the larval stage lasts from 45 to 60 days, a relatively long planktotrophic period (Ayal and Safriel, 1982b:397). However, the protoconch (Figure 126D) is not indicative of a long larval stage, as it is not highly sculptured and has a weak sinusigeral notch. *Cerithium scabridum* has been calculated to have a life span of 2 years (Ayal and Safriel, 1982b:395).

Pashtan and Ritte (1977:258) found several levels of genetic difference in terms of allele frequencies and frequencies of specific genotypes between source populations from the Red Sea and colonist populations in the Mediterranean. The relative frequency of heterozygotes was lower in the Mediterranean than in the Red Sea. Lavie and Nevo (1986a:99) suggested that high levels of genetic variability in *C. scabridum* in the Mediterranean may be correlated with its broad ecological niche and direct development. A study on the pollution effects of the heavy metals cadmium and mercury on the population genetic structure of *C. scabridum* was conducted by Lavie and Nevo (1986a), who recorded differential survivorship of allozyme genotypes specific for each kind of pollutant and their interaction.

DISCUSSION.—Among Red Sea and Persian Gulf cerithiids, *C. scabridum* is distinguished by its relatively small size, elongate, slender, white shell with angulate whorls and spiral rows of tan-brown spots. The sculpture of two dominant nodulose spiral cords per whorl is distinctive, as are the 5 beaded-spinose spiral cords on the body whorl and the moderately excavated shell base.

This species shows a great amount of intraspecific variation in size and shell sculpture, which has been noted by other workers (Barash and Danin, 1977:93; Jousseaume, 1930:280). Some individuals are unusually larger than normal (Figure 125A). Although most specimens have two dominant spiral cords per whorl, some have 3 or even 4 cords of equal strength (Figure 125C). The number of axial ribs also vary from 12 to 16 (see Table 40). Within a single population, there may be considerable differences in the degree and kind of sculpture between individuals, and particularly in the variation of nodular development (USNM 708980). There is also a great size difference between individuals (see Table 40).

A number of authors have commented on the resemblance of *C. scabridum* to the sympatric *C. ruppelli* Philippi (Cooke, 1885:43; Tryon, 1887:124; Kobelt, 1898:150–151; Sturany, 1903:52; Jousseaume, 1930:280). The latter species (Figure 119) is a much larger shell, has a longer siphonal canal, and comprises phenotypes sculptured with 4 spiral cords per whorl or one spiral cord per whorl. *Cerithium scabridum* also may be confused with elongate phenotypes of the sympatric *Clypeomorus bifasciata* (Sowerby), which lives in the high intertidal zone and is about the same size as the *C. scabridum*. *Clypeomorus bifasciata* has a more solid shell with a very short siphonal canal, and without the excavated shell base. It is sculptured with three beaded spiral cords per whorl, and lacks the angulate whorls of *C. scabridum*. *Cerithium zonatum* (Wood) (Figure 142) occurs on east African coast of the Indian Ocean, and may be confused with *C. scabridum*. *Cerithium zonatum*, however, has three or four spinose spiral cords per whorl of which the central one is the largest, frequently forming a median peripheral keel of spines.

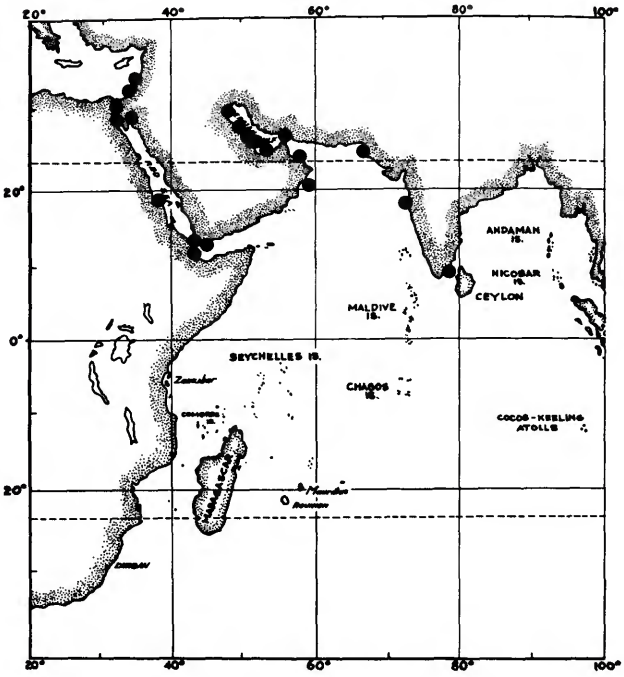

FIGURE 128.—Geographic distribution of *Cerithium scabridum* Philippi.

FOSSIL RECORDS.—*Cerithium scabridum* has been recorded from the Pleistocene of French Somalia, near Obock (Abrard, 1942:60, pl. 6: fig. 25). *Cerithium rufonodulosum* E.A. Smith, 1901, originally described as a Recent species, has been shown to be a Pleistocene fossil washed out of raised beaches along the banks of the Swartkops River, South Africa (Kilburn and Tankard, 1975:197–198, fig. 8a). Kilburn and Tankard demonstrated that the morphological differences between *C. scabridum* and *C. rufonodulosum* are very small and regarded the relationship between the two taxa as a subspecific one. *Cerithium scabridum* differs from *C. scabridum rufonodulosum* only in having less prominent tubercles.

GEOGRAPHIC DISTRIBUTION (Figure 128).—*Cerithium scabridum* appears to be endemic to the Red Sea, Arabian Sea, and Persian Gulf. Although reputed to be common in the Gulf of Mannar (Satyamurti, 1952:86), this report and the few museum records from western and southern India and Ceylon need reconfirmation. *Cerithium scabridum* is notable among the Red Sea species that have colonized the eastern Mediterranean Sea

after immigration through the Suez Canal (Barash and Danin, 1972:309–310, 1977:93–94; Ayal and Safriel, 1977:257–258). It appears to be well established along the coast of Israel (Figure 124F) and Lebanon, and has recently colonized the east coast of Sicily (Barash and Danin, 1977:93). Kilburn and Tankard (1975:198) cite it as occurring as far south as the Mascarene Islands and Quirimba Island, Mozambique, but I have not seen specimens from these regions.

SPECIMENS EXAMINED.—MEDITERRANEAN SEA: Beirut, Lebanon (USNM 656911); Shiqmona, Israel (TAU 6889); Haifa Harbor, Israel (BMNH, TAU 6887a,b, USNM 862608); Yafo, Israel (ANSP); between Haifa and Jaffa, Israel (AMNH); Jaffa, Israel (TAU 6892). RED SEA: Ismailia, Egypt (MCZ); Great Bitter Lakes, Egypt (MCZ, RMGM); Suez, Egypt (USNM 23175, 128594, 305049); Abu Zneima, Gulf of Suez, Egypt (USNM 794186); Port Sudan, Sudan (USNM 862611). GULF OF ADEN: Djibouti, French Somalia (MNHNP); Aden (USNM 306152, 608860); Gold Mohur, W Aden (RMGM); Khar Maksar, Aden (BMNH); Slave Id, Aden (BMNH).

ARABIAN SEA: Muscat, Oman (USNM 798222); Mothercat Beach, N end Masirah Id, Oman (USNM 788727). PERSIAN GULF: Kuwait (USNM 862612); off Manifah, Saudi Arabia (USNM 862607); Ras Tanura, Saudi Arabia (AMNH); Zaal Id, Tarut Bay, Saudi Arabia (USNM 597640); Tarut Bay, Saudi Arabia (AMNH); Saihut, Saudi Arabia (USNM 597673, 617109); Damman, Saudi Arabia (USNM 629255, 708974, 708977, 708980); between Dhahran and Damman, Saudi Arabia (USNM 633241); 26°02′N, 50°05′E, Half Moon Bay, Saudi Arabia (USNM 633607); El Azzizia, Saudi Arabia (USNM 597666, 597671); Badiyaa, NW Bahrain (MCZ); Durhan, Qatar (MCZ); Omm Said, Qatar (BMNH); Janna Id, United Arab Emirates (USNM 633601); W end of Halat al Bahraini, United Arab Emirates (BMNH); Abu Dhabi, United Arab Emirates (BMNH); Khor Hulaylah, United Arab Emirates (USNM 862609); Hormuz Id, Iran (MCZ). PAKISTAN: 3 m, intertidal, Oyster Rocks, Karachi Harbor, Sind Prov, Pakistan (LACM 79-9). INDIA: Chaupati Beach, Bombay (USNM 862610); Tuticorn (MCZ, USNM 336219).

Cerithium scobiniforme, new species

FIGURES 129, 130

DESCRIPTION.—*Shell* (Figure 129): Shell fusiform, slender, comprising 10–14 straight-sided to weakly inflated whorls, and reaching 27.6 mm length and 10.4 mm width. Protoconch unknown. Early teleoconch whorls highly inflated, sculptured with 2 weak spiral bands. Adult teleoconch whorls with overall coarse, cancellate, rasp-like sculpture of 3 or 4 spiral cords crossed by 13–19 weak, colabral axial ribs; crossover points spinose and interspaces with many fine spiral lines. Acute subsutural ramp present. Penultimate whorl sometimes with fourth spiral cord partially overlapped by body whorl. Suture distinct. Body whorl elongate, sculptured with 5 main spinose, spiral cords. Base of body whorl sharply excavated and sculptured with one spiral, spinose, or beaded spiral cord. Aperture strongly fusiform, nearly one-fourth the shell length. Anterior siphonal canal relatively long, tightly constricted, and strongly reflected dorsally and to left of shell axis. Columella concave, thick, with strong columellar lip. Anal canal distinct, bordered with parietal columellar tooth. Outer lip of aperture convex, strongly crenulate. Shell color white with occasional small, black, spiral spots and bluish black anterior canal. Outer lip of aperture frequently bluish black. Occasional black spiral spots. Measurements (Table 41). Periostracum thin, transparent.

Radula: Type-2 radular ribbon (Figure 3B) very small, delicate. Rachidian tooth triangular in outline with slightly concave front and with long central posterior projection and pair of basal ridges on basal plate; cutting edge with large, pointed, central main cusp flanked on each side by 2 small denticles. Lateral tooth having broad basal plate with long, lateral, posterior projection, and posteriorly projecting median buttress with small pustule. Marginal teeth with long thin shafts, curved, serrated tips, and narrow bases. Inner marginal tooth with long main cusp, 3 inner flanking, pointed denticles, and 2 outer flanking denticles. Outer marginal tooth same, but without outer flanking denticles.

Anatomy: Operculum and animal are unknown.

HOLOTYPE.—USNM 859930, 24.9 mm × 8.8mm (Figure 129E).

PARATYPES.—LACM 76702, 6 specimens; USNM 859931, 2 specimens.

TYPE LOCALITY.—1.5 mi S of Estango Id, Port Dimalosan, Cagayan Prov, NE Luzon, Philippines.

ETYMOLOGY.—From the Latin *scobina* (a wood file), and *forma* (form), in reference to the rasp-like sculpture.

ECOLOGY.—Museum records indicate that *C. scobiniforme*, new species, occurs subtidally, in shallow water, on sand and coral rubble. The ratchet sculpture and long reflected anterior canal suggest that it is a burrower. Eggs, larvae, and mode of development are unknown.

DISCUSSION.—The distinguishing features of this new species are the white, cancellate, spinose shell, coarsely sculptured with weak axial riblets and 3 spiral, spinose cords per whorl, the strongly excavated shell base with thick, fusiform aperture, and the dark bluish black anterior siphonal canal. *Cerithium scobiniforme*, new species, does not appear to be common, and may be confused with *C. salebrosum* Sowerby (Figure 122).

There is not a great deal of intraspecific variation in shell sculpture in this species. Nearly all specimens have pure white shells and dark bluish black canals, but there is some variation in the intensity and extent of the dark pigment. Some individuals have a white outer lip (Figure 129C,D) while in others it is black (Figure 129A,B,E). Occasionally, dark spots are randomly distributed on the shell (Figure 129), and some individuals are nearly melanistic (LACM 76782, Figure

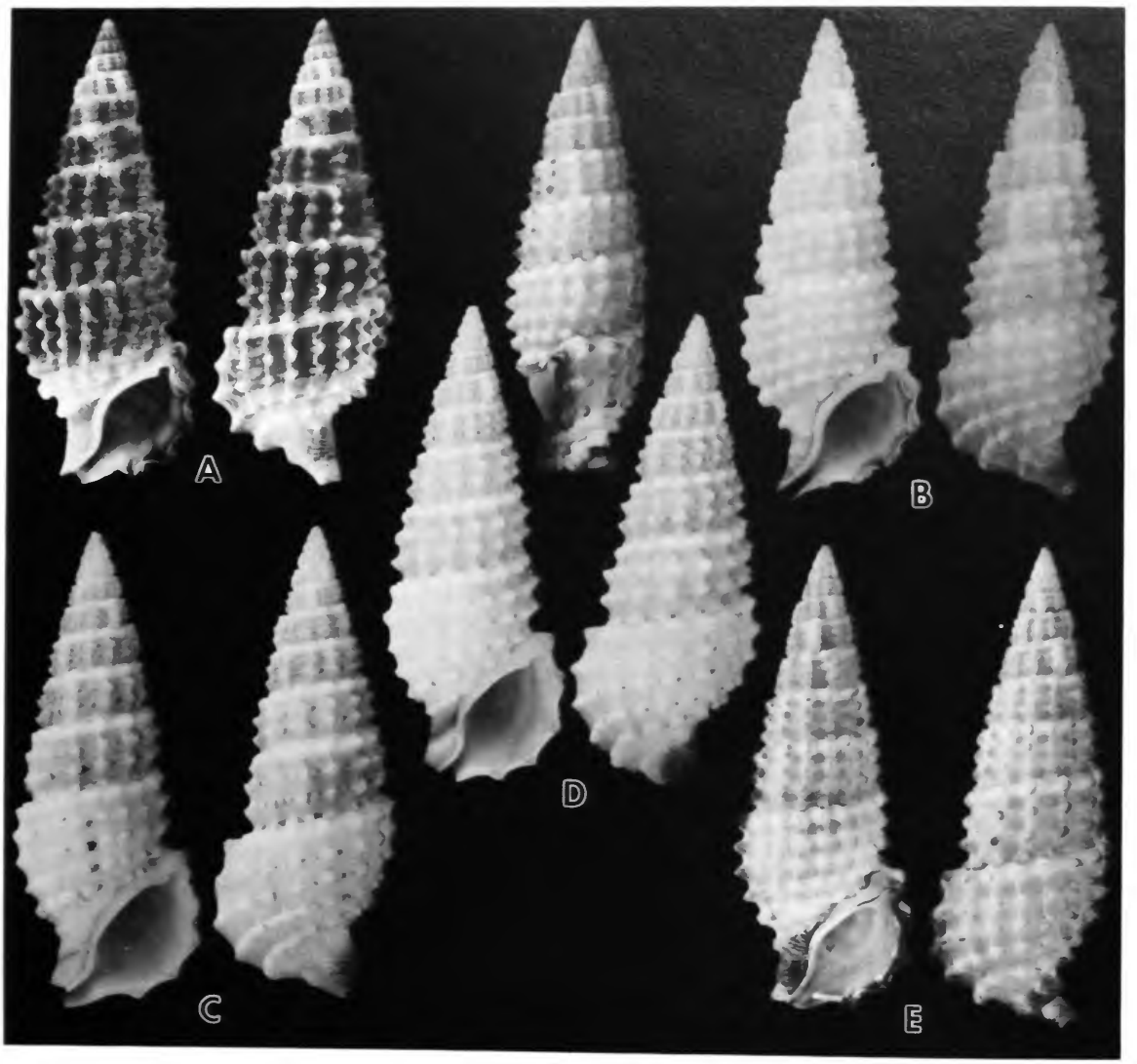

FIGURE 129.—*Cerithium scobiniforme*, new species: A, darkly pigmented form, Luzon, Philippines, 19.4 mm (LACM 76782); B, Koror, Palau, 17.5 mm (ANSP 202770); C, Net Pt, Ponape, Caroline Ids, 19.4 mm (LACM 6850); D, Net Pt, Ponape, Caroline Ids, 19.4 mm (LACM 6850); E, holotype, Pt Dimalonsan, Luzon, Philippines, 24.9 mm (USNM 859930).

TABLE 41.—Shell morphometrics of *Cerithium scobiniforme*.

Character	$\bar{x}$ (n = 16)	sd	v	Range
Shell length	21.1	5.0	25.3	12-27.6
Shell width	7.3	1.6	2.7	4.9-10.4
Aperture length	5.8	1.2	1.5	4.1-8
Aperture width	3.4	0.6	0.4	2.4-4.2
Number of whorls	11.6	2.7	7.4	10-14
Number spiral cords	3.1	0.2	0.1	3-4
Number axial ribs	16.4	1.9	3.6	13-19

129A). Specimens examined from Luzon, Philippines (AMS), had an unusual color pattern of brown spiral bands.

Cerithium scobiniforme, new species, closely resembles *C. salebrosum* Sowerby (Figure 122), with which it is sympatric, but differs in being more coarsely sculptured with only 3 spinose spiral cords per whorl and in having a body whorl with five spiral cords rather than the 6 cords of *C. salebrosum*. *Cerithium scobiniforme* also has a darkly pigmented anterior canal and aperture in contrast to the all white *C. salebrosum*. Some coarsely sculptured individuals of *C. salebrosum* (Figure

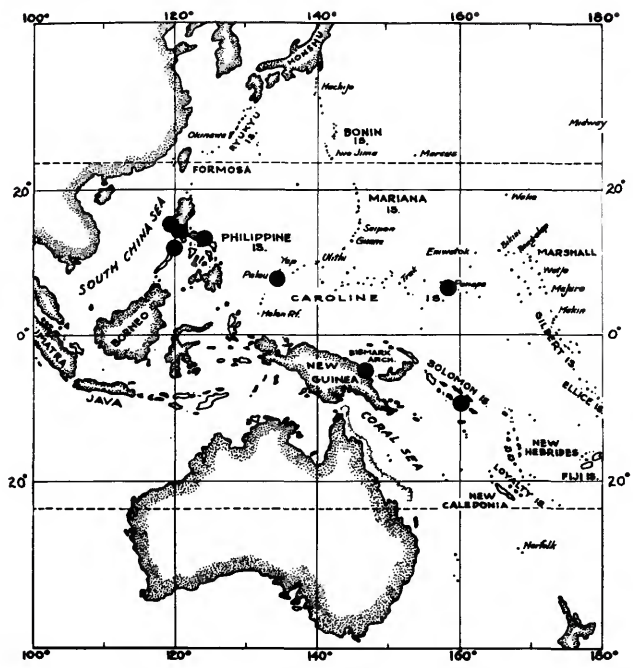

FIGURE 130.—Geographic distribution of *Cerithium scobiniforme*, new species.

