

Genus *Clypeomorus* Jousseaume
(Cerithiidae: Prosobranchia)

RICHARD S. HOUBRICK

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ABSTRACT

Houbrick, Richard S. Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology*, number 403, 131 pages, 62 figures, 33 tables, 1985.—The genus *Clypeomorus* Jousseaume is confined to tropical intertidal habitats in the Indo-Pacific and is characterized by low spired, variably sculptured, frequently beaded shells.

All species are eurytopic and style-bearing microphagous herbivores, having taenioglossate radulae. Internal anatomy is cerithioid: pallial gonoducts are open, males are aphyllate and produce spermatophores. Development may be planktonic or nonplanktonic. The genus dates from the Miocene and represents a major cerithiid adaptive radiation onto hard substrata in the intertidal zone.

Twelve living *Clypeomorus* species are recognized: *C. bifasciata* (Sowerby), *C. brevis* (Quoy and Gaimard), *C. batillariaeformis* Habe and Kosuge, *C. pellucida* (Hombron and Jacquinot), *C. petrosa* (Wood), *C. purpurastoma*, new species, *C. inflata* (Quoy and Gaimard), *C. irrorata* (Gould), *C. admirabilis*, new species, *C. subbrevicula* (Oostingh), *C. adunca* (Gould), *C. nympa*, new name. Three subspecies, *C. bifasciata persica*, new subspecies, *C. petrosa chemnitziana* (Pilsbry), *C. petrosa gennesi* (Fischer and Vignal), and three fossil species, *C. verbeekii* (H. Woodward), *C. tjilonganensis* (K. Martin), and *C. alasaensis* Wissema also are recognized. A cladistic analysis of *Clypeomorus* species using 20 characters comprising 50 character states derived from shell, radula, and anatomical features was made. Three clades or groups of closely related species were recognized but were not given higher taxonomic status because of unresolved polychotomies that might be clarified when additional anatomical data become available. The relationships of two species, *C. adunca* and *C. nympa*, remain unclear, and in the case of the latter taxon, allocation to *Clypeomorus* is questionable. A description and taxonomic discussion of the genus is presented and status of the type-species, *Clypeomorus clypeomorus* (= *C. bifasciata*) resolved. The synonymy, description, ecology, intra- and inter-specific variation, biogeography, fossil records, and a list of material examined are discussed and presented for each species.

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Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia)

Richard S. Houbrick

Introduction

The genus *Clypeomorus* comprises twelve living species, three subspecies, and three fossil species. In the literature, they are frequently assigned to the genus *Cerithium* Bruguière, but they differ from other cerithiids by their low-spined, frequently beaded shells. All members of this tropical group occur in intertidal habitats and are epifaunal herbivores. They are usually common, occur in large populations, and have shells that show wide sculptural variability. Some species show considerable phenotypic differences. Among species, there is normally great variation in the range of shell length, and in several species local populations of dwarfed individuals occur. *Clypeomorus* species are recorded in the fossil record as far back as the Miocene and are today endemic to the Indo-Pacific.

Nothing has been published on the gross anatomy of *Clypeomorus* species with the exception of the paper by Cannon (1975), who presented an accurate account of the reproductive structures of *Clypeomorus batillariaeformis* (cited as *Cerithium moniliferum* Kiener). In general, the basic anatomy of these cerithiids is not unlike that of *Cerithium* or *Rhinoclavis* species (Houbrick, 1974, 1978a). The median to proximal portion of the outer lamina of the open pallial oviduct contains

both a spaceous spermatophore bursa and a smaller, more proximal seminal receptacle. Aphallate males have open pallial gonoducts and produce spermatophores. Fertilization is internal and development may be planktotrophic or lecithotrophic. The anatomical groundplan of *Clypeomorus bifasciata* is typical of the genus and is presented here in detail (p. 27). Departures from this pattern in other *Clypeomorus* species, particularly in the arrangement of the pallial gonoducts, are discussed separately under each species treatment.

Several *Cerithium* species have been shown to have extreme levels of genetic variability (Ritte and Pashtan, 1982), and this phenomenon appears to be reflected in sculptural variability throughout the entire *Cerithium* (sensu lato) group. Because of this variation, specific determination is difficult, and utilization of many characters derived from radulae and shells of numerous specimens is sometimes necessary for identification of *Clypeomorus* species. Shells of immature snails are especially difficult to place. Some *Clypeomorus* species reviewed in this monograph may comprise undetected sibling species or subspecies, and several species appear to be undergoing incipient speciation, particularly at the edge of their geographic ranges. The group may indeed prove to be as complex as *Littorina* in regard to cryptic species. Although I have been deliberately conservative in my recognition of species, I have called attention to species-

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complexes or local populations where I suspect incipient speciation may exist. Resolution of these problems is best left to local workers who have the time and techniques to solve them.

LIST OF RECOGNIZED TAXA

(* denotes extinct taxa)

- Clypeomorus bifasciata* (Sowerby, 1855)
C. b. persica, new subspecies
Clypeomorus brevis (Quoy and Gaimard, 1834)
Clypeomorus batillariaeformis Habe and Kosuge, 1966
Clypeomorus pellucida (Hombron and Jacquinot, 1852)
Clypeomorus petrosa (Wood, 1828)
C. p. chemnitziana (Pilsbry, 1901)
C. p. gennesi (Fischer and Vignal, 1901)
Clypeomorus purpurastoma, new species
Clypeomorus inflata (Quoy and Gaimard, 1834)
Clypeomorus irrorata (Gould, 1849)
Clypeomorus admirabilis new species
Clypeomorus subbrevicula (Oostingh, 1925)
Clypeomorus adunca (Gould, 1849)
Clypeomorus nymphea, new species
 * *Clypeomorus verbeekii* (Woodward, 1880)
 * *Clypeomorus tjilonganensis* (K. Martin, 1899)
 * *Clypeomorus alasaensis* Wissema, 1947

MATERIALS AND METHODS

SPECIMENS EXAMINED.—Because *Clypeomorus* species are variable in shell sculpture and have widespread geographical ranges, careful inspection of numerous samples from as many localities as possible is required before one is able to develop a “feel” for the species and their variations. When dealing with species that have widespread geographical ranges, one can never know the entire range of variation that exists within a species or determine the genetic variation present throughout its range. Living populations of *Clypeomorus* species were examined and dissections of animals made at the Mid-Pacific Marine Laboratory, Enewetak Atoll (formerly known as Eniwetok Atoll), The University of Guam Marine Laboratory, Guam; the Marine Laboratory of the University of the South Pacific, Suva, Fiji; the Orstrom Laboratory and various other sites in New Caledonia; the Marine Laboratory of the Australian Museum, Lizard Island, Queensland,

Australia; and several sites on the Bataan Peninsula, Luzon, Philippines. The types of most taxa and thousands of lots comprising numerous specimens were examined from major museum collections throughout the world. Types of species examined are noted in the synonymies or text. All others are noted in the “Materials Examined.” 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), London
DMNH	Delaware Museum of Natural History, Greenville
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHNG	Muséum National d'Histoire Naturelle, Geneva
MNHNP	Muséum National d'Histoire Naturelle, Paris
NM	Natal Museum, Pietermaritzburg
NMV	National Museum, Victoria
NSMT	National Science Museum, Tokyo
RGM	Rijksmuseum van Geologie en Mineralogie, Leiden
UF (or FSM)	Florida State Museum, Gainesville
USNM	U.S. National Museum Collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
WAM	Western Australian Museum, Perth
ZMA	Zoologisch Museum, Amsterdam

CHARACTERS STUDIED.—The characters were divided into three groups: mensural, meristic, and qualitative. All shell characters were analyzed using adult snails. It should be noted that *Clypeomorus* species, without exception, have their earliest whorls eroded, rendering measurements of exact length impossible; however, if one excludes badly eroded specimens, reasonable estimates of shell length may be made. The immense ranges of many of the species and the rarity and restricted distributions of others presented many problems for comparative phenetic or cladistic analyses. Collection and analysis of morphometric and meristic data were time con-

suming and not always productive. Different phenotypes exist in many parts of the ranges of most species, and adequate material was frequently lacking from key areas. Dissection of poorly preserved material yielded incomplete comparative observations. I attempted to examine living populations and dissect as many narcotized species as possible during field trips to various parts of the western Pacific. Comparative observations made on living animals allowed me to confirm some ideas derived from prior inspection of museum material. Nevertheless, the survey of taxa for many critical characters is unfortunately incomplete. Many taxa need more detailed analysis than was possible during this study. The following is a list of characters used in this study, some of which were used for cladistic analysis.

Shell: A list of the shell characters used in this study follows:

Mensural: Shell length; shell width; apical angle of shell; aperture length; aperture width; shell length/shell width; shell length/aperture length; shell length/radula length.

Meristic (includes presence or absence of a character): Number of whorls in teleoconch; number of spiral cords on penultimate whorl; number of beads on penultimate whorl; number of axial ribs on penultimate whorl; presence or absence of spiral cords; presence or absence of beads on penultimate whorl; presence or absence of axial ribs; presence or absence of denticles on outer lip; presence or absence of varices.

Qualitative: Thickness of columellar callus; sculpture of early whorls; alignment of beads; placement of major varix on penultimate whorl.

Anatomy: For anatomical studies, only adults were used. I tried to examine living snails whenever possible. The body color was recorded and dissection of internal anatomy made under water, to which an aqueous solution of Methylene Blue was added to enhance nervous tissue and glandular structures. Carmine particles were used to determine ciliary movements in the pallial gonoducts and stomach. Of the twelve species discussed in this monograph, dissections of six taxa were made: *C. bifasciata*, *C. brevis*, *C. batil-*

lariaeformis, *C. petrosa*, *C. irrorata*, *C. nympha*. Anatomical material of the remaining species was either lacking, fragmentary, or poorly preserved. The pallial complex and delicate pallial gonoducts frequently are destroyed during preservation leaving intact only the muscular head-foot, kidney, and digestive gland-gonad complex. Only preserved or dried material was available for some species. Of the six species dissected, *Clypeomorus bifasciata* was studied in greatest detail. The paucispiral operculum is basically the same in all *Clypeomorus* species and is not useful as a taxonomic character at the species level.

Radula: Radular measurements were made on wet mounts with an ocular micrometer. The radulae of all species were examined on a Cambridge Mark II stereoscan electron microscope. A list of radular characters follows:

Mensural: Radula length; radula length/shell length ratio.

Meristic: Number of teeth rows; number of cusps on rachidian tooth; number of lateral cusps on rachidian tooth; number of cusps on lateral tooth; number of cusps on inner marginal tooth; number of cusps on outer marginal tooth.

Qualitative: Shape of rachidian tooth; shape of lateral tooth extension; shape of marginal cusps; shape of glabrella and rachidian basal plate.

Most anatomical structures are of generic value and characters best utilized for taxonomic purposes at the specific level are those derived from the reproductive systems. The layout of the female pallial gonoducts, particularly the placement of the sperm gutter and seminal receptacle in the outer laminar wall, is a useful discriminating tool. Care must be taken, however, to have only ripe, healthy, adult snails, because the pallial oviducts change during ontogeny and tend to degenerate in old snails. Moreover, many specimens are infested with trematode parasites and have undergone parasitic castration. It should be pointed out that the pallial gonoducts are secondarily derived from the ectoderm and may not be truly homologous between species. Therefore, despite their usefulness for specific determination, their value in determining polarity for

cladistic analysis or for phylogenetic speculation is questionable. Other discriminating characters are the shape of the inhalant siphon and associated papillae, and the shape and thickness of the jaws.

ECOLOGICAL DATA.—Observations and habitats, substrate preferences, and vertical distribution along the shore were helpful in solving some taxonomic problems. Data on reproductive biology and descriptions of egg masses, embryos, and larvae provide more holistic descriptions of taxa and were incorporated into each species treatment, when possible.

STATISTICAL TESTS.—Standard statistical tests were made on the morphological data. For taxa that were morphologically close, Chi Square, Student's T, Analysis of Variance, and Student-Neuman-Keul's Post Hoc Comparison were used.

CLADISTIC ANALYSIS.—A cladistic analysis of *Clypeomorus* species using 20 characters comprising 50 character states was made using the Wagner 78 algorithm (Ferris, 1970; Wiley, 1981: 178–192). This program produced computer generated cladograms that served as a basis for deriving a phylogenetic classification. Polarity was established primarily by outgroup comparison of presumed homologous structures derived from the shell, radula, and animal (for details of the cladistic methodology, see page 9). Taxonomic and phylogenetic results derived solely by rigid adherence to cladistic methodology were avoided. All available evidence, such as that derived from the fossil record, biogeography of species, and developmental and ecological biology, was considered to develop a synthetic classification.

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Systematics

In this monograph I attempt to provide taxonomic stability for *Clypeomorus* species and to indicate "problem" taxa that need further, more detailed study. Accordingly, a generic analysis is presented below, as well as discussions of nomenclatural history, phylogeny, and zoogeography. A brief account of doubtful *Clypeomorus* species follows. The basic format used for each species consists of: (1) a synonymy and description of the shell, radula, and anatomy; (2) a table of shell measurements and, where possible, a similar table of radular measurements; (3) remarks on the synonymy, a summary of the ecology, and a discussion of interspecific relationships and in-

traspecific variation; (4) the fossil records of each species and a summary of the geographic range, accompanied by a map; and (5) a list of the material examined.

The following hierarchic classification is used in this report:

Superfamily CERITHIACEA Fleming, 1822

Family CERITHIIDAE Fleming, 1822

Subfamily CERITHIINAE Fleming, 1822

Genus *Clypeomorus* Jousseau, 1888

Clypeomorus Jousseau, 1888:171; 1930:270.—Thiele, 1929:213–214.—Wenz, 1938:767–768.—Cotton, 1952: [1].—Shuto, 1969:67.—Cernohorsky, 1972:70.—Houbert, 1975:16.

TYPE-SPECIES.—*Clypeomorus clypeomorus* Jousseau, 1888 (= *Clypeomorus bifasciata* (Sowerby, 1855)), by tautonymy.

NOMENCLATURE.—This genus was proposed to accommodate *Clypeomorus clypeomorus* Jousseau, 1888, which I regard as a Red Sea morph of *Clypeomorus bifasciata* (Sowerby). Jousseau (1888:171) included six species in his new genus, the last of which, *Clypeomorus clypeomorus*, is the type-species of the genus by tautonymy. A short, squat shell with a very short anterior siphonal canal, contracted columella, and a surface sculpture of numerous tubercles are the conchological characters Jousseau considered distinctive of the genus. As examples of the new taxon he listed *Cerithium morus* Lamarck, 1822 (= *Clypeomorus bifasciata* (Sowerby, 1855)), *Cerithium rugosum* (Wood, 1828) (= *Clypeomorus brevis* Quoy and Gaimard, 1834), *Cerithium moniliferum* Kiener, 1841 (= *Clypeomorus batillariaeformis* Habe and Kosuge, 1966), *Cerithium nigrofasciatum* Sowerby, 1865 (= *Clypeomorus bifasciata* (Sowerby, 1855)), and *Cerithium tessellatum* Sowerby, 1855 (= *Cerithium zonatum* (Wood, 1828)). Of these, *Cerithium zonatum* should be excluded from *Clypeomorus*, because it is a *Cerithium* species and its resemblance to *Clypeomorus* is only superficial. I also exclude *Cerithium caeruleum* Sowerby, 1855, and *Cerithium lineatum* Dunker (sic) (= *Rhinoclavis aspera* (Linnaeus,

1758)), which Jousseume included as a *Clypeomorus* species. These should all be referred to other cerithiid genera because they differ from the true *Clypeomorus* group in shell physiognomy, radular characters, anatomy, and habitat.

Jousseume (1888:173) commented on the similarity between *Clypeomorus clypeomorus* and *Cerithium carbonarium* Philippi, 1848, as depicted by Sowerby (1865; pl. 9: fig. 59), and included the latter species in the genus *Clypeomorus*. Despite the overall similarity, the resemblance is purely superficial and convergent; I have previously shown that *C. carbonarium* is a synonym of *Batillaria sordida* (Gmelin, 1791) and a member of the family Potamididae H. and A. Adams, 1854 (Houbrick, 1978b). Jousseume (1888:173) also noted a close resemblance between *Clypeomorus clypeomorus* and *Cerithium moniliferum* Kiener (= *Clypeomorus batillariaeformis* Habe and Kosuge, 1966) but remarked that the former species was shorter and fatter and had more prominent tubercles.

I regard Jousseume's species, *Clypeomorus clypeomorus*, as a Red Sea variety of the more widely distributed *Clypeomorus bifasciata* (Sowerby). The Red Sea populations of *Clypeomorus bifasciata* are more fully discussed on pages 41–43.

A description of the generic characters of *Clypeomorus* given herein is broader than if based on the Red Sea forms alone, and includes conchological, anatomical, radular, and ecological characters shared by all members of the group.

DIAGNOSIS.—Shell small, not exceeding 3 cm length, short, squat and rounded with a teleoconch of 8 or 9 inflated whorls. Body whorl wide. Aperture round-ovate and about one-third the length of the shell. Columella deeply concave and with slight callus on body whorl. Outer lip rounded, moderately thick. Anterior siphonal canal very short, deeply incised and directed leftward about 45 degrees to shell axis. Anal canal distinct, forming a deeply incised groove that extends well into shell aperture. Shell sculpture usually of 2 or 3 nodulose spiral cords crossed by weaker axial elements and presenting an overall beaded appearance of varying inten-

sity. Incised spiral lines sometimes present. Protoconch normally eroded in adults. Suture moderately incised and slightly wavy. Periostracum thin. Operculum thin, corneous, brown and ovate with paucispiral sculpture and an eccentric nucleus. Animal microphagous herbivore with long taenioglossate radula (2+1+1+1+2) comprising numerous rows of teeth with rounded cusps and spoon-shaped or spatulate marginal teeth. Jaws, a pair of salivary glands that pass through the nerve ring but lie mostly anterior to it, a well-developed esophageal gland, a style sac, and crystalline style are present (Figure 13A,D). Nervous system epiathroid, moderately condensed. Dorsal two-thirds of mantle edge fringed with short pallial tentacles. Eyes prominent, located at outer base of each tentacle. Pallial gonoducts open, sexes separate, males aphaallic. Spermatophore bursa and seminal receptacle in proximal medial lamina of female pallial oviduct. Sperm dimorphic. Reproduction oviparous. Larvae lecithotrophic or planktotrophic. Habitat intertidal.

ETYMOLOGY.—*Clypeomorus* is a feminine noun from the Latin *clipeus* (shield) and *morus* (a mulberry tree; probably in error for *morum*, *i*, a mulberry). Note that the name *Clypeomorus* is feminine; therefore, specific names should agree in gender. Most authors have mistakenly regarded it to be masculine. Jousseume (1888) himself erred in this regard, but later (1930:270) he cited *Clypeomorus pupa* as an example of the group, using a feminine ending.

REMARKS.—*Clypeomorus* differs from most *Cerithium*, *Rhinoclavis*, and *Pseudovertagus* species in having a short squat shell with a truncated anterior canal and an overall sculpture of two to three spiral cords bearing numerous rounded beads. The name, *Clypeomorus*, aptly describes the beaded, mulberry-like appearance. In general, members of this genus are smaller and less elongate than other cerithiids and have larger, more rounded apertures. They also have long radular ribbons and the shell length/radula length index has a low value. In females, the seminal receptacle is a single chamber, usually

proximal and adjacent to the spermatophore bursa whereas in *Cerithium*, *Rhinoclavis*, and *Pseudovertagus*, it is frequently digitate and normally lies in the tissue of the mid-section of the outer wall of the spermatophore bursa. While there is an esophageal gland in all *Clypeomorus* species examined, this is not always so in other cerithiids. The radular teeth of *Clypeomorus* species tend to have blunt, spatulate cusps and the edges of the marginal teeth are spoon-like, bearing few denticles. This is in contrast to *Cerithium*, *Rhinoclavis*, and *Pseudovertagus* species, all of which have more numerous, sharply pointed cusps and denticles on their lateral and marginal teeth. Finally, *Clypeomorus* species are all confined to the intertidal zone, usually on coarse, rocky substratum, whereas most other cerithiid species are mostly subtidal and occupy more diverse ecological niches. *Clypeomorus* comprises fifteen living and three extinct taxa. Of the Recent taxa, twelve are accorded specific rank and three subspecific rank. Tables 3 and 4 provide an indication of the variability in shell and radular parameters among the living taxa.

ECOLOGY.—*Clypeomorus* species live in the intertidal zone where they are found on exposed rocky or limestone substrata and rubble. They may also occur on softer substrata in less exposed situations. Many are able to withstand long hours of exposure. Normally found in marine environments, some species such as *Clypeomorus brevis* (Quoy and Gaimard, 1834), *Clypeomorus pellucida* (Hombron and Jacquinot, 1852) and *Clypeomorus bifasciata* (Sowerby, 1855), also occur in estuarine habitats. Most species are common and frequently occur in conspicuous populations of high density. This is particularly true of *Clypeomorus bifasciata*, *Clypeomorus batillariaeformis*, and *Clypeomorus petrosa* (Wood, 1828). All members of the genus are style-bearing, microphagus herbivores and have relatively long radular ribbons in comparison to other cerithiid taxa. This is probably due to the common origin of the group, as well as to similar mode of feeding on hard substrata. They are an adaptive group of cerithiids that has fully exploited the inter-

tidal portion of the littoral zone. Where several congeners are sympatric the main mode of ecological segregation is that of habitat, i.e., particular substratum and exact location of the species in the intertidal zone. Although detailed studies have not been made, niche partitioning appears to be trophic and is reflected in radular differences as related to feeding. Size also appears to segregate some sympatric species, e.g., *Clypeomorus petrosa* and *Clypeomorus purpurastoma*. Although the data are fragmentary, reproductive anatomy and developmental modes of some species are specialized, and undoubtedly serve to segregate congeners. Most species are more active at night, but their behavior has not been carefully studied. Table 1 provides a summary of ecological distributions among *Clypeomorus* species. As may be seen in this table, the reproductive modes of only two species are known.

Recent papers dealing with the ecology of the intertidal zone of various Indo-Pacific regions that mention *Clypeomorus* species of questionable identity include those of Taylor and Lewis (1970), Taylor (1971), Atapattu (1972), Morton (1973), Smythe (1979), Thomassin and Galenon (1977), Chelazzi and Vannini (1979), and Ayal and Safriel (1981). These and similar shorter papers should be approached with caution because of the probable misidentification of most *Cerithium* (sensu lato) and *Clypeomorus* species.

PHYLOGENY.—The earliest unequivocal *Clypeomorus* fossil dates from the Miocene and is from the Indo-Pacific region, where the genus is now endemic. The relationship of this genus to other cerithiid genera is unclear. There are older Eocene fossils from Europe that bear an overall similarity to the *Clypeomorus* physiognomy. These are members of the genera *Benoistia* Cossmann, 1899, and *Brachytrema* Morris and Lycett, 1851; but it is doubtful that there is any close relationship by way of direct lineage. No intermediate fossils from the late Tertiary are known. The similarity is probably due to convergence.

Shell characters, arrangement of the pallial oviducts, and a common intertidal habitat tend

TABLE 1.—Ecological distribution and developmental modes of *Clypeomorus* species (x = categories; 0 = not known; H = high tidal zone; M = middle tidal zone; L = low tidal zone).

Species	Habitat			Zonation			Reproduction	
	Rocky shore	Sand/mud flat	Mangrove	H	M	L	Direct	Indirect
<i>C. bifasciata</i>	x	x	0	x	0	0	0	x
<i>C. brevis</i>	x	x	0	x	0	0	0	0
<i>C. batillariaeformis</i>	x	0	0	0	x	0	x	0
<i>C. pellucida</i>	0	0	x	x	0	0	0	0
<i>C. petrosa</i>	x	0	0	x	x	0	0	0
<i>C. purpurastoma</i>	x	x	0	0	0	x	0	0
<i>C. inflata</i>	x	0	0	0	0	0	0	0
<i>C. irrorata</i>	x	0	0	0	x	0	0	0
<i>C. admirabilis</i>	x	x	0	x	0	0	0	0
<i>C. subbrevicula</i>	x	0	0	0	x	0	0	0
<i>C. adunca</i>	x	0	0	0	0	0	0	0
<i>C. nympha</i>	x	0	0	0	x	0	0	0

to support the concept that the Indo-Pacific *Clypeomorus* group is monophyletic; nevertheless, the possibility exists that convergence has masked phylogenetically divergent lineages and that the group is polyphyletic. For instance, the western Atlantic *Cerithium lutosum* Menke, 1828, and eastern Pacific *Cerithium menkei* Carpenter, 1857 are both intertidal species that appear to have shell characters fitting the limits of *Clypeomorus*. The internal anatomy of the pallial oviducts of *Cerithium lutosum*, however, is very different from that of *Clypeomorus* species for which the anatomy is known.

Clypeomorus may be derived from the *Thericium* Monterosato, 1890, lineage. I have previously considered this group as a subgenus of *Cerithium* Bruguière, 1789 (Houbrick, 1974:38), but *Thericium* has been recently accorded generic rank by Gründel (1982:40), and I am inclined to agree with him. Many Tethyan cerithiid fossils that were assigned in the older literature to *Pithocerithium* Sacco, 1895 (a synonym of *Thericium*), closely resemble modern Indo-Pacific *Clypeomorus* species. It is not unreasonable to suggest that the *Clypeomorus* lineage evolved from the large Tethyan assemblage of *Thericium* that is now of worldwide distribution. This probably occurred

by an adaptive radiation into the rich, heterogeneous intertidal zone of the tropical Indo-Pacific.

The basic shell physiognomy of living *Clypeomorus* species reflects the radiation of this group into the intertidal zone. Selective pressures, such as hard substratum, high energy conditions, exposure to air during tidal changes, euryhaline conditions, and predation pressures unique to the intertidal biotope, have all contributed to the basic shell design. It is obvious that an obese, stocky, thick shell with a large aperture is advantageous to a snail exposed to the extremes of temperature and salinity that occur in a rocky intertidal, high energy environment. A large aperture is correlated with a larger foot and enables the animal to clamp down on the surface with more efficiency. In contrast, a long tapering shell, typical of most other cerithiids, is a distinct disadvantage in this kind of habitat. The selective advantage of the overall beaded sculpture, so typical of *Clypeomorus* species, is more difficult to assess. The many beads may serve to deflect the lamellar flow of water over shell. They undoubtedly add strength to the shell by endowing it with many "points d'appui" and tend to line up as varices or lattice-like lines. Vermeij (1978:26) has suggested that beaded sculpture in high interti-

dal snails is a heat regulatory device.