122, E) resemble *C. scobiniforme*, but there do not appear to be any intergrades. *Rhinoclavis aspera* (Linné) also resembles *C. scobiniforme* in sculpture, but the former species is a much larger, more robust species and has a prominent, median columellar plait and a long, reflected, siphonal canal.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 130).—This species has a narrow geographic range, and appears to be confined to reefs around high islands, archipelagos, and large land masses. It has been found in the Philippines, Caroline Islands, New Guinea, and the Solomons.

SPECIMENS EXAMINED.—PHILIPPINES: 1.8–9.1 m, 2.4 km S of Estagno Id, Port Dimalonsan, Cagayan Prov, NE Luzon (LACM 76702); Masinloc Bay, Luzon (USNM 862518); Villa Carmen, Bataan Prov, SW Luzon (LACM 96399); Awasan Beach, Tagkawayan, Quezon Prov, Luzon (AMS); 1.8–9.1 m, W part of Boculud Pt, Tabaco Harbor, Albay Prov, SW Luzon (LACM 76841); 9.1 m, 2.08 km N of Cabadea Pt, Cagnasag Id, Albay Prov, SW Luzon (LACM 76782); Isla Santa Rosa, off Mactan Id, Cebu (AMNH 210336); 3.6–7.2 m, E side Jagoliao Id, NW end Bohol (ANSP 231484); Culion, Calamian Gp, Palawan (LACM 76776).

NEW GUINEA: Hansa Bay, Madang Prov, Papua (Brussels Museum); 1–3 m, Mililat Harbor, Astrolabe Bay, Madang Prov, Papua (LACM 80-17); inlet, N end of Kranket Id, Madang Prov, Papua (AMS). SOLOMON ISLANDS: NW coast of Guadalcanal (USNM 821473). CAROLINE ISLANDS: Palau (USNM 636458); 1.8 m, 0.8 km SE of main dock, Koror Ids, Palau (ANSP 202770); 0.9–1.5 m, Net Point, Ponape (LACM 68-50).

Cerithium tenellum Sowerby, 1855

FIGURES 131–134

Cerithium tenellum Sowerby, 1855:857, pl. 180: figs. 88–90 [lectotype: BMNH 19861801, 17.5 mm × 6.6 mm, and 10 paralectotypes, 19861802-11, herein selected; type locality: herein restricted to Tawitawi Id, Sulu Archipelago, Philippines]; 1865, pl. 11: fig. 71a,b.—Tryon, 1887:132, pl. 23: figs. 10, 11.—Kobelt, 1898:213–214, pl. 38: figs. 2, 3.

Cerithium NovaeHiberniae [sic] A. Adams in Sowerby, 1855:857, pl. 180: figs. 84, 85.

Cerithium filosum Sowerby, 1865, pl. 12: fig. 82 [lectotype: BMNH 19861711, 1 paralectotype 19861712; type locality: Burias, Philippines; not *Cerithium filosum* Philippi, 1849, nor *Cerithium filosum* Gould, 1849].—Tryon, 1887:125, pl. 21: fig. 25.

Cerithium tenuifilosum Sowerby, 1866, pl. 12: fig. 307 [replacement name for *Cerithium filosum* Sowerby, 1865].—Cernohorsky, 1972:64, pl. 14: fig. 3.

Cerithium tomlini Hedley, 1914:717–718, pl. 85: fig. 89 [not *Cerithium tomlini* Preston, 1905, pl. 180: fig. 85 of Sowerby, 1855, designated as type of *tomlini* by Hedley, 1914].

Cerithium mysterium Hedley, 1917:708–709 [replacement name for *Cerithium tomlini* Hedley, 1914].

Cerithium (Clypeomorus) tenellum Sowerby.—Kaicher, 1956, pl. 3: fig. 13.

Cerithium salebrosum Sowerby.—Demond, 1957:292–293, fig. 9 [not *Cerithium salebrosum* Sowerby, 1855; is *Cerithium tenellum* Sowerby, 1855].

Cerithium (Proclava) kobelti Dunker.—McNeil, 1960:41–42, pl. 11: fig. 21 [not *Cerithium kobelti* Dunker, 1877; is *Cerithium tenellum* Sowerby, 1855].

Cerithium tenellum Sowerby.—Cernohorsky, 1972:65, pl. 14: fig. 4 [not *Cerithium tenellum* Sowerby; is *Cerithium torresi* E.A. Smith, 1884].

Cerithium (Thericium) mysterium Hedley.—Cernohorsky, 1978:52, pl. 13: fig. 9.

DESCRIPTION.—*Shell* (Figures 131, 132): Shell turreted, fusiform, comprising up to 16 convex-angulate whorls, reaching 31 mm length and 12.5 mm width. Protoconch unknown. Early teleoconch whorls (Figure 133B) straight-sided, sculptured with 3 or 4 spiral lirae; axial ribs appearing on fifth to sixth whorl. Adult teleoconch whorls with weak to moderate subsutural ramp and usually sculptured with 0–4 main spiral cords with fine spiral lirae in interspaces, having 0–24 axial ribs sometimes strongly angulate at whorl periphery. Sculpture highly variable, ranging through absence of spiral sculpture to fine cancellate, nodulose, or heavily beaded shells. Suture wavy, distinct, slightly impressed. Body whorl convex, elongate, sculptured with 4 or 5 main spiral cords and large varix opposite outer lip of aperture. Siphonal constriction moderate. Anterior siphonal canal short, moderately reflected dorsally to left of shell axis. Anal canal well developed, bordered by strong parietal columellar plait. Columella concave, with thickly calloused lip. Aperture fusiform-ovate, a little more than one-third the shell length. Edge of outer lip thick, crenulate, strongly convex and rounded, but slightly concave at suture. Shell color white, commonly with spiral rows of small, light tan or brown spots on interspaces between

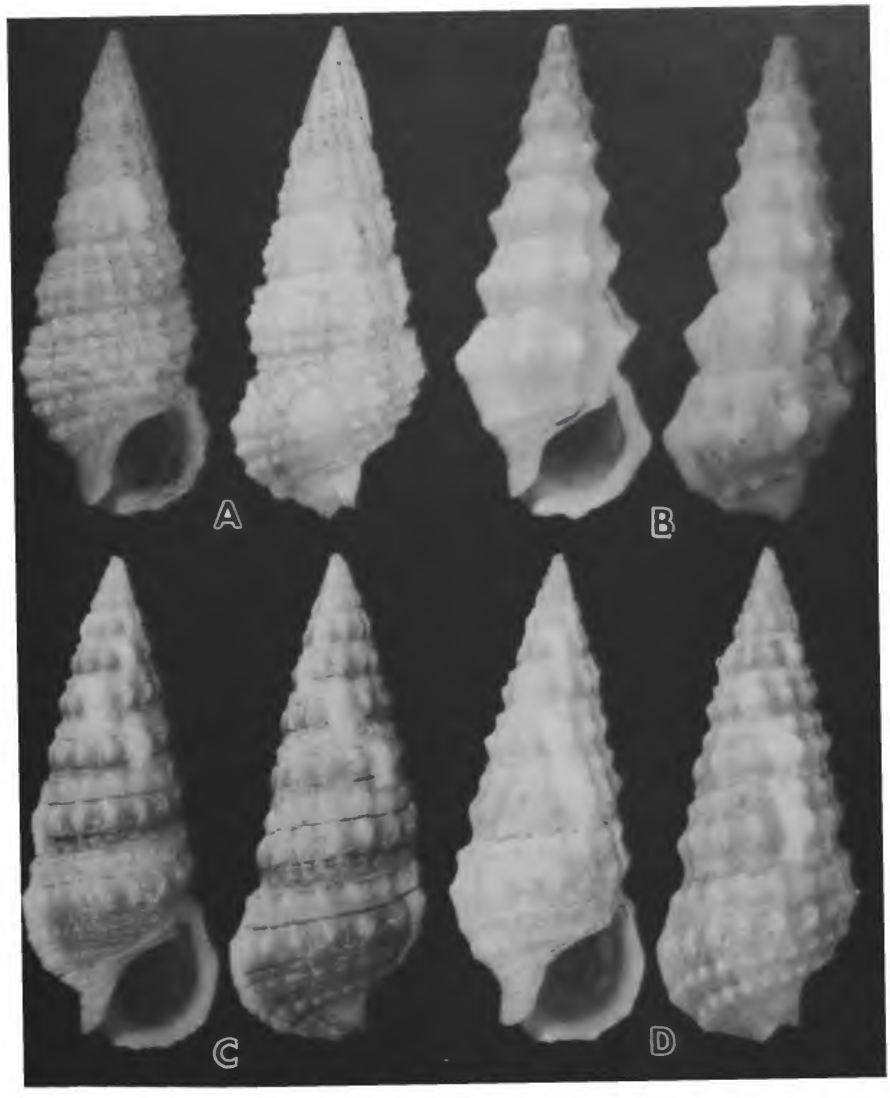

FIGURE 131.—Types of nominal taxa synonymous with *Cerithium tenellum* Sowerby. A, lectotype of *Cerithium filosum* Sowerby, Burias, Philippines, 21.8 mm (BMNH 19861711); B, specimen (non-type) selected by Hedley to represent *Cerithum mysterium* Hedley, replacement name for *Cerithium novaehiberniae* A. Adams, 24.4 mm (BMNH 3971741708); C, atypical, brightly pigmented paralectotype of *Cerithium tenellum* Sowerby, Philippines (BMNH 19861802); D, lectotype of *Cerithium tenellum* Sowerby, Philippines, 17.5 mm (BMNH 19861801).

major spiral cords. Shell occasionally brownish to pink. Aperture shiny white. Measurements (Table 42). Periostracum not evident. Operculum (Figure 133A) paucispiral and with microscopic scales on unattached surface.

Radula (Figure 133D-I): Type-1 radular ribbon (Figure 3A) short, a little under one-tenth the shell length. Rachidian tooth (Figure 133H,I) squarish; basal plate having median posterior projection with small central pustule and pair of basal incised ridges; anterior front with median concavity, and cutting edge comprising elongate, arrow-shaped main cusp flanked on each side by 2 or 3 very small, rounded denticles. Lateral tooth (Figure 133G,H) having elongate lateral, posterior extension, and strong central buttress extending posteriorly on basal plate; cutting edge with long pointed main cusp one pointed, inner flanking denticle and 2 or 3 outer flanking, narrow, pointed denticles. Marginal teeth (Figure 133F) with long narrow shafts, curved and serrated at tips. Inner marginal tooth with long main cusp, 3 inner flanking, pointed denticles

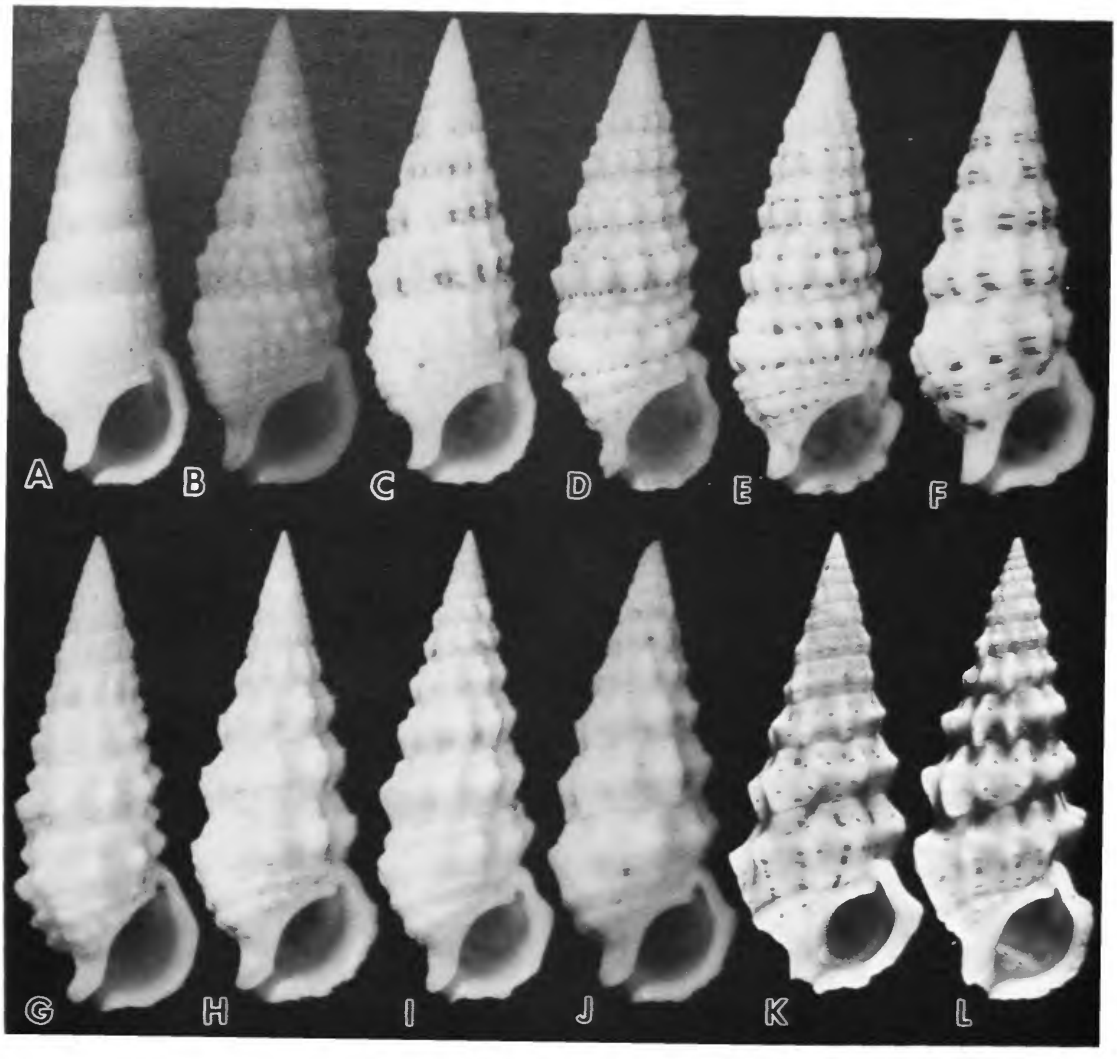

FIGURE 132.—Phenotypic variation in *Cerithium tenellum* Sowerby. A-C, all Bikini Atoll, Marshall Ids, 21 mm, 20.5 mm, 19.8 mm, respectively (USNM 580640); D,E, both Dirk Hartog Id, Western Australia, 24.1 mm, 20.8 mm, respectively (WAM 457-76); F, Île des Pins, New Caledonia, 24 mm (USNM 692935); G, Bikini Atoll, Marshall Ids, 20 mm (USNM 580640); H-J, all Île des Pins, New Caledonia, 27.3 mm, 33 mm, 27 mm, respectively (USNM 692935); K, Big Upolu Cay, off Cairns, Queensland, Australia, 29.2 mm (AMS); L, Undine Reef, off Cairns, Queensland, Australia, 27.5 mm (AMS).

TABLE 42.—Shell morphometrics of *Cerithium tenellum*.

Character	$\bar{x}$ (n = 18)	sd	v	Range
Shell length	24.8	4.1	16.1	18.2–31
Shell width	8.8	1.6	2.5	6.5–12.5
Aperture length	5.1	0.8	0.6	5.2–9.2
Aperture width	5.0	0.8	0.6	3.7–6.5
Number of whorls	14.1	0.8	0.6	13–16
Number spiral cords	1.8	1.8	3.3	0–5
Number axial ribs	13.3	5.2	27.2	0–24

and 2 outer flanking, pointed denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Unknown.

SYNONYMIC REMARKS.—Extreme variability in shell sculpture has led to the proposal of many names for this species. The earliest available names are *Cerithium novaehiberniae* A. Adams in Sowerby, 1855, and *C. tenellum* Sowerby, 1855. *Cerithium novaehiberniae* is conspecific with *C. tenellum* and merely represents a highly ribbed form of the latter. Sowerby's (1855) fig. 83 is an intermediate form between *tenellum* and

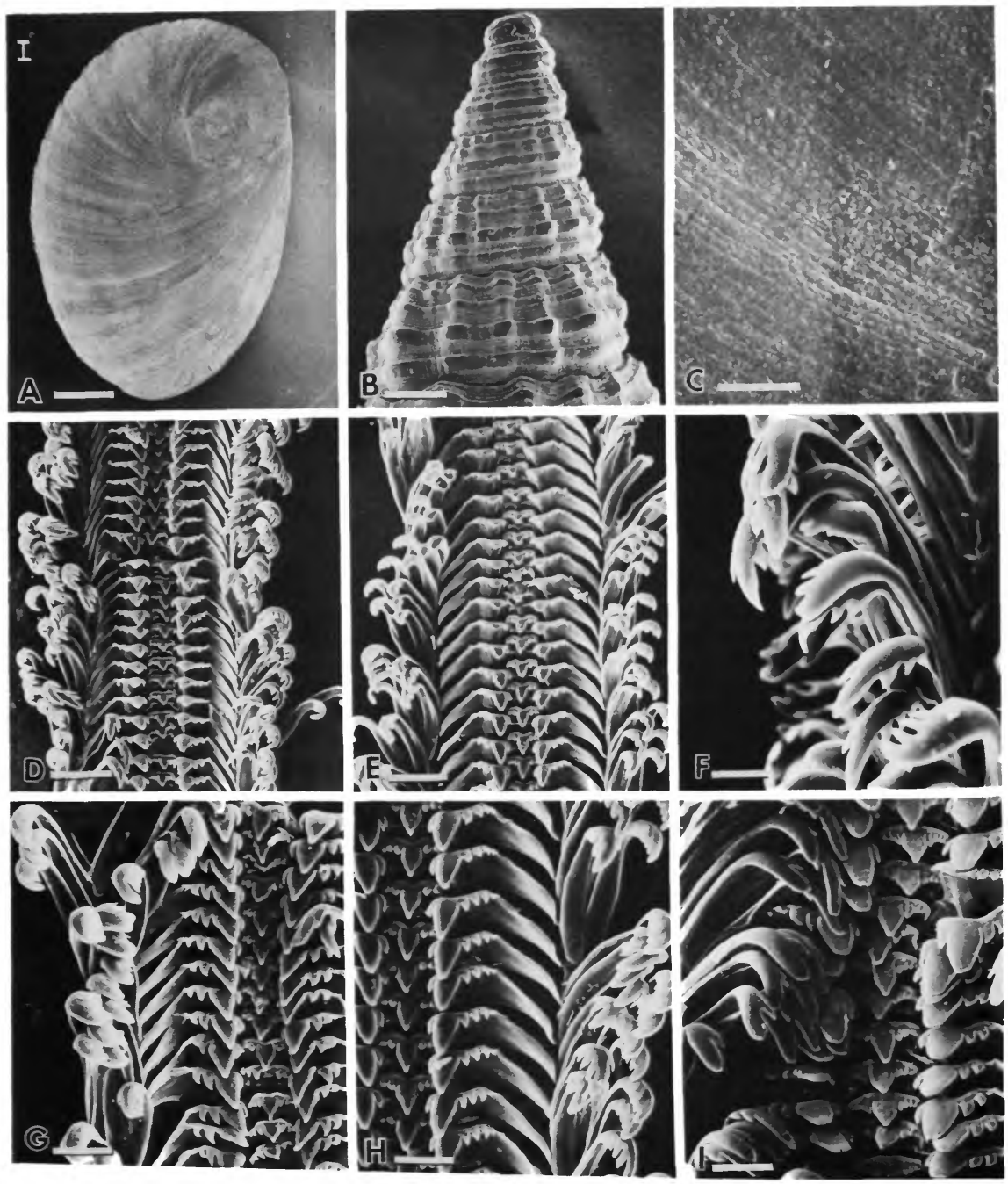

FIGURE 133.—SEM micrographs of operculum, shell and radula of *Cerithium tenellum* Sowerby. A, operculum, Îlots Degnala, Uvea Atoll, Loyalty Ids (bar = 0.4 mm; USNM 692973); B, early whorl sculpture, Bikini Atoll, Marshall Ids (bar = 0.25 mm; USNM 580640); C, detail of opercular surface (bar = 50 µm; USNM 692973); D, radula with marginals spread open, Dirk Hartog Id, Western Australia (bar = 125 µm; USNM 862648); E, radula with marginals spread open, Olango, Cebu, Philippines (bar = 125 µm; ANSP 231859); F, marginal teeth, Dirk Hartog Id, Western Australia (bar = 75 µm; USNM 862648); G, half row, Uvea, Loyalty Ids (bar = 75 µm; USNM 692973); H, half row, Olango, Cebu, Philippines (bar = 50 µm; ANSP 231849); I, marginal teeth folded over ribbon, Tryon Id, Queensland, Australia (bar = 60 µm; AMS).

novaehiberniae, while fig. 84 represents a highly ribbed form, given the name *mysterium* by Hedley (1914). A shell labeled *C. novaehiberniae* in the British Museum (BMNH 3971741708) does not match Sowerby's fig. 84, but looks very much like the shell figured by Sowerby (1865, fig. 71a,b) as *C. novaehiberniae* and is depicted herein (Figure 131B). This highly ribbed shell was designated as the type of *C. tomlini* by Hedley (1914), but as this name was preoccupied, the name *C. mysterium* Hedley, 1917, was later proposed and has recently been applied to this phenotype (Cernohorsky, 1978:52). Hedley (1917) referred to Sowerby's fig. 85 as representing the *Cerithium* species he intended to describe as *C. tomlini* and stated that he regarded *C. novaehiberniae* A. Adams as a composite species. Although the name *novaehiberniae* precedes *tenellum* in Sowerby's *Thesaurus*, the confusion caused by the different Sowerby figures of *C. novaehiberniae*, and the lack of a type specimen compel me to select the name *tenellum* as the valid one. The type material of *C. tenellum* consists of 11 shells, some of which are atypically pigmented. One of these highly pigmented morphs were figured by Sowerby (1855, figs. 88, 90) is shown herein (Figure 131D), and his depictiom has undoubtedly led subsequent workers to apply the name *tenellum* to other species, and in particular to *C. torresi* E.A. Smith (see Cernohorsky, 1972:65, pl. 14: fig. 4). A white shell (BMNH 19861801) corresponding closely to Fig. 89 of Sowerby, is herein selected as the lectotype of *C. tenellum* (Figure 131D). The name *Cerithium tenuifilosum* Sowerby, 1866, a replacement name for *Cerithium filosum* Sowerby, 1855, which is preoccupied, has been applied to *C. tenellum* (see Cernohorsky, 1972:64), but the lectotype of *C. filosum* (Figure 131A) is conspecific with *C. tenellum*.

ECOLOGY.—*Cerithium tenellum* is a shallow, subtidal, infaunal species, common on sandy lagoon bottoms around coral reefs. There is nothing recorded about this species in the ecological literature. *Cerithium tenellum* is common in the sediments on One Tree Id, Queensland, Australia, where it occurs in densities in excess of 700 per square meter. It is most common in coarse gravel-type sediments close to the reef crest, but is active only at night when about 70 percent of the population comes to the surface to feed. Snails appear to actively graze across the surfaces of large, dead, coral fragments (G. Skilleter, in litt.). I have observed this speciesburrowing in clean white sand in the lagoon of Enewetak Atoll, where it lives in microsympatry with *C. salebrosum*, *Rhinoclavis fasciata*, and *Rhinoclavis aspera*. Drilled shells are common and indicate heavy predation by naticid snails. At One Tree Id, *C. tenellum* lays its gelatinous egg masses on coral fragments during December -January (G. Skilleter, in litt.). Egg mass morphology and larvae remain undescribed.

DISCUSSION.—An overall white shell with a few weak spirals of brown dots and with a variable sculpture of axial, angulate ribs occasionally overlain by spiral cords are the distinguishing characters of this species.

Cerithium tenellum is perhaps, one of the more variable Indo-Pacific *Cerithium* species. Large phenotypic differences exist between and within some populations. Strong selection pressures between phenotypes within different habitats may account for some of the observed differences, and several geographical clines appear to be present. In Micronesian and Melanesian populations, shell sculpture tends to be weak or moderate, with equal spiral and axial elements presenting an overall fine, beaded effect (Figure 132A–C), although some nodulose forms are occasionally found (Figure 132G). In the reef areas of Queensland, Australia and in New Caledonia, shells tend to lack spiral cords, but have strong thick axial ribs and are strongly nodose (Figure 132H–L). These phenotypes have been given the name *Cerithium mysterium*. However, there are Micronesian (USNM 580640; Figure 132G) and Queensland (AMS) populations in which a complete transition from virtually smooth shells to the highly ribbed *mysterium* shells occur. A specimen from Green Id, Queensland (AMNH, labeled as *C. tomlini*, has upper whorl sculpture typical of *C. tenellum*, while the last three whorls have the strong axial ribbing typical of *mysterium* phenotypes. In Western Australia, populations that live in coarse sediments tend to have 2 or 3 knobby spiral cords per whorl and the spiral rows of brown dots are larger and more numerous (Figure 132D,E). Finally, on both sides of Australia, shells living on algal covered, soft sediment bottoms are virtually smooth, the only sculpture being the former growth varices. Micronesian specimens of this species may be confused with the sympatric *C. salebrosum* Sowerby (Figure 122), with which they share a common sandy habitat and similar white color. *Cerithium tenellum* differs from *C. salebrosum* in lacking the excavation and sharp constriction of the shell base, and does not have as rugose a sculpture. *Cerithium torresi* E.A. Smith (Figure 135) also resembles *C. tenellum* in sculpture but the color of the former species is darker and it has more spiral beaded cords than the latter.

FOSSIL RECORDS.—This species, cited as *Cerithium (Proclava) kobelti* Dunker, has been reported from the Pliocene of Okinawa (McNeil, 1960:41–42, pl. 11: fig. 21), but this is the only recorded fossil of *C. tenellum*.

GEOGRAPHIC DISTRIBUTION (Figure 134).—*Cerithium tenellum* has a limited distribution in the Indo-west-Pacific. Although only a few specimens from SE Asia and Indonesia have been seen, *C. tenellum* appears to be very common in Western Australia. In the Pacific it occurs from the Philippines south to Queensland and throughout Melanesia as far as Fiji. In Micronesia it is known only from the Caroline and Marshall islands, where it is very common. A single record from Johnston Id needs reconfirmation.

SPECIMENS EXAMINED.—INDIAN OCEAN ISLANDS: E of N Lagoon, West Id, Cocos Keeling Ids (ANSP 289268). THAILAND: Ao Ra Wai, Goh Phuket (USNM 701397). PHILIPPINES: Cebu, Cebu (MCZ 22699); Salpa Id, 2 km S of Olango Id, Cebu (ANSP 230445); Salpa Id, off Olango, Cebu (ANSP 230445); Cawhegen Id, off Olango, Cebu (ANSP

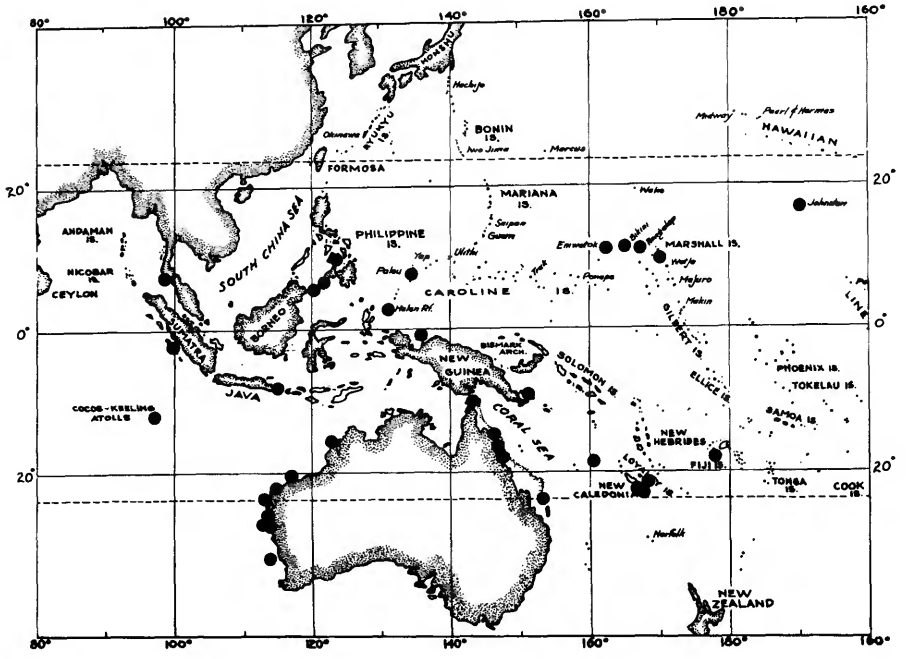

FIGURE 134.—Geographic distribution of *Cerithium tenellum* Sowerby.

231849); Little Santa Cruz Id, Zamboanga, Mindanao (USNM 862832); Tengolan Id, Basilian Id (USNM 619796); Siasi Id, Sulu Archipelago (ANSP 318701); Tabaan, Simaluc Id, Tawitawi (USNM 243700). INDONESIA: *Siboga* Exp, Sumatra (ZMA); Bali (AMS C60967).

WESTERN AUSTRALIA: SE of Beacon Id, Houtman Abrolhos Ids (WAM 458-76); W side Wooded Id, Houtman Abrolhos Ids (WAM); SW of Rat Id, Houtman Abrolhos Ids (AMS, WAM); S end of Long Id, Houtman Abrolhos Ids (USNM 801602, 801608); Mangrove Id Gp, Houtman Abrolhos Ids (WAM); Bill Bay, 3.2 km S Pt Maud, Cardalia Station (WAM); Point Charles (ANSP 267944); SE of Dirk Hartog Id (WAM); Surf Pt, Dirk Hartog Id (USNM 862648, WAM 457-76); Pt Gregory, NW side Peron Peninsula, Shark Bay (WAM); lagoon 1.6 km N Denham, Shark Bay (WAM); N of Carnarvon, below Quobba Light (WAM); Pt Quobba (AMS); W of Pt Cloates (WAM); Pt Cloates, N of Shark Bay (AMS); N Fraser Id, Pt Cloates (WAM); N side Naval Base, Exmouth Gulf (AMS); S of Cape Murat, Exmouth Gulf (WAM); Turtle Beach, W side NW Cape (AMS); Thevenard Id, N of Shark Bay (AMS); Rosemary Id, Dampier Archipelago (WAM); Ico Id (WAM); Catamaran Bay, W side King Sound, near Cape Levique (AMS). QUEENSLAND, AUSTRALIA: Murray Id, Torres Strait (AMS C29542, C295383, USNM 273843); Hospital Pt, Thursday Id, Torres Strait (AMS); Three Islands, N of Cooktown (AMS C57675); Lizard Id (AMS, USNM 216424, 766774, 783653); Undine Reef, N of Cairns (AMS); Rudder Reef, NE of Pt Douglas (AMS C114894); Low Isles, near Pt Douglas (AMS); Michaelmas Cay, off Cairns (AMS C53541); Big Upolu Cay, NE of Cairns (AMS); Green Id, off Cairns (AMS, USNM 781468); Buchan's Pt (AMS); near jetty, Hayman Id (USNM 704902); Langford Reef (USNM 845795); Hook Id (AMS); Brampton Id (AMS); Capre Cay, Swains Reef (AMS); Thomas Cay, Swains Reef (AMS); Gillett Cay, Swains Reef (AMS); Tryon Id, Capricorn Gp (AMS); Heron Id, Capricorn Gp (USNM 431834); W end Heron Id, Capricorn Gp (USNM 704883); Masthead Id, Capricorn Gp (AMS C19096); North West Id, Capricorn Gp (AMS); N of One Tree Id, Capricorn Gp (AMS); Lady Musgrave Id, Bunker Gp (AMS).

CORAL SEA: Anchorage Cay, Chesterfield Reef (AMS). NEW GUINEA: Mios Woendi, Schouten Ids, Irian Jaya (USNM 542684); reef E of Noesi, Mios Woendi, Schouten Ids, Irian Jaya (AMNH); 4.8 km N of Rani Id, Schouten Ids, Irian Jaya (ANSP); 0.8 km E of Noekori Id, E Padaido Ids, Irian Jaya (ANSP); 0.8 km E of Kaipoeri Village, Koeroedoi Id, Geelvink Bay, Irian Jaya (ANSP); E side Rouw Id, Aeori Ids, Geelvink Bay, Irian Jaya (ANSP); N shore Matas Id, Aeori Ids, Geelvink Bay, Irian Jaya (ANSP); Kula Id, Lusancay Ids, Trobriand Gp, Papua (AMS). LOYALTY ISLANDS: Ile des Pins (USNM 692864, 692865, 692868, 692890, 692935); Ilots Deguala, Uvea Atoll (USNM 692973); Lifu (AMS C30718, MCZ). NEW CALEDONIA: Oubatche (AMS C4036); Poe, Bourail (AMS C107111); Noumea (MNHNP); reef near Kunie, Ile des Pins (AMS). FIJI: Wadingi Id, Maunaunca Gp (USNM 824827); Nadi, Viti Levu (AMS C67596).

CAROLINE ISLANDS: N of Ngapalt Pass, E Babelthuap Id,

Palau (ANSP); E of Melekeiok, E Babelthuap, Palau (ANSP); 0.8 km S of Helen Reef, Helen Id (ANSP). MARSHALL ISLANDS: Rigili Id, Enewetak Atoll (USNM 581243, 581590); Japtan Id, Enewetak Atoll (USNM 582524); Muti Id, Enewetak Atoll (USNM 716365); Igurin Id, Enewetak Atoll (USNM 581374, 582312, 582626); Jieori Id, Enewetak Atoll (USNM 582499); Enewetak Id, Enewetak Atoll (USNM 582286, 660660, 770577, 809773); NW side Yuroshi Id, Bikini Atoll (USNM 579810); Bikini Id, Bikini Atoll (USNM 579314, 579717, 580566, 582779, 582862, 582983, 582984, 583023, 583660, 583851, 583922, 583950, 584915, 585182); W end Rukoji Id, Bikini Atoll (USNM 579782); Enyu Id, Bikini Atoll (USNM 579230, 580640, 580890, 580953, 581030, 581408, 586380); Rongelap lagoon, Rongelap Atoll (USNM 584290, 584301); Burok Id, Rongelap Atoll (USNM 583994); Rongelap Id, Rongelap Atoll (USNM 583345, 585492); Likiep Atoll (USNM 596144); Nado Id, Likiep Atoll (USNM 615328, 615355); Kwajalein Atoll (USNM 587400). JOHNSTON ISLAND: (ANSP).

Cerithium torresi E.A. Smith, 1884

FIGURES 135–137

Cerithium torresi E.A. Smith, 1884:65, pl. 5: fig. O [holotype: BMNH 188212698; type locality: Torres Strait; 14.2 mm × 5.4 mm].—Tryon, 1887:136, pl. 23: fig. 14.—Kobelt, 1898:244, pl. 42: fig. 14.