The number and exact identity of fossil *Clypeomorus* species is difficult to determine due to the comparative rarity of fossils and the fragmentary, often eroded, state of available specimens. Most were described in the literature as *Cerithium* species and were frequently assigned erroneous names. For these reasons, I have not seriously regarded literature citations of fossil *Clypeomorus* species unless the figured specimens are easily determined or voucher specimens were examined. I conservatively estimate that there are three extinct species in the genus: *Clypeomorus verbeekii* (Woodward, 1880), *Clypeomorus alasaensis* Wissema, 1947, and *Clypeomorus tjilonganensis* (K. Martin, 1899). Other extinct *Clypeomorus* species may be *Cerithium fennemai* K. Martin, 1899, and *Cerithium ickei* (Schepman, 1906) (not Vignal, 1909). I did not examine specimens of the former species, and its exact allocation is not clear. *Cerithium ickei* was originally allocated to *Clava* (= *Rhinoclavis* Swainson, 1840), but it was later excluded from that genus (Houbrick, 1978a:20). Although the shell of this species resembles somewhat those of *Clypeomorus* species, not enough material is available to make a generic assignment at this time.

Members of the family Cerithiidae underwent a great adaptive radiation in the early Tertiary when most of the genera, including *Clypeomorus*, appeared. The *Clypeomorus* group first appears in the Miocene and probably represents a major adaptive radiation into the intertidal zone. Although some species are now extinct, many taxa have survived and remain unchanged to the present. I regard many of the Recent species to be conspecific with these fossils. I have previously stated that nearly all of the living western Atlantic *Cerithium* species were represented in the Pliocene and Pleistocene epochs (Houbrick, 1974:35). Of the seventeen living Indo-Pacific rhinoclavid snails, comprising the genera *Rhinoclavis* Swainson, 1840, *Pseudovertagus* Vignal, 1904, and *Clavocerithium* Cossmann, 1920, only five species are unrepresented in the fossil record (Houbrick, 1978a).

Some *Clypeomorus* fossils that appear to be conspecific with some living species are summarized in Table 2. As can be seen, some taxa have fossil records extending back in geological time as far as the Miocene.

One of the problems in deriving a species phylogeny was the lack of anatomical information about some species. While *Clypeomorus bifasciata* is well known anatomically, other species are poorly understood, and the anatomy of some, such as *Clypeomorus inflata* and *Clypeomorus subbrevicula*, remains virtually unknown. It is thus impossible to compare homologous anatomical features among all species. The same problem exists with shell characters and radulae of some uncommon species such as *Clypeomorus adunca*, resulting in a poor comparative statistical database. Habitat and developmental data are also lacking for some species. Summaries of shell and radular statistics are in Tables 3 and 4, respectively.

The cladistic method was chosen rather than a phenetic approach based on degree of similarity, because it allowed me to use comparative cerithiid morphology to establish polarities. Characters and scoring of character states selected to determine phylogenetic relationships are presented in Table 5, providing a summary of their distribution among *Clypeomorus* species. Many of these characters are derived from Tables 3 and 4. The genus *Cerithium* is morphologically most like *Clypeomorus*, and among *Cerithium* species, *Cerithium lutosum* Menke, 1828, is closest to *Clypeomorus* species in shell shape, sculpture, habitat, and is anatomically well known to me. For these reasons, it was chosen as the outgroup representative. Due to the probability of convergence and parallelism, polarities of shell characters (Table 5, characters 1–10) as established by outgroup comparison are, at best, unsatisfactory. The presence of beaded sculpture (character 1), axial ribs (character 4), and spiral cords (character 5) are common sculptural features among many *Cerithium* species and are considered to be generalized rather than derived characters. A pupiform shell (character 3) occurs rarely among

TABLE 2.—Fossil records of extant *Clypeomorus* species.

Species	Epoch	Locality	Source	As cited in source
<i>C. bifasciata</i>	Late Miocene	Enewetak	Ladd (1972:40, pl. 9: fig. 11)	<i>Cerithium (Concerithium) aff. egenum</i> (Gould)
	Late Pliocene	New Hebrides	Abrard (1946:56, pl. 4: fig. 20)	<i>Cerithium (Pithocerithium) morum</i> Lamarck
	Holocene	Philippines	Popenoe and Kleinpell (1978:40, pl. 2: fig. 21)	<i>Clypeomorus morus</i> (Lamarck)
<i>C. batillariaeformis</i>	Holocene	W. Australia	This paper	—
	Late Pliocene	Philippines	Shuto (1969:67–68, pl. 2: figs. 6, 12)	<i>Clypeomorus tuberculatus</i> (Linnaeus)
	Pleistocene	Saipan	Ladd (1972:37–38, pl. 9: figs. 7, 8)	<i>Cerithium (Thericium) alveolus</i> Hombrom and Jacquinet
<i>C. pellucida</i>	Holocene	Enewetak	Ladd (1972:37–38, pl. 9: figs. 7, 8)	<i>Cerithium (Thericium) alveolus</i> Hombrom and Jacquinet
	Miocene	Timor	Tesch (1920:53, pl. 130: fig. 179)	<i>Cerithium patulum</i> Sowerby
<i>C. petrosa</i>	Pliocene	Timor	Martin (1884:153–154, pl. 8: fig. 180)	<i>Cerithium echinatiformis</i> K. Martin
	Pleistocene	French Somalia	Abrard (1942:60, pl. 6: fig. 26)	<i>Cerithium (Pithocerithium) petrosus</i> (Wood)
<i>C. inflata</i>	Late Pliocene	New Hebrides	Abrard (1946:56)	<i>Cerithium (Pithocerithium) petrosus</i> (Wood)
	Pliocene	Timor	Tesch (1920:55–56, pl. 131: fig. 180)	<i>Cerithium inflata</i> Quoy
<i>C. irrorata</i>	Pliocene	Timor	Tesch (1920:56, pl. 130: fig. 181)	<i>Cerithium obesum</i> Sowerby

TABLE 3.—Comparison of shell parameters (mean values) among *Clypeomorus* taxa (l/w = length/width; l/al = length/aperture length).

Taxon	n	Length	Width	Aperture length	Aperture width	No. beads on penultimate whorl	l/w index	l/al index
<i>C. bifasciata</i>	439	20.13	9.65	5.82	3.65	16.23	2.23	3.45
<i>C. b. persica</i>	20	15.81	7.58	3.70	3.40	12.85	2.09	4.27
<i>C. brevis</i>	35	15.79	7.32	4.26	3.28	13.03	2.15	3.71
<i>C. batillariaeformis</i>	50	27.10 ^a	9.92	7.59	4.19	15.00	2.73	3.57
<i>C. pellucida</i>	25	22.65	10.33	6.32	4.93	11.76	2.19	3.58
<i>C. petrosa</i>	30	27.03	13.11	7.73	5.89	13.90	2.06	3.50
<i>C. p. chemnitziana</i>	30	27.52	12.73	9.61	6.34	23.00	2.16	2.86
<i>C. p. gennesi</i>	30	24.36	11.93	6.74	5.31	17.00	2.04	3.61
<i>C. purpurastoma</i>	30	21.16	9.41	5.49	3.99	19.30	2.24	3.85
<i>C. inflata</i>	30	22.49	12.58	7.84	6.23	11.00	1.87	2.87
<i>C. irrorata</i>	30	21.25 ^b	9.37	5.76	4.66	11.20	2.27	3.69
<i>C. admirabilis</i>	25	22.03	10.93	6.34	5.02	8.82	2.01	3.47
<i>C. subbrevicula</i>	31	20.25	11.77	8.00	6.00	13.10	1.73	2.53
<i>C. adunca</i>	15	17.50 ^c	8.67	8.38	3.93	0	2.01	2.09
<i>C. nympa</i>	38	14.10	6.78	3.07	2.90	15.07	2.07	4.59

^a n=7; ^b n=8; ^c n=1.

cerithiids and is here considered derived. The polarities of characters 6–9 are derived from outgroup comparison alone. Radula length (characters 10, 11) is more suggestive of the coarseness of the food and amount of work done in feeding than it is of phylogenetic relationship (Fretter and Graham, 1962:172). Radular characters of the outgroup, *Cerithium lutosum*, are assumed to be generalized as this species grazes on microalgae on moderately coarse surfaces. Departures from this layout such as changes in cusp form (character 12), rachidian shape (character 14), lateral tooth extension (character 17), and shape of cusps on marginal teeth (character 18) are considered derived states and probably reflect adaptations to new substrata types. No meaningful interspecific anatomical comparisons were possible because these characters were lacking for too many species. Nevertheless, the placement of the seminal receptacle (character 19) in the proximal wall of the outer lamina of the pallial oviduct does seem to be a derived state because this structure is medianly placed in all other *Cerithium* species examined.

Figure 1 represents a cladogram derived from Table 5 and the addition of a few other characters not listed therein. Six different runs, resulting from a reshuffling of taxa, showed identical cladograms. Each was derived with a total of 42 character state changes among the 20 characters. In the cladogram (Figure 1), character numbers from Table 5 are shown above stem lines and the changes in character states are depicted by the numbers beneath the lines. Of these 42 changes, eight (in characters 2,6,7,12,19) are reversals. Parallelism occurs in character 2, which changes to character state 1 in two lineages. The cladogram (Figure 1) is interpreted as dividing the twelve living species of *Clypeomorus* into three clades that appear to share a common shell physiognomy, and to a lesser degree, radular morphology. Differences in radular groupings shown in Figure 2 are subtle and based on generalized tooth shape and dentition patterns. The radulae depicted in the square are hypothesized to be the most generalized (plesiomorphic)

and the two major groups below it, to the left and right, are considered to be more specialized (apomorphic) and correspond with stem 1 and stem 8 in Figure 1. Stem 1 includes the problematic taxa *nympha* and *adunca*, both discussed in more detail below. Note that an unresolved polychotomy occurs in the lineage derived from stem 1. In this clade, *Clypeomorus batillariaeformis* and *C. pellucida* are probably a sister group but are separated in the cladogram because the latter species has become highly modified by its unique, low energy habitat on intertidal mangrove roots. *Clypeomorus petrosa*, comprising three subspecies, and *C. purpurastoma* are closely related and are probably a sister group. This is masked in the cladogram by *C. nympha*, which is very similar to *C. purpurastoma* in shell form but differs in the layout of its pallial oviducts, suggesting convergence in the shell. Thus, *Clypeomorus nympha* may be misplaced in the genus *Clypeomorus*. Stem 8, which originally contained an unresolved trichotomy, was resolved by the addition of character “a” that separates the *brevis-bifasciata* clade from the others. The great number of character changes (7) associated with *Clypeomorus adunca* casts suspicion on its proper placement in the cladogram and undoubtedly accounts for the polychotomy in stem 1. *Clypeomorus adunca* (Figure 3) stands apart from all other species both in its smooth sculpture and in its short, atypical radula. The unique shell and radula suggest an unusual habitat, but nothing is known of the ecology of this rare species, and its relationships remain unresolved.

Some of these clades may represent separate adaptive radiations because they correlate with different habitats. Because anatomical and ecological information about some species is incomplete and homologies uncertain, the polarities of many characters are unresolved. Thus, recognition of these clades does not necessarily imply that they are phylogenetic units and they are not given taxonomic status herein.

The twelve living species comprise three species-groups or clades (A, B, C) that appear to share a common shell physiognomy. While these

TABLE 4.—Patterns of *Clypeomorus* radular dentition (sl/rl = shell length/radula length).

Species	n	Mean length	Mean no. rows	sl/rl index	Number of cusps			
					Rachidian	Lateral	Inner marginal	Outer marginal
<i>C. bifasciata</i>	12	4.17	98.33	5.12	3-5	4-5	4	3
<i>C. brevis</i>	12	4.04	94.67	4.46	3-5	4-5	4	3
<i>C. batillariaeformis</i>	12	4.31	85.50	5.83	3-5	4-5	4	3
<i>C. pellucida</i>	7	4.88	84.71	4.91	3-5	4	4	3
<i>C. petrosa</i>	5	4.85	83.40	5.32	3-5	4-5	4	3
<i>C. purpurastoma</i>	9	3.30	82.60	6.91	3-5	4	4-5	3-4
<i>C. inflata</i>	1	9.00	153.00	2.70	3	3	3	2
<i>C. irrorata</i>	5	7.44	139.00	2.54	3	3	3	2
<i>C. admirabilis</i>	1	9.00	126.00	2.80	3	1	3	2
<i>C. subbrevicula</i>	10	7.00	139.00	2.94	3	4	3	2
<i>C. adunca</i>	1	2.90	90.00	7.59	3	3	4	3
<i>C. nympha</i>	10	2.29	64.12	5.79	3-5	4	4	3

TABLE 5.—Comparison of 12 species of *Clypeomorus* and one of *Cerithium*, using 20 characters and 48 character states (A = *Cerithium lutosum* Menke, outgroup; B = *Clypeomorus bifasciata*; C = *C. brevis*; D = *C. batillariaeformis*; E = *C. pellucida*; F = *C. petrosa*; G = *C. purpurastoma*; H = *C. inflata*; I = *C. irrorata*; J = *C. admirabilis*; K = *C. subbrevicula*; L = *C. adunca*; M = *C. nympha*).

Character	A	B	C	D	E	F	G	H	I	J	K	L	M
SHELL													
1. Beaded sculpture present (0) absent (1)	0	0	0	0	0	0	0	0	0	0	1	0	0
2. Varix placement lateral (0) dorsal (1) mixed (2)	0	0	0	1	1	1	1	1	2	0	0	1	1
3. Pupate shell absent (0) present (1)	0	0	0	0	0	1	1	0	0	0	0	0	1
4. Axial ribs present (0) absent (1)	0	0	0	0	0	0	0	0	0	0	0	1	0
5. Spiral cords present (0) absent (1)	0	0	0	0	0	0	0	0	0	0	0	1	0
6. Number of spiral cords 3+ (0) 2 (1) 0 (2)	0	0	1	0	0	0	0	0	1	1	1	2	0
7. Beads on penultimate whorl 0-12 (-2) 13-15 (-1) 16-18 (0) 19-25 (1)	0	-1	-1	-1	-1	1	-2	-2	-2	-1	-2	-1	0

clades are somewhat arbitrary, they probably reflect a historical adaptive radiation that is reflected by changes in radular morphology.

Clade A centers around the ubiquitous *Clypeomorus bifasciata* (the *Clypeomorus morus* of authors) and its close relative, *Clypeomorus brevis* (Figure 4). These species are dorsoventrally flattened, have a large varix opposite the outer lip, and have thick, spirally beaded cords and numerous aligned beads. They live in an identical rocky, high intertidal habitat and may be closely related. The geographic distribution of *Clypeomorus brevis* follows the Pacific Plate boundary in contrast to that of *Clypeomorus bifasciata*, which is more widespread.

Clade B, comprising *Clypeomorus batillariaeformis*, *C. pellucida*, *C. purpurastoma*, *C. petrosa*, and *C. nympa*, occurs in the upper midtidal to low intertidal zones and is well represented by the common *Clypeomorus batillariaeformis* (Figure 5a) (previously known as *Clypeomorus moniliferum*). *Clypeomorus pellucida* (Figure 5b) has an unusual shape and sculpture due to its low energy habitat on mangrove roots. All species in this group are characterized by shells with a prominent hump-like varix located between an angle of 90–40 degrees perpendicular to the plane of the aperture, when the shell is viewed anteriorly. *Clypeomorus petrosa* (Figure 6a), comprising three subspecies, and *Clypeomorus purpurastoma* (Figure

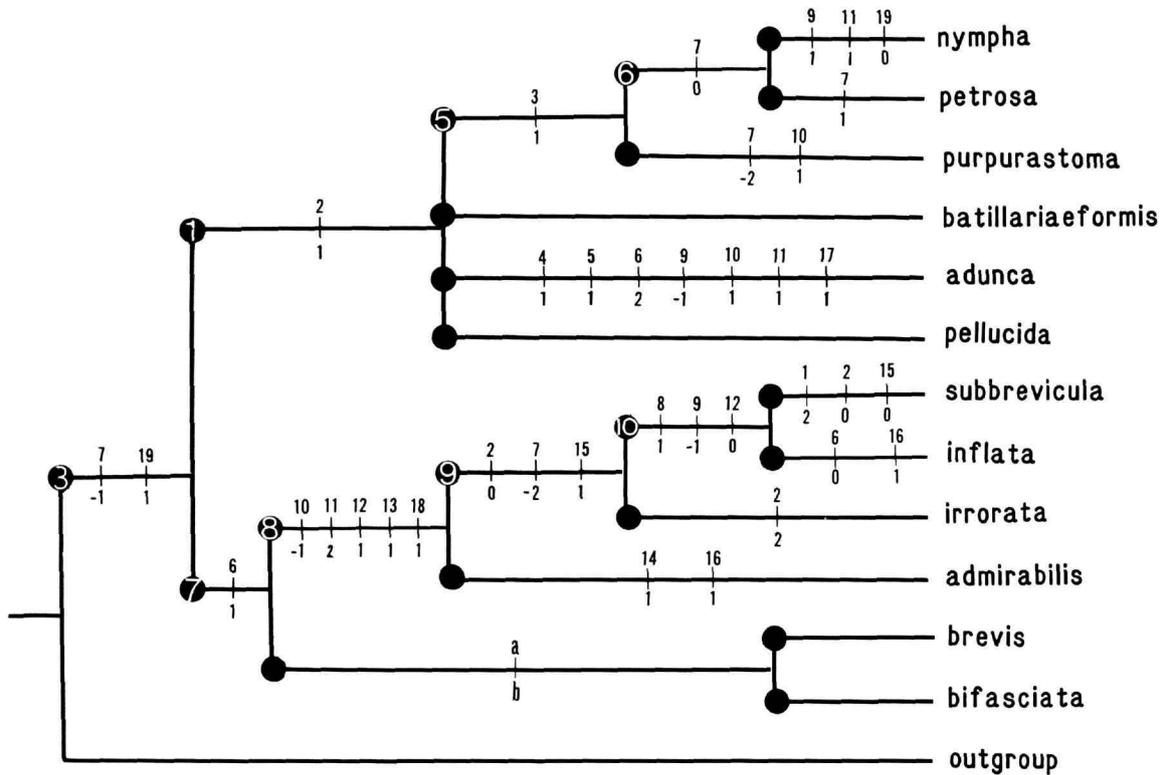


FIGURE 1.—Hypothesis of relationships among *Clypeomorus* species based on cladistic analysis of morphological characters. Numbers above stem lines refer to characters, numbers below stem lines refer to changes in character states. Major stems are indicated by numbers within circles. Nodes are represented by vertical lines of cladogram. Cladogram constructed from data in Table 5.

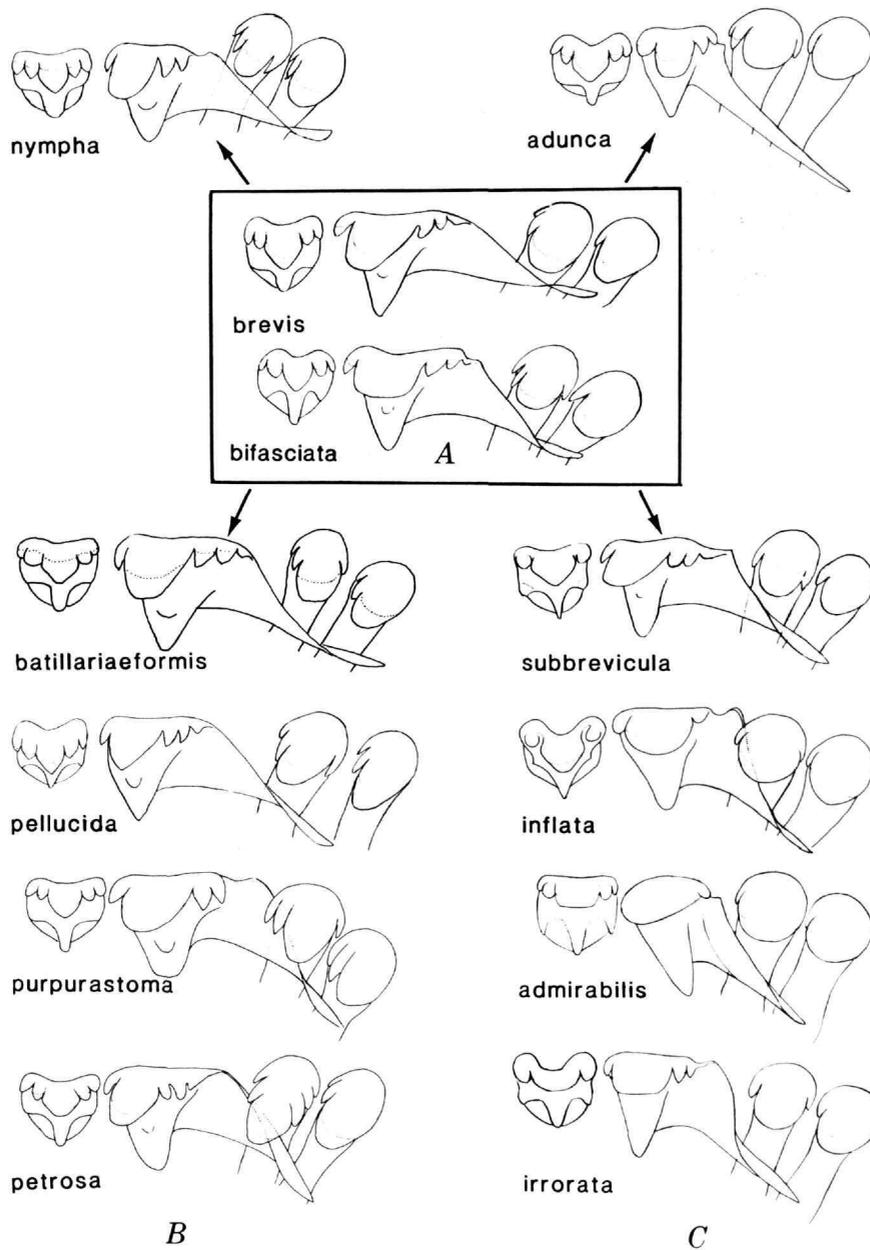


FIGURE 2.—Patterns of *Clypeomorus* radular morphology. Radulae in box (A) represent the generalized (plesiomorphic) state hypothesized to have become modified into more specialized (apomorphic) states as illustrated by two radular groups beneath box (B and C). The three morphological groups (A, B, and C) correspond to three clades discussed in text and shown in Figure 1. *Clypeomorus nympha* and *Clypeomorus adunca* are placed above the box because of their uncertain taxonomic position.

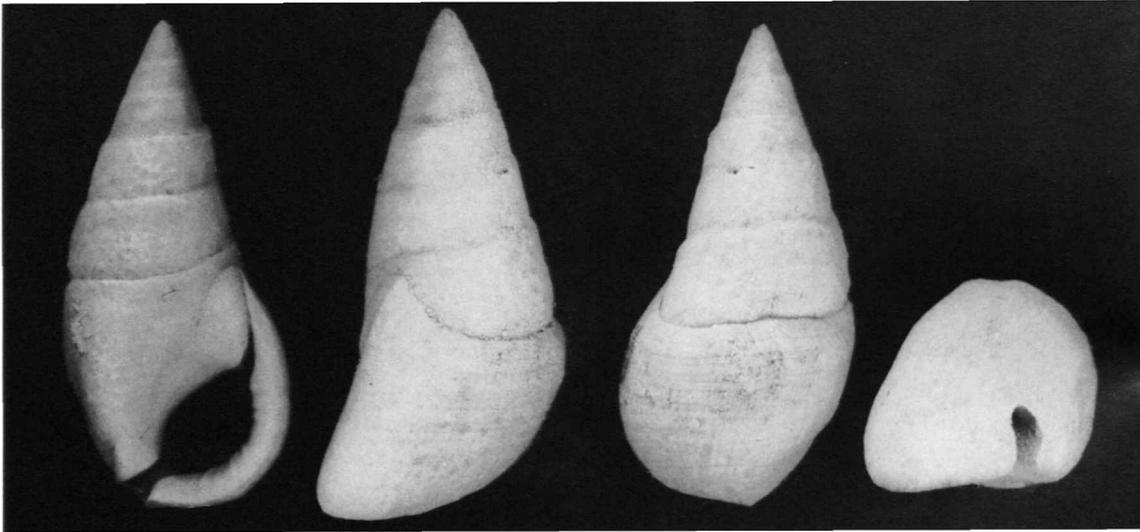


FIGURE 3.—*Clypeomorus adunca*. (Shell whitened with ammonium hydroxide to enhance sculptural details.)

6b) each have pupiform shells. *Clypeomorus batil-lariaeformis* and *Clypeomorus pellucida* (Figure 5a, b) usually have an upper midtidal habitat, while *Clypeomorus petrosa* lives on rocky benches or rocks at the low to mid-intertidal zone, and *Clypeomorus purpurastoma* (Figure 6b) occurs on rocks in the low midtidal to low intertidal zones. *Clypeomorus nympa* (Figure 6c) is doubtfully assigned to this clade, although it closely resembles *Clypeomorus purpurastoma*, and lives on algal mats of intertidal benches on low lying coral islands. Both species are unique in having violet colored apertures. The allocation of *Clypeomorus nympa* to *Clypeomorus* remains uncertain (see discussion under *C. nympa*).

Stem 8 gives rise to clade C (Figure 1), a well-defined group characterized by numerous changes in character states in its branches. This clade was also derived from other data sets that included characters rejected from the final list of characters used to formulate the cladogram presented herein. It reflects radular patterns detected before the cladogram was made. For these reasons stem 8 represents the most accurate

branching sequence in the cladogram. All four species in clade C, *C. subbrevicula*, *C. inflata* (Figure 7a,b), *C. irrorata*, and *C. admirabilis* (Figure 8a,b), have restricted geographic distributions and only one, *C. irrorata*, is known in the fossil record (Pliocene). These taxa may represent newly evolved species and appear so on the cladogram, with the exception of *C. admirabilis*. On the other hand, they may be species whose ranges have narrowed and some, such as *Clypeomorus admirabilis*, new species, probably evolved as a result of a vicariant event in the geology of northern Australia (page 58). Species of the clade C live primarily in the upper midtidal zone among cobbles and rocky rubble, are uncommon, and not well known. They possess radulae of a similar pattern that contrast with other *Clypeomorus* radulae in having the tooth cusps markedly spatulate and rachidian teeth with elongated basal plates. In this group, shell sculpture may be relatively smooth, as in *Clypeomorus irrorata*, or rugose as in *Clypeomorus admirabilis*, new species. A strong varix usually occurs on the body whorl at a 90° angle to the aperture plane when the



FIGURE 4.—Representatives of clade A (as defined on page 14): *a*, *Clypeomorus brevis*; *b*, *Clypeomorus bifasciata*. Note dorsoventral flattening and large varix opposite outer lip. (Specimens whitened with ammonium hydroxide to enhance sculptural details.)

shell is viewed anteriorly. *Clypeomorus irrorata* and *C. admirabilis*, new species, are morphologically close, while *C. subbrevicula* differs in having a more beaded sculpture and a radula that appears to be intermediate with those of species in group two.