Clypeomorus sordidula (Gould).—Habe, 1964:41, pl. 12: fig. 22 [not *Cerithium sordidula* Gould, 1849; is *Cerithium torresi* E.A. Smith, 1884].

Proclava pfefferi (Dunker).—Habe, 1964:41, pl. 12: fig. 19 [not *Cerithium pfefferi* Dunker, 1882; is *Cerithium torresi* E.A. Smith, 1884].

Cerithium tenellum Sowerby.—Cernohorsky, 1972:65, pl. 14: fig. 4 [not *Cerithium tenellum* Sowerby, 1855; is *Cerithium torresi* E.A. Smith, 1884].

DESCRIPTION.—*Shell* (Figure 135A-HJ): Shell elongate, turreted, moderately slender, comprising about 14 moderately inflated cancellate, beaded whorls and reaching 25 mm length and 9.5 mm width. Protoconch (Figure 135H) 2.5 whorls with deep sinusigeral notch; sculpture unknown. Early teleoconch whorls (Figure 135J) impressed presuturally, sculptured with dominant axial ribs crossed over by 2 or 3 spiral cords. Adult teleoconch whorls impressed presuturally and with overall cancellate sculpture comprising 3 or 4 main spiral cords, fine spiral lirae, and subsutural cincture of 1 or 2 finely beaded spiral threads; spiral sculpture crossing over 11–17 very weak to strong axial ribs; nodules or beads occur at cross-over points. Suture impressed. Prominent, wide varices randomly distributed. Body whorl narrow, sculptured with subsutural cincture and 5 main, spiral, beaded cords and numerous spiral, finely beaded threads. Large varix opposite outer lip of aperture. Body whorl with moderately excavated base and strong siphonal constriction. Aperture ovate, a little less than one-fourth the shell length. Anterior siphonal canal moderately long, well defined, constricted, reflected dorsally and to left of shell axis. Anal canal defined by parietal columellar tooth extending into aperture. Columella concave, with strong callus and moderate columellar lip. Outer lip thick, crenulate, and with spiral denticles on inside. Shell color dirty white overlain by broad brown or grayish blue bands; varices, beads, aperture lip, columella, and apex white. Interior of aperture lip with gray or brown spiral bands. Measurements (Table 43). Periostracum thin, tan. Operculum (Figure 135I) corneous, ovate, tan, and paucispiral with eccentric nucleus.

Radula (Figure 136): Type-1 radular ribbon (Figure 3A) short, about one-tenth the shell length. Rachidian tooth (Figure 136B-D) triangular shaped having basal plate with pair of basal ridges and long, triangular, median-posterior extension; anterior front concave and cutting edge with large, pointed main cusp flanked on each side by two pointed denticles. Lateral tooth (Figure 136C,D) with wide central buttress bearing weak pustule, and having long, lateral, posterior extension on broad basal plate; cutting edge with broad, spoon-shaped, main cusp flanked by one sharp, inner denticle and 2 or 3 sharp, outer denticles. Marginal teeth (Figure 136B-D) with long shafts having sharply hooked, spoon-like tips. Inner marginal tooth with long, spatulate main cusp, two inner-flanking denticles, and one outer flanking denticle. Outer marginals same, but lacking outer-flanking denticles.

Anatomy: Head-foot yellowish white with gray stripes and white and black blotches on snout, tentacles, and sides of foot. Mantle dark brown with axial, yellow flammules. Snout long, extensible with bilobed tip. Cephalic tentacles very long and slender. Foot narrow, long, and crescent-shaped anteriorly. Sole of foot white. Mantle edge with moderate to small papillae.

SYNONYMIC REMARKS.—*Cerithium torresi*, although relatively common in the Indo-West Pacific, has been mentioned seldom in the literature since its description. Habe (1964:41, pl. 12: fig. 22) and Cernohorsky (1972:65, pl. 14: fig. 4) have both figured *C. torresi*, but have applied other names to it. *Cerithium eximium* Sowerby, 1855, is a name found on some museum labels for this species, but the type material of *C. eximium* is conspecific with *Rhinoclavis (Proclava) sordidula* Gould, 1849. Both Sowerby's (1865) and Kobelt's (1898) figures of *Cerithium eximium* are clearly representations of *Rhinoclavis sordidula*. I previously overlooked the name *eximium* and did not place it into the synonymy of *Rhinoclavis sordidula* (Houbrick, 1978b). Another name applied to this species in museum collections and in some books (Cernohorsky, 1972:65) is *C. tenellum*, but this is a different species frequently cited as *C. tenuifilosum* Sowerby, 1866.

ECOLOGY.—This species occurs in low-intertidal to shallow subtidal, low-energy zones on muddy sand flats among rocks and rubble, and sometimes near grass beds high in organic content. It appears to need an organic-rich environment subject to runoff from the shore. I observed living populations at Kissing Point, Townsville, and at Geoffrey Bay, Magnetic Id, Queensland, Australia. They were found in the former location crawling in soft, terrigenous sediment with the potamidid, *Cerithidea cingulata* (Gmelin). In Geoffrey Bay, a large

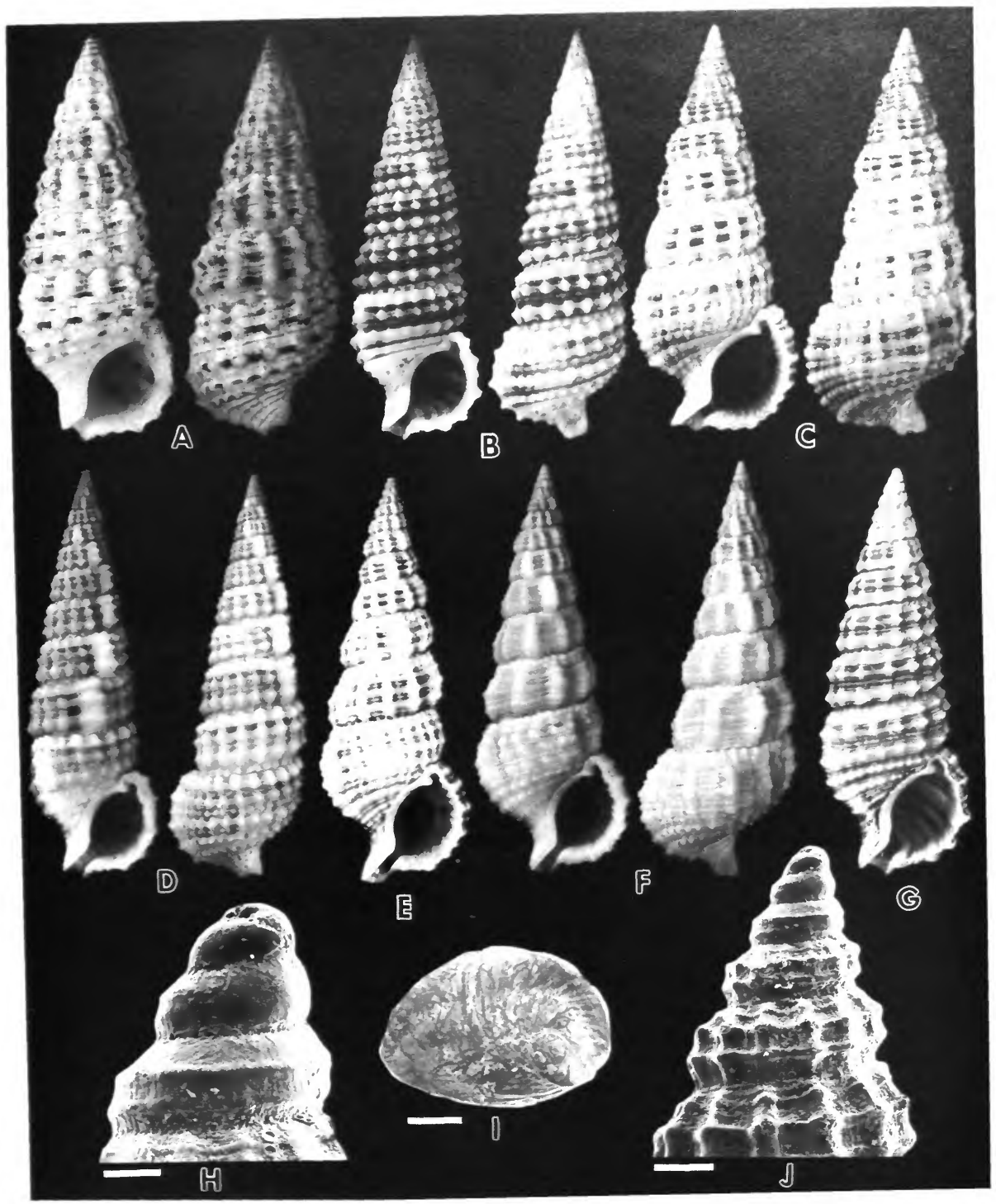

FIGURE 135.—*Cerithium torresi* E.A. Smith, showing phenotypic variation. A, holotype of *Cerithium torresi* E.A. Smith, Torres Strait, 14.2 mm (BMNH 188212698); B, Augustus Id, Western Australia, 21.6 mm (MCZ); C-F, all from one population of Karaitivu Id, Ceylon, 26.6 mm, 21 mm, 32 mm, 29.8 mm, respectively (ANSP 84422); G, Pelau Besar, Malacca, Malaysia, 18.8 mm (USNM 660964); H, SEM of protoconch, Hervey Bay, Queensland, Australia (bar = 85 μm; AMS); I, operculum, Port Darwin, Northern Territory, Australia (bar = 0.5 mm; AMS); J, SEM of sculpture of early whorls, Hervey Bay, Queensland, Australia (bar = 0.21 mm; AMS).

TABLE 43. Shell morphometrics of *Cerithium torresi*.

Character	$\bar{x}$ (n = 17)	sd	v	Range
Shell length	21.0	2.7	7.2	15.8–25
Shell width	7.3	1.1	1.2	5.3–9.5
Aperture length	5.5	0.6	0.3	4.3–6.5
Aperture width	3.7	0.5	0.2	2.8–4.5
Number of whorls	14.0	0.8	0.6	13–16
Number spiral cords	3.3	0.5	0.2	3–4
Number axial ribs	15.1	1.8	3.1	11–17

population occurred in muddy sand on an intertidal rocky flat adjacent to a fringing reef. Both populations were observed in June, when all specimens examined were sexually immature.

The eggs and larvae of *C. torresi* are undescribed, but there is probably a planktotrophic larval stage, as the protoconch shown in Figure 135H, although too eroded to see sculptural details, has a deep sinusigeral notch.

DISCUSSION.—The distinguishing characters of this species are a long tapering shell having slightly convex whorls and thick former varices, and an overall beaded appearance due to sculpture of three, sometimes four spiral cords crossed by 14–17 axial riblets forming lines of white axial beads. A large lateral varix is opposite the outer lip. The aperture is internally pigmented with widely spaced, brown lines.

There is some intraspecific variation in shell sculpture, particularly in the development of axial ribs. Some phenotypes (Figure 135F) have very strong ribs. Shell color is normally white with many bluish brown to brown spiral bands (Figure 135B,D) in the interspaces between sculptural elements,

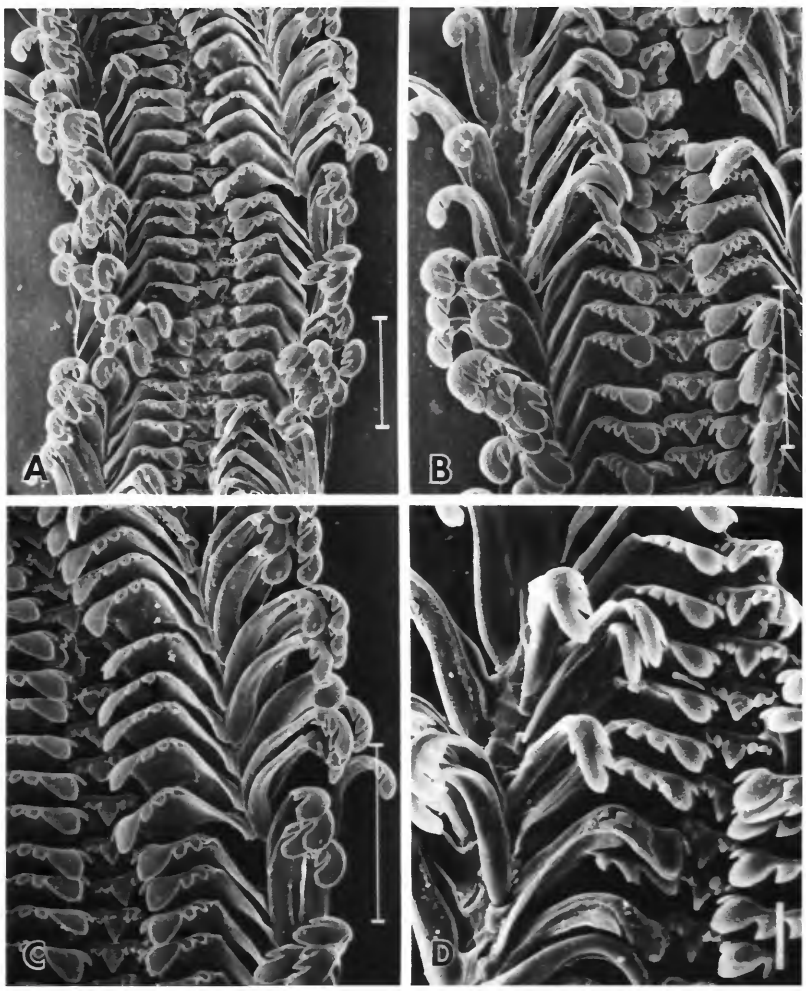

FIGURE 136.—SEM of radula of *Cerithium torresi* E.A. Smith. A, radula with marginals spread open (bar = 100 μm; MCZ 725); B, half row, Augustus Id, Western Australia (bar = 100 μm; MCZ 725); C, half row, Augustus Id, Western Australia (bar = 100 μm; MCZ 725); D, half row with marginals folded over ribbon, Karaitivu Id, Ceylon (bar = 43 μm; ANSP 84422).

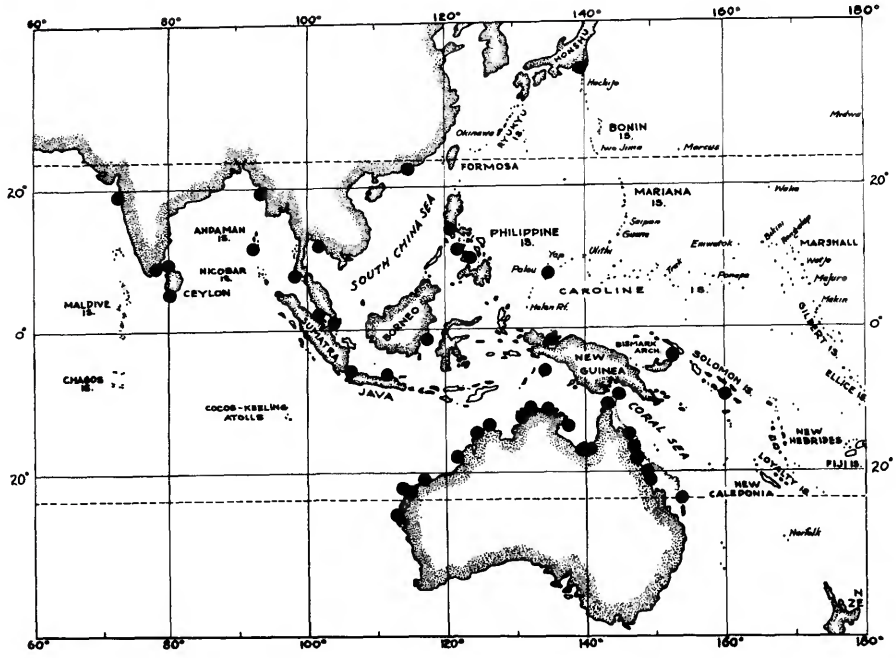

FIGURE 137.—Geographic distribution of *Cerithium torresi* E.A. Smith.

presenting an overall dusky appearance. However, some shells are dark brown or tan (Figure 135F) and may lack spiral bands of pigment while others may be devoid of all pigment (Figure 135E).

This species is easily confused with *Cerithium dialeucum* Philippi, 1849 (Figure 47), which generally has a larger, wider shell with more angulate whorls, a subsutural cincture of two thin, finely beaded threads, and fewer beaded, axial riblets. The major cusps on the central and lateral radular teeth of *C. dialeucum* (Figure 48) are longer and more pointed than those of *C. torresi*. As the early whorls of these two species are very similar, juveniles are difficult to identify.

Another congener with which *C. torresi* may be confused is *Cerithium balteatum* Philippi, 1848 (Figure 17). The latter species is usually smaller, with a more deeply impressed suture and sutural ramp, strongly constricted and excavated at its base, and with the anterior canal directed forward in line with the shell axis. There are four major spiral cords rather than three, as in *C. torresi*, and in general, fewer and wider pigment bands. *Rhinoclavis (Proclava) kochi* (Pfeiffer), called *Cerithium eximium* Sowerby in some collections, should also be compared with *C. torresi*, as some forms of the latter closely resemble it, although they never have the central columellar plait found in *Rhinoclavis* species.

The shell morphology of *C. torresi* does not vary much throughout its geographic range. However, shells from India and Ceylon (Figure 135F) have wider body whorls and are sculptured with finer spiral cords and excised lines and tend to have few or no beads on the axial riblets. They are also more variable in color. There appears to be more variation within a given population than in other parts of the range. This same trend is seen in populations that occur in deeper, subtidal habitats, such as found off Queensland.

FOSSIL RECORDS.—None recorded.

GEOGRAPHIC DISTRIBUTION (Figure 137).—*Cerithium torresi* has an Indo-West Pacific distribution, and is confined to tropical continental margins and large continental archipelagos of the Pacific and Indian Ocean basins. In the Indian Ocean it occurs on the coast of western India, in the Andaman Islands, and throughout SE Asia and the Indonesian archipelago to western Australia. In the western Pacific it is found from the Ryukyu Islands, south through the Philippines and Palau, to New Guinea and Queensland, Australia.

SPECIMENS EXAMINED.—INDIAN OCEAN ISLANDS: Andaman Ids (BMNH 190010162-3). INDIA: Bandra, N of Bombay (USNM 443630); Bombay (AMS, BMNH Winkworth Coll 1838, BMNH 1909923240241, NM FA197, USNM 91057); Chapauti Beach, Bombay (USNM 701820, 701828); Karwar, N Kanara (USNM 443666); Tuticorn (BMNH Winkworth Coll 1838, USNM 347476, 841364). CEYLON: N tip of Eluvaitivu Id, N Ceylon (ANSP); 1.8–5.5 m, 9.6 km SW of Karaitivu Id, N Ceylon (ANSP 84422, DMNH 933, 71987, MCZ 215564); W side of Weligama Bay, S Ceylon (ANSP). BURMA: Ramree Id, Arakan Coast (BMNH Biggs Coll 2258). THAILAND: SW end of Rawal Beach, Phuket (LACM 85-4); Sriracha, SE Thailand (USNM 363653). MALAYSIA: Sin-

gapore (AMS, ANSP, BMNH 19061030162183, BMNH 1924129102103); NE end, Sentosa Id, Singapore (AMS); Siglap, Singapore (BMNH Winkworth Coll 1838); Pulau Besar, Malacca Strait (USNM 660955, 660964). CHINA: Stanley Beach, Hong Kong Id, Hong Kong (AMS); Hong Kong (AMS C33580, ANSP). JAPAN: Misaki, Sagami, Hondo Ids (AMS C1544). PHILIPPINES: Bagac, Bataan, Luzon (USNM 774972); Manila Harbor, Luzon (USNM 243827); Manila, Luzon (LACM 34625); Cabcaben, SE Bataan, Luzon (ANSP); San Juan, Tayabas Bay, Batangas Prov, Luzon (AMS C108261); Iloilu, Panay (USNM 383966, 383974); Miranda Beach, Pont Verda, Negros (ANSP); 1.8–6 m, channel between Mandane and Mactan Id, E Cebu (ANSP). INDONESIA: Sembuga, 14 km E of Balikpapan, E Kalamantan, Borneo (AMS); Singkep (ZMA); 6°S, 106°10′E, Keledjitan, Bantam, Java (USNM 260540); Tjiperwagaran, Bantam, Java (USNM 260568); Jepara, Java (USNM 767460); 12.8 km SW of Tg Ratoe, Maikoor, Aru Ids, Moluccas (WAM).

WESTERN AUSTRALIA: Williamia, Useless Inlet, Shark Bay (AMS C69243); Denham, Shark Bay (AMS); 1–5 m, 4 km ESE from Petit Pt, Shark Bay (WAM); tidal creek at Little Lagoon near Denham, Shark Bay (WAM); 4 km NW of Denham, Shark Bay (WAM); Faure Id, Faure Flat, Shark Bay (WAM); Dirk Hartog Id (AMS C70177); Monkey Mia, E side of Peron Peninsula, Shark Bay (AMS); Sam's Creek, Port Sampson (WAM); Pelican Pt, Carnarvon (WAM); Carnarvon (AMS); 25 km N of Ningaloo Homestead, North West Cape (WAM); near Charles Knife Rd, Exmouth Gulf (WAM); 30.6 km S of Exmouth Township (AMS); SE of Exmouth Township, S of Learmouth (AMS); E side of Exmouth Township (AMS); between Cape Duprey and Cape Malauet, Barrow Id (USNM 694107); Long Id, near Dampier Archipelago (AMS); Dampier (WAM); Roebuck Bay, Broome (AMS); Black Ledge, 6.4 km E by S of Broome (ANSP); 3.2 km SW of jetty, Broome (ANSP); Entrance Point, Broome (ANSP); Augustus Id (MCZ 725); Vansittart Bay (WAM). NORTHERN TERRITORY, AUSTRALIA: Daly River (AMS C19488); WSW of Darwin (AMS); Talc Pt, off Darwin (AMS); Fannie Bay, Darwin (AMS); Port Darwin (BMNH Piele Coll. 2242); East Arm, Darwin Harbor (AMS); East Pt, Darwin (AMS); Nightcliff Pt, Darwin (USNM 602148); Smith Pt, Port Essington (MCZ); Maningrida, Arnhem Land (AMS); Bickerton Id, Gulf of Carpentaria (USNM 602239); Groote Eylandt, Gulf of Carpentaria (AMS); N Id, Pellew Gp (AMS C71334).

QUEENSLAND, AUSTRALIA: Forsyth Id, Wellesley Gp, Gulf of Carpentaria (AMS); Mornington Id, Wellesley Gp, Gulf of Carpentaria (AMS); Sweers Id, Wellesley Gp, Gulf of Carpentaria (AMS); Karumba, Gulf of Carpentaria (AMS); Mapoon, Gulf of Carpentaria (AMS C14285); Terry Beach, W side of Prince of Wales Id, Torres Strait (AMS); Friday Id, Torres Strait (AMS); S side of Thursday Id, Torres Strait (AMS); Hospital Pt, Thursday Id, Torres Strait (AMS C105905); Stover Bay, Somerset, Cape York Peninsula (AMS); Somerset, Cape York Peninsula (AMS); 16–22 m, Albany Passage, Torres Strait (AMS); 11 m, 14°32.2′S, 144°53.4′E, 18 m, 15°44′S, 145°27′E (AMS); Starcke River, N of Cooktown (AMS); between Mossman and Daintier (AMS); Four Mile Beach, Port Douglas (AMS); Trinity Bay (AMS); 55 m, 16°33′S, 146°09′E, NE of Cairns, (AMS); Buchan's Pt, N of Cairns (AMS); Yule Pt, N of Cairns (AMS); Clump Pt, Mission Beach (AMS); S Mission Beach, S of Innisfal (AMS); Kurrimine Beach, Near Silkwood (AMS); Horseshoe Bay, Magnetic Id (USNM 824821, 836876); Picnic Bay, Magnetic Id, off Townsville (AMS); Geoffrey Bay, Magnetic Id (USNM 836906); Bowen (AMS); Black Id, Langford Reef, near Bowen (AMS, WAM 1018-84); Edgecumbe Bay (AMS); Hook Id (AMS); Lindeman Id, Cumberland Gp, N of Mackay (AMS); Shoal Pt, Mackay (AMS, WAM); 21°24′S, 149°19′E, Pt Perpetua, Sarina Beach (AMS); N Keppel Id, Keppel Bay (AMS); Shoal Bay Rocks, Keppel Bay (AMS); Pt Vernon, Hervey Bay (AMS); Scarness, Torquay, Hervey Bay (AMS); Pialba, Hervey Bay (AMS); Dundowran Beach, near Pialba, Hervey Bay (AMS); 27°40′E, 153°30′S, Stradbroke Id (WAM); Airlie Beach (AMS). NEW GUINEA: 0.8 km E of Kaipoeri Village, Koe Roedoi, Geelvink Bay, Irian Jawa (ANSP); 22–55 m, 2.4 km SW of Yule Id, Papua (AMS); 15–40 m, Nodup, Rabaul, Papua (AMS). SOLOMON ISLANDS: E Honiara, Guadalcanal (LACM 78-422). PALAU: 4.8 km NE of Eil Malk, E of Yoo Passage (ANSP).

Cerithium traillii Sowerby, 1855

FIGURES 138–140

Cerithium traillii Sowerby, 1855:871, pl. 182, figs. 173, 174 [holotype: BMNH 1986181; type locality: Singapore]; 1865, pl. 4: fig. 24.—Tryon, 1887:871, pl. 25: fig. 47 [part only].—Kobelt, 1893:99, pl. 20: figs. 1, 2.

Clypeomorus trailli [sic] (Sowerby).—Habe, 1964:41, pl. 12: fig. 24.—Cernohorsky, 1972:71, pl. 16: fig. 10.

Clypeomorus traillii (Sowerby).—Springsteen and Leobrera, 1986:60, pl. 13: fig. 11 [not *Cerithium traillii* Sowerby; is *Cerithium pacificum*, new species].

DESCRIPTION.—*Shell* (Figure 138): Shell large, turreted, elongate, with broad base, comprising up to 17 straight-sided whorls, and attaining 48 mm length and 17.4 mm width. Protoconch unknown. Early teleoconch whorls sculptured with 3 weak spiral lirae crossed by strong axial ribs. Adult teleoconch sculptured with 3 major beaded spiral cords, weak spiral lirae with tiny beads in interspaces, and microscopic spiral incised lines. Beads sometimes aligned to form 24–45 weak axial ribs, but ribs normally absent. Several varices randomly distributed. Suture moderately impressed, distinct. Body whorl large, wide and with large, thickened varix opposite outer lip of aperture; sculptured with 5 major beaded spiral cords, with weaker beaded cords in interspaces. Base of body whorl moderately excavated, sculptured with 4 or 5 narrow, beaded spiral cords. Anterior siphonal canal short, tubular, well defined, slightly turned to left of shell axis. Aperture ovate, large, a little more than one-third the shell length. Columella concave, with thickened lip. Anal canal

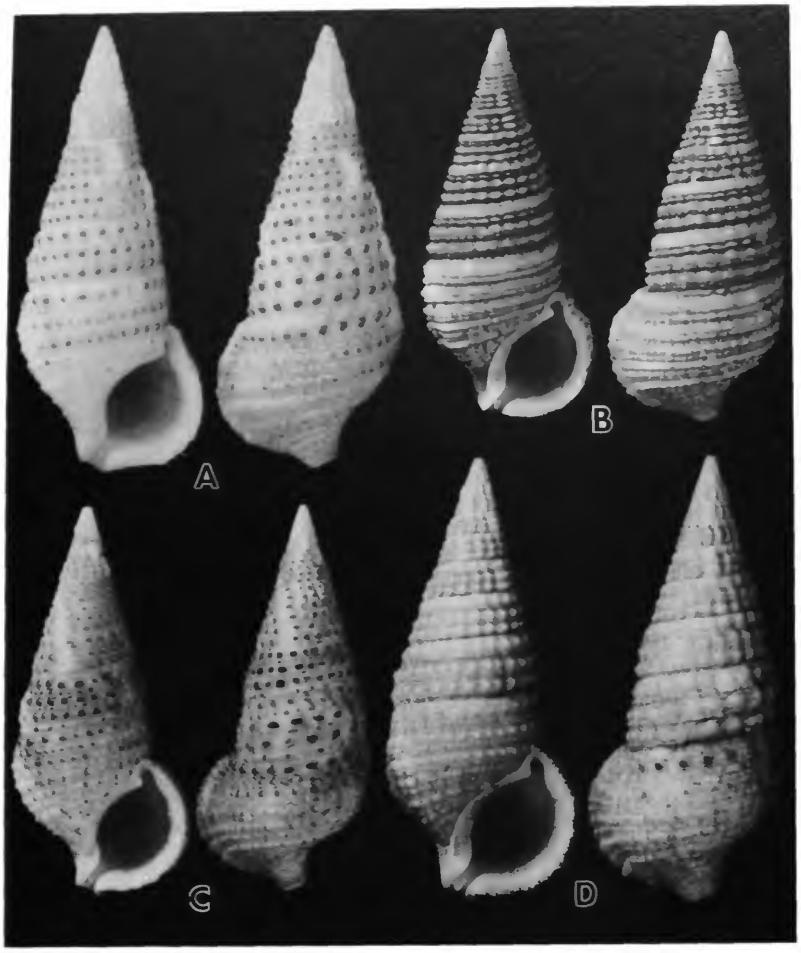

FIGURE 138.—*Cerithium traillii* Sowerby. A, holotype, Singapore, 41.1 mm (BMNH 1986181); B, Yap, Caroline Ids, 37.4 mm (USNM 634325); C, Kepple Harbor, Malaysia, 41.8 mm (USNM 660839); D, Yap, Caroline Ids, 35.2 mm (USNM 630812).

large, bordered with strong, parietal, columellar plait. Outer lip of aperture convex, rounded, weakly crenulate, and thickened at edge. Shell color white, with wide to narrow, spiral tan bands, broad tan blotches, and frequently with brown beads. Varices, early whorls and aperture white. Measurements (Table 44). Periostracum thin, light tan.

Radula (Figure 139): Type-1 radular ribbon short, about one-thirteenth the shell length. Rachidian tooth (Figure 139D) rounded-triangular, having basal plate with short median posterior extension and pair of basal ridges; anterior front weakly concave, and cutting edge with large, spade-shaped main cusp flanked on each side by 2 weak denticles. Lateral tooth (Figure 139C) with broad, long median buttress extending posteriorly and with long, lateral, posterior extension on basal plate; cutting edge with large pointed main cusp, one inner-flanking denticle, and 2 outer-flanking, pointed denticles. Marginal teeth (Figure 139C) spatulate with broad bases and tapering, curved, serrated tips. Inner marginal tooth with broad, elongate, main cusp, 3 inner flanking denticles, and 2 outer flanking denticles. Outer marginal tooth same, but lacking outer flanking denticles.

Anatomy: Ctenidium brown, hypobranchial gland bright green.

Type-A pallial oviduct. Outer edge of anterior medial lamina with short sperm gutter opening into blind anterior pocket and continuing posteriorly to enter spermatophore bursa.

SYNONYMIC REMARKS.—This species, uncommonly cited in popular shell books, is sometimes confused with *Cerithium zonatum* or listed as one of that species' many synonyms. Tryon (1887:871) suggested that *C. traillii* is a form of *C. zonatum,* and Cernohorsky (1972:71) also noted its resemblance to the latter species. The holotype of *C. traillii* (Figure

TABLE 44.—Shell morphometrics of *Cerithium traillii*.

Character	$\bar{x}$ (n = 6)	sd	v	Range
Shell length	39.7	4.1	16.4	35.4–48
Shell width	15.4	1.6	2.4	12.9–17.4
Aperture length	12.8	1.3	1.6	10.8–14.3
Aperture width	8.8	1.0	1.1	6.8–10
Number of whorls	16.0	0.6	0.3	15–17
Number spiral cords	3.0	–	–	3
Number beads	32.3	6.7	44.9	25–45

138A) is typical of the species. This species is herein accorded full specific status on the basis of the anatomy of the pallial oviduct.

Several authors have assigned *C. traillii* to *Clypeomorus* Jousseaume, but its elongate shape, large size, and moderately elongate anterior canal separate it from that genus, and the anatomy of the pallial oviduct clearly places it into *Cerithium*. The shell depicted by Springsteen and Leobrera (1986, pl. 13: fig. 11) as *Clypeomorus traillii* (Sowerby) is not this species.

ECOLOGY.—Nothing has been published about the habitat of this species. *Cerithium traillii* appears to be limited to the turbid waters and terrigenous sediments found along continental shores and around large, high islands associated with archipelagos. This species was observed under rocks on a shallow mid- to low intertidal reef flat at Cockle bay, Magnetic Id, Queensland, Australia. It was not common there, and does not appear to occur in large populations anywhere in its range. Eggs, larvae, and developmental biology are unknown.

DISCUSSION.—*Cerithium traillii* is distinguished by its large, elongate shell with straight-sided whorls, sculpture of three finely beaded, spiral cords per whorl, and by a large body whorl. Former growth varices are uncommon or weak except for the major one on the body whorl. Axial ribbing is strong on

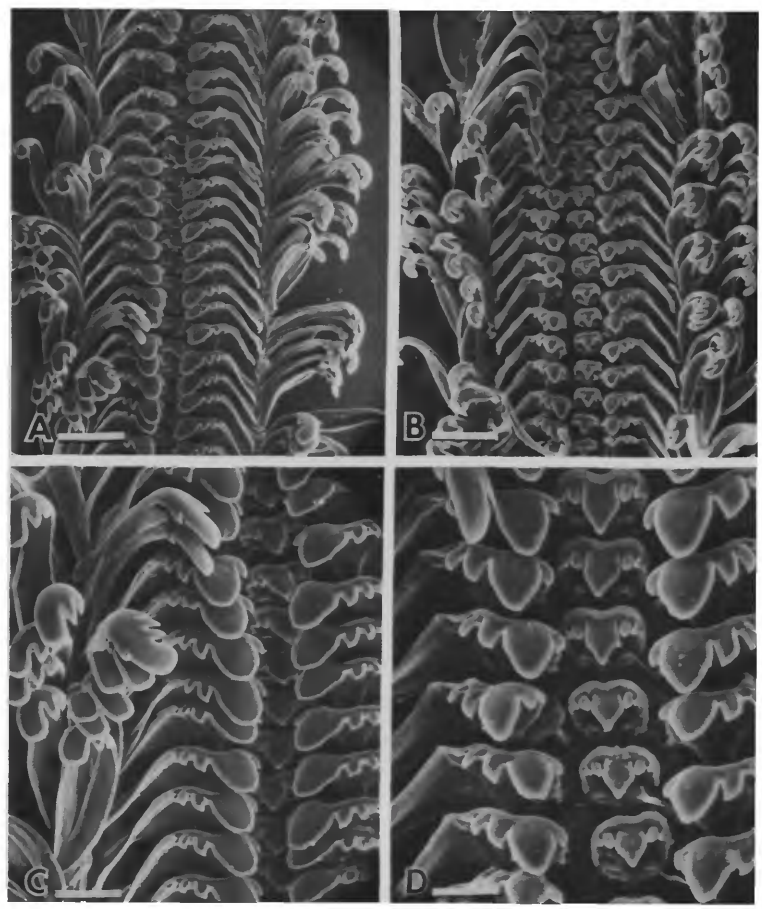

FIGURE 139.—SEM of radula of *Cerithium traillii* Sowerby: A, radula with marginals spread open, Koror Id, Palau (bar = 0.15 mm; USNM 621154); B, radula with marginals spread open, Bohol, Philippines (bar = 115 µm; ANSP 231483); C, half row, Palau (bar = 75 µm; USNM 621154); D, detail of rachidian and lateral teeth, Bohol, Philippines (bar = 43 µm; ANSP 231483).