ZOOGEOGRAPHY.—The genus *Clypeomorus*

may have originated in the Tethys Sea, but it is now endemic to the Indo-Pacific region. The earliest unequivocal Indo-Pacific *Clypeomorus* fossil dates from the Miocene of Timor (Tesch, 1920:55). A few species from other regions, such as *Cerithium lutosum* Menke, 1828, from the Caribbean, *Cerithium menkei* Carpenter, 1857, from

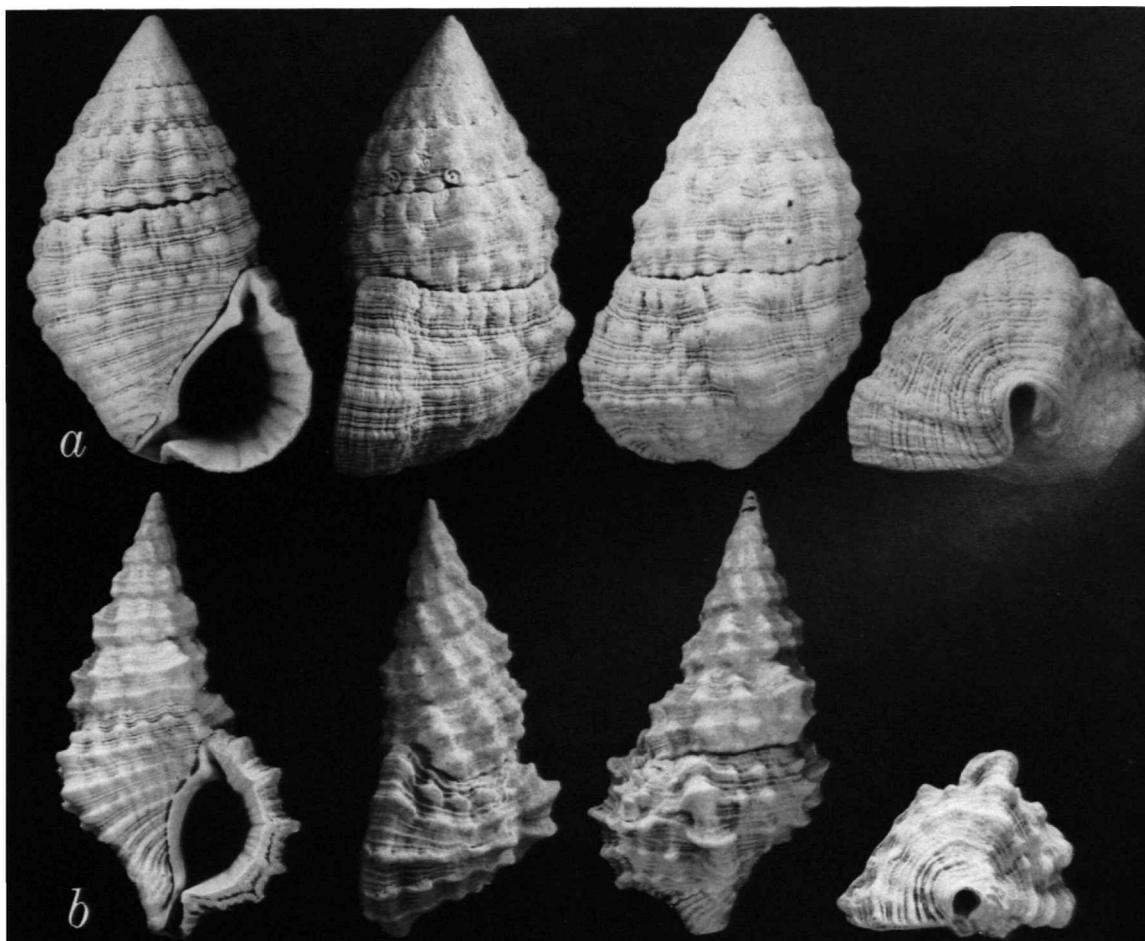


FIGURE 5.—Two of the species in clade B (page 14): *a*, *Clypeomorus batillariaeformis*; *b*, *Clypeomorus pellucida*. Note dorsal varix on both species. *Clypeomorus pellucida* is highly specialized due to its unique habitat on mangroove roots. (Shells whitened with ammonium hydroxide to enhance sculptural details.)

the Eastern Pacific, and the Trinidad fossil, *Cerithium harrisi* Maury, 1912, resemble *Clypeomorus* species in shell sculpture and habitat preference. This may be due to convergence, because *Cerithium lutosum* differs in anatomy from *Clypeomorus*.

The most species-rich regions for *Clypeomorus* are the Philippine and Indonesian archipelagos, where ten species occur. The arc of large, moun-

tainous islands from New Guinea to the Fiji Islands supports seven species. To the North, the Ryukyu Islands, a transitional zone between tropical and temperate faunas, has six species. As may be seen in Figure 9, the number of species gradually diminishes on the low-lying, island groups and atolls of the Central Pacific and Indian Ocean. This trend is also seen in volcanic islands, such as the Tuamotus, near the eastern edge of

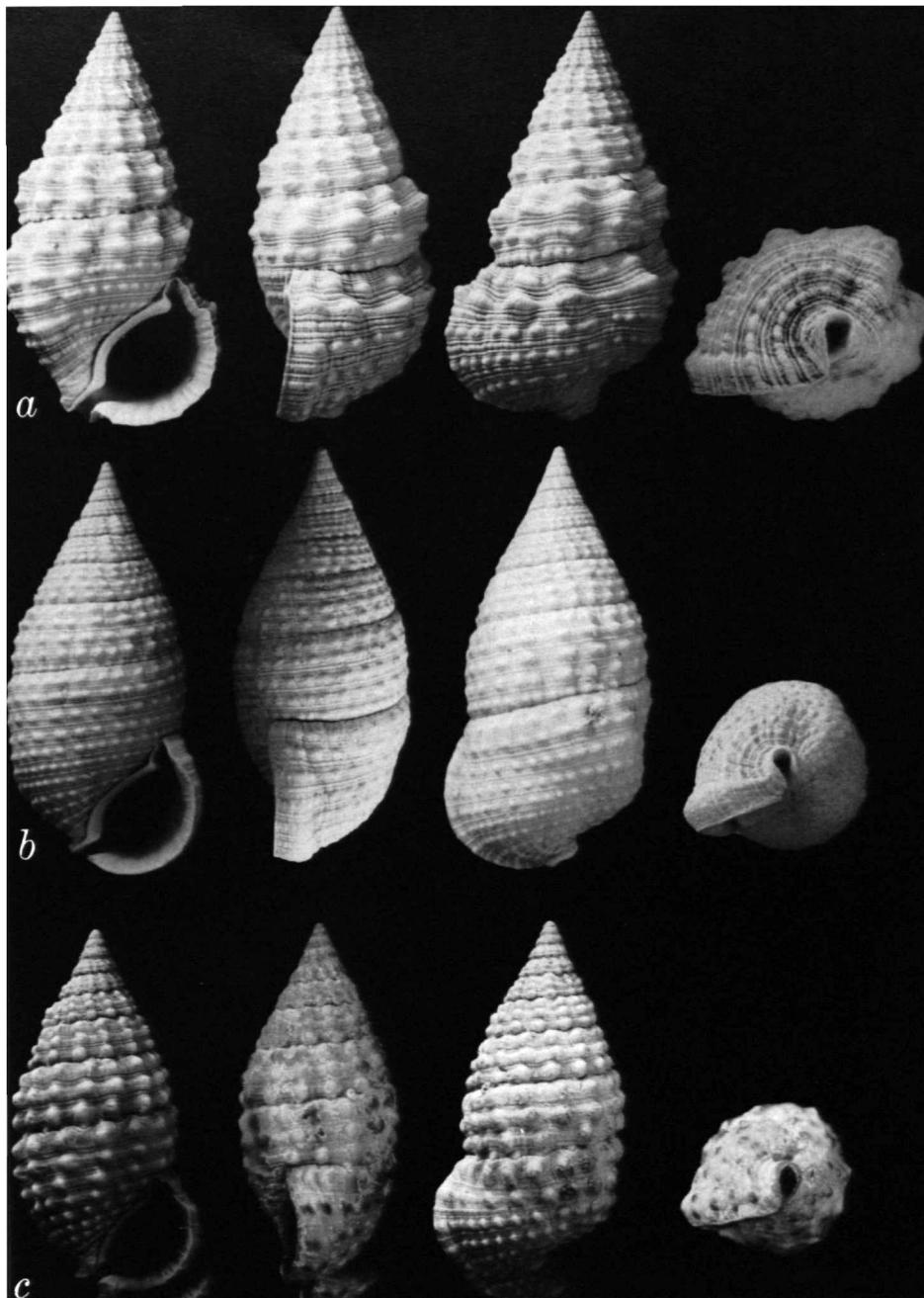


FIGURE 6.—Species in clade B (page 14): *a*, *Clypeomorus petrosa*; *b*, *C. purpurastoma*; *c*, *C. nympa*. Note dorsal varix and pupiform shells. *Clypeomorus nympa* is doubtfully assigned to the genus. (Shells whitened with ammonium hydroxide to enhance sculptural details.)



FIGURE 7.—Species in clade C (page 16): *a*, *Clypeomorus inflata*; *b*, *C. subbrevicula*. Note inflated shape and numerous, incised spiral lines. (Shells whitened with ammonium hydroxide to enhance sculptural details.)

the range, which have fewer habitats than continental islands. Restricted areas, like the Persian Gulf, the Red Sea, and a few outlying island groups, such as the Austral and Cook Islands, support only one species. The number of species recorded for the South China coasts and upper Marianas may be low because of poor data from these regions. One species, *Clypeomorus brevis*, is largely confined to low lying islands of the Pacific plate. Several of the more uncommon *Clypeomorus* species, which, judging from the fossil record,

formerly had wider geographic ranges, are now restricted to limited localities in the Philippine and Indonesian archipelagos.

Speciation, which seems to occur in regions restricted and somewhat isolated from the general Indo-Pacific, can probably be explained by vicariant events. These regions are exemplified by northwestern Australia, the Persian Gulf, southern Japan, and the Austral Islands.

SPECIES WRONGLY ATTRIBUTED TO *Clypeomorus*.—A number of *Cerithium* species are com-

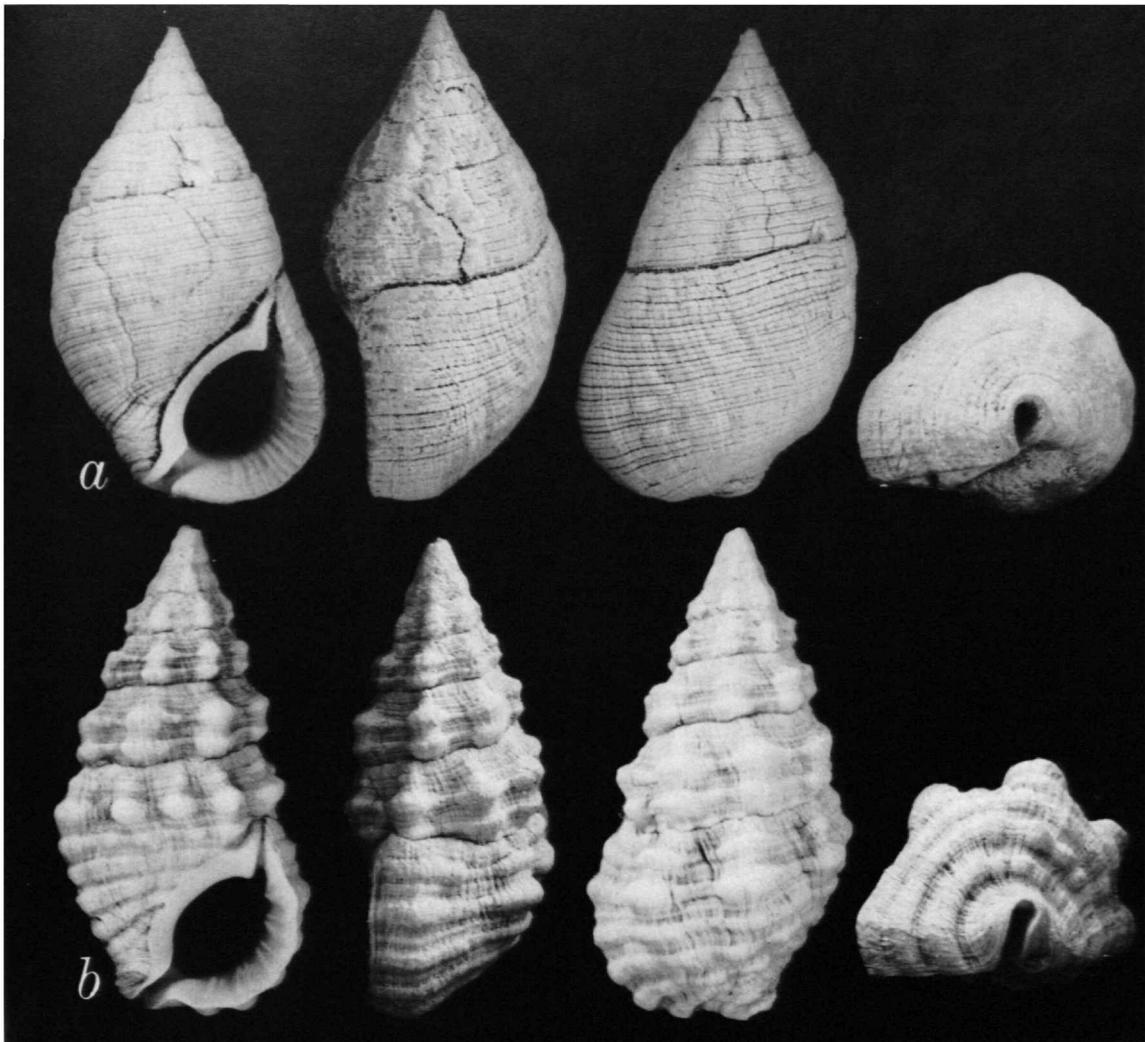


FIGURE 8.—Species in clade C (page 16): *a*, *Clypeomorus irrorata*; *b*, *Clypeomorus admirabilis*. Compare radulae of these two species in Figures 45 and 48. (Shells whitened with ammonium hydroxide to enhance sculptural details.)

monly confused with *Clypeomorus* species: *Cerithium caeruleum* Sowerby, 1855, is frequently referred to *Clypeomorus* by authors, and indeed, the knobby squat shell does superficially resemble many *Clypeomorus* species. However, *Cerithium caeruleum* is sculptured with spines or tubercles rather than beads, and the anatomy of this species departs from typical *Clypeomorus*

anatomy: the distal portion of the osphradium does not turn away from the ctenidium at the inhalant siphon and the seminal receptacle is in the median portion of the outer lamina of the pallial oviduct.

Some populations of *Cerithium zonatum* (Wood) look very much like *Clypeomorus* species and this species is frequently found living in

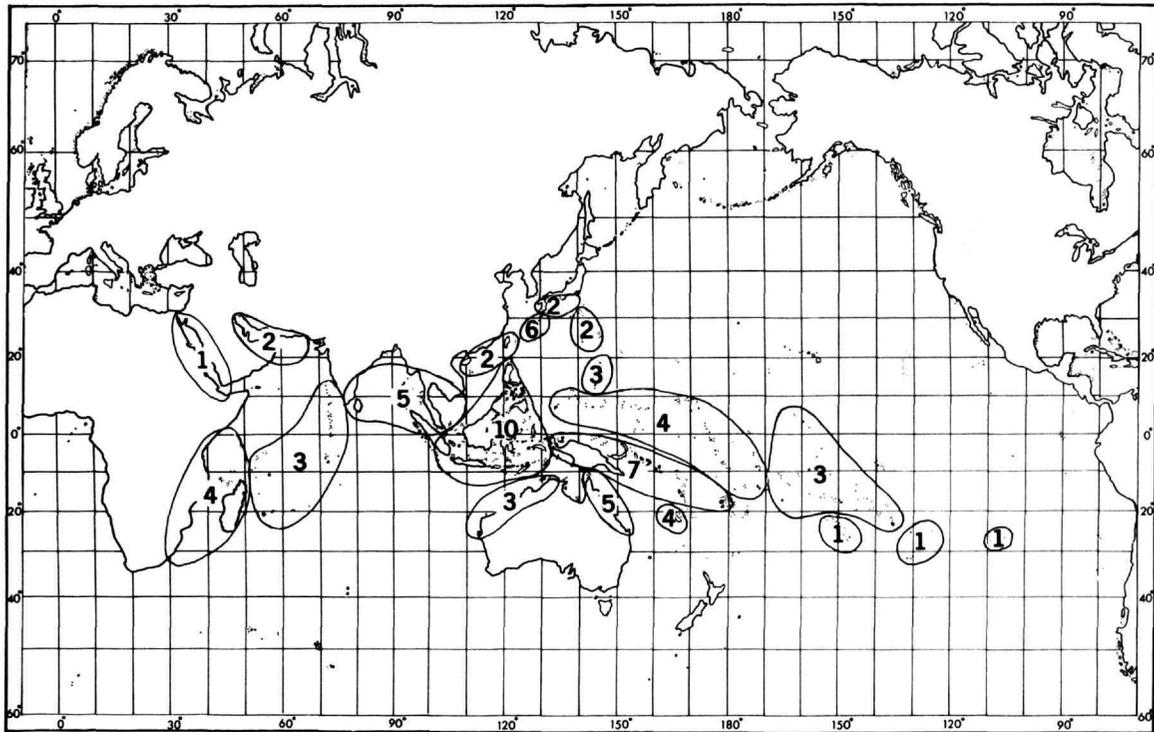


FIGURE 9.—Number of living species of *Clypeomorus* inhabiting selected areas of Indo-West-Pacific Provenge. Insufficiently collected areas omitted. Some regions, such as the South China coast are poorly represented in collections and probably support more species than indicated.

microsympatry with *Clypeomorus bifasciata*, which it closely resembles. The anatomy of the pallial oviduct of *Cerithium zonatum*, as well as examples of shells from populations in other parts of its range, exclude it from *Clypeomorus*.

In the New World, several *Cerithium* species have shells that are very similar to those of *Clypeomorus* species. These are *Cerithium lutosum* Menke, 1828, from the Caribbean, and *Cerithium menkei* Carpenter, 1857, from the eastern Pacific. The anatomy of the pallial oviduct of *Cerithium lutosum* is unlike that of *Clypeomorus*. *Cerithium menkei* is the Panamic geminate form of *C. lutosum*, so it is unlikely that its pallial oviduct differs from that of *C. lutosum*. I thus exclude these two species from *Clypeomorus*, as well as the Miocene fossil, *Cerithium harrisi* Maury, 1912, from Trinidad, which appears to be closely related to *Cerithium lutosum*.

Another problematic species is *Clypeomorus nympa*, new name (formerly known as *Cerithium sejunctum* Iredale, 1929), which is frequently confused with *Clypeomorus purpurastoma*. Although herein allocated to *Clypeomorus* rather than to *Cerithium*, its placement is debatable, because it appears to share characters with both genera. Shell form and sculpture and its intertidal habitat indicate an allocation to *Clypeomorus*, but the anatomy of the pallial oviducts is more like *Cerithium* species.

Among extinct cerithiids, *Cerithium ickei* (Schepman, 1906; not Vignal, 1909, nor Martin, 1914) bears some resemblance to the *Clypeomorus* shell shape, but its sculpture, deeply impressed suture, and long anterior canal suggest allocation to *Cerithium* Bruguière. It was incorrectly attributed to *Clava* (= *Rhinoclavis* Swainson) by Schepman (1906:189), for it does not have the central

columellar plait distinctive of *Rhinoclavis* species.

Cerithium fennemai K. Martin, 1899, may be a *Clypeomorus* species, but it is known to me only by the holotype (RGM 10373), a small shell with a damaged outer lip. The sculpture of 4 or 5 spiral cords per whorl is more like that seen in some *Cerithium* species; thus, its characters are equivocal rendering an assignment to *Clypeomorus* premature until more comparative material is available.

***Clypeomorus bifasciata* (Sowerby),
new combination**

Among *Clypeomorus* taxa, the *bifasciata* complex comprises one of the most geographically widespread groups, and presents a number of taxonomic problems (see below). Populations from southern Japan, Western Australia, the Red Sea, and the Persian Gulf may be separate subspecific or specific taxa; but the evidence for recognition of most of these groups as distinct taxa does not now seem convincing, and only populations from the Persian Gulf are herein considered as a valid subspecies.

Populations from the other regions mentioned above should be studied more carefully, in situ, by local workers who have access to living specimens and can observe ecological, physiological, and morphological traits in greater detail.

***Clypeomorus bifasciata bifasciata* (Sowerby),
new combination, new status**

Figures 10–17

- Cerithium morus* Lamarck, 1822:75 [lectotype, here selected: MNHNG 1097/38, no locality cited; not *Cerithium morus* Bruguière, 1792].—Quoy and Gaimard, 1834:118–119, pl. 54: figs. 13–15.—Kiener, 1841–1842:52–53, pl. 15: fig. 1.—Deshayes in Lamarck, 1843:302–303.—Hombron and Jacquinot, 1852, pl. 24: figs. 15–16, 18; 1854:104.—Sowerby, 1855:870, pl. 182: figs. 159–161; 1865, pl. 7: fig. 42.—E.A. Smith, 1884:63–65 [in part].—Tryon, 1887:133, pl. 24: figs. 32, 33, 35, 39, 40.—Kobelt, 1890:80–81, pl. 15: figs. 6, 7.—Martens, 1897:172–173.—Schepman, 1909:160.—Dance, 1974:68, unnumbered fig.
- Cerithium concisum* Hombron and Jacquinot, 1852, pl. 24: figs. 1–2 [holotype: MNHNP, no number; type-locality:

“Oceanie”; not *Cerithium concisum* Matheron, 1843]; 1854:102–103.—Dautzenberg and Fischer, 1905:124–125, 132.—Fischer, 1906:408.—Couturier, 1907:155.—Oostingh, 1923:70–72; 1925:44.

- Cerithium gemmulatum* Hombron and Jacquinot, 1852, pl. 24: figs. 3, 4, 7, 8, 9, 10, 39–41 [in part; lectotype: MNHNP, no number; type-locality: Solomon Is; Torres Straits; Vavao; not *Cerithium gemmulatum* de Serres, 1840]; 1854:102–103.—Tryon, 1887:134, pl. 25: figs. 57–58.
- Cerithium vittatum* Sowerby, 1855:874, pl. 183: fig. 193 [lectotype, here selected: BMNH 1907-12-30-362-3; no locality cited; not *Cerithium vittatum* Lamarck, 1804].—Tryon, 1887:134, pl. 25: fig. 55.
- Cerithium bifasciatum* Sowerby, 1855:874, pl. 183: fig. 198 [holotype: BMNH, not registered; type-locality: St. Nicholas Id, off Cebu, Philippines; not *Cerithium bifasciatum* Locard, 1886]; 1865, pl. 5: fig. 34.—Tryon, 1887:134, pl. 24: figs. 39–40, pl. 25: fig. 55.—Kobelt, 1889:115, pl. 22: figs. 8, 9.—Martens, 1897:171.
- Cerithium Hanleyi* [sic] Sowerby, 1855:874, pl. 183: fig. 193 [type not found, no locality cited; fig. 193 here selected to represent lectotype].—Tryon, 1887:135, pl. 24: fig. 42.—Kobelt, 1898:239, pl. 42: fig. 3.—Dance, 1974:67, text fig.
- Cerithium rubro-lineatum* Sowerby, 1855:874, pl. 183: fig. 199 [type not found, no locality cited, fig. 199 here selected to represent lectotype].—Tryon, 1887:135.—Kobelt, 1898:241–242, pl. 42: figs. 8, 9.
- Cerithium humile* Dunker, 1861:9, pl. 2: fig. 17 [type not found, fig. 17 here selected to represent lectotype; no locality cited; Okinawa here selected as type-locality]; 1882:106.—Lischke, 1869:72; 1871:50, pl. 3: fig. 18 [not figures 19, 20].—Tryon, 1887:134, pl. 25: fig. 66.
- Cerithium moniliferum* Kiener.—Sowerby, 1865, pl. 4: fig. 20 [not *Cerithium moniliferum* Kiener, 1841; is *Cerithium bifasciatum* Sowerby, 1855].
- Cerithium nigro-fasciatum* Sowerby, 1865, pl. 9: fig. 58 [type not found, fig. 58 here selected to represent lectotype; type-locality: Philippines].—Tryon, 1887:134, pl. 24: fig. 40.
- Cerithium obesulum* Sowerby, 1865, pl. 20: fig. 149, pl. 12 [supplementary]: fig. 318.—Tryon, 1887:139, pl. 26: fig. 93.—Kobelt, 1895:171, pl. 32: fig. 9.
- Cerithium Uranus* [sic] Bayle, 1880:251 [new name for *Cerithium vittatum* Sowerby, 1855].
- Clypeomorus clypeomorus* Jousseaume, 1888:171 [lectotype, here selected and figured, fig. 10a, MNHNP, no number; type-locality: Obock, French Somaliland]; 1930:270–272.—Fischer, 1901:112.
- Cerithium morus* Lamarck var. *moniliferum* Dufresne.—Schepman, 1895:162; 1909:161.—Horst and Schepman, 1899: 228.
- Cerithium oceanicum* Hedley, 1899:431–432, fig. 19 [holotype: AMS c5939; type-locality: Funafuti, Ellice Id].
- Cerithium concisum moniliferum* Kiener.—Oostingh, 1923:

- 72–73 [not *Cerithium moniliferum* Kiener, 1841].
Clypeomorus penthusarus Iredale, 1929:278 [new name for *Cerithium morus* Lamarck, 1822].
Cerithium (Pithocerithium) morum Lamarck.—Abrard, 1946: 56.
Clypeomorus concisum (Hombron and Jacquinot).—Wissema, 1947:71 [not *Cerithium concisum* Hombron and Jacquinot, 1852].
Cerithium morus Bruguière.—Demond, 1957:292, fig. 8 [not *Cerithium morus* Lamarck, 1822; is *Clypeomorus batillariaeformis* Habe and Kosuge, 1966].
Cerithium tuberculatus (Linnaeus).—Shuto, 1969:67–68, pl. 2: figs. 6, 12 [not *Cerithium tuberculatum* Linnaeus, 1758; is *Cerithium bifasciatum* Sowerby, 1855].
Cerithium (Conocerithium) aff. egenum.—Ladd, 1972:40, pl. 9: fig. 11 [not *Cerithium egenum* Gould, 1849; is *Cerithium bifasciatum* Sowerby, 1855].
Clypeomorus moniliferus (Kiener).—Cernohorsky, 1972:70 [in part: pl. 16: fig. 5, only].
Clypeomorus humile (Dunker).—Shirai, 1977:275 [not *Cerithium humile* Dunker, 1861; is *Clypeomorus batillariaeformis* Habe and Kosuge, 1966].
Clypeomorus morus (Lamarck).—Popenoe and Kleinpell, 1978:40, pl. 2: fig. 21.