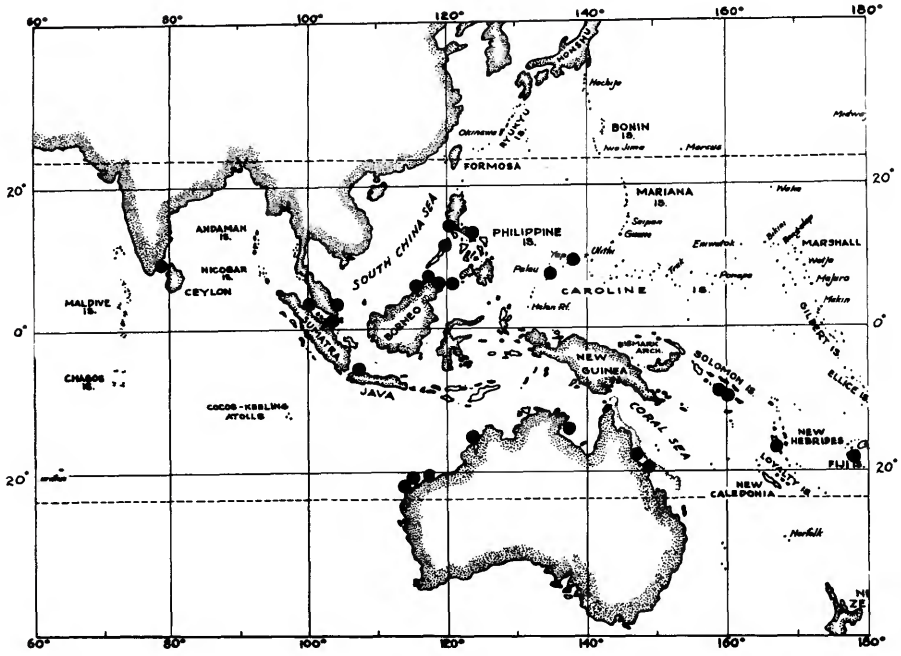

FIGURE 140.—Geographic distribution of *Cerithium traillii* Sowerby.

the early whorls but disappears on the adult teleoconch. The dominant spiral sculpture of tiny, smooth beads becomes weak on the last two whorls. There does not appear to be a great amount of interspecific variation in the shell of this species.

As noted above, *Cerithium traillii* is morphologically close to *C. zonatum* Wood (Figure 141), and had been considered a subspecies of the latter species by Tryon (1887:871). Immature and dwarfed specimens of *C. traillii* closely resemble *C. zonatum*, and are not easily separated from it. Indeed, it is difficult to find any conchological autapomorphies that clearly define *C. traillii*. However, it is ecologically distinct from *C. zonatum*. At Magnetic Id, Queensland, Australia, I found *C. traillii* was confined to low intertidal, protected, reef flats among coral rubble, while *C. zonatum* occurred on algal mats or in sea-grass beds in the mid- to low intertidal zones. The pallial gonoducts of the two species are quite different; *C. traillii* has Type-A layout whereas *C. zonatum* has a Type-B arrangement. *Cerithium traillii* is clearly a distinct species.

FOSSIL RECORDS.—This species has been recorded from the Pliocene of East Borneo by Beets (1950:307–308). The Pliocene fossil, *Cerithium niasensis* Icke, from Nias, Indonesia, was depicted by Wissema (1947:63–64, pl. 3: figs. 68, 69), who suggested that it resembled *C. traillii;* I concur in this observation.

GEOGRAPHIC DISTRIBUTION (Figure 140).—*Cerithium traillii* has an Indo-West Pacific distribution. It occurs in India, SE Asia, the Indonesian Archipelago, and along the tropical coasts of Australia. In the Western Pacific, it is found from the Amami Islands, Japan (Habe, 1964:41), south to the Philippines and throughout Melanesia, as far east as Fiji.

SPECIMENS EXAMINED.—INDIA: Tuticorn (BMNH). THAILAND: Koh Samui (USNM 360916); Taluei Id (USNM 361190). MALAYSIA: SE side Cape Rachado, Negril Sembilan, Malacca Strait (USNM 774485); Negril Sembilan, W Malaysia (USNM 778485); off Mersing, E coast Malaysia (WAM); Sembilan Id, W Singapore (CAS 39514); Palau Anyut, Malacca Strait (USNM 660909); Pulau Hantu, SW of Singapore (USNM 701337); Palau Hantu, SW of Keppel Harbor (USNM 660839); Pulau Sebarok, S Singapore (WAM); Pulau Brani, Singapore (BMNH); Tanjong Aru, Jesselton, N Borneo (USNM 658508); 2.4 km from Sandakan, N Borneo (USNM 658131); Kudat, N Borneo (USNM 666752). PHILIPPINES: Talaga, Bataan Prov, Luzon (WAM); Apat Bay, S Quezon, Luzon (WAM); E Quezon, Luzon (WAM); Maricaban Id, Luzon (USNM 8628410; Albay Prov, Luzon (WAM); Northern Culion, Palawan (WAM); Walan Id, Sulu Archipelago (WAM). INDONESIA: Haarlem Id, Batavia Bay, Java (ZMA); Djakartabasi, Leiden Id, Java (ZMA); Leiden Id, Batavia Bay, Java (ZMA); Purmerend Id, Batavia Bay, Java (ZMA).

WESTERN AUSTRALIA: Bundegi Reef, NW Cape (WAM); Malus Id, Dampier Archipelago (WAM); NW Id, Montebello Id (WAM); Delambre Id, Dampier Archipelago (WAM 87976); Yampi Sound (WAM). NORTHERN TERRITORY, AUSTRALIA: Groote Id (WAM). QUEENSLAND, AUSTRALIA: Cockle Bay, Magnetic Id (USNM 842741);

South Molle Id (USNM 845804). SOLOMON ISLANDS: Pavuvu Id, Russell Gp (USNM 488306, 488384); NW coast, Guadalcanal (USNM 831472). NEW HEBRIDES: 168°06'E, 17°44'44"S, Efate Id (USNM 786939, 786951, 787023, 787118,). FIJI: Viti Levu Bay, Viti Levu (USNM 824788); Suva, Viti Levu (USNM 531960). CAROLINE ISLANDS: Palau (USNM 636208, 636576, 636634, 636700); Koror Id, Palau (USNM 621154); Tomil Harbor, Yap (USNM 485808, 634325); Yap (USNM 630812).

Cerithium zonatum (Wood, 1828), new combination

FIGURES 141–145

?Cerithium heteroclites Lamarck, 1822:74 [holotype: MHNG 109733; type locality: Nouvelle Hollande (Australia), 33 mm].

Strombus zonatus Wood, 1828:34, pl. 4: fig. 7 [type not located; type locality: not given; neotype herein designated: USNM 862848, Bandicoot Bay, Barrow Id, Western Australia, 25.2 mm × 10.2 mm,].—Hanley, 1856:215, pl. 4: fig. 7.

Cerithium lemniscatum Quoy and Gaimard, 1834:119–120, pl. 54: figs. 16–18 [holotype: MNHNP, no number; type locality: Vanikoro; not *Cerithium lemniscatum* Brongniart, 1823].—Kiener, 1842:42–46, pl. 16: fig. 4.—Sowerby, 1855:873, pl. 183: fig. 187; 1865, pl. 5: fig. 27a,b.—Tryon, 1887:135, pl. 24: fig. 38.—Kobelt, 1893:116–117, pl. 22: figs. 10, 11.

Cerithium luctuosum Hombron and Jacquinot, 1852, pl. 23: figs. 12, 13; 1854:99 [holotype, MNHNP, no number; type locality: Raffles Bay, Singapore].—Tryon, 1887:135, pl. 25: fig. 56.

Cerithium millepunctatum Hombron and Jacquinot, 1852, pl. 24: figs. 13, 14 [holotype: MNHNP, no number; type locality: Hogoleu; 21 mm × 8.2 mm; not *Cerithium millepunctatum* Eudes-Deslongchamps, 1842]; 1854:103–104.—Tryon, 1887:136, pl. 25: fig. 60.—Kobelt, 1898:277–278, pl. 47: fig. 5.

Cerithium alternatum Sowerby, 1855:872, pl. 179: fig. 70 [lectotype, herein selected: BMNH 19861671, 2 paralectotypes 19861672-3; type locality: Ticao Id, Philippines; 34.2 mm × 13.38 mm; not *Cerithium alternatum* Hutton, 1873]; 1865, pl.4: fig. 22.—Tryon, 1887:135, pl. 25: figs. 48–50.—Kobelt, 1895:191, pl. 35: figs. 2, 3.

Cerithium splendens Sowerby, 1855:873, pl. 183: fig. 191 [lectotype: BMNH 19071028103; type locality: Philippines, herein restricted to Bohol; 36.4 mm × 14.28 mm]; 1865, pl. 3: fig. 19.—Tryon, 1887:135, pl. 25: figs. 51–53.—Kobelt, 1893:125–126, pl. 24: fig. 1.

Cerithium tesselatum Sowerby, 1855:867, pl. 181: figs. 134, 135 [lectotype, herein selected: BMNH 19861841; 2 paralectotypes 19861842-3; type locality: Darnley's Id, Australia; 20.8 mm × 10 mm]; 1865, pl. 10: fig. 66.—Tryon, 1887:127, pl. 22: fig. 59.—Kobelt, 1895:195, pl. 35: fig. 11.—Cernohorsky, 1972:71, pl. 16: fig. 8.

Cerithium Hanleyi [sic] Sowerby, 1855:874, pl. 183: fig. 194 [erroneously cited as fig. 193; holotype: BMNH, 19071028221; type locality: not cited, herein restricted to Cebu, Philippines; 14 × 6.4 mm].—Tryon, 1887:135, pl. 24: fig. 42.—Kobelt, 1898:239, pl. 42: fig. 3.—Dance, 1974:67, text fig.

Cerithium gemma Sowerby, 1855:873, pl. 178: fig. 51 [lectotype, herein selected: BMNH 19861721, 1 paralectotype 19861722; type locality: Luzon; 17.8 mm × 6.78 mm]; 1865, pl. 10: fig. 70.—Tryon, 1887:134, pl. 24: fig. 41.—Kobelt, 1895:215, pl. 38: fig. 7.

Cerithium nitidum Sowerby, 1855:872, pl. 183: figs. 180, 181 [lectotype, herein selected: BMNH 19861751, 2 paralectotypes 19861752-3; type locality: Bohol, Philippines; 25.2 mm × 10.4 mm; not *Cerithium nitidum* MacAndrew and Forbes, 1847; not *Cerithium nitidum* Hombron and Jacquinot, 1852; nor *Cerithium nitidum* Zekeli, 1852]; 1865, pl. 5: fig. 28.—Tryon, 1887:135, pl. 25: fig. 54.—Kobelt, 1895:190.

Cerithium purpurascens Sowerby, 1855:872, pl. 183: figs. 182–186 [lectotype, herein selected: BMNH 19861761, 1 paralectotype 19861762; type locality: Philippines; 21.86 mm × 9.82 mm]; 1865, pl. 6: fig. 36.

Cerithium asperum Pease, 1861:433 [holotype: BMNH, 1961203; type locality: Sandwich Is; 15 mm × 7 mm; not *Cerithium asperum* Bruguière, 1792, nor *Cerithium asperum* Rouillier, 1848].—Kobelt, 1895:198, pl. 35: fig. 16.—Dautzenberg and Bouge, 1933:304.—Kay, 1965:47, pl. 5: figs. 11, 12.

Cerithium robustum Sowerby, 1865, pl. 7: fig. 44 [holotype: BMNH, 1986183; type locality: Panay, Philippines; 35.3 mm × 14.5 mm].—Tryon, 1887:135, pl. 25: fig. 50.—Kobelt, 1893:118–119, pl. 23: fig. 1.

Cerithium gentile Bayle, 1880:248 [new name for *Cerithium nitidum* Sowerby, 1855].—Kobelt, 1895:190, pl. 35: fig. 1.

Cerithium traillii kikaiensis Pilsbry, 1904:25, pl. 4: fig. 38 [holotype: ANSP 86001, type locality: Kikai, Osumi, Japan; 15.8 mm × 6.8 mm].

Cerithium philippinense Cossmann, 1906:123, footnote [new name for *Cerithium lemniscatum* Quoy and Gaimard, 1834].

Cerithium probleema Iredale, 1929:270 [new name for *Cerithium lemniscatum* Quoy and Gaimard, 1834]; 1930:78.

Clypeomorus zonatus (Wood).—Cernohorsky, 1972:71, pl. 16: fig. 9, 9a.—Springsteen and Leobrera, 1986:63, fig. 5.

Cerithium (Cerithium) tenellum Sowerby.—Springsteen and Leobrera, 1986:63, fig. 10 [not *Cerithium tenellum* Sowerby, 1855; is *Cerithium zonatum* (Wood, 1828)].

DESCRIPTION.—*Shell* (Figures 141, 142): Shell turreted, elongate, comprising up to 12 inflated, angulate whorls and reaching 35 mm length and 14.3 mm width. Protoconch (Figure 141F) small, comprising 2 whorls; protoconch 1 smooth, bulbous; protoconch 2 weakly sculptured with three weak spiral threads, weak subsutural pustules, and with sinusigeral notch. Early teleoconch whorls (Figure 141H) convex, with broad, sloping, subsutural ramp, and sculptured with 2 spiral cords and many microscopic, spiral incised lines; strong axial ribs appearing after third whorl. Adult teleoconch whorls usually angulate, sculptured with 3 or 4, major spiral cords becoming beaded or spinose where crossed by 11–50 weak axial ribs; spiral cord at whorl periphery largest and with strongest beads or spines. Interspaces between cords with fine spiral lirae and many fine spiral incised lines. Periphery of last three whorls usually most spinose. Weak varices randomly distributed. Suture distinct, incised, wavy. Body whorl large, sculptured with 5, sometimes 6 beaded to spinose, major, spiral cords and with smaller beaded cords in interspaces. Body whorl tessellate when cord development more equal and less spinose. Moderate varix on body whorl opposite outer lip of aperture. Base of body whorl not excavated; moderately to weakly constricted and with short, tubular anterior siphonal canal weakly reflected dorsally to left of shell axis. Aperture ovate, a little more than one-third the shell length. Anal canal well developed, bordered with parietal columellar plait. Columella concave, thick with moderate columellar lip. Outer lip of aperture slightly thickened at edge, sharply crenulate, and with internal spiral grooves. Shell color highly variable, with white background, overlain by tan to brown blotches and having spiral rows of brown spots and alternating broad brown and white spiral bands. Aperture white, but upper columella frequently violet or mauve. Measurements (Table 45). Periostracum thin, tan.

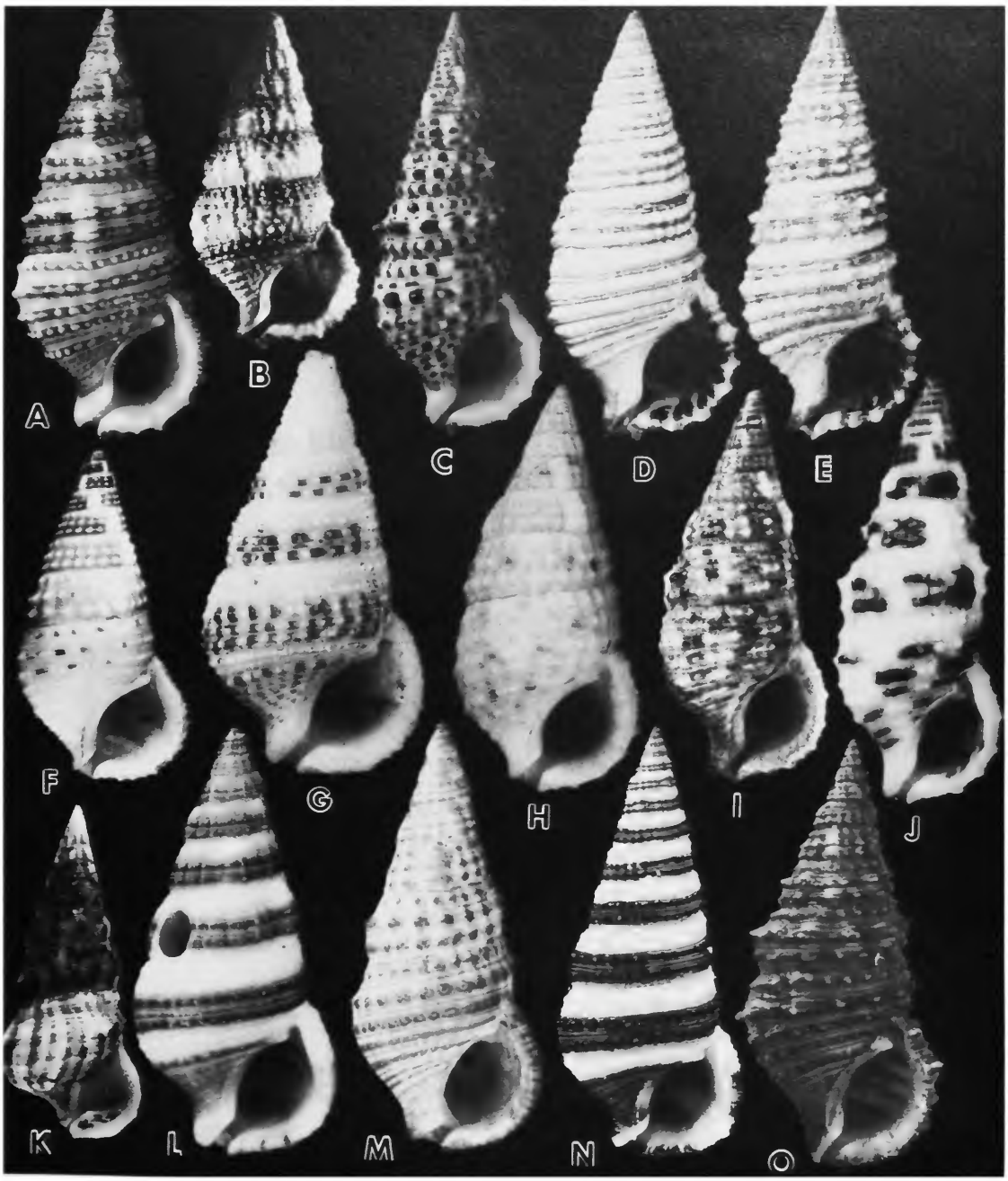

FIGURE 141.—Types of nominal taxa synonymous with *Cerithium zonatum* (Wood). A, lectotype of *Cerithium nitidum* Sowerby, Bohol, Philippines, 25.2 mm (BMNH 19861751); B, holotype of *Cerithium lemniscatum* Quoy and Gaimard, 31 mm (MNHNP); C, lectotype of *Cerithium splendens* Sowerby, Philippines, 36.4 mm (BMNH 19071028103); D, holotype of *Cerithium robustum* Sowerby, Panay, Philippines, 35.3 mm (BMNH 1986183); E, lectotype of *Cerithium alternatum* Sowerby, Ticao Id, Philippines, 34.2 mm (BMNH 19861671); F, holotype of *Cerithium luctuosum* Hombron and Jacquinot, Raffles Bay, Singapore, 32 mm (MNHNP); G, lectotype of *Cerithium tesselatum* Sowerby, Damley's Id, Australia, 20.8 mm (BMNH 19861841); H, holotype of *Cerithium traillii kikaiensis* Pilsbry, Kikai, Osumi, Japan, 15.8 mm (ANSP 86001); I, holotype of *Cerithium millepunctatum* Hombron and Jacquinot, Hogoleu, 21 mm (MNHNP); J, lectotype of *Cerithium gemma* Sowerby, Luzon, Philippines, 17.8 mm (BMNH 19861721); K, holotype of *Cerithium heteroclites* Lamarck (MHNG 109733); L, holotype of *Cerithium hanleyi* Sowerby, 14 mm (BMNH 19071028221); M, holotype of *Cerithium asperum* Pease, Hawaii, 15 mm (BMNH 1961203); N, neotype of *Cerithium zonatum* Wood, Bandicoot Bay, Barrow Id, Western Australia, 25.2 mm (USNM 862848); O, lectotype of *Cerithium purpurascens* Sowerby, Philippines, 21.9 mm (BMNH 19861761).