DESCRIPTION.—*Shell* (Figures 10, 11; Table 6): Shell thick, obese with teleoconch of 8–9 inflated whorls. Length/width index 2.09. Adult whorls slightly flattened dorsoventrally. Protoconch unknown. Penultimate whorl sculptured with 3 dominant equally spaced, spiral, beaded cords. The beads are rounded, smooth, and are aligned axially on the spiral cords forming ribs, especially on earlier whorls and on narrow morphs. Between each of the dominant spiral cords are 5, smaller, spiral lirae, 2 of which are tiny and 3 a little larger. The lirae are incised with many microscopic spiral lines, and axial divisions on lirae appear scale-like. Basic sculpture of penul-

timate whorl repeated on the other whorls of teleoconch. Former varices present only on right and left side of shell, dividing it into dorsal and ventral halves. Suture incised and slightly wavy. Body whorl fat, sculptured with 6 dominant, beaded, spiral cords on inflated portion of whorl. At siphonal constriction are 2 more spiral cords of a scaly appearance. Minor lirae and incised spiral lines lie between the dominant spiral cords of the body whorl. Siphonal constriction begins at midpoint of the aperture. Aperture ovate, about one-third the length of the shell, Columella concave with moderate parietal callus covering portion of body whorl. Outer lip thick, rounded, moderately crenulate and with beveled, thickened inner portion that is lined with numerous denticle-like lirae. Outer lip straight, aperture parallel to plane of substrate. Anterior inhalant siphonal canal short, deeply incised and slightly reflected, directed leftward about 45 degrees to shell axis. Anal canal at posterior of aperture, adjacent to body whorl and forming distinct, deeply incised groove bordered with columellar parietal plait that extends well into aperture of shell.

Periostracum thin, not evident. Shell color exceedingly variable, but normally comprising

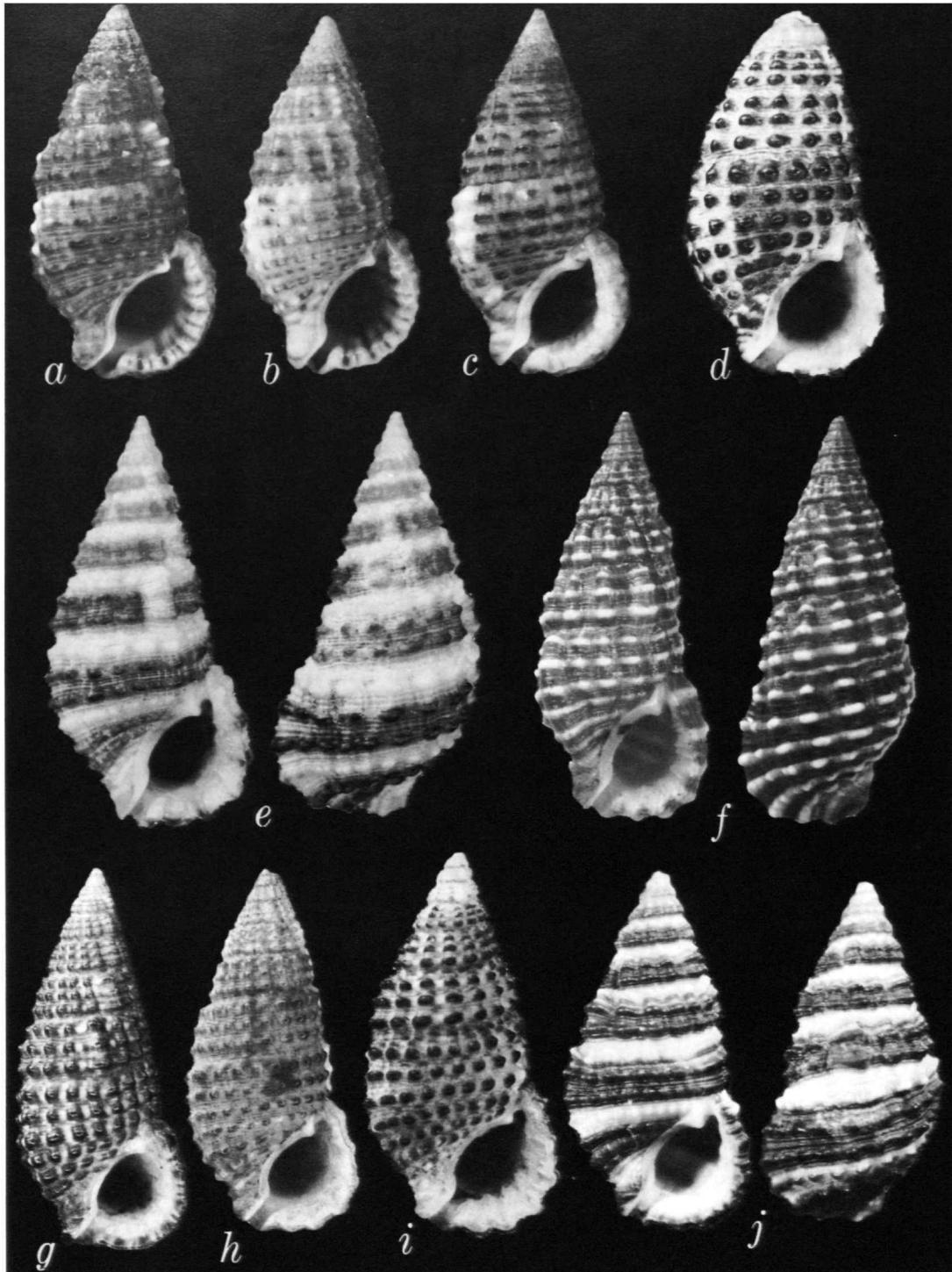
TABLE 6.—Analysis of shell parameters of *Clypeomorus bifasciata bifasciata* (measurements in mm).

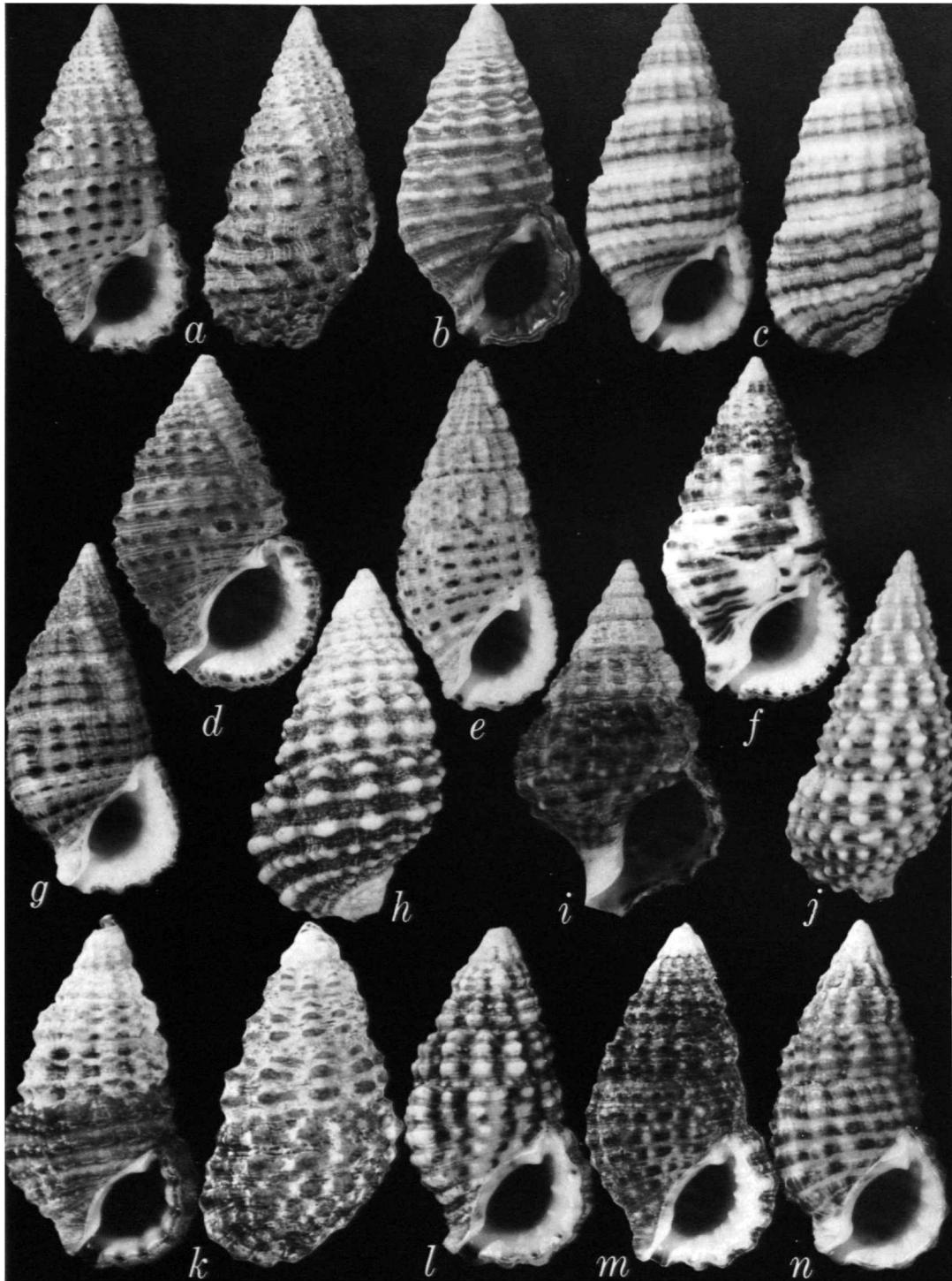
Character	n	\bar{x}	sd	Range
Shell length	439	20.13	3.88	10.9–29.7
Shell width	439	9.65	1.86	5.0–6.4
Aperture length	439	5.82	1.15	2.9–9.0
Aperture width	439	3.65	0.76	2.0–6.4
No. beads per whorl	30	16.23	2.19	13–22

Length/width index: 2.09

Shell length/aperture length index: 3.45

FIGURE 10.—Types of taxa synonymous with *Clypeomorus bifasciata* (Sowerby, 1855): a, lectotype of *Clypeomorus clypeomorus* Joussemae, 1888, MNHNP, no number, from Obock, Gulf of Aden (16.7 × 7.6 mm); b, paralectotype of *Clypeomorus clypeomorus*, NMHNP, from Massaouah, Gulf of Aden (15.2 × 6.9 mm); c, paralectotype of *Clypeomorus clypeomorus*, NMHNP, from Obock, Gulf of Aden (16.5 × 7.5 mm); d, holotype of *Cerithium concisum* Hombron and Jacquinot 1852, NMHNP, from "Oceanie" (21 × 11.2 mm); e, holotype of *Cerithium bifasciatum* Sowerby, 1855, BMNH, not registered, from St. Nicholas, Cebu, Philippines (25.8 × 11.6 mm); f, lectotype of *Cerithium vittatum* Sowerby, 1855, BMNH 1907.12.30.362.3, no locality cited (20.2 × 8.4 mm); g, lectotype of *Cerithium gemmulatum* Hombron and Jacquinot, 1852, NMHNP, no number, from Torres Strait (24.5 × 6.8 mm); h, paralectotype of *Cerithium gemmulatum*, NMHNP, from the Solomon Islands (23.8 × 10 mm); i, paralectotype of *Cerithium gemmulatum*, NMHNP, from the Solomon Islands (22.5 × 10.4 mm); j, lectotype of *Cerithium nigrofasciatum* Sowerby, 1855, from the Philippines (21.9 × 10.8 mm).





gray, brown, or black blotches on a white background and darkly pigmented beads. Darker pigments sometimes arranged in spiral bands. Aperture, collumella white; weak brown spots sometimes at edge of inner lip.

Operculum thin, corneous ovate, paucispiral with nucleus near periphery. Attachment scar on obverse elliptical, occupying about one-third of surface.

Radula (Figure 12; Table 7): Radular ribbon relatively long, about 4 mm in length and comprising about 98 rows of teeth. Shell length/radula length index 5.12. Rachidian tooth (Figure 12*f*) pentagonal, having a basal plate with long, pointed basomedial projection that is flanked by a pit-like depression on each side. Top of rachidian tooth straight, cutting edge with wide, central, triangular cusp flanked by 1, rarely 2, smaller rounded cusps on each side. Lateral tooth (Figure 12*b,d,f*) trapezoidal with long, twisted basolateral extension that inserts onto basal radular membrane, basal plate of lateral tooth with long basal inner extension. Top of lateral tooth straight with cutting edge comprising small, blunt inner denticle, large, wide, spatulate cusp and 2 or 3 smaller, blunt denticles. Tips of marginals (Figure 12*e*) sharply curved, spoon-shaped, comprising large rounded central

TABLE 7.—Analysis of radular parameters of *Clypeomorus bifasciata bifasciata* (measurements in mm).

Character (n=12)	\bar{x}	sd	Range
Radula length	4.17	0.56	4.07–4.73
Rows of teeth	98.33	11.69	90–104
Shell length	21.33	2.00	17.08–23.64

Shell length/radula length index: 5.12

cusps that is flanked by 2 smaller blunt cusps on inner side and 1 blunt small cusp on outer side. Outer marginal tooth differs in lacking outer cusp.

Animal (Figure 13A,C,F): Color of head-foot variable, but usually olive brown to whitish tan covered with tiny opaque white dots and larger black maculations. Top half of mantle edge bifurcate in cross section comprising smooth outer edge and inner edge bearing papillae (Figure 13E, *mp*). Underside of inhalant siphon (Figure 13E, *inh*) bright yellow bordered with black. Head moderately elongate bearing long tentacles (Figure 13E, *t*). Right side of foot has long ciliated groove (Figure 13E, *cg*) leading from exhalant siphon to base of foot. No ovipositor seen on females.

Within the pallial complex the brown bipectinate osphradium (Figure 13E, *os*) extends the length of the mantle cavity becoming thin and worm-like near the inhalant siphon (Figure 13E, *inh*) where it turns to the left and away from the ctenidium. Filaments of the osphradium are squarish or block-like. The ctenidium (Figure 13E, *ct*) extends the length of the mantle cavity. The hypobranchial gland (Figure 13E, *hg*) is thick, glandular, and is divided lengthwise by a central furrow. The anus (Figure 13D,E, *a*) opens anterior to the pallial gonoduct. The pallial gonoducts of both sexes are open, and when the mantle cavity is opened by a dorsal longitudinal cut, each is seen to comprise a medial (outer) lamina (Figure, 13C,F, *ml*) on the right and a lateral (inner) lamina (Figures 13C,F, *ll*) on the left. The pallial gonoducts appear white and glandular, especially in females.

The reproductive tract comprises the gonads

FIGURE 11.—*Clypeomorus bifasciata*, showing variation in shell form, sculpture, and color (all specimens shown at same size; an immature specimen (*i*) is presented for comparison with adults): *a*, Po Bui Island, Sandakan, N Borneo (USNM 232865, 28.6 mm); *b*, Wakanura, Kyushu, Japan (USNM 228240, 17.1 mm); *c*, Mbweni, Zanzibar (USNM 604220, 25.7 mm); *d*, Goa, India (USNM 442931, 23.9 mm); *e*, Eman Point, Marong, Bataan, Luzon, Philippines (USNM 774756, 26.8 mm); *f*, (Pago Pago Harbor, Tutuila, Samoa (USNM 774538, 21.2 mm); *g*, Eman Point, Marong, Bataan, Luzon, Philippines (USNM 774756, 23.4 mm); *h*, Heron Island, Queensland, Australia (USNM 623098, 12.3 mm); *i*, immature specimen, Eman Point, Marong, Bataan, Luzon, Philippines (USNM 623098, 12.3 mm); *j*, Eaglehawk Islands, Dampier Archipelago, Western Australia (WAM 868-76, 20.2 mm); *k*, Nagasaki, Kyushu, Japan (USNM 228241, 19.6 mm); *l*, Point Quobba, Western Australia (WAM 867-76, 19 mm); *m*, Hahajima, Ogasawara, Bonin Islands (USNM 175584, 16 mm); *n*, Troughton Island, Western Australia (WAM 874-26, 26 mm).

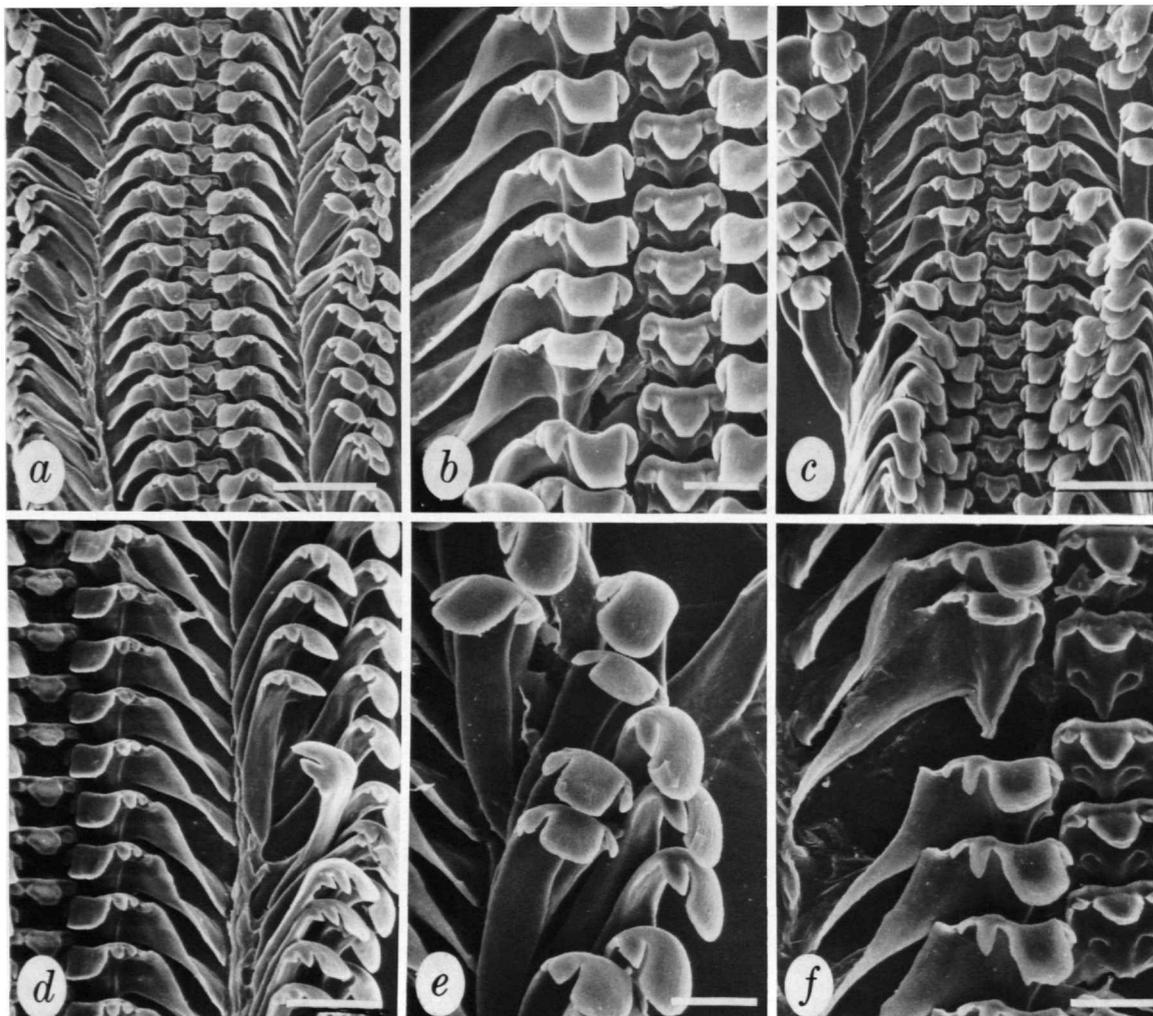


FIGURE 12.—SEM micrographs of radula of *Clypeomorus bifasciata*: *a*, general view of radula with marginal teeth folded back, Apra Harbor, Guam, USNM 774776 (bar = 150 μm); *b*, detail of lateral and rachidian teeth in specimen from Ngo Bay, New Caledonia, USNM no number (bar = 50 μm); *c*, general aspect of radula in specimen from N'Go Bay, New Caledonia, USNM no number (bar = 150 μm). Marginal teeth folded back in upper portion of specimen; *d*, half row of radula showing insertion of lateral and marginal teeth onto radular membrane, Cabago Point, Looc Bay, Bagac, Bataan, Luzon, Philippines, USNM 774746 (bar = 75 μm); *e*, detail of cusps on tips of marginal teeth, Eman Point, Morong, Bataan, Luzon, Philippines, USNM 774756 (bar = 50 μm); *f*, detail of rachidian and lateral teeth in specimen from Cabago Point, Looc Bay, Bagac, Bataan, Luzon, Philippines, USNM 774746 (bar = 50 μm).

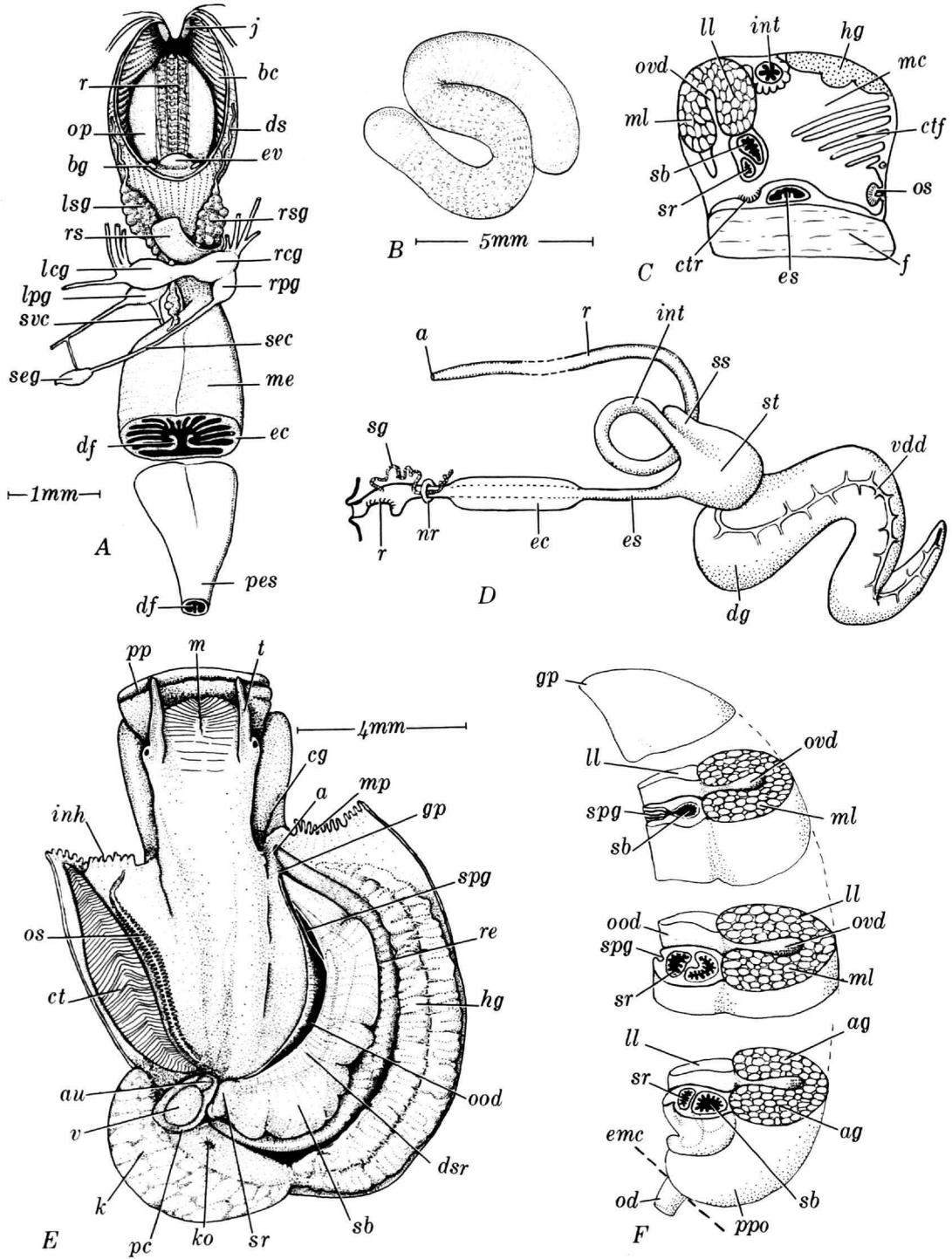
in the upper whorls, the renal gonoducts, and the pallial gonoducts. In females, the glandular gonoduct is divided into a proximal albumen gland (Figure 13F, *ag*) and a mid capsule gland. The medial lamina bears the spermatophore bursa (Figures 13C,E,F; 14, *sb*), the sperm collecting gutter (Figures 13E,F; 14, *spg*), and the seminal receptacle (Figures 13C,E,F; 14, *sr*) while the lateral lamina is partially fused to the mantle wall. At the edge of the distal end of the medial lamina there is a deep ciliated gutter, the sperm collecting gutter (Figures 13E,F; 14, *spg*), which bifurcates and leads into 2 different areas of the lamina: (1) it becomes a wide, shallow sperm gutter along the edge of the lamina, opening into the seminal receptacle (Figures 13C,E,F, *sr*) at the proximal end; (2) it runs deep into the tissue of the medial lamina, becoming a long ciliated tube leading into a wide spermatophore bursa (Figures 13C,E,F; 14, *sb*), interiorly lined with fine transverse plications. The complex seminal receptacle (Figure 13E, *sr*) is ovate in shape and lies at the proximal end of the medial lamina. It does not have an internal opening into the spermatophore bursa. It opens at its proximal end into the proximal pallial oviduct, presumably at the site of fertilization. Externally, but within the mantle cavity, the seminal receptacle (Figure 13E, *sr*) appears as a white bulbous sac at the proximal end of the pallial gonoduct adjacent to the pericardium. The lateral lamina of the pallial oviduct is fused to the body wall of the snail at its outer edge and is longitudinally divided into a thin, transparent section and a thickened inner area, which in turn is transversely divided into thick glandular folds comprising a proximal albumen gland and a median capsule gland. Adjacent to the proximal end of the lateral lamina there is a highly ciliated glandular tract (Figure 13C, *ctr*) on the floor of the mantle cavity opposite the medial lamina. The alimentary tract includes a pair of chitinous jaws (Figure 13A, *j*) and a large buccal mass. A large pair of latero-posterior muscles connect the odontophore to the body wall along with numerous thin muscular strands, which encircle the entire buccal mass. A

pair of salivary glands (Figure 13A, *lsg*, *rsg*) lie anterior to the nerve ring (Figure 13D, *nr*) but a small portion of the left gland passes through the ring. Each salivary gland has a thin, moderately long duct (Figure 13A, *ds*), which runs along the side of the buccal mass and enters at the midlateral portion of the buccal cavity (Figure 13A, *bc*). Posterior to the nerve ring, the midesophagus widens considerably to form a large midesophageal crop lined with many digitate folds (Figure 13A, *ec*). The stomach (Figure 13D, *st*) is typically cerithioid with complex folds and sorting surfaces, a gastric shield, style sac (Figure 13D, *ss*) and crystalline style, which is about the length of the snout of the snail. In the upper intestine (Figure 13D, *int*), the feces are molded to form ovoid fecal pellets that are stacked transversely in the lower intestine.