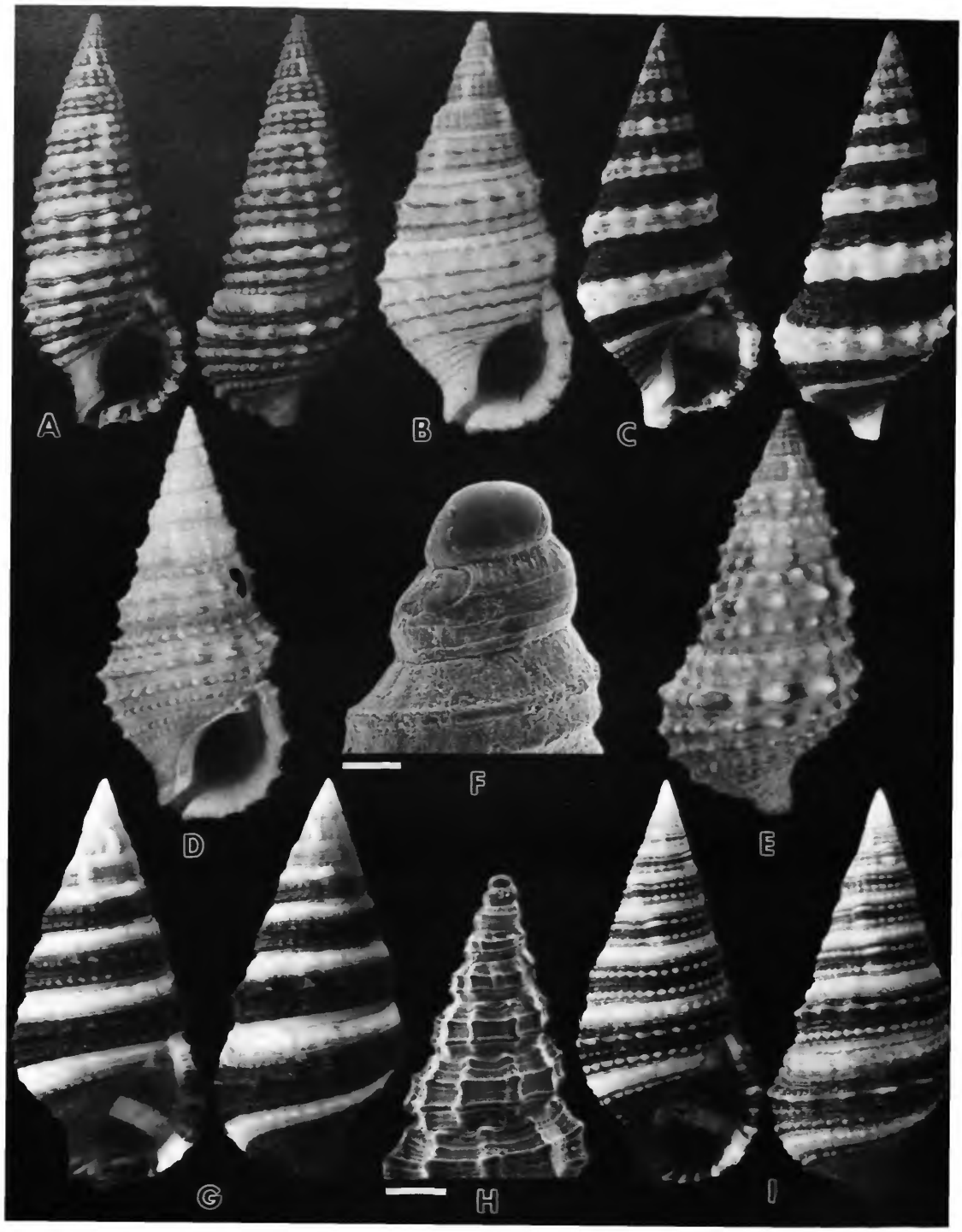

FIGURE 142.—Phenotypic variation in *Cerithium zonatum* (Wood): A, Singapore, 31.1 mm (USNM 77068); B,D,E, all paralectotypes of *Cerithium purpurascens* Sowerby, Philippines, 18.8 mm, 22.9 mm, 26 mm, respectively (BMNH); C, Yule Id, Papua New Guinea, 27.8 mm (USNM 617601); F, SEM of protoconch, Mahe, Seychelles (bar = 68 μm; ANSP 310484); G, Davao Bay, Mindanao, Philippines, 17.5 mm (USNM 596963); H, SEM of early whorl sculpture, Mahe, Seychelles (bar = 43 μm; ANSP 310484); I, Davao Bay, Mindanao, Philippines, 27.5 mm (USNM 596963).

TABLE 45.—Shell morphometrics of *Cerithium zonatum*.

Character	$\bar{x}$ (n = 17)	sd	v	Range
Shell length	22.0	7.5	55.6	11.1–35
Shell width	8.9	3.0	9.0	4.5–14.3
Aperture length	6.7	2.3	5.1	3.8–10.5
Aperture width	4.5	1.6	2.7	2.4–7.6
Number whorls	11.3	0.8	0.6	10–12
Number spiral cords	3.4	0.5	0.2	3–4
Number nodes	25.0	10.1	101.9	12–50

Radula (Figure 143): Type-1 radular ribbon (Figure 3A). Rachidian tooth (Figure 143D) triangular, with long, median, posterior, basal projection and pair of basal ridges on basal plate; anterior edge slightly concave at center and cutting edge with large, spade-shaped, main cusp flanked on each side by 2 small denticles. Lateral tooth (Figure 143D) with long, broad, posteriorly projecting, median buttress having small central pustule, and with long, lateral, posterior projection on basal plate; cutting edge with large, pointed main cusp, one inner-flanking denticle, and 2 outer-flanking denticles. Marginal teeth (Figure 143B,D) with narrow shafts, broader at bases and with curved, serrated tips. Inner marginal tooth with long main cusp, 3 inner-flanking denticles, and 2 outer-flanking denticles. Outer marginal tooth same, but lacking outer-flanking denticles.

Anatomy: Animal flesh-colored to orange, flecked with yellow and black blotches and striped with black on snout and tentacles. Mantle edge orange and black and fringed with many minute cream-colored papillae. Mantle papillae around inhalant siphon darker. Mantle surface orange, with brown stripes.

Osphradium black, equal in length to ctenidium. Ctenidium gray, narrow with long finger-like filaments. Hypobranchial gland wide, thick, folded transversely, and secreting copious mucus.

Salivary glands comprised of thin, convoluted tubes passing through nerve ring. Esophageal gland of moderate size.

Type-B pallial oviduct (Figure 4B) with short anterior sperm

FIGURE 143.—Radula of *Cerithium zonatum* (Wood). A, radula with marginals spread open, Nouméa, New Caledonia (bar = 125 μm; USNM 724094); B, marginal teeth folded over ribbon, Pago Bay, Guam (bar = 88 μm; USNM 774773); C, radula with marginals spread open, Pago Bay, Guam (bar = 125 μm; USNM 774773); D, half row, Nouméa, New Caledonia (bar = 88 μm; USNM 724094).

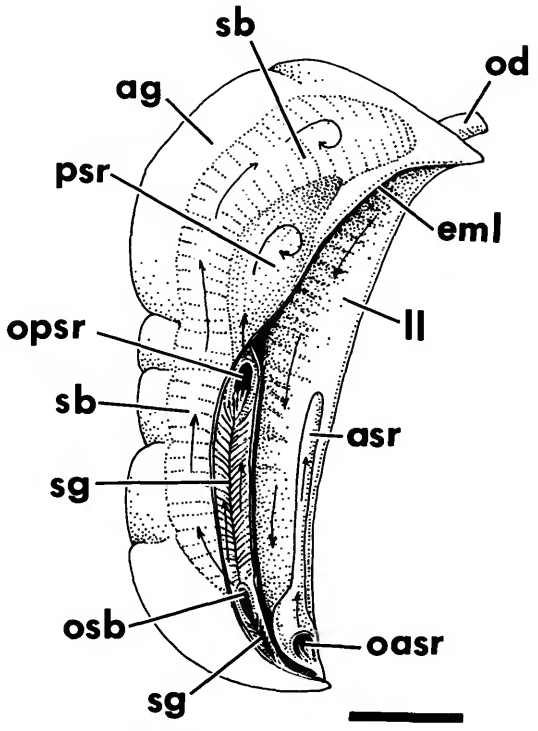

FIGURE 144.—Pallial oviduct of *Cerithium zonatum*, 4.5 mm length. Arrows signify ciliary currents (bar = 1 mm). (Abbreviations: *ag* = albumin gland; *asr* = anterior seminal receptacle; *eml* = free edge of medial lamina; *ll* = lateral lamina; *od* = coelomic oviduct; *opsr* = opening of posterior seminal receptacle; *osb* = opening of spermatophore bursa; *psr* = posterior seminal receptacle; *sb* = spermatophore bursa; *sg* = sperm gutter.)

gutter (Figure 144, sg) leading to anterior opening of spermatophore bursa (Figure 144, osb) and large spermatophore bursa (Figure 144, sb). Sperm gutter continues (Figure 144, sg2) behind opening to spermatophore bursa, opening medianly (Figure 144, osr) into pink, sac-like posterior seminal receptacle in edge of posterior medial lamina (Figure 144, psr). Lateral lamina (Figure 144, ll) thin-walled, with opening at anterior edge of lamina leading into anterior seminal receptacle, an elongate narrow pouch (Figure 144, asr).

SYNONYMIC REMARKS.—This very variable species has been the recipient of more names (19) than any other *Cerithium* species. The excessive nomenclatural problems associated with *C. zonatus* are due to the failure of previous authors to appreciate the full range of variation and their unacquaintance with the many names already available. Many of the proposed names are preoccupied and a number of replacement names have been published, further complicating the synonymic history of this taxon. The result is that *Cerithium zonatum* has been largely ignored or confused with other species in the modern literature. For example, Hinton's (1972) popular *Guide to the Shells of New Guinea and the Central Indo-Pacific* illustrates four specimens of *C. zonatum* on pl. 2: figs. 4–7, but does not identify them, remarking that further research is needed. Springsteen and Leobrera (1986:63, pl. 14: figs. 5, 10) correctly identified the banded specimen in fig. 5 as *C. zonatum* (cited as *Clypeomorus*), but the 3 specimens in fig. 10, all typical *C. zonatum*, are incorrectly called *C. tenellum* Sowerby.

An early available name may be *Cerithium heteroclites* Lamarck, 1822. A shell in the Geneva Natural History Museum, reputed to be the holotype of this species (Figure 141K), has a label written in Lamarck's hand citing New Holland (Australia) as a locality. However, the specimen is difficult to attribute to any known species because it is badly deformed, especially on the body whorl. It is probably *Cerithium atratum* Born, a western Atlantic species, but it may also be a deformed specimen of *Cerithium zonatum* (Wood), which fits the cited locality. For this reason, it is cited as a synonym of *Cerithium zonatum* with a query. If it is shown that this specimen is truly conspecific with *C. zonatum*, the name *heteroclites* has priority. Kobelt's (1898:253) concept of *C. heteroclites* was formed by the illustrations of Potiez and Michaud (1838:365, pl. 31: figs. 21, 22), which do not match the putative holotype in the Geneva Museum but appear rather to represent a potamidid snail.

The earliest available name is *Cerithium zonatum* (Wood, 1828). This name was recently used by Cernohorsky (1972:7) and Springsteen and Leobrera (1986:63), who allocated it to the genus *Clypeomorus* Jousseaume. Although the type of *C. zonatus* has not been found, Wood's illustration of this species is excellent and not likely to be taken for any other Indo-Pacific *Cerithium* species. As this species is common and widespread, a neotype for *C. zonatum* (Wood, 1828) is herein selected to stabilize the name (USNM 862848, Bandicoot Bay, Barrow Id, Western Australia). The neotype (Figure 141N), is similar in form and color to Wood's fig. 7.

Eight of the above synonyms are Sowerby names, seven of which were proposed in 1855 in the *Thesaurus Conchyliorum* for different phenotypes that, upon examination of many thousands of specimens, are seen to intergrade. Sowerby (1855, 1865) treated large and small phenotypes as separate taxa. One of his nomina, *C. hanleyi* (Figure 141L), clearly conspecific with *C. zonatum*, was not included in his subsequent *Cerithium* monograph (Sowerby, 1865). Of the Sowerby taxa, *C. tesselatum* (Figure 141G) is merely a broad, finely sculptured phenotype of *C. zonatum*. Tryon (1887:135) treated many of these Sowerby names as synonyms or varieties of each other. The types of all of these synonymous taxa are shown in Figure 141.

ECOLOGY.—Little has been written about the ecology of this species. Maes (1967:113) recorded it (cited as *C. purpurascens* Sowerby) to be abundant on seaweeds in the hot (36°–39°C) waters of the inner lagoons at Cocos Keeling. A large population I observed at Cockle Bay, Magnetic Id, Queensland, Australia, lived on an intertidal reef flat among sea grasses and coral rubble. Most individuals occurred on the surface but some

were found under rocks. This species was also observed living on algal mats and marine angiosperm grass beds around Guam. Museum records record *C. zonatum* from a number of different intertidal habitats, but normally it is found in the low intertidal zone among algal-covered rocks or in grass beds. Populations living on hard substrates in the high intertidal zone tend to comprise individuals with stubbier shells and larger nodes, while those from low-energy, sand-mud habitats have small, weakly sculptured shells. The spawn and larvae of this species are unknown, but the protoconch (Figure 142F) has the sculpture and deep sinusigeral notch suggestive of a veliger larva, and the extensive geographic range also indicates a planktotrophic life history.

DISCUSSION.—*Cerithium zonatum* is best recognized by its beaded, spinose, colorful shell and by the angulate, spinose, peripheral, spiral cord on the penultimate and body whorls. The mauve columella, unexcavated, broad shell base and short anterior canal are other identifying features. Many shells frequently have broad alternating bands of brown and white; hence, the name *"zonatum."*

The overall prickly sculpture and frequent colorful aspect of this shell help to identify it, but there are some phenotypes with less pronounced sculpture that are difficult to recognize as this species. The dominant spiral cords vary from 3 or 4 per whorl, and there is very wide variation in the number of beads (11–33) on the peripheral cord of the penultimate whorl (see Table 45). A possible correlation between habitat and shell morphology may exist; shells from populations living in marine grass beds are usually elongate and have spinose beads on the last three whorls; those from intertidal algal mats and rocky shores tend to be shorter and stubbier and resemble *Clypeomorus* species; shells from muddy, sandy habitats have a finer, tessellated sculpture. This putative phenotypic response to habitat needs careful study.

The types of synonymous taxa of *C. zonatum* (Figure 141) illustrate the morphological diversity seen in sculpture and color of this species. Some morphs are heavily beaded (Figure 141C,E,O), while others have an overall tessellate appearance (Figure 141F-H,L,N) due to equal development of all spiral cords and numerous weak beads. Some phenotypes are smaller than normal and have about 24 beads on the penultimate whorl, presenting a smooth beaded aspect (Figure 141G,L). These forms appear to be common in the Ryukyus and were given subspecific status by Pilsbry (1904), who named them *kikaiensis* (Figure 141H). However, identical phenotypes also occur in other parts of the range with many intermediates in some populations from Thailand (USNM 405967), the Philippines (USNM 233010), Australia (USNM 847053), Guam (USNM 243736, 838786, 847273), and also in Japan (USNM 343854). It is impossible to adequately separate the *kikaiensis* phenotypes from more typical forms in many populations. The lack of a distinct geographic range and many widespread phenotypic intergrades preclude subspecific recognition of the *kikaiensis* phenotypes.