The epiathroid nervous system is tightly condensed at the nerve ring. The *rpg* ratio of Davis et al. (1976:263) (length of the pleuro-esophageal connective divided by the sum of the lengths of the supraesophageal ganglion, the pleuro-esophageal connective, and the right pleural ganglion) is 0.61, close to the values of 0.59 observed in *Cerithium* species (Houbrick, 1980:132). The higher the value, the more loosely condensed the nervous system. This indicates that the *Clypeomor* group is relatively advanced compared with other groups such as the potamidids.

REMARKS.—The history of the taxon is complex, as exemplified by the lengthy synonymy. Long known as *Cerithium morus* Lamarck, 1822, this species has been cited by many authors under this name. Dodge (1956:290) noted that “the *morus* of modern authors is the *morus* of Lamarck.” A great deal of confusion exists in the literature because of misidentification and assignment of other taxa to the species *morus* Lamarck. The synonymy presented above clarifies much of this. Many of these names are preoccupied or were based on mixed lots of several species when originally proposed. I have examined the type-material of most of these taxa and many are figured in this paper (Figures 10, 15).

Kobelt (1889:241) considered *Cerithium vitta-*



tum, *Cerithium uranus*, and *Cerithium hanleyi* to be synonyms of *Cerithium rubrolineatum*, which I regard as a synonym of *Clypeomorus bifasciata*. The earliest available name is *Cerithium bifasciatum* Sowerby, 1855.

It has been difficult to assign a definite publication date to the names *Cerithium gemmulatum* and *Cerithium concisum* of Hombron and Jacquinot. These names first appear in the Atlas that was issued in the years 1841–1854. The text appeared in 1854. The names of both taxa appear on plate 24 of the Atlas, but there is no indication as to which year the plate was pub-

FIGURE 13.—Anatomical structures and spawn mass of female *Clypeomorus bifasciata*: A, diagrammatic representation of anterior alimentary tract showing interrelationships of buccal mass, salivary glands, nerve ring, and midesophagus; B, spawn mass from Guam; C, section through mantle cavity of female showing relationship of pallial oviducts to other mantle organs; D, generalized diagram of alimentary tract; E, mantle organs exposed by dorsal longitudinal cut in mantle (the visceral whorls are removed and the kidney has been pulled back exposing the pericardium and proximal pallial oviduct); F, diagrammatic representation of female pallial oviduct sectioned to show internal arrangement of ducts. (Abbreviations: *a* = anus; *ag* = albumin gland; *au* = auricle; *bc* = buccal cavity; *bg* = buccal ganglion; *cg* = ciliated groove; *ct* = ctenidium; *ctf* = ctenidial filament; *ctr* = ciliated tract; *df* = dorsal fold of esophagus; *dg* = digestive gland; *ds* = duct of salivary gland; *dsr* = distal seminal receptacle; *ec* = midesophageal crop; *emc* = end of mantle cavity; *es* = esophagus; *ev* = esophageal valve; *f* = foot; *gp* = gonoduct pore; *hg* = hypobranchial gland; *il* = inner lamina; *inh* = inhalant siphon; *int* = intestine; *j* = jaw; *k* = kidney; *ko* = kidney opening; *leg* = left cerebral ganglion; *ll* = lateral lamina; *lpg* = left pleural ganglion; *lsg* = left salivary gland; *m* = mouth; *mc* = mantle cavity; *me* = midesophagus; *ml* = medial lamina; *mp* = mantle papillae; *nr* = nerve ring; *od* = oviduct; *ood* = opening to pallial oviduct; *op* = odontophore; *opg* = opening to pallial gonoduct; *os* = osphradium; *ovd* = oviducal groove; *pc* = pericardium; *pes* = posterior esophagus; *pp* = propodial groove; *ppo* = proximal pallial oviduct; *r* = radula; *rcg* = right cerebral ganglion; *re* = rectum; *rpg* = right pleural ganglion; *rs* = radula sac; *rsg* = right salivary gland; *sb* = spermatophore bursa; *sec* = supraesophageal connective; *seg* = supraesophageal ganglion; *sg* = salivary gland; *spg* = sperm gutter; *sr* = seminal receptacles; *ss* = style sac; *st* = stomach; *svc* = subvisceral connective; *t* = tentacle; *v* = ventricle; *vvd* = vas deferens.)

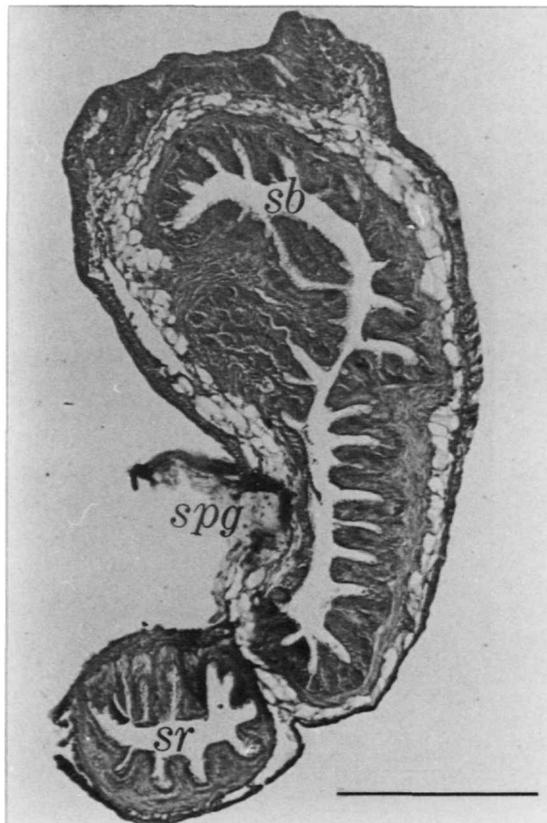


FIGURE 14.—Histological section through proximal part of outer lamina of pallial oviduct showing spermatophore bursa (*sb*), seminal receptacle (*sr*), and sperm gutter (*spg*) (bar = 0.25 mm).

lished. According to Dr. Philippe Bouchet (in litt.) of the Muséum National d'Histoire Naturelle, Paris, plate 24 of Hombron and Jacquinot was published between December 1851 and December 1852, as indicated by the stamp appearing on it in the French National Library. I have cited the year 1852 as the appropriate date. As can be seen in the synonymy above, both names are preoccupied.

The name *Cerithium morus* Lamarck, 1822, cannot be used because it is preoccupied by Bruguière's (1792) use of this name. I have previously shown (Houbrick, 1978b:643) that

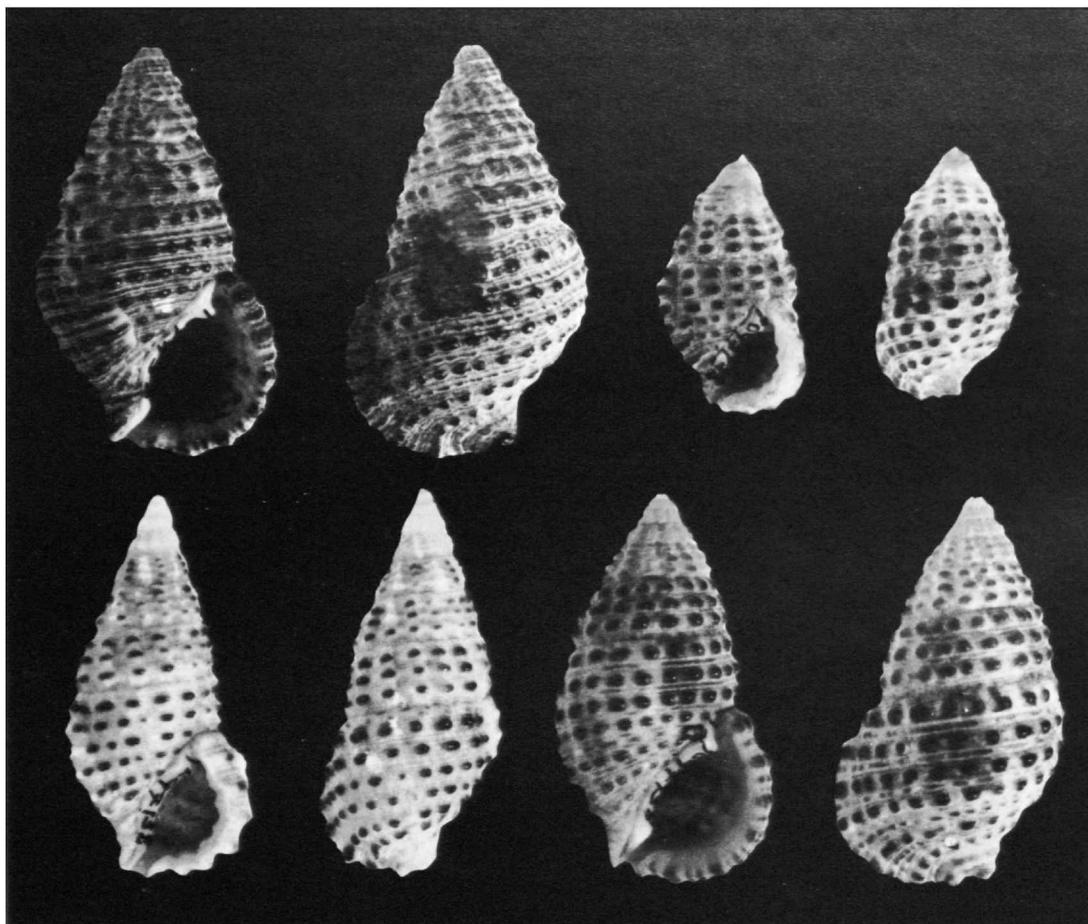


FIGURE 15.—Types of *Cerithium morus* Lamarck, 1822 (= *Clypeomorus bifasciata* (Sowerby)), National Muséum d'Histoire Naturelle, Geneva, no. 1097/38. Largest specimen selected as lectotype.

Brguière's name is a synonym of *Batillaria sordida* (Gmelin, 1791), at least in part. All of Bru-guière's (1792:500) figure references in his original description represent *Batillaria sordida* with the exception of figure 89 of Lister (1770), which is not clearly attributable to any species. I examined Lamarck's type material in the Geneva Museum. With the largest of the specimens (26.5 × 13.5 mm) is a written label in Lamarck's hand that matches the length cited in his original description, 26 mm ("11 lignes et demie," Lamarck,

1822:75). This specimen is here regarded as the lectotype of *Cerithium morus* Lamarck (Figure 15). The three remaining paratypes are similar in sculpture to the lectotype.

I regard *Cerithium gemmulatum* Hombron and Jacquinet, 1852, to be conspecific with *Clypeomorus bifasciata*. The five paratypes in the Paris Museum constitute a mixed lot: three are *Clypeomorus bifasciata* (two from Torres Strait and one from the Solomon Islands) and the other two are *Clypeomorus batillariaeformis* Habe and Kosuge

(the *Cerithium moniliferum* Kiener, 1841, of authors), both from Vavao. I select the largest of the two specimens from Torres Straits (24.5 × 6.8mm) as the lectotype of *Cerithium gemmulatum* (Figure 23a). The name *gemmulatum* is preoccupied.

Clypeomorus clypeomorus Jousseaume, 1888, is here regarded as a Red Sea phenotype of *Clypeomorus bifasciata*.

Cerithium metcalfi Sowerby, 1855, is probably conspecific with *Clypeomorus bifasciata*. Sowerby's (1855) figures of the former also resemble *Cerithium inflatum* Quoy and Gaimard, 1834, as was noted by Tryon (1887:132). A search for the type material of *Cerithium metcalfi* at the British Museum (Natural History) was unsuccessful; consequently, its exact identity remains uncertain.

E.A. Smith (1884:63) noted the perplexing taxonomic problems of *Clypeomorus bifasciata* complex and in his synonymy listed *Clypeomorus moniliferum* Kiener (= *Clypeomorus batillariaeformis* Habe and Kosuge), and *Clypeomorus carbonarium* Sowerby (= *Batillaria sordida* (Gmelin)). These two species are distinct, valid taxa and must be excluded from the synonymy of *Clypeomorus bifasciata*.

Cernohorsky's (1972:70, pl. 16: figs. 3–5) depiction of *Clypeomorus moniliferus* (= *Clypeomorus batillariaeformis* Habe and Kosuge) consists of a mixed lot: although his figure 5 represents true *Clypeomorus bifasciata*, figure 4 is somewhat equivocal, while figure 3 is *Clypeomorus batillariaeformis*. Cernohorsky (1972:70) erroneously placed *Clypeomorus bifasciata* (cited as *Clypeomorus morus* Lamarck) into the synonymy of *Clypeomorus batillariaeformis* (cited as *Clypeomorus moniliferum*). As I have already shown, these two species are distinct. Cernohorsky (1972:71) also regarded *Cerithium vittatum* Sowerby, 1855, and *Cerithium uranus* Bayle, 1880, as synonyms of *Cerithium zonatum* (Wood, 1828) (cited as a *Clypeomorus*); but examination of the types convinces me that *Cerithium vittatum* is conspecific with *Clypeomorus bifasciata*. Moreover, Wood's (1828) species, *zonatum*, is not a member of the genus *Clypeomorus*, but is a true *Cerithium*.

Wissema (1947:71) considered *Cerithium moniliferum* Kiener, 1841 (= *Clypeomorus batillariaeformis* Habe and Kosuge) to be a synonym of *Clypeomorus conisum* (= *Clypeomorus bifasciata*) and indicated that his material belonged "to the var. *moniliferum* (Kiener), which certainly is not of specific rank." I believe his remarks show that his specimens were erroneously identified as *Clypeomorus bifasciata* (cited as *Clypeomorus concisum*) and I have indicated his error in the synonymy presented above.

Schepman (1909:160) and Oostingh (1923:72) regarded *Cerithium moniliferum* Kiener (= *Clypeomorus batillariaeformis* Habe and Kosuge) as a synonym of *Clypeomorus bifasciata* but the sympatric geographic distribution of the two, as well as a careful study of shell sculpture, anatomy, and ecology of the former species do not support this view. *Cerithium obscurum* Hombron and Jacquinet, 1852, was erroneously placed into the synonymy of *Clypeomorus bifasciata* by Oostingh (1923:71; cited as *Clypeomorus concisum*) but is a synonym of *Clypeomorus batillariaeformis* Habe and Kosuge.

ECOLOGY.—This species is an epifaunal inhabitant of the high intertidal zone and usually occurs in dense populations on hard or loose rocky substrata. Occasionally it is found on softer substrata. I observed *Clypeomorus bifasciata* living in the upper intertidal zones in Fiji, Guam, the Philippines, New Caledonia, and Queensland, Australia. Museum collection records confirm the fact that this species lives in similar habitats of the upper intertidal throughout its range. At Pago Bay, Guam, I observed a population of *Clypeomorus bifasciata* living on the undersides of rocks during the day, during which they appear to be avoiding high temperatures and desiccation. Animals are more active during incoming tides and at night. At Lizard Island, Queensland, Australia, this species lives among rocks at the high tide mark, where it is partially buried in coarse sand between rocks at low tide. This population was more active at higher tides and at night and comprised many individuals of highly polymorphic color patterns. Another population,

of low density, from a mangrove swamp at Apra Bay, Guam, was found living on stones and roots at the high tide mark adjacent to the gray, muddy sand. This kind of estuarine habitat is less common for *Clypeomorus bifasciata* than rocky intertidal habitats. *Clypeomorus bifasciata* is abundant in the Philippines where I observed large populations living on the rocky, high, intertidal zone along the western Bataan peninsula. In Fiji, a population from Lauthala Bay lived at the upper intertidal zone on beach rock covered with fine silt and sediment. Identical habitats were observed along the southeastern shore of New Caledonia where this species is common. In all of these localities, with the exception of Guam, the populations of *Clypeomorus bifasciata* are sympatric with those of *Clypeomorus batillariaeformis*, which live in the mid-intertidal zone. Yaron (1979:234) observed the Red Sea form of this species (cited as *Clypeomorus moniliferus*) living around stones in wet sand above rocky slabs in the high tidal zone at Ras Bourka, Gulf of Aqaba, where it partially buried in the sand during low tides, emerging at the incoming tide. According to Ayal (in litt.), the Red Sea morph is very common in the Gulf of Aqaba and Gulf of Suez where it occupies the highest tidal zone of all cerithiids. It lives in these areas in crevices and under stones in the barnacle zone and the limpet zone and is active mainly during night ebb tides.

The reproductive biology of this widespread species needs detailed study. A number of papers have dealt with its reproduction, but most taxa cited in these papers are probably misidentified. Natarajan (1957) has described the egg masses of *Clypeomorus bifasciata* (cited as *Cerithium morus*) and records ribbon-like masses ranging from 60 to 185 mm in length, each containing an average of 9100 eggs. Hatching took place in 3 days and the presence of free swimming veliger larvae with well-developed velar lobes suggested a long pelagic phase. A more recent paper by Rao and Ramasarma (1980) described similar development for *Clypeomorus clypeomorus* Jousseaume, a name given to the Red Sea morph of *Clypeomorus bifasciata*. These authors compared

their species with what they cite as *Cerithium morus*, another synonym of *Clypeomorus bifasciata*. It is thus unclear what species they had. Kasinathan and Govindan (1975:96–97) recorded egg masses of *Clypeomorus bifasciata* (cited as *Cerithium morus*) deposited in the form of folded ribbons containing great numbers of small eggs that, upon hatching, had a short pelagic larval phase of about 48 hours; thus, they may be *Clypeomorus bifasciata*. None of these papers illustrate the cited species. I observed a population of *Clypeomorus bifasciata* at Pago Bay, Guam, which spawned in October 1978. Spawn are deposited on the undersurfaces of rocks and comprise sheet-like jelly masses about 45 mm long, when uncoiled, and 4.5 mm wide. They are filled with rows of tiny eggs, each 0.1 mm in diameter, and arranged in layers, three deep (Figure 13b). The spawn masses are numerous: e.g., a rock with an undersurface of 16 × 18 cm had six egg masses attached to it. Although spawn are exposed during low tides, they remain moist. Larvae are free swimming, but the length of the pelagic phase is unknown.

The large buccal mass and relatively long radular ribbon, as well as the rocky microhabitat of this species, indicate that it grazes on microalgae associated with a hard substratum. Stomach contents of dissected specimens from all localities where I worked consisted of coarse sand grains, detrital particles, diatoms, and filamentous green algae. The tiny fecal pellets are ovoid and are made up of sand grains, algal fragments, and detrital particles.

DISCUSSION.—*Clypeomorus bifasciata* has long been identified or confused with other similar taxa. Frequently, several *Clypeomorus* and *Cerithium* species are "lumped" with it and given various names. Conversely, this taxon has undergone excessive "splitting" as is evident from the lengthy and complex synonymy. The differing generic and subgeneric assignments of this taxon also reflect the taxonomic instability. As a result, most of the biological literature about the species is useless, because the names cited are usually incorrect or suspect. This is particularly true of

papers that do not illustrate the nominal species with which they are concerned. For these reasons, I have disregarded most of the anatomical, life history, and ecological observations cited in the literature and have relied on my own field and laboratory observations. I have also chosen to disregard locality records cited in the literature; consequently, I believe that the ranges and ecological limits cited in this paper are substantially accurate.

Variability in shell size and color is common and has led to an excess of names, but the shell form and sculpture of *Clypeomorus bifasciata* are fairly constant. Because of their high intertidal habitat, most specimens frequently have badly eroded shells that usually lack a protoconch. The presence of sympatric congeners with similar shells that live in the same intertidal habitat in a given locality and the mixing of other species due to hermit crab transport of empty shells is reflected by the innumerable mixed lots encountered in most museum collections. All of these factors have contributed to a taxonomic morass of misidentification seldom encountered with any other cerithiid taxon.

The congener most frequently confused with *Clypeomorus bifasciata* is *Clypeomorus batillariaeformis* Habe and Kosuge, 1966, previously known in the literature as *Cerithium moniliferum* Kiener, 1841. These two species are usually sympatric and abundant throughout most of their respective ranges. Because they have the same basic shape and size, they are frequently collected together and found mixed in museum collections. In the field, the two species are ecologically segregated by their vertical distribution in the intertidal zone: *Clypeomorus bifasciata* is found in the high intertidal zone while *Clypeomorus batillariaeformis* occurs below it in the upper midtidal zone. The two species are frequently found adjacent to each other and their ecological distribution may be further complicated by vertical irregularities of the substratum in the intertidal zone. This is particularly true of rocky intertidal habitats along reef fronts.

The easiest way to distinguish adult specimens

of the two species is to compare the placement of the major varix on the body whorl. In *Clypeomorus bifasciata*, the varix is on the body whorl directly opposite the outer lip, while in *Clypeomorus batillariaeformis* the varix occurs on the right dorsal surface of the body whorl at an angle of 40 degrees to the plane of the aperture, when viewed anteriorly (Figure 16). *Clypeomorus bifasciata* is also characterized by its rounded whorls and its dorsoventrally compressed shell. The beaded sculpture tends to be aligned both axially and spirally. The anterior canal is relatively wide and the thick outer lip is crenulated and has an inner thickened, lirate, beveled slope that leads into the aperture. The plane of the outer lip runs parallel to the shell axis. When the shell is viewed anteriorly, the lower part of the outer lip is usually below the siphonal canal and does not seem to close over it. In contrast, when viewed anteriorly, *Clypeomorus batillariaeformis* has a more oval, rounded shell, and the whorls are more elongate and straight sided. The aperture is more rounded, the anterior siphonal canal narrower, and the outer lip thinner and relatively smoother than in *Clypeomorus bifasciata*. The inner surface of the outer lip is not thick and lirae are weak if present. When viewed anteriorly, the lower portion of the outer lip seems to close over the anterior siphonal canal. The beaded sculpture rarely is axially aligned. Figure 16 illustrates the main differences between these two confusing species. If the comparisons noted above are used, most identifications may be made without trouble; but there are some morphs of both species that are very difficult to determine with accuracy. Immature specimens of these species are exceptionally difficult to identify. In the field, the two species, although sympatric, rarely mix together in a single population; consequently, any immature snails found within a population are probably conspecific. Museum lots having immature shells should not be relied on as being conspecific because they frequently contain mixed samples. The possibility of hybrids should be considered.

Clypeomorus bifasciata is frequently confused

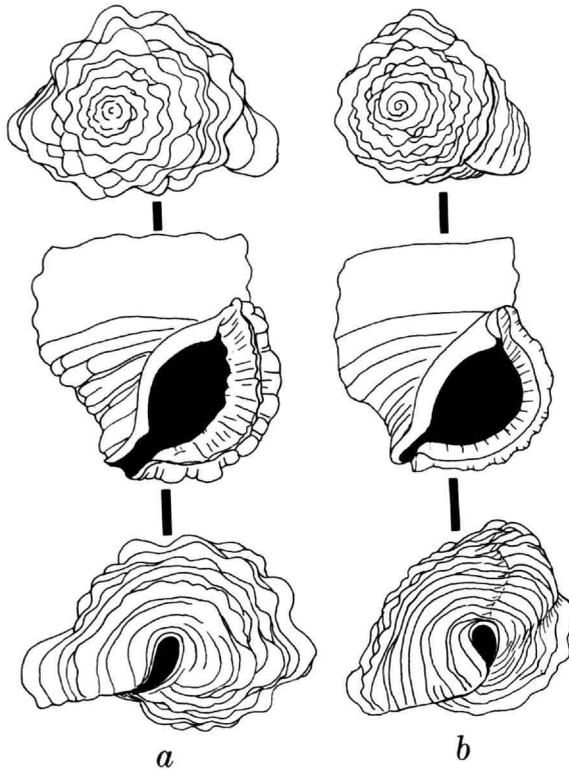


FIGURE 16.—Shell comparisons between (a) *Clypeomorus bifasciata* and (b) *Clypeomorus batillariaeformis*. Note placement of penultimate varix in both taxa and thicker, beveled lip in *C. bifasciata*.

with its parapatric congener, *Clypeomorus brevis* (Quoy and Gaimard, 1834), with which it is morphologically closely allied. The latter species is significantly smaller than *Clypeomorus bifasciata* and differs from it in having only two primary spiral cords of nodules per whorl and a more rugose, reticulate appearance. Moreover, *Clypeomorus brevis* is essentially restricted to the central and south Pacific Island groups and is not sympatric with *Clypeomorus bifasciata* to any degree, except in the Moluccas. I regard these two species as sister groups: both share the same habitat and have almost identical shell morphology and gross anatomy. They fit the concept of a superspecies as defined by Mayr (1969:52), and as such may also be regarded as semispecies.

Another common sympatric congener fre-

quently found in the intertidal habitat and confused with *Clypeomorus bifasciata* is *Clypeomorus petrosa* (Wood, 1828). The latter species lives in the midtidal zone and has a fat shell with strongly convex, angulate whorls and an irregular sculpture of elongate spiral nodes and beads. The major varix is on the dorsal surface of the body whorl. *Clypeomorus petrosa* is usually a much larger, more nodulose snail than is *Clypeomorus bifasciata*.

Cerithium zonatum (Wood, 1828) is also sympatric with *Clypeomorus bifasciata*, although it normally occurs at the low tide mark. Some populations of *Cerithium zonatum*, in response to high energy, rocky environments, tend to comprise stocky morphs and are most likely to be misidentified as *Clypeomorus bifasciata*. While both species have an overall beaded sculpture and the major varix of the body whorl is located directly opposite the outer lip, they are quite distinct in all other conchological features. *Cerithium zonatum* generally has a more elongate shell with straight sided whorls and is sculptured with four major beaded spiral cords and several minor beaded spiral lirae on the penultimate whorl. The beads tend to be sharply pointed. In contrast, *Clypeomorus bifasciata* has only three major beaded spiral cords and if smaller spiral lirae are present, they are never beaded.

Clypeomorus subbrevicula (Oostingh, 1925) also resembles *Clypeomorus bifasciata* in its beaded sculpture, but the former species has a limited range in the western Pacific and does not have the heavy varix opposite the outer lip.

An ecophenotypic response is seen in some populations: those from more open oceanic, high energy, rocky habitats tend to be squatter, thicker, and have more distinct beading than those from more sheltered, estuarine situations where the substrate is generally softer. In sheltered habitats, shells are smaller, more slender, and have less distinct beaded sculpture. Because these morphological trends occur throughout the range of *Clypeomorus bifasciata* I do not regard populations exhibiting such trends to have subspecific status.

Within the range of *Clypeomorus bifasciata*

there are three geographically separate populations comprising individuals that are morphologically distinct from the typical form and that may fall into the category of subspecies. Two of these morphs were given specific names: these are *Clypeomorus clypeomorus* (Jousseume, 1888), which is limited to the Red Sea, and *Clypeomorus humilis* (Dunker, 1861) from southern Japan and the Ryukyu Islands. The third population is confined to the Persian Gulf and is herein recognized as a valid subspecies. Specimens from the Red Sea comprise individuals that are smaller, more slender, and have rounder body whorls than those of typical *C. bifasciata* morphs (Figure 10a–c). Moreover, they tend to have a color pattern of black spiral dots on a yellowish background. Nevertheless, neither measurements of shell characters nor radular and anatomical morphology show any significant differences between these Red Sea forms and typical *C. bifasciata*, which is an extremely variable species. The morphological differences seen in Red Sea populations occur in other populations in the Indo-Pacific but in lower frequencies. Although the name *Clypeomorus clypeomorus* Jousseume has been applied to the Red Sea forms, the morphological differences between it and *C. bifasciata* do not justify recognition of a distinct taxon, even at the subspecific level. The observed differences may be due to ecological conditions and isolation of the Red Sea. Red Sea populations should be more carefully studied in situ because they may be taxonomically distinct.

The name *Clypeomorus humilis* (Dunker) has been given to specimens from southern Japan and Ryukyu Islands (Figure 11b,k,l), which tend to be more darkly pigmented and have the apertural part of the body whorl flattened. They are sculptured with more deeply incised spiral lines than typical *Clypeomorus bifasciata* morphs. The beads are more spirally elongated and overall sculpture tends to be more rugose, approaching that of *Clypeomorus brevis* (Quoy and Gaimard). There are many intergrades between these morphs and typical forms, the radula shows no distinct characteristics, and their anatomy has not been examined. For these reasons, I do not now

accord *C. humilis* subspecific status but point out that further study may show the Japanese populations are a distinct subspecies.

Several other geomorphological trends are apparent. For instance, populations of *Clypeomorus bifasciata* from the continental margins of the Indian Ocean exclusive of Australia comprise large individuals with wider, dorsoventrally flattened shells (Figure 11c,d). Curiously, this trend also is seen in some Guam populations. In Fiji, Samoa, and New Caledonia, populations consist of individuals with longer, more slender shells; moreover, populations of dwarf individuals are occasionally seen there. In the tropical portions of northern Australia, dwarf individuals are common. Populations from the north and northwest of Australia tend to be striped or spotted with light brown (Figure 11h,j,n).

Many populations comprise dwarf individuals. I have observed such populations in splash pools above the high tide zone at Lizard Island, Queensland, Australia, and noted that populations of normal-size individuals existed farther down in the intertidal zone. Vermeij (1980:389) commented that growth rate in most intertidal organisms declines in upshore direction because time available for feeding is reduced. My observations on this species support his hypothesis.

FOSSIL RECORDS.—This species has been recorded from the late Pliocene of Efate, New Hebrides, by Abrard (1946:56; cited as *Cerithium (Procerithium) morum* Lamarck) and in the late Pliocene of the Philippines (Shuto, 1969:67–68; cited as *Clypeomorus tuberculatus* (Linnaeus)). It has also been found in Upper Miocene formations of Enewetak, Marshall Islands, and was cited by Ladd (1972:40) as *Cerithium (Concerithium) aff. egenum* (Gould). I have examined late Pliocene fossils from the Vigo Formation of the Bondoc Peninsula, Tayabas Province, Luzon, Philippines, that are conchologically conspecific with living *Clypeomorus bifasciata*. This material is housed at the California Academy of Sciences (CAS 41087) and has been cited by Popenoe and Kleinpell (1978:40, pl. 2: fig. 21), as *Clypeomorus morus* (Lamarck). I have also examined fossils of *Clypeomorus bifasciata* of indeterminate age found

in an emergent beach deposit at Barrow Island, Western Australia. Pleistocene fossils of this species also occur at Rottneest Island, Western Australia. The present southern range of *Clypeomorus bifasciata* in Western Australia is Shark Bay, but other tropical species occur as fossils in southwestern Australia indicating that the area was once warmer. A summary of the above records is shown in Table 2.

GEOGRAPHIC DISTRIBUTION (Figure 17).—*Clypeomorus bifasciata* is a widely distributed intertidal species that is confined mostly to the continental regions and high island groups of the western Pacific and Indian Ocean. The eastern limits of this species are the Mariana, Caroline, and Solomon islands groups with an extension into the central south Pacific via Fiji and the Samoan Islands. I have examined a few lots from the Marshall Islands, but *Clypeomorus bifasciata* appears to be rare there; the few samples in museums probably represent temporary populations. In the Indian Ocean, this species occurs in the Red Sea, Persian Gulf, and as far south as Durban, South Africa, and in Australia, south to

Shark Bay, Western Australia. It is also commonly found along the Asian subcontinent and among the Indian Ocean island groups. I have seen no specimens from Cocos-Keeling Islands.

MATERIAL EXAMINED.—RED SEA: 10 km N of Ras-Sudar, Gulf of Suez, Egypt (USNM 719193, 794188); Abu Zneima, Gulf of Suez, Egypt (USNM 794187); 40 mi (64 km) S of Suez, Gulf of Suez, Egypt (USNM 788100); Eilat, Gulf of Aqaba, Israel (NM G4719, G4723, USNM 671280, 672285, 786804); Fara'um, Gulf of Aqaba, Israel (USNM 769975); Ras Abu Galum, Gulf of Aqaba, Egypt (USNM 794178); 20 mi (32 km) N of Halieb, Egypt (USNM 788172, 788176); 0.5 mi (0.8 km) NNW of Inst. Oceanography and Fisheries, Hurghada, Egypt (USNM 719193); E end Dessie Id, 22 mi (35 km) off Massawa (ANSP 309141); Dessei Id (NM G1554, F9820); Kebri Id, Dalalk Arch (USNM 702539); Port Sudan, Sudan (BMHN, no number); Ras Mujallab Heidi, Aden (BMNH, no number); Jiddah Harbor, Saudi Arabia (USNM 637011); 20 mi (32 km) N of Jiddah, Saudi Arabia (USNM 425587). PERSIAN GULF: Kuwait (ANSP

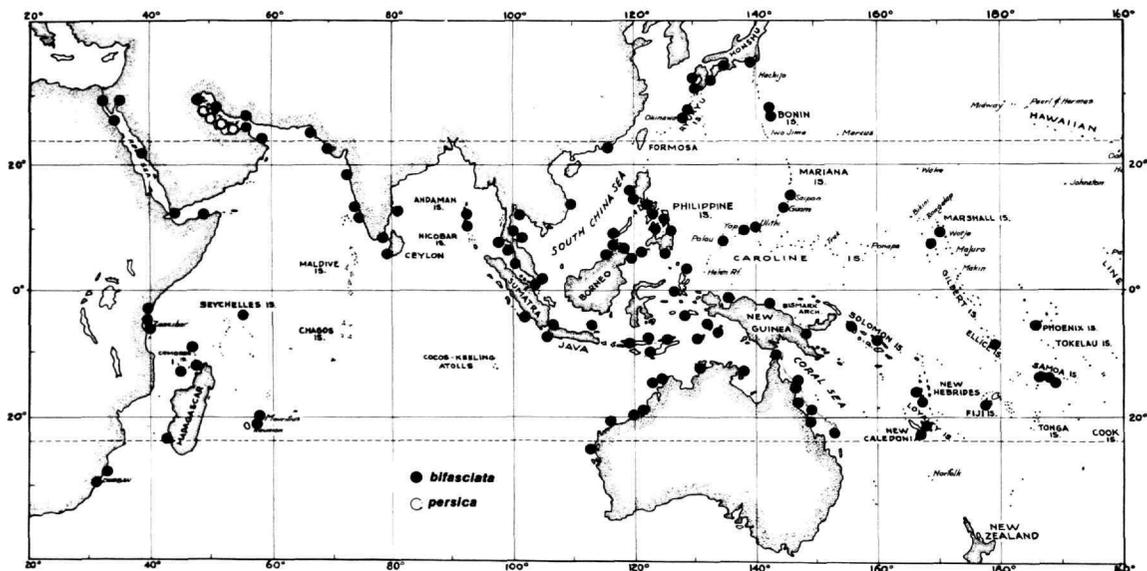


FIGURE 17.—Geographic distribution of *Clypeomorus bifasciata bifasciata* (solid circle) and *Clypeomorus bifasciata persica*, new subspecies (open circle).

212180, 219070, USNM 653489); Salmya, Kuwait (USNM 769627, 769631, 774589, 779629); Janna Id, United Arab Emirates (USNM 633592); Bushier, Iran (BMNH, no number); Hormuz Id, Iran (BMNH, no number, MCZ 246793); Bunder Abbas, Strait of Hormuz, Iran (USNM 605415). GULF OF OMAN: Muscat, Oman (USNM 657373, 657383, 798215, 91067, NM G673). ARABIAN SEA: N end of Masirah Id, Oman (USNM 788725). PAKISTAN: N side Akha Pt, Gulf of Kutch (ANSP 294822); Bay of Kutch (USNM 716654); Mangora Beach, Sind (USNM 605737). EAST AFRICA: Bawe Id, Zanzibar (USNM 597188); Mbweni, Zanzibar (USNM 604220); Ras Chokir, Dar es Salaam, Tanzania (USNM 703854); Oyster Bay, Dar es Salaam, Tanzania (USNM 786805); Mboa Maji, Tanzania (USNM 703949); Mboa Maji, 9 mi (14.5 km) S of Dar es Salaam, Tanzania (USNM 774551). MADAGASCAR: Baie d'Ambaro (USNM 776881); Ambatomboka or Crater Pt, Nossi-Bé (USNM 776664); Antsaokoabe Beach, Nossi-Bé (USNM 719547); Antsaokoabe Beach, Nossi-Bé (USNM 719549); Pt Fièvre, Nossi-Bé (USNM 719992); 100 yds (91 m) off Centra d'Océanographie pier, 13°24'S, 48°17'E, Nossi-Bé (USNM 719444); 13°24'S, 48°17'E, Pt Fièvre, Nossi-Bé (USNM 719456); 13°24'S, 48°18'E, Pt Fièvre, Nossi-Bé (USNM 719295); 13°24'S, 48°18'E, off Ambanoro Village, Nossi-Bé (USNM 719262); 13°24'S, 48°18'E, Pt Fièvre, Nossi-Bé (USNM 719292); 13°24'S, 13°24'S, 48°18'E, Pt Fièvre, Nossi-Bé (USNM 719222); Tuléar, N side of Fierenana (USNM 774468).

INDIAN OCEAN ISLANDS: Mahe, Seychelles (BMNH, no number); Baie Ternay, Mahé, Seychelles (BMNH, no number); near Case Noyale, Mascarene Ids, SW of Mauritius (USNM 716988); Mauritius (USNM 75536); settlement, Aldabra (BMNH, no number); Andaman Ids (USNM 173053). INDIA: Bandra, N of Bombay (USNM 443715, 774528); Chaupati Beach, Bombay (USNM 774526, 774527); Bombay (USNM 90832); Vengurla, N of Goa (USNM 443219); St George's Id, Goa (USNM 443156);

Goa (USNM 442931); Waltair (USNM 783670); CEYLON: Colombo (LACM, no number). MALAY ARCHIPELAGO: Palau Hantu, SW of Keppel Harbor, Malaysia (USNM 660837); Sekudu Id, Straits of Johore, Malaysia (USNM 660741); Pelau Besar, Malacca Strait, Malaysia (USNM 660950, 660969, 660978); Kampong Layang, near Chang, NE of Singapore, Malaysia (USNM 660675); Raffles Light, Singapore (USNM 655511); Singapore (USNM 336227); NE coast St John's Id, S of Singapore, Malaysia (USNM 660762); Negri Sembilan, W Malaysia, 2°28'N, 101°51'E (USNM 778488); Lang Kawi Ids, W Pulau Tanjung Dendong, Kedah State, Malaysia, 6°25'30"N; 99°54'45"E (USNM 778615); Lang Kawi, Ids, NW Pulau Langgun, Kedah State, Malaysia, 6°27'N, 99°53'10"E (USNM 778612). THAILAND: Taluei Id (USNM 361188); Goh Huyong, Similan Ids (USNM 661190); Pulau Tanga, Butang Ids (USNM 661637, 774484); Koh Chala (USNM 405927, 427351); Sriracha, Gulf of Siam (USNM 405798, 405808); SE Rayong (USNM 363652); Laem Sing (USNM 361401); Koh Chang (USNM 361367, 529532); Koh Kut (USNM 405832, 419783, 419890); SE Koh Samet (USNM 419276); Koh Tao (USNM 774454, 774461); Koh Pangam, Gulf of Siam (USNM 384127); Koh Samui (USNM 360917, 405632); Maprao Id (USNM 360906); Angtong Id (USNM 361261). VIETNAM: Dong Hai (USNM 783671). INDONESIA: Benkoelen, Sumatra (USNM 363878); Pelaboean Ratoe, Preager, Java (USNM 260591); Wijnkoopsbaai, W Java (ZMA 10424); Keledjitan, Bantam, Java (USNM 774568); Pruput, Bantam, Java (USNM 260580); Cape Tandjung, Ndorotai, 3 mi (4.8 km) NNE Reo, Flores (FSM 24771); Maumere, Flores (FSM 24766, 24768); Morotai, Halmahera Group, (USNM 542546); Telok Slawi, Komodo Id (USNM 632192, 632201, FSM 24758, 24759); W end Seman Id, Lesser Sundas (FSM 24767); Pombo Id, Haruku Strait, E of Ambon (USNM 746559); S end Kajoa Id, Moluccas (USNM 746399); Nuhu Jaan, Elat Bay, W coast Nuhu Tjut, Kai Ids, Moluccas (USNM 747144);

W side Mitak Id, Jamdena Straits, Tanimbar, Moluccas (USNM 747544); Aroe Id, Moluccas (ZMA, no number); Seleo Id, off NW Aitape, New Guinea (USNM 616004); Seleo Id, Aitape, New Guinea (USNM 774554); Sorendidori, E side Soepiori Id, Schouten Ids, New Guinea (ANSP 207471); 1 mi (1.6 km) E of dock at Biak, New Guinea (ANSP 206465); NORTH BORNEO; Labuan (USNM 336245, 347481); Gaya Id, Jesselton (USNM 658325); Bohaydulong Id (USNM 658029); Kupang, Timor; Kudat Bay (FSM 24774); Si Amil Id (USNM 233063); Po Bui Id, Sandakan (USNM 232865); Taganak Id (USNM 243943, 243944).

PHILIPPINES: (numerous localities throughout archipelago). AUSTRALIA: 1 mi (1.6 km) NE Gantheaume Pt, Broome, W Australia (ANSP 232669); Troughton Chain, W Australia (WAM 874-26); Big Pt, Cape Voltaire, Admiralty Gulf, W Australia (WAM no number); Vansittart Bay, W Australia (WAM no number); Cape Keraudren, W Australia (WAM no number); Anchorage Bay, Rosemary Id, Dampier Archipelago, W Australia (WAM no number); Eaglehawk Ids, Dampier Archipelago (WAM 868-76); Bay of Rest, Exmouth Gulf, W Australia (WAM no number); 5 mi (8 km) fence, S of Northwest Cape, W Australia (WAM no number); W side of Barrow Id, W Australia (USNM 691586); Useless Loop, Shark Bay, W Australia (WAM, 2 lots); Quobba Station, 40 mi (64 km) W of Carnavon, W Australia (WAM no number); Pt Quobba, W Australia (WAM 867-76); Port Hedland, W Australia (USNM 801603); Geraldton, W Australia (WAM no number); Port Bradshaw, near Cape Arnhem, Northern Territory (USNM 602121); NE end, Groote Eylandt Id, Gulf of Carpentaria, Northern Territory (USNM 602127, 602134); Bickerton Id, Gulf of Carpentaria, Northern Territory (USNM 602231); Yirrkala, Arnhem Land, Northern Territory (USNM 602327); Thursday Id, Queensland (LACM no number, USNM 613610); Orpheus Id, Palm Ids, Queensland (ANSP 138850); Pandora Reef, Queensland (ANSP 133074); near Mackay, Flat Top Id, Queensland (USNM

622989); Heron Id, Queensland (USNM 623098); South Brook Id, Queensland (USNM 623107, 623108); Lizard Id, Queensland (USNM 806059), JAPAN: Chiba (ANSP 243225); Shirahama, Wakayama Prefecture (ANSP 244160); Arasaki, Yokosuka City, Miura Peninsula, Honshu (ANSP 320690); Nagasaki, Kyushu (USNM 228241); Mogi (USNM 233147); Wakanura, Kyushu (USNM 228240); Fukura, Awaji (USNM 343853); Sagami Bay, Kanagawa Prefecture, Honshu (USNM 563878); Sagami Bay, Honshu (ANSP 243224); Hirado, Hizen (USNM 178968, 273121, 343852, BMNH 1907.9.10.13-15); Shimoda (USNM 1602); Mogi-Bakau (USNM 273034); Enoshima (USNM 127610); Kii (LACM 1199). RYUKYU ISLANDS: Kiraisima (USNM 774512); Gima, Kume Shima (USNM 613723, ANSP 243225); Naha, Okinawa (USNM 363729); Chishima, Okinawa (USNM 633815); Ukibara-Shima, E of Okinawa (USNM 670494); Kadena Circle, Okinawa (USNM 789377); Smugglers Cove, Okinawa (LACM no number); Fitzwoody Reach, Naha Air Force Base, Okinawa (LACM no number); Okinawa (ANSP 234666); 2 mi (3 km) N of Naha, Okinawa (ANSP 302847). BONIN ISLANDS: Bonin Id (USNM 343851); Hahajima, Ogasawara (USNM 175584). CHINA: Cape d'Aguilar, Hong Kong Id (USNM 621999); Kowloon, Hong Kong (USNM 233245). MARIANA ISLANDS: Saipan (LACM, no number); Cocos Id, S of Guam (LACM, no number); Apra Harbor, Guam (USNM 243623, 243626, 243737, 243747, 774573, 774776); Marine Lab, Pago Bay, Guam (USNM 774774); Oca Pt, Guam (USNM 487100). CAROLINE ISLANDS: Palau Ids (USNM 636056, 636360); Koron, Palau Ids (USNM 621155, 636197, 776669); Ulithi (USNM 602382); Tomil Harbor, Yap (USNM 634243); Ant Atoll, E Carolines (LACM 68-54). SOLOMON ISLANDS: Yoi Id (USNM 774522); Nudha Id, Indispensable Strait, Central District (LACM 78-69.29); Bougainville (ANSP 267104). NEW HEBRIDES: SW Efate Id (USNM 787661, 787662, 787832, 787986, 787987); Point d-Arbel, Efate Id (USNM

787505); 168°19'06"E, 17°44'44"S, Efate Id (USNM 787005). NEW CALEDONIA: Tomo, Bay de St Vincent (USNM 725141); Bay de Prony (USNM 774511); E side, Kuakue Bay (USNM 693728); N side N'Go Bay (USNM 725005, 725011); Mbo Id, 12 mi (19 km) W of Noumea (USNM 724305); Pointe aux Long Cous, Noumea (USNM 724213); Touaourou (USNM 724672, 724683, 724687). MARSHALL ISLANDS: Kwajalein Atoll (USNM 587347); Nado Id, Likiep Atoll. FIJI: near mouth of Lami River, Viti Levu (USNM 532479); 1.5 mi (2.5 km) N of Suva, Viti Levu (USNM 532471); Cuvu Id, Nandronga, Viti Levu (USNM 774548); SW side Vendraa shallows, Viti Levu (USNM 694531); Fiji Ids (USNM 42211, 76594, 76642, 76689, 88007, 88014, 88015, 90831, 91032, 91034, 91041, 91831); Lauthala Bay, Suva, Viti Levu (USNM 794743, 794745, 794746); Daumba Reef, Nauva, Viti Levu (USNM 794747); Sooloo (USNM 18627); Astrolabe Reef, Yanuyanu-i-loma Id (LACM); Vanga Bay, Mbengga Id (LACM). SAMOA: Ofu (LACM); Apia (USNM 774535, 774541); Apia Harbor, Upolu (USNM 774533); Namua Id, Upolu (USNM 698935); Matautu-Lefagu Bay, Upolu (USNM 698792, 698800); Upolu (ANSP 198481); Felialupo Rd, W side of Savii (USNM 774544); Outer reef, Apia (USNM 573938); Tutuila Id (USNM 488642, 589288, 774451, 774452, 774534); Fagaalu, Tutuila (USNM 699017, 774536, 774537); Fagaitua Bay, Tutuila (USNM 704692); Tafuna Cove, Tutuila (USNM 699206, 774521); Asili, Tutuila (USNM 774553); Pago Pago Harbor, Tutuila (USNM 13044, 603279, 774538); Fagaitua Bay, Tutuila Id (LACM); Goat Id, Tutuila (LACM). PHOENIX ISLANDS: Hull Id (USNM 774562).

Clypeomorus bifasciata persica, new subspecies

Figures 17, 18

DESCRIPTION.—Shell (Figure 18; Tables 8, 9). Adult shell turreted, reaching 20 mm in length and having teleoconch of 9.5 whorls with an

TABLE 8.—Analysis of shell parameters of *Clypeomorus bifasciata persica* (measurements in mm).

Character (n=20)	\bar{x}	sd	Range
Shell length	15.81	1.95	12.22–19.64
Shell width	7.58	0.89	6.28–10.07
Aperture length	3.70	0.49	2.93–4.92
Aperture width	3.40	0.45	2.64–4.26
No. beads on penultimate whorl	12.85	2.18	10–17
No. whorls	9.50	1.24	7–11

apical angle of about 40 degrees. Length/width index 2.08. Protoconch unknown. Early whorls usually eroded, bearing sculpture of 3 spiral, beaded cords aligned to form axial riblets. Whorls moderately inflated. Penultimate whorl sculptured with 3 nodulose cords, the largest of which are anterior. Beads are large, round, almost knob-like and smooth, and somewhat axially aligned. There are about 13 beads on the anterior spiral cord of the penultimate whorl. Tiny spiral lirae occur between beaded spiral cords but are weak or nearly lacking. Former varix present on body whorl opposite outer lip. Body whorl large, wide, sculptured with about 6 dominant, wide, beaded spiral cords, each separated from the other by a thin, spiral, beaded cord. Shell base wide, solid and with only a slight siphonal constriction. Aperture ovate, a little less than one-third the shell length. Columella concave with slight columellar callus. Outer lip thick, beveled interiorly and with interior denticles. Anterior siphonal canal short, deeply incised. Shell color somewhat variable, but of a spotted or checkered appearance due to blackish background covered with white beads. Periostracum not evident. Operculum and radula essentially same as in nominate subspecies. Animal, radula, and reproductive biology unknown.

HOLOTYPE.—ANSP 263194, Ras Tanura, Saudi Arabia (15.5 × 7.2 mm).

PARATYPES.—USNM 838028, Ras Tanura, Saudi Arabia.

ETYMOLOGY.—Named after the Persian Gulf.