There are a number of cerithiid species, some sympatric, with which *C. zonatum* may be confused. Among sympatric congeners, *C. traillii* Sowerby (Figure 138) is most similar in shell morphology, but it is a much larger species with finer beaded spiral sculpture and fewer varices. The pallial oviducts of *C. zonatum* differ significantly from those of *C. traillii* (see "Discussion" under *C. traillii*, p. 191). Another sympatric species, *C. scabridum* Philippi (Figure 122), closely resembles *C. zonatum*, but the former species usually has a much smaller shell with only 3 spiral beaded cords per whorl, and lacks the median, sharply noded, peripheral cord of *C. zonatum*. *Cerithium torresi* E.A. Smith (Figure 135) also resembles this species but differs in having stronger axial sculpture and in lacking the pointed spiral row of nodes on the whorl periphery. *Clypeomorus bifasciata* (Sowerby) and *Clypeomorus batillariaeformis* (Habe and Kosuge) frequently live adjacent to populations of *C. zonatum* in the intertidal zone, and these three taxa frequently have convergent shell sculpture (see Houbrick, 1985:36, 56). The two *Clypeomorus* species have much shorter anterior siphonal canals and completely lack the minor beaded spiral cords that occur on *C. zonatum*.

FOSSIL RECORDS.—No fossils are cited in the literature, but Miocene fossils from Enewetak and Bikini Atolls, Marshall Islands, called *Rhinoclavis marshallensis* by Ladd (1972:34–35, pl. 8: fig. 12), have an overall tessellate sculpture and shell shape that closely resembles the morphology of some phenotypes of *C. zonatum*.

GEOGRAPHIC DISTRIBUTION (Figure 145).—*Cerithium zonatum* has a wide Indo-Pacific distribution, ranging from the Arabian Gulf and eastern Africa, east throughout the Indian Ocean and the Malaysian Archipelago and into the western Pacific. In the Pacific, it occurs from Japan to south Queensland, Australia, throughout Melanesia, and from the Carolines east through the Marshall Islands to Samoa and Tonga, in Micronesia.

SPECIMENS EXAMINED.—EAST AFRICA: SE Lunga Bay, Mozambique (NM H1866); NW of Choca, SW Conducia Bay, Mozambique (NM H1857); Conducia Bay, Mozambique (NM H247); Bagamoyo, Eastern Prov, Tanzania (USNM 774561). ARABIAN SEA: Mothercat Beach, N end Massirah Id, Oman (USNM 862837). MADAGASCAR: Tulear (MNHNP, USNM 862949); Nossi Bé (USNM 720027). INDIAN OCEAN ISLANDS: Seychelles (USNM 634722); Anse a la Mouche, Mahé, Seychelles (USNM 749632); SW of Cerf Id, NE Mahé, Seychelles (ANSP 311863); S of landing, Addu Atoll, Maldives (BMNH); lagoon side, S tip Home Id, Cocos Keeling Ids (USNM 656258, 656416); N tip of West Id, Cocos Keeling Ids (ANSP 287836); 0.8 km E of N Lagoon, West Id, Cocos Keeling Ids (USNM 656303); E of North Lagoon, West Id, Cocos Keeling Ids (ANSP 289268); N of Pula Maria, Cocos Keeling Ids (USNM 656363); N Keeling, Cocos Keeling Ids (USNM 589140).

INDIA: Bombay (USNM 774497). THAILAND: Off Ao

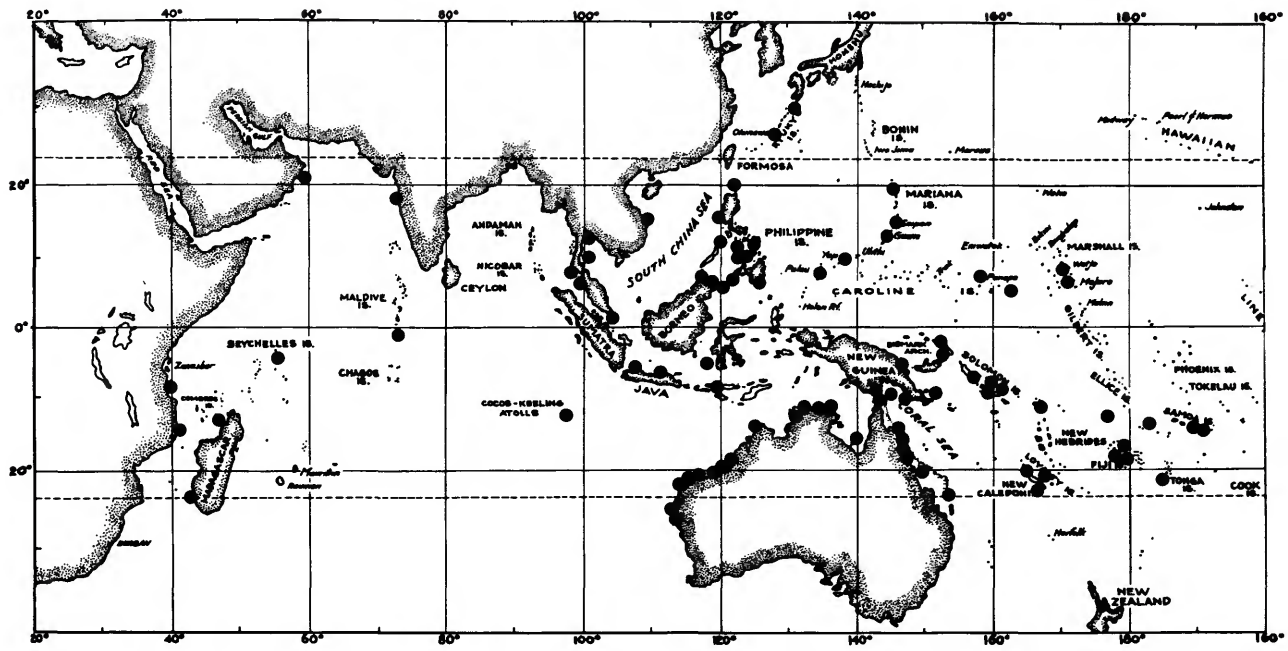

FIGURE 145.—Geographic distribution of *Cerithium zonatum* (Wood).

Rawai, Koh Phuket, Thailand (USNM 661793); Ao Ra Wai, Goh Phuket (USNM 716401); Srirachi, Gulf of Thailand (USNM 405801); Koh Maprao (USNM 361339); Koh Tao (USNM 405947, 405967, 419685, 419697). MALAYSIA: Pulau Gasing, off Tg Rhu, Pulau Langkawi, W Malaysia (WAM); W side Palau Singa Besar, Pulau Langkawi, W Malaysia (AMS); Negril Sembilan, W Malaysia (USNM 778491); Pulau Babi, W Malaysia (WAM); Cape Rachado, Malacca Strait, W Malaysia (USNM 661007); Palau Anyut, Malacca Strait, W Malaysia (USNM 660906); off Mersing, Pu Sebarok, SW Singapore (WAM); Sedkudu Id, Strait of Johor, W Malaysia (USNM 774486); Singapore (USNM 305989, 770608); NE coast E St John's Id, S of Singapore (USNM 660809); Palau Salu, S Singapore (AMS C138729, WAM); NE end Sentosa Id, Singapore (WAM); Sisters Id, Singapore (AMS); E Malaysia (WAM); Kudat Bay, N Borneo (USNM 632230); W Marudu Bay, N Borneo (USNM 632204); Berhala Channel, Sandakan, N Borneo (USNM 657948, 657949); Sibuan Id, N Borneo (USNM 657698). VIET NAM: Chu Lai Bay (USNM 762771).

JAPAN: Kikaigashima, Osumi (USNM 175589, 343856); Yakushima Id, Osumi (USNM 343854, 563890). RYUKYU ISLANDS: Okinawa (USNM 670891, 671093, 671103); Akamaru-zaki, Okinawa (ANSP 302774); Kadena Circle, Okinawa (USNM 664632, 664633); Ukibara Shima, E of Okinawa (USNM 670495, 774530); Machinato, Okinawa (LACM 29254, 29344); Yakata, Katabaru, Onna Village, Okinawa (USNM 812950, 821283); Itoman, Okinawa (ANSP 279927); Saedake, Okinawa (LACM 27623); Metasaki, Okinawa (LACM 71932); Moon Beach, Okinawa (USNM 838529, 838786); Kue Channel, Okinawa (LACM 29329).

PHILIPPINES: Sabatan Id, Batan Gp (USNM 243913, 243914, 243919, 243925); Subic Bay, Luzon (USNM 593863); Jamelo Bay, Luzon (USNM 635365); Maricaban Id, Luzon (USNM 232979); Pt Naso, Panay (USNM 243898); S Bias Bay, W Daco Id, Negros (USNM 808024); Guijulugan, Negros (USNM 244051); Cebu, Cebu (USNM 243794); Mactan Id, Cebu (USNM 774509); Tabisay, Cebu (USNM 419434); Catbalogan, Samar (USNM 232950, 232952, 243727, 243733); San Juanico Strait, off Samar (USNM 233010, 243867, 243869); Gavilan Pt, near Campo Islam, Mindanao (USNM 619910, 619914); Mariqui, Mindanao (USNM 619841); Little Santa Cruz Id, Zamboanga, Mindanao (USNM 244032); Manicaan, Mindanao (USNM 619713); Panubigan Ids, Mindanao (USNM 619825); Sinonog Id, Mindanao (USNM 619859); Davao, Mindanao (FSM, USNM 596963); Pangpuyan Id, Mindanao (USNM 619890, 619921, 619925); Apal, Mindanao (USNM 232974); Bagbagon, near Basilan Pt, Mindanao (USNM 619998, 620000, 620102); Basilan Id, Mindanao (USNM 620034, 620037, 620056); Babag, near Taluksangay, Basilan, Mindanao (USNM 619666, 775127); Busuanga, Calamian Gp (USNM 233013); Culion, Calamian Gp (USNM 303690); Tagbayag Bay, Palawan (USNM 244194, 244197, 244198); Cabaluay, SE Sulu Sea (USNM 619625); Bolong, near Sangali, SE Sulu Sea (USNM 619650); Marike, Logey, SE Sulu Sea (USNM 619803); Ladang, Sacol Id, SE

Sulu Sea (USNM 619676, 619715); Jolo (USNM 233114); Sangboy Id, near Jolo (USNM 619615); Simaluc Id, Tawitawi (USNM 232982, 232983, 232986, 239604, 239707); Tataan, Simaluc Id, Tawitawi (USNM 243696); Gochenaur (USNM 217267). INDONESIA: Pulau Melila, off Sumatra (USNM 661973); Batavia Bay, Java (ZMA); Jepara, Java (USNM 767484); Komodo Id (FSM 24758); 2°30′S, 128°E, Laut Seram, Pitt Pass, Gomomo Id, Celebes (USNM 233072).

WESTERN AUSTRALIA: Pt Gregory, NW side Peron Peninsula, Shark Bay (WAM); Williamia, Useless Inlet, Shark Bay (AMS); Denham, Shark Bay (WAM); Herald Bight, Shark Bay (AMS C69328); mouth of Gascoyne River, Carnarvon (WAM); Quobba Station, 64 km N of Carnarvon (WAM); N Cardabia Homestead (WAM); Norwegian Bay, Ningaloo Station, NW Cape (WAM); Yardie Creek, NW Cape (AMS C70180, WAM); 8 km S of NW Cape (WAM); Exmouth Gulf (NM G2787); E side Exmouth Gulf (AMS); N side naval base, Exmouth Gulf (AMS); W of Shall Id, Passage Ids (WAM); Barrow Id (WAM); Bandicoot Bay, Barrow Id (USNM 691704); S end Flacourt Bay, Barrow Id (WAM); E side Withnell Bay, Dampier Archipelago (WAM); Eaglehawk Id, Dampier Archipelago (WAM); NE end of Enderby Id, Dampier Archipelago (WAM); Malus Id, Dampier Archipelago (WAM); Back Beach, Dampier Archipelago (WAM); Monte Bello Id (AMS C69265); Cape Keraudren (WAM); N Turtle Id, off Port Hedland (AMS); Gantheaume Pt, Broome (NM G4931); Riddell Beach, Broome (WAM); SE Wood Id, E of Cockatoo Id (WAM); Vansittart Bay (WAM); Port Sampson (WAM). NORTHERN TERRITORY, AUSTRALIA: Grose Id, W of Darwin (AMS); Aravu Pt, Coburg Peninsula (AMS); NE end Smith Pt, Coburg Peninsula (AMS); Boucaut Bay (AMS); Cape Wessel (WAM 871-76). QUEENSLAND, AUSTRALIA: Bountiful Id, Gulf of Carpentaria (AMS); Murray Id, Torres Strait (AMS C29539); Hospital Pt, Thursday Id, Torres Strait (AMS); Friday Id, Torres Strait (AMS); Prince of Wales Id, Torres Strait (AMS); Somerset, Cape York Peninsula (AMS C108321); Yam Id, Torres Strait (AMS); Palm Bay (ZMA); Northwest Id, Capricorn Gp (AMS); Three Id, Cape Flattery (AMS C41319); Wanga Reef off Daintree, N of Cairns (AMS); Snapper Id, near Daintree River, N of Cairns (AMS); Low Isles, Pt Douglas (AMS C76027, USNM 623126); Batt Reef, E of Pt Douglas (AMS); Four Mile Beach, Pt Douglas (AMS); Alexander Reef, off Pt Douglas (AMS); Double Id, N of Cairns (AMS); Yule Pt, N of Cairns (AMS); Cockle Bay, Magnetic Id (AMS); Geoffrey Bay, Magnetic Id (AMS, USNM 842875); Hayman Id, Whitsunday Gp (AMS C70759, USNM 704929); Sinclair Bay, Cape Glochester (AMS); Edgecumbe Bay, Bowen (AMS); Hook Id (AMS); Hamilton Id, Whitsunday Passage (AMS); Heron Id, Capricorn Gp (USNM 623011).

NEW GUINEA: Seleo Id, Aitape, Papua (USNM 616028); Islet, N end Kranket Id, Madang, Papua (AMS C61610); Kula Id, Lusancay Ids, Trobriand Gp (AMS C95231); Daru, Papua (AMS); Yule Id, Papua (USNM 617601, 617602); Port Moresby Bay, Papua (CAS, MCZ, USNM 613593); Bootless Inlet, Motupore Id, Papua (WAM). BISMARCK ARCHIPELAGO: New Britain (AMS); Mongop, New Ireland (AMS C98254). SOLOMON ISLANDS: 3.2 km W Kia Village, NW end Santa Isabel (LACM 78-614); Loulasi Id, off Aoki, W coast Malaita Id (AMS); Munda, New Georgia (USNM 821469); Pavuvu Id, Russell Gp (USNM 488369). SANTA CRUZ ISLANDS: Vanikoro (AMS). LOYALTY ISLANDS: Lifu (AMS, USNM 423321). NEW CALEDONIA: Île Art (USNM 806109); Touho (AMS); Bourail (AMS); Paagoumene (AMS); causeway to Presque Île Ducos, Nouméa (AMS); Anse Vata, near Nouméa (AMS); Île St Marie, Nouméa (AMS); Point Magin, near Nouméa (USNM 724094); 2 km S of Conception (USNM 724529). FIJI: Tuakoi Pt, S side Rotuma (USNM 685900); SW side Ovatoa, Vanua Levu (USNM 774545, 774550); N coast Verevere Id, Vanua Levu (USNM 694818); Namotu Id (AMNH 202729); Nadi, Viti Levu (AMS C675978, USNM 638461, 638561); S side Mathuata Id, Viti Levu (USNM 694349, 694351); Nananu-i-Ra, Viti Levu (USNM 638548); 2.4 km NE of Mbau Id, Viti Levu (USNM 531724); Suva, Viti Levu (USNM 531940, 531967, 532079, 633165); Tavula, Viti Levu (LACM 77-35); near Seine Bay, Matuku (USNM 686402).

MARIANA ISLANDS: Maug Id (USNM 486731); Tanapag Harbor, Saipan (USNM 607847); Tumon Bay, Guam (USNM 592820, 592821, 592823); bomb craters, Piti Bay, Guam (USNM 842628); Asan Pt, Guam (ANSP 337178, USNM 774777); Apra Bay, Guam (USNM 232945, 243620, 243736, 243738, 243744); Pago Bay, Guam (USNM 774766, 774773, 847273, 853041); Cocos Id, Guam (USNM 853080). CAROLINE ISLANDS: Palau (USNM 636531); Angaus Id, Palau (USNM 616959); Yap (USNM 630820, 630821); Yaptown, Yap (USNM 634301); Timil Harbor, Yap (USNM 634337, 774566); Ponape (AMS, USNM 42453); Mutunlik, Kusai Id (USNM 609566); Stoney Id, (AMS). MARSHALL ISLANDS: Kwajalein, Kwajalein Atoll (USNM 587354); S end Imrodj Id, Jaluit Atoll (USNM 660234); Enybor Id, Jaluit Atoll (USNM 659396); N of Jabor Id, Jaluit Atoll (USNM 659076); Hejatto Id, Jaluit Atoll (USNM 660198). WALLIS AND HOORN ISLANDS: Wallis Id (MNHNP); Nukuhifala (USNM 676432); Mata Utu, W coast Uvea (USNM 675991). SAMOA: Apia (USNM 573862, 573901); Tutuila Id, E Samoa (ANSP 233856); Pago Pago (USNM 574059); Pago Pago Harbor, Tutuila, E Samoa (AMS C71693); Fagaitua Bay, Tutuila (USNM 704711); Ofu, Manu'a Gp (USNM 381218, 381219). TONGA: 2.4 km from Nuku'alofa, Tongatapu (USNM 683988).

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