DISCUSSION.—This subspecies is easily recog-

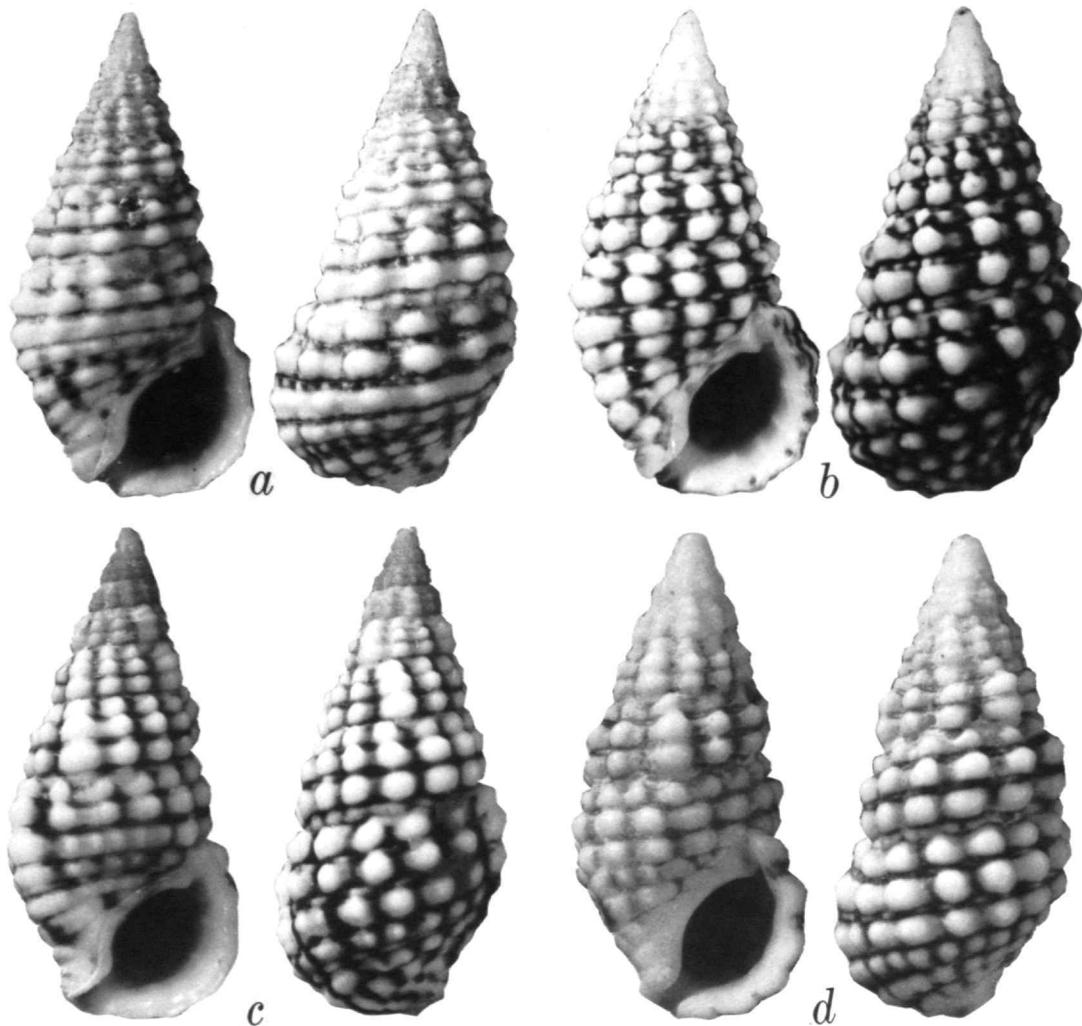


FIGURE 18.—*Clypeomorus bifasciata persica*, new subspecies, showing variation in shell sculpture (note thick spiral cords on wide siphonal neck and large, rounded beads on spiral cords of teleoconch): *a*, Ras Tanura, Saudi Arabia, USNM 597606 (17 × 7.7 mm); *b*, holotype, ANSP 263194, Ras Tanura, Saudi Arabia (15.5 × 7.2 mm); *c*, Khawr Hulaylah, near Dubayy, United Arab Emirates, NM g6961 (14.2 × 6.3 mm); *d*, Bahrain Id, Bahrain, AMNH 109730 (14.9 × 6.6 mm).

nized by its black and white checkered appearance and distinctive sculpture of white, large, rounded beads (Figure 18). The anterior spiral cords usually bear the largest beads, which tend to be drawn out spirally. In contrast to the typical subspecies, the tiny spiral lirae are diminished or

lacking. Another distinctive feature of *Clypeomorus bifasciata persica* is the thick siphonal neck at the shell base. The typical subspecies has a more constricted siphonal neck and the beaded spiral cords on the body whorl are thinner. Inspection of length/width, length/aperture length ratios,

TABLE 9.—Comparison of shell characters between *Clypeomorus bifasciata bifasciata* and *C. bifasciata persica* showing T test values ($T = P < .01$) for two-tailed test.

Character	<i>C. b. bifasciata</i>				<i>C. b. persica</i>				T
	n	\bar{x}	sd	s	n	\bar{x}	sd	s	
Length/width ratio	12	1.66	0.80	0.58	20	2.10	0.14	0.02	4.40
Length/aperture length ratio	12	3.48	0.16	0.23	20	4.31	0.47	0.21	4.88
No. beads*	30	16.23	2.19	4.65	20	12.85	2.18	4.75	5.54

* Number of beads on dominant spiral cord of penultimate whorl.

and counts of beads show nearly equal variances and normal distributions of characters for both subspecies. A two-tailed T test for unequal numbers (Table 9) was made and shows significant differences in length/width and length/aperture length ratios between the two subspecies ($T=4.40$, $P<.01$; $T=4.88$, $P<.01$, respectively). The number of beads on the spiral cord of the penultimate whorl is significantly lower in *Clypeomorus bifasciata persica* ($P<.01$).

I regard the subspecific status of *C. b. persica* with uncertainty. No intergrades between the two subspecies were seen. There are collections in some museums from the northern and eastern sides of the Gulf in which all individuals are clearly typical *C. b. bifasciata* forms (p. 39). Specimens from these regions are uncommon and the possibility exists that *C. b. persica* forms may also live in the eastern Gulf. If so, it would be best to accord *persica* specific status because it seems unlikely that two subspecies occur in a region as small as the Persian Gulf. The Persian Gulf populations need more careful study based on well-documented material and on-site investigation.

Geologically, the Persian Gulf is young and was formed by downwarping of the eastern Arabian Plate when it broke away from the African continent. Eastward migration of the Plate began in the Miocene but the Persian Gulf probably formed in the late Pliocene. During each of the Pleistocene glacial periods the Gulf has been reduced to the status of an estuary. The most recent such episode ended less than 20,000 years ago. The Persian Gulf was filled again during the "Flanderian Transgression" and reached its pres-

ent level about 5000 years ago (Kassler, 1973). *Clypeomorus bifasciata persica* may represent an adaptation to recent geological events and to a stressful environment of high temperature and salinity.

GEOLOGICAL DISTRIBUTION (Figure 17).—This subspecies most commonly occurs on the western side of the Gulf. The eastern side and the Gulf head appear to support only populations of the nominate subspecies.

MATERIAL EXAMINED.—PERSIAN GULF: EI Azzizia, 5 mi (8 km) S of Al Khubar, Saudi Arabia (USNM 597672); Ras Tanura, Saudi Arabia (USNM 597606, ANSP 263194); Dammam, Saudi Arabia (USNM 629256); Maza'am well, E of Dammam Dome, Saudi Arabia (USNM 708991); Abu Ali, Saudi Arabia (USNM 783081); Ras Mishab, Saudi Arabia (USNM 622149); Ras Noma, Bahrain (USNM 806482); Bahrain Id (AMNH 190730, ZMA); Khawr Hulaylah, near Dubayy, United Arab Emirates (NM 66961).

Clypeomorus brevis (Quoy and Gaimard)

Figures 19–21

Strombus rugosus Wood, 1828:13, 34, pl. 4: fig. 10 [holotype: BMNH, no number; type-locality: not given, cited in index as *Cerithium rugosum*; not *Strombus rugosus* Lamarck, 1804].

Cerithium brevis Quoy and Gaimard, 1834:116–117; 1833, pl. 54: figs. 9–12 [nonbinomial, holotype: MNHNP, no number; type-locality: Tonga Tapu].—Kobelt, 1898:226, pl. 40: figs. 1, 2.—Tryon, 1887:134, pl. 24: fig. 35.

Cerithium musiva Hombron and Jacquinot, 1852, pl. 24: figs. 23, 24 [holotype: MNHNP, no number; type-locality: Samoa]; 1854:104.—Tryon, 1887:134, pl. 24: fig. 47.

- Cerithium musiva* var. *albida* Hombron and Jacquinot, 1852, pl. 24: fig. 25 [holotype: MNHNP, no number; type-locality: "Océanie"]; 1854:104.
- Cerithium acutum* Hombron and Jacquinot, 1852, pl. 24: figs. 26, 27 [holotype: MNHNP, no number; type-locality: Raffles Bay; not *Cerithium acutum* Deshayes, 1833, nor Kiener, 1841, nor Muenster, 1841]; 1854:105.—Tryon, 1887:134, pl. 25, fig. 65.
- Cerithium rugosum* (Wood).—Sowerby, 1865, pl. 7: fig. 45a,b.—Sowerby, 1855:874, pl. 183: figs. 195–197.—Tryon, 1887:134, pl. 24: figs. 36, 37, 47.
- Cerithium patiens* Bayle, 1880:249 [new name for *Strombus rugosus* Wood].—Tryon, 1887:134, pl. 24: figs. 36, 37, 47.
- Cerithium breve* var. *ellicensis* Hedley, 1899:432, fig. 20 [holotype: AMS c5940; type-locality: Funafuti Atoll, Ellice Islands].
- Clypeomorus brevis* (Quoy and Gaimard).—Cernohorsky, 1972:70–71, pl. 16: figs. 6, 7.—Salvat and Rives, 1975:270, fig. 69.—Rehder, 1980:39.
- Clypeomorus bifasciatus* (Sowerby).—Shirai, 1977:275, unnumbered illustration [not *Cerithium bifasciatus* Sowerby; is *Cerithium brevis* Quoy and Gaimard].

DESCRIPTION.—*Shell* (Figures 19, 21; Table 10): Shell thick, squat, with average length of 15.79 mm, having teleoconch of 9–10 angulate, inflated whorls and apical angle of 40 degrees. Each whorl sculptured with 12–14 strong axial ribs and 2 strong spiral cords that are beaded where they cross axial ribs, presenting an overall rugose cancellate appearance. Numerous, tiny, spiral incised lines present on each whorl. Two dominant spiral cords on lower two-thirds of each whorl; a third, weaker, spiral cord usually present on upper part of each whorl, more defined on penultimate whorl. Axial ribs tend to align with

each other on all whorls except penultimate and body whorls. Early whorls (Figure 19*m*) sculptured with 2 dominant and several minor spiral cords but usually eroded or decollate; protoconch unknown. Suture distinct, wavy, and impressed. Body whorl inflated, nearly one-half the shell length and sculptured with 6 beaded spiral cords; sharp siphonal constriction after last spiral cord. Prominent thick varix on edge of outer lip. Strong former varix on body whorl opposite outer lip dividing shell into dorsal and ventral halves. Former varices randomly present on other whorls. Body whorl slightly fattened ventrally. Aperture enameled, ovate, about one-third the length of the shell. Columella concave with moderate callus. Anterior siphonal canal short, deeply incised and slightly reflected, directed leftward about 45 degrees to shell axis. Anal canal directed posteriorly, deeply incised, extending well into aperture and defined by parietal columellar plait. Outer lip thick, crenulate, and with thick interior denticles. Edge of outer lip parallel to shell axis. Outer lip extends slightly onto penultimate whorl. Periostracum very thin, usually eroded. Shell color white with brown to gray spiral lines, spots or blotches that may rarely

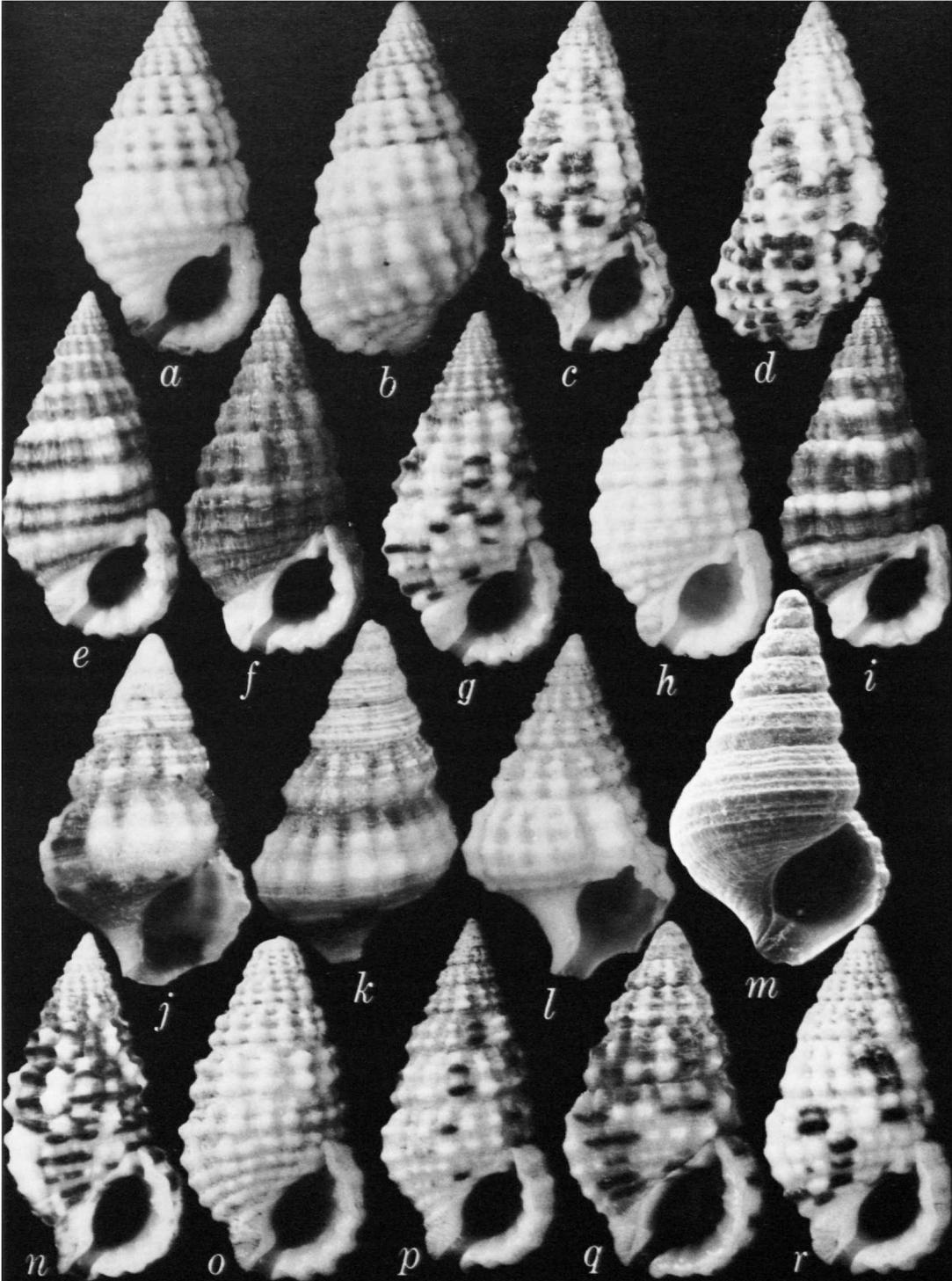
TABLE 10.—Analysis of shell parameters of *Clypeomorus brevis* (measurements in mm).

Characters (n=35)	\bar{x}	sd	Range
Shell length	15.79	4.59	7.48–24.28
Shell width	7.32	2.13	3.52–11.42
Aperture length	4.26	1.32	1.72–7.47
Aperture width	3.28	0.98	1.55–5.42
No. of whorls	9.11	1.05	7–11
No. beads per whorl	13.03	1.29	10–15

Length/width index: 2.16

Shell length/aperture length index: 3.71

FIGURE 19.—*Clypeomorus brevis*: *a, b*, stocky, albino morph, Likiep Atoll, Marshall Islands, USNM 596102 (21.1 × 10 mm); *c, d*, large, slender morph showing common color pattern, Nukualofa, Tongatapu, Tonga, USNM 613541 (27.9 × 12.6 mm); *e-i*, various colored individuals from single population, Engebi Island, Enewetak Atoll, Marshall Islands, USNM 587604 (all specimens about 20 × 10 mm); *j, k*, juvenile showing distinctive spiral sculpture on early teleoconch, Oneroa Island, Raroia, Tuamotu Islands, USNM 721190 (4.1 × 2.3 mm); *l*, immature specimen with undeveloped outer lip, Toms Island, Palmerston Island, N Cook Islands, USNM 685167 (12.2 × 6.6 mm); *m*, juvenile showing early sculpture (SEM ×50); *n*, typical color pattern on shell from Palmyra Island, N Line Islands, USNM 348471 (19.7 × 9.1 mm); *o*, albino morph, Anchorage Island, Suvarov, N Cook Islands, USNM 704447 (19.2 × 9.5 mm); *p*, Dwarf shell, N end of Whale Island, Suvarov Island, N Cook Islands, USNM 704549 (15.3 × 6.8 mm); *q*, shell from dwarf population living on gravel flats of lagoon shore, N end Oneroa Island, Raroia, Tuamotu Islands, USNM 721190 (8.9 × 4.6 mm); *r*, typical color form from Ryukyu Islands, USNM 666625 (21.5 × 10.7 mm).



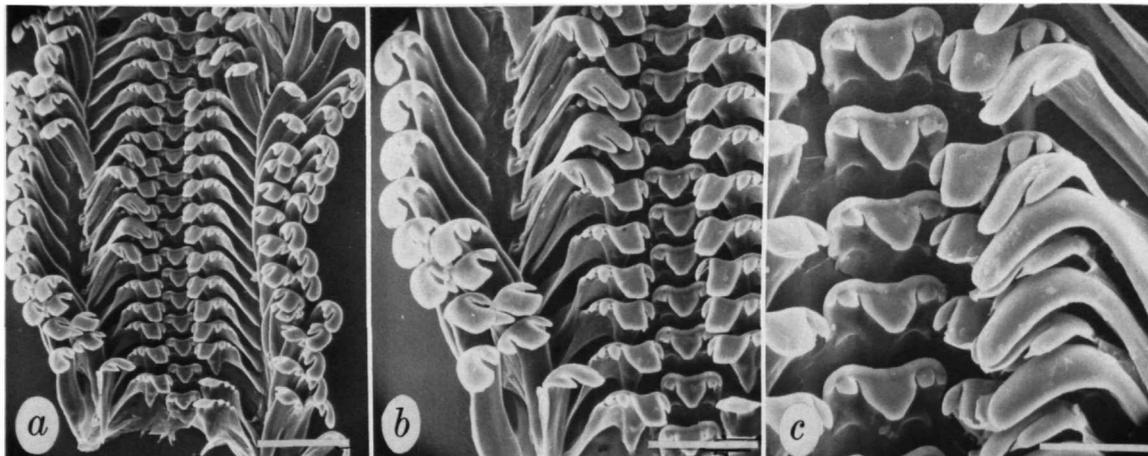


FIGURE 20.—SEM micrographs of radula of *Clypeomorus brevis*: *a*, general view of radular ribbon (bar = 150 μ m); *b*, detail of lateral and marginal teeth (bar = 100 μ m); *c*, detail of rachidian and marginal teeth (bar = 50 μ m).

become bands. Shell occasionally melanistic. Operculum thin, corneous, ovate, paucispiral with subcentral nucleus adjacent to anterior siphonal canal.

Radula (Figure 20; Table 11): Radular ribbon about 4 mm long and comprising 95 rows of teeth. Shell length/radula length index 4.46. Rachidian tooth pentagonal, about 66 μ m wide. Basal plate of rachidian tooth (Figure 20*c*) with short, basomedial projection flanked on each side by pit-like depression. Top of rachidian tooth concave with wide, spade-like central cusp flanked by 1, sometimes 2, tiny, blunt denticles on each side. Lateral tooth rhomboidal, having very long, twisted, basolateral projection that inserts onto basal radular membrane. Basal plate of lateral tooth (Figure 20*b*) has long, median, buttress-like projection that is directed downward. Top of lateral tooth concave, serrated with small, pointed, inner denticle, a large, wide, squarish, spade-like cusp, and two smaller, pointed denticles. Where serration on top of lateral tooth ends, upper basal plate has a flange before sharply extended basolateral projection. Marginal teeth (Figure 20*b,c*) long, curved, and spatulate. Base of inner marginal tooth rounded where inserted onto radular membrane. Tip of

TABLE 11.—Analysis of radular parameters of *Clypeomorus brevis* (measurements in mm).

Character (n=12)	\bar{x}	sd	Range
Radula length	4.04	0.26	3.69–4.61
Rows of teeth	94.67	4.72	89–102
Shell length	18.00	1.20	16.11–20.43

Shell length/radula length index: 4.46

inner marginal tooth sharply curved and spoon-like, divided into 2, rounded, inner denticles, a broad, squarish, large cusp and 1 small, sharp denticle. Outer marginal tooth same, only lacking outer denticle.

Animal: Internal anatomy essentially same as in *Clypeomorus bifasciata*. Base color white-yellow with brown blotches on head-foot; sole of foot white, propodial mucus gland present. Head and snout broad and short. Cephalic tentacles striped with brown and snout lined with fine transverse brown lines. Dorsal part of mantle edge has fine papillae; ventral part smooth. Inhalant siphon marked by fold in mantle edge and has slightly larger papillae. Osphradium dark brown; ctenidium white, hypobranchial gland wide, comprised of transverse folded ridges. Anus and pal-

lial gonoduct openings near mantle edge. Sperm collecting gutter runs along edge of medial lamina, a bright yellow spermatophore bursa and a white-lobed seminal receptacle at the proximal end of the medial lamina. Buccal mass of moderate size.

REMARKS.—While *Strombus rugosus* Wood, 1828, is the earliest name for this species, it is preoccupied by an earlier use of that name by Lamarck (1804). Bayle (1880) proposed a replacement name for *Cerithium rugosum* but was unaware that there was an earlier name for this species, *Cerithium brevis* Quoy and Gaimard, 1834. I have examined the types of all taxa listed in the above synonymy and am satisfied that they are conspecific (Figure 21). The various taxa of Hombron and Jacquinot (1852) are color variations of *Clypeomorus brevis*. *Cerithium breve* var. *ellicensis* Hedley, 1899 (Figure 21j) is merely a dwarf morph of *Clypeomorus brevis*. Shirai (1977, unnumbered illustration) erroneously figured *Clypeomorus brevis* under his description of *Clypeomorus bifasciata*.

ECOLOGY.—This species is an epifaunal member of the intertidal zone where it is usually found on a hard substrate. It normally occurs along the sheltered shore of fringing reefs, or on exposed beach rock or rocky areas and shallow ponds on the lagoon sides of low lying, oceanic islands. It is able to spend long periods of time out of the water and can withstand high salinities and temperatures. *Clypeomorus brevis* is a common species and has been recorded in densities of more than 79 snails per square meter (Kay and Switzer, 1974:286). I have observed a population of this species on Sand Island, Enewetak Atoll, Marshall Islands, which lived on exposed beach rock at the high intertidal zone. There it occurred in densities of several individuals per square meter. Snails were on the exposed surface of the beach rock, did not clump, and did not seem to seek shelter from the hot sun. This population was immersed in sea water only at high tide. Museum records of this species from localities throughout its geographic range indicate a similar habitat. *Clypeomorus brevis* may also occur on coarse sandy substrates, such as noted by Kay and Switzer

(1974:282) at Fanning Island. Kay (1971:268) observed that it lived in more estuarine areas of the lagoon shore where the water is brackish. Kay and Switzer (1974:286) determined that this species can withstand salinities as high as 55 ‰ but becomes inactive in salinities lower than 27 ‰.

Poli and Salvat (1976:249) observed that this species is common in some shallow ponds (*hoas*) associated with the lagoon of Taiaro Atoll, Tuamotus. These ponds are occasionally flooded by the sea, causing a sharp rise in the population, which is exterminated by subsequent drying, leaving behind vast numbers of shells.

Clypeomorus brevis grazes on microalgae. Its fecal pellets are tiny and comprised of dark brown or greenish algal particles and detritus.

Predation on this species was not observed, but it may be eaten by gastropod predators during high tides. Many shells show signs of apertural breakage caused by crabs. In an aquarium, I observed *Cymatium nicobaricum* (Röding, 1789) eat three specimens of *Clypeomorus brevis* even though many other snails were present as potential food. It is commonly parasitized by trematodes.

DISCUSSION.—Adult *Clypeomorus brevis* specimens are variable both in color and shell size. The rugose, cancellate sculpture with heavy beading and denticulate, thickened outer lip are less variable and easily identify this species, even juveniles (Figure 19j,l). Color pattern ranges from pure white (Figure 19a) to a nearly brown-black color (Figure 19f), but most specimens are light colored and spotted with brown or dark gray. Former varices are always white. Individual populations shown polymorphic color patterns (Figure 19e-i). Some populations in the Marshall Islands, Tokelau Islands, and Society Islands and especially the Tuamotus are comprised of dwarf individuals (Figure 19o,p). These populations appear to be randomly distributed throughout the above-mentioned island groups and are confined to supratidal environments, such as splash pools. According to Vermeij (1980:389), the growth rate of many invertebrates declines in an upshore direction, which may explain the presence of tiny



FIGURE 21.—*Clypeomorus brevis* (Quoy and Gaimard, 1834) and types of synonymous taxa: *a*, lectotype of *Cerithium breve* Quoy and Gaimard, 1834, NMHNP, no number, Tonga (in type collection revised by P.H. Fischer MNHNP); *b*, *c*, paralectotypes of *Cerithium breve*, NMHNP, no number, Tonga; *d*, holotype of *Cerithium acutum* Hombron and Jacquinot, 1852, NMHNP, no number, Raffles Bay (19.2 × 8.4 mm); *e*, holotype of *Cerithium musiva* Hombron and Jacquinot, 1852, NMHNP, no number, Samoa (17.4 × 9.1 mm); *f*, *g*, holotype of *Strombus rugosus* Wood, 1828, BMNH, no number, no locality given (27.5 × 11.5 mm); *h*, *i*, holotype of *Cerithium musiva* var. *alba* Hombron and Jacquinot, 1841, NMHNP, no number, "Oceainie" (18 × 8.3 mm); *j*, holotype of *Cerithium breve* var. *ellicensis* Hedley, 1899, AMS c.5940, Funafuti Atoll, Ellice Islands (10 × 5 mm).

snails in these environments. Populations of normal-sized individuals occur throughout the same islands. The largest individuals I examined are from the Gambier Islands and Tonga.

This species resembles *Clypeomorus bifasciata* (Sowerby) in overall shell morphology and radular characters and is probably closely related to it. *Clypeomorus brevis* replaces *Clypeomorus bifas-*

ciata in the central Pacific. The two species share similar habitats and appear to occupy the same niche in their respective ranges.

FOSSIL RECORDS.—This species has not been recorded as a fossil in the literature.

GEOGRAPHIC DISTRIBUTION (Figure 22).—This species is largely confined to low lying, island groups in the central Pacific and is endemic to the Pacific Plate (sensu Springer, 1982), where it is very common throughout most of the atolls of Micronesia and Polynesia. It is an “island loving,” atoll species not normally found in continental regions or on large mountainous islands. There are a few reliable records, based on large lots of live-collected specimens, from the western Pacific (Okinawa, N. Borneo, Moluccas), which probably represent fringing, opportunistic populations. The same holds true for those populations from New Ireland, the New Hebrides, and New Caledonia. The record from Easter Island mentioned by Rehder (1980:39) is based on a single, dead, beachworn specimen (ANSP 315542) and needs to be reconfirmed. A single record from Hawaii (USNM 42213) is probably

based on incorrect data, because *Clypeomorus brevis* has never been subsequently collected there. This species is apparently absent from the Austral Islands. Although the mode of reproduction and development of *Clypeomorus brevis* are not known, its distribution throughout the numerous island groups of the central Pacific Ocean indicate that it probably has pelagic larvae.

MATERIAL EXAMINED.—INDONESIA: Pombo Id, Haruku Strait, E of Ambon (USNM 746559); Batu Sapi, Sandaken, Sabah, North Borneo (AMNH); Ashmore Reefs, West Ids, Timor Sea (USNM 80607). NEW HEBRIDES: Pointe d'Arbel, Efate Id (USNM 787503). NEW IRELAND: (USNM 120680). NEW CALEDONIA: Îlot Maitre, S by W of Nouméa (ANSP 272319). LOYALTY ISLANDS: E side of Lifu (USNM 801435). RYUKYU ISLANDS: (USNM 666625); Kadena Circle, Okinawa (USNM 664653). PALAU ISLANDS: Angaur Id (USNM 616983). CAROLINE ISLANDS: Kapingamarangi Atoll (USNM 610884); Ulithi Atoll (USNM 612458); Yap (USNM 630814). W. SAMOA: Matantu-Lefagu Bay, Upolo (USNM

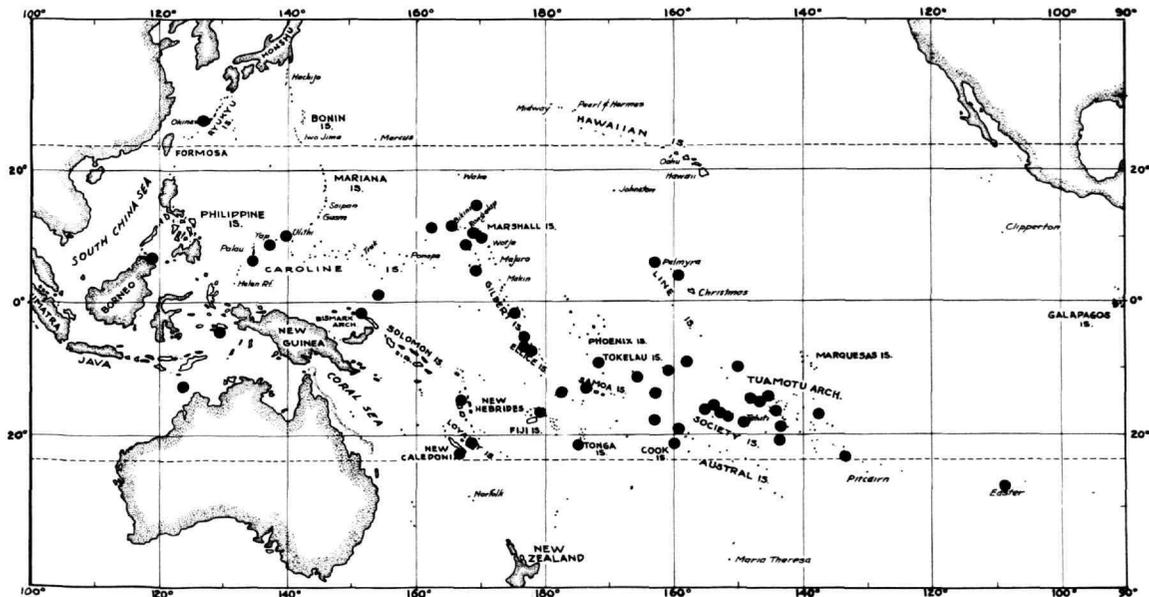


FIGURE 22.—Geographical distribution of *Clypeomorus brevis* (Quoy and Gaimard, 1834).

698802); W side of Vailele Bay, Upolo Id (ANSP).

MARSHALL ISLANDS: Engebi Id, Enewetak Atoll (USNM 587575, 587604); Rijoru Id, Enewetak Atoll (USNM 581958); Iguirin Id, Enewetak Atoll (USNM 655735); Aramit Id, Enewetak Atoll (USNM 587492); Enewetak Id, Enewetak Atoll (USNM 587575, 587604); W side of Elizabeth Id, Jaluit Atoll (USNM 659187); SW of Jabor Village, Jaluit, Jaluit Atoll (USNM 659550); W of N end of Lijeron Id, Jaluit Atoll (USNM 659887); Sydneytown, S of Jabor (USNM 659564, 659635, 659713); Lagoon side, S of end of Mejato Id, Jaluit Atoll (USNM 660209, 660212); N point of Enybor Id, Jaluit Atoll (USNM 659334, 659391); Likiep Atoll (USNM 596102, 596182); Rikararu Id, Likiep Atoll (USNM 615392); Likiep Id, Likiep Atoll (USNM 599542); lagoon side, Nado Id, Likiep Atoll (USNM 615324, 615370); Ailuk Id, seaward reef, Ailuk Atoll (USNM 615078); Taongi Atoll (USNM 693873); Wotho Id, Wotho Atoll (USNM 614413); Lae Id, lagoon side, Lae Atoll (USNM 614982, 614991); Pokak Atoll (USNM 615903); Bikini Id, Bikini Atoll (USNM 580428); Uorikku Id, Bikini Atoll (USNM 580061); E central part, Enyu Id, Bikini Atoll (USNM 580952, 584907); N side, W central part, Namu Id, Bikini Atoll (USNM 580523); Chieerete Id, Bikini Atoll (USNM 579565); Bokororyuru Id, Bikini Atoll (USNM 583111); Yurochi Id, Bikini Atoll (USNM 579813); Yomyaran Id, Bikini Atoll (USNM 580511); Kwajalein Atoll (USNM 587348); windward side, Kwajalein Id, Kwajalein Atoll (USNM 614760); reef flat, between Loi and S. Loi Ids, Kwajalein Atoll (USNM 614743). **ELLICE ISLANDS:** main island, Vaitupu (USNM 685939, 686061); lagoon side, Nui (USNM 685864, 685880, 685891); windward side, Nanomea (USNM 433799); main island, Nukulailai (USNM 685798). **GILBERT ISLANDS:** Abemama (USNM 434003). **WALLIS and HORN ISLANDS:** W shore, Faioa (USNM 676069); shore line, Nukuhifala (USNM 676416, 676434). **FIJI:** inlet by Yanuca Id, Viti Levu (FSM 24773). **TONGA:** Nukualofa, Ton-

gatapu (USNM 613541); Tongatapu (USNM 161526). **TOKELAU ISLANDS:** Etena, SW coast, Swains Id (USNM 768398); E of Taulaga Village, shore of lake, Swains Id (USNM 704308); lagoon shore, N side, Fakaofu Islet, Fakaofu (USNM 768098); lagoon, Fenua Loa, S point, Fakaofu (USNM 768173); Tokelau Islet, NE Nukunonu (USNM 768616).

COOK ISLANDS: Mehaumatic Lagoon, Manihiki Atoll (ANSP); Penrhyn Id (AMNH); N end, Whale Id, Suvorov (USNM 704549); N of old jetty, lagoon shore, Anchorage Id, Suvorov (USNM 704447); W side, lagoon reef flats, Whale Id, Suvorov (USNM 704558); reef S of Navana Village, Rakahanga (USNM 704356); near Tauhuna Village, Manihiki (USNM 704409); Toms Id, Palmerston (USNM 685112, 685115, 685162, 685167); off Aroa Creek, SW Rarotonga (USNM 708752); Avatiu harbor to Motu Tou, Rarotonga (USNM 684426); E of mouth of South River, N coast, Rarotonga (USNM 732597); Avarua harbor, N Rarotonga (USNM 684963; ANSP); jetty near airport, Aitutaki (USNM 684963); Akaiami Id, Aitutaki (USNM 630795); N tip Aitua, Aitutaki (USNM 684836); E side Akitua, NE Aitutaki (ANSP); 0.5 mi (0.8 km) N of Amori, W Aitutaki (ANSP). **SOCIETY ISLANDS:** off Hotel Arahiri, Tahiti (USNM 668452); S side Motu Tipaemanu, Raiatea (USNM 675218); S side Motu Toahutu, Tahaa (USNM 674159); Motu "I Atara" Tahaa (USNM 674292); SE side, Motu Ahi, Maupiti (USNM 706343); N of village, E side of lagoon, Scilly (USNM 705341); between Pererau Fai and Araara Pupu, District of Anua, Bora Bora. **TUAMOTUS:** Lagoon shore, Oneroa Id, Raroia (USNM 721075); lagoon shore, N end Oneroa Id, Raroia (USNM 721190, 721216); channel, N of Kahongi Id, Raroia (USNM 720407, 720494); E edge of Motufano Id, Raroia (USNM 721240); island, second channel, E of Kakapuka, Raroia (USNM 723026); lagoon side, Ohava Id, Raroia (USNM 720510); Gavariuari Id, Raroia (USNM 723178, 723257); Garumaoa Id, Raroia (USNM 723373); N of Okaea Id, Raroia (USNM 722900); S end of Garumaoa Id, Raroia (USNM

697561); Onigehiuhui Id, Raroia (USNM 722937); NE side, Tevu Kamaruia Id, Takume (USNM 723725); Otakareva Islet, Toau Atoll (ANSP); Maiai Id, Tikehau (USNM 629578, 629589); lagoon near village, Tatakoto Atoll (USNM 782717); reef flat, N side Puka Puka (USNM 789797); W end, Tatakoto Atoll (USNM 782676); reef flat, W of landing, NE side Anaa (USNM 788979); Avatori Pass, E side Îlot Brander, Rangiroa Atoll (USNM 782765); Takaroa Id (ANSP); S of W point of Northeast Id, Anuanuraro, Îles Duc de Gloucester (USNM 725227). GAMBIA ISLANDS: near Gatavake, W of Rikitea, Mangareva Id (USNM 638053); Baie de Gatavake, Mangareva Id (USNM 776448); N part of barrier reef, Motu Tepapuri (USNM 726375); NW coast, Aukena Id (USNM 726262). N LINE ISLANDS: lagoon, SE Fanning Id (USNM 700069); Palmyra Id (USNM 348470, 348471, 487404); Coopers Id, Palmyra Id (USNM 613475, ANSP 315959). S LINE ISLANDS: S part of W coast, Nake Id, Caroline Id (USNM 725113); N shore of South Id, Caroline Id (USNM 725058); channel near South Id, Caroline Id (USNM 726044). EASTER ISLAND: (ANSP 315542).

***Clypeomorus batillariaeformis* Habe and Kosuge**

FIGURES 23–27

Cerithium moniliferum "Dufresne" Kiener, 1841, pl. 16: fig. 3 [possible paratype: MNHNG, no number; type-locality: l'Océan Indien; not *Cerithium moniliferum* Deshayes, 1833, nor H.C. Lea, 1843; nomen dubium]; 1842:49–50.—Deshayes in Lamarck, 1843:319.—Sowerby, 1855:91, pl. 182 [in part: fig. 164 only]; 1865; pl. 4: fig. 20 [not *Clypeomorus batillariaeformis* Habe and Kosuge, 1966; is *Cerithium bifasciatum* Sowerby, 1855].—Tryon, 1887:134, pl. 24: fig. 35 [not *Clypeomorus batillariaeformis* Habe and Kosuge, 1966; is *Cerithium bifasciatum* Sowerby, 1855].—Kobelt, 1898:126–127, pl. 24: figs. 2, 3 [not *Clypeomorus batillariaeformis* Habe and Kosuge, 1966; is *Cerithium bifasciatum* Sowerby, 1855].—Dautzenberg, 1929:479–480.

Cerithium gemmulatum Hombron and Jacquinot, 1852 pl. 24: figs. 3, 4, 7, 8, 9, 10, 39–41 [in part; lectotype and paralectotype: MNHNP, no number; type-locality: Vavu;

not *Cerithium gemmulatum* de Serres, 1840]; 1854:102–103.

Cerithium obscurum Hombron and Jacquinot, 1852, pl. 24: figs. 5, 6 [holotype: MNHNP, no number; type-locality: Îles Solomon; not *Cerithium obscurum* Deshayes, 1833]; 1854:102–103.

Cerithium baccatum Hombron and Jacquinot, 1852, pl. 24: figs. 11, 12 [holotype: MNHNP, no number; type-locality: Raffles Bay; not *Cerithium baccatum* Brongniart, 1823, nor Kiener, 1841]; 1854:102–103.

Cerithium concisum moniliferum Kiener.—Oostingh, 1923:72–73. [not *Cerithium concisum* Hombron and Jacquinot, 1852].

Cerithium morus Bruguière.—Demond, 1957:292, fig. 8 [not *Cerithium morus* Lamarck, 1822: is *Clypeomorus batillariaeformis* Habe and Kosuge, 1966].

Clypeomorus batillariaeformis Habe and Kosuge, 1966:328–329, pl. 29: fig. 13 [holotype: NSMT 38674, 26.4 × 12.0 mm; type-locality: Arafura Sea, Northern Territory, Australia].—Inaba and Oyama, 1977:26.

Clypeomorus tuberculata (Linnaeus).—Shuto, 1969:67–68, pl. 2: figs. 6, 12 [not *Cerithium tuberculatus* Linnaeus, 1758: is *Clypeomorus batillariaeformis* Habe and Kosuge, 1966].

Clypeomorus moniliferus (Kiener).—Cernohorsky, 1972:70 [in part, pl. 16: figs. 3, 4 only].

Cerithium (*Theridium*) *alveolus* Hombron and Jacquinot.—Ladd, 1972:37, pl. 9; figs. 7, 8 [not *Cerithium alveolus* Hombron and Jacquinot, 1852: is *Clypeomorus batillariaeformis* Habe and Kosuge, 1966].

Cerithium wainngoli Ladd, 1972:40, pl. 10: figs. 6, 7 [holotype: USNM 650515; type-locality: Vanua Mbalavu, Fiji].

Clypeomorus humilis (Dunker).—Shirai, 1977:275 [not *Cerithium humilis* Dunker, 1861: is *Clypeomorus batillariaeformis* Habe and Kosuge, 1966].

DESCRIPTION.—*Shell* (Figures 23–25; Table 12): Shell thick and stocky, teleoconch comprising 7 slightly inflated whorls. Length/width index 2.73. Adult whorls round in cross section. Apical angle 40 degrees. Penultimate whorl sculptured with 3 dominant, equally spaced, spiral, beaded cords. Middle cord strongest and with largest beads. Anterior cord frequently smaller and with less distinct beads than other two cords. There are about 15 beads per whorl. Beads smooth, rounded, slightly drawn out, usually not axially aligned. Fine spiral lirae between dominant spiral cords are sometimes sculptured with tiny beads. Of the minor spiral lirae, median

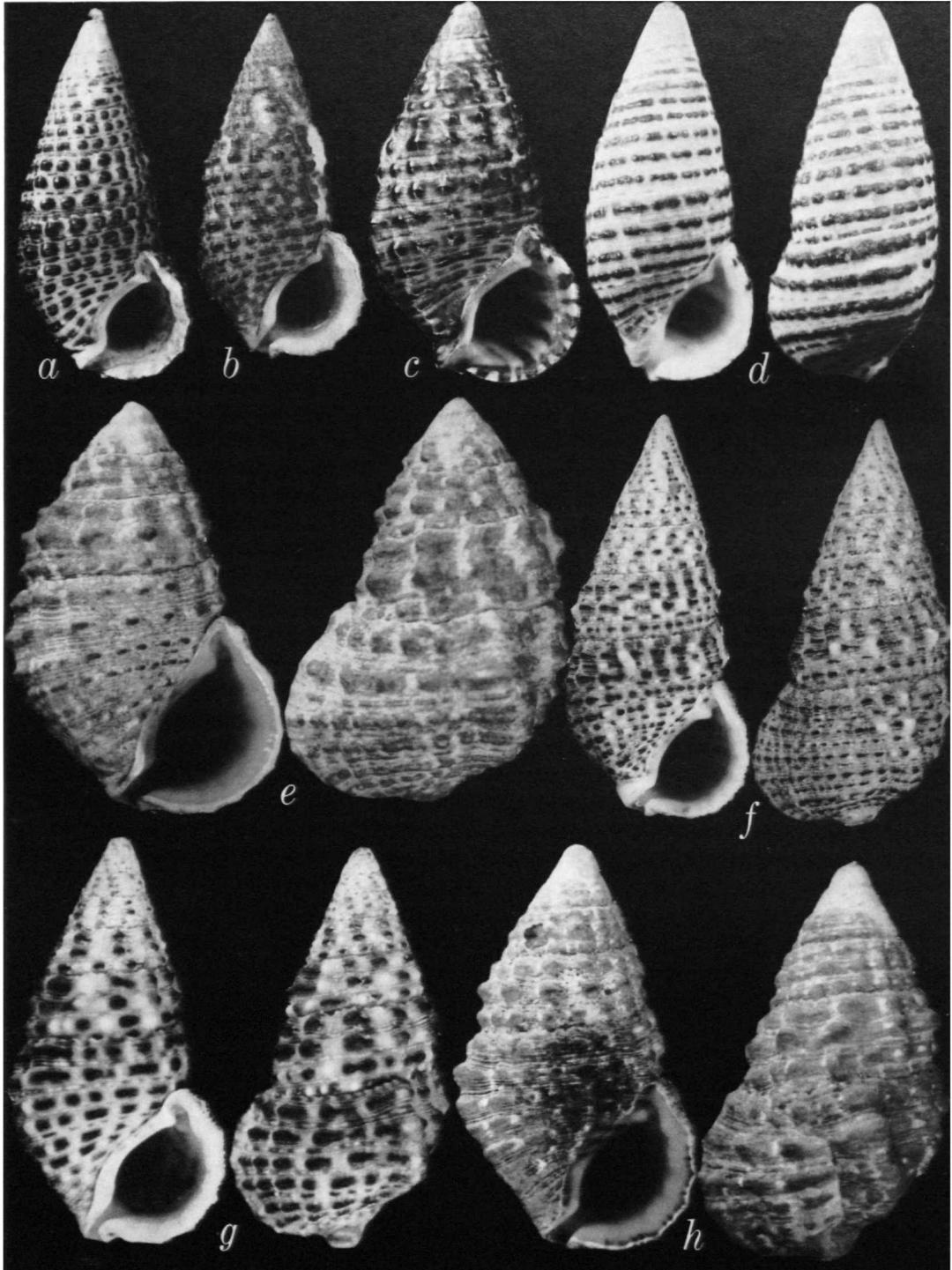


TABLE 12.—Analysis of shell parameters of *Clypeomorus batillariaeformis* (measurements in mm).

Character (n=50)	\bar{x}	sd	Range
Shell width	9.92	2.61	3.45–15.25
Shell length (last 3 whorls)	16.29	4.08	5.50–25.15
Aperture length	7.59	2.00	2.70–11.60
Aperture width	4.19	1.28	1.15–6.90
No. beads/cord on penultimate whorl	15	3.28	9–22
No. of whorls	7	1.20	5–11

one between dominant spiral cords is frequently largest. Sculpture of other whorls same as penultimate whorl, but early whorls usually badly eroded. Body whorl with prominent, hump-like, dorsal varix at angle of 120 degrees to the right of the apertural plane, when shell viewed anteriorly. Other former varices randomly distributed on teleoconch whorls. Suture slightly incised, indistinct, and wavy, round, with large varix on right dorsal surface and sculptured with 6 or 7 dominant spiral, beaded cords. Numerous fine spiral lirae between dominant spiral cords of body whorl are most pronounced at siphonal constriction, which begins at midpoint of aperture. Aperture ovate, about one-third the length of the shell. Columella concave with slight callus. Outer lip moderately thick, rounded, smooth, sometimes weakly crenulate. Inner surface of

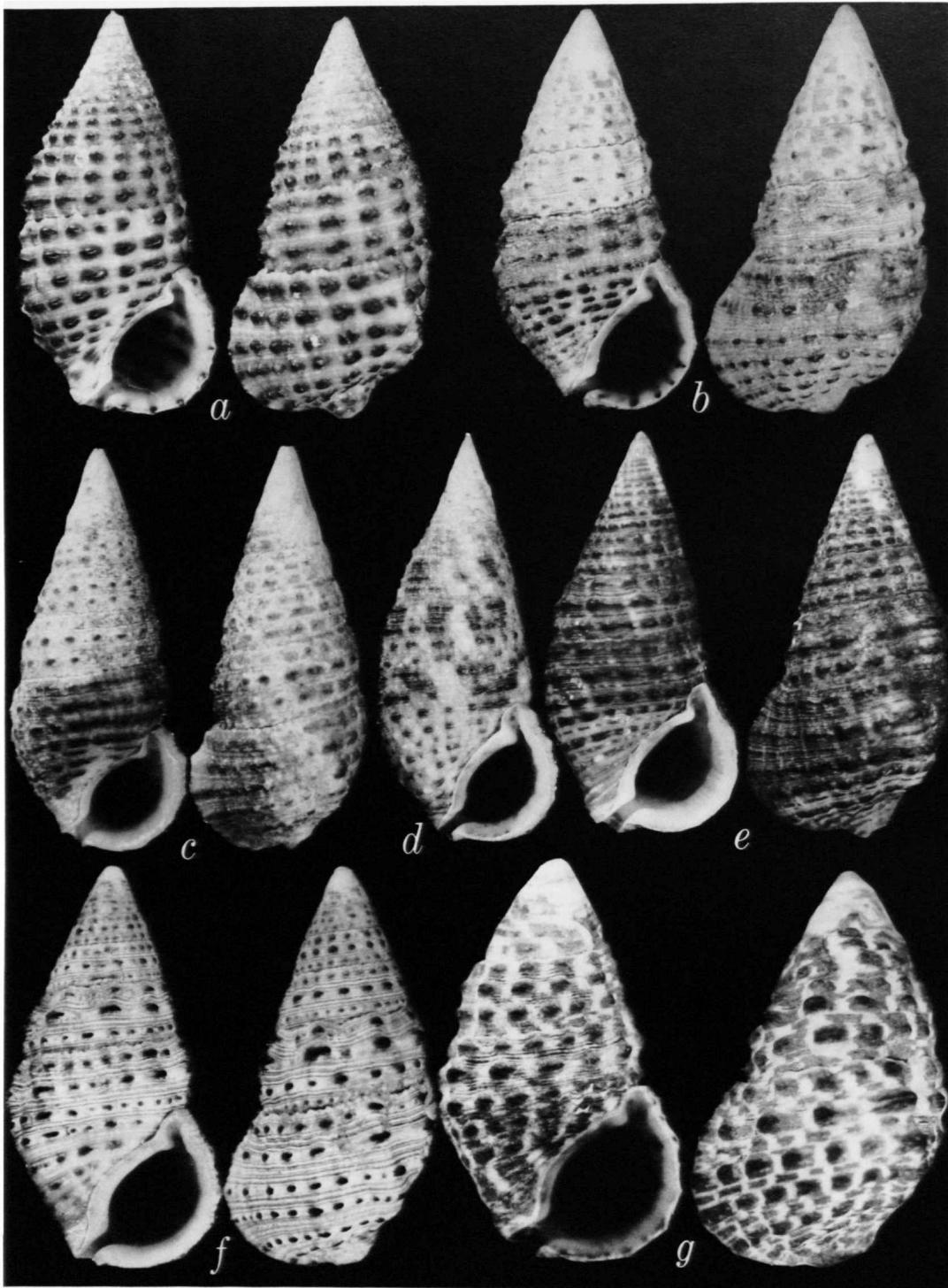
outer lip has fine spiral lirae. Plane of outer lip, when viewed from left side of shell, nearly in line with shell axis. Lower part of outer lip is even with end of anterior siphonal canal. Anterior siphonal canal short, narrow, deeply incised, slightly reflected and directed leftward about 45 degrees to shell axis. Base of outer lip partially obscures siphonal canal when shell is viewed anteriorly. Anal canal defined by columellar plait at posterior of aperture adjacent to body whorl and forming deeply incised groove extending well within aperture.

Periostracum thin, tan, usually worn or lacking. Shell color dark brown to buff, frequently grayish with black to dark brown beads, which may be drawn out to form short lines. Aperture and columella white. Operculum thin, tan, corneous, ovate, and paucispiral with nucleus near periphery.

Radula (Figure 25; Table 13): Radular ribbon relatively long, about 4.0 mm in length and with 86 rows of teeth. Shell length/radula length index 5.83. Rachidian tooth pentagonal, about 60 μ m long. Basal plate of rachidian (Figure 25b) has long, triangular-shaped basomedial projection that is flanked by a pit-like depression on each side. Top of rachidian slightly concave, with wide triangular central cusp flanked by 1 rounded cusp (rarely 2) on each side. Lateral tooth (Figure 25d,f) rhomboidal with long twisted basolateral projection inserting onto basal radular membrane. Long inner basal projection buttresses tooth. Top of lateral tooth slightly concave, serrated with small blunt inner cusp, a large wide spade-shaped cusp, and 2 to 3 smaller blunt cusps. Marginal teeth (figure 25e,f) long, spatulate, rounded at bases and having curved spoon-shaped tips. Tip of inner marginal with 2 small inner denticles, a wide rounded central cusp, and a single small outer denticle. Tip of outer marginal same only lacking outer cusp.

Animal: Basic anatomy very similar to that described for *Clypeomorus bifasciata* (page 27). In contrast to *C. bifasciata*, dorsal mantle edge bears small numerous papillae. Pair of salivary glands

FIGURE 23.—*Clypeomorus batillariaeformis* Habe and Kosuge, 1966 (with exception of specimen *a*, showing variation in shell form, sculpture and color): *a*, lectotype of *Cerithium gemmulatum* Hombron and Jacquinot, 1852, NMHNP no registry number = *Clypeomorus bifasciata* (Sowerby), Torres Strait, *Astrolabe* Expedition (24.6 mm); *b*, paralectotype of *Cerithium gemmulatum*, NMHNP no registry number, Vavau, *Astrolabe* Expedition (25.2 mm); *c*, lectotype of *Cerithium obscurum* Hombron and Jacquinot, 1852, NMHNP no registry number, Solomon Islands (21.1 mm); *d*, holotype of *Cerithium baccatum* Hombron and Jacquinot, 1852, MNHNP no registry number, Raffles Bay (28.5 mm); *e*, reef near Cebu, Philippines (USNM 243791, 18.8 mm); *f*, Malcochin Harbor, Linapacan, Philippines (USNM 243860, 30.1 mm); *g*, Okinawa (USNM 617090, 27 mm); *h*, Koh Tao, Thailand (USNM 419697, 20.7 mm).



←
FIGURE 24.—*Clypeomorus batillariaeformis* showing variation in shell form, sculpture, and color (all specimens shown at same size); *a*, Huron Gulf, New Guinea (USNM 487891, 21.5 mm); *b*, Malcochin Harbor Linapacan, Philippines (USNM 243860, 26.6 mm); *c*, Chango Islands, W Zanzibar (ANSP 214371, 26.6 mm); *d*, Laam Son, W Phuket Island, Thailand (ANSP 286013, 27.8 mm); *e*, Bandra, N of Bombay, India (USNM 443607, 26.6 mm); *f*, Okinawa (USNM 617090, 26.3 mm); *g*, dwarf variety, Likiep Atoll (Tomassin collection no. 914, 11.5 mm).

anterior to nerve ring with left gland partially passing through ring. Salivary glands large, long, worm-like, and not as compact and tangled as in *C. bifasciata*. Ducts of salivary glands empty into buccal cavity slightly forward of midbuccal mass. Rectum large and wide. Reproductive system very much like that of *C. bifasciata*. Detailed description of male and female pallial gonoducts given by Cannon (1975). Reproduction lecitho-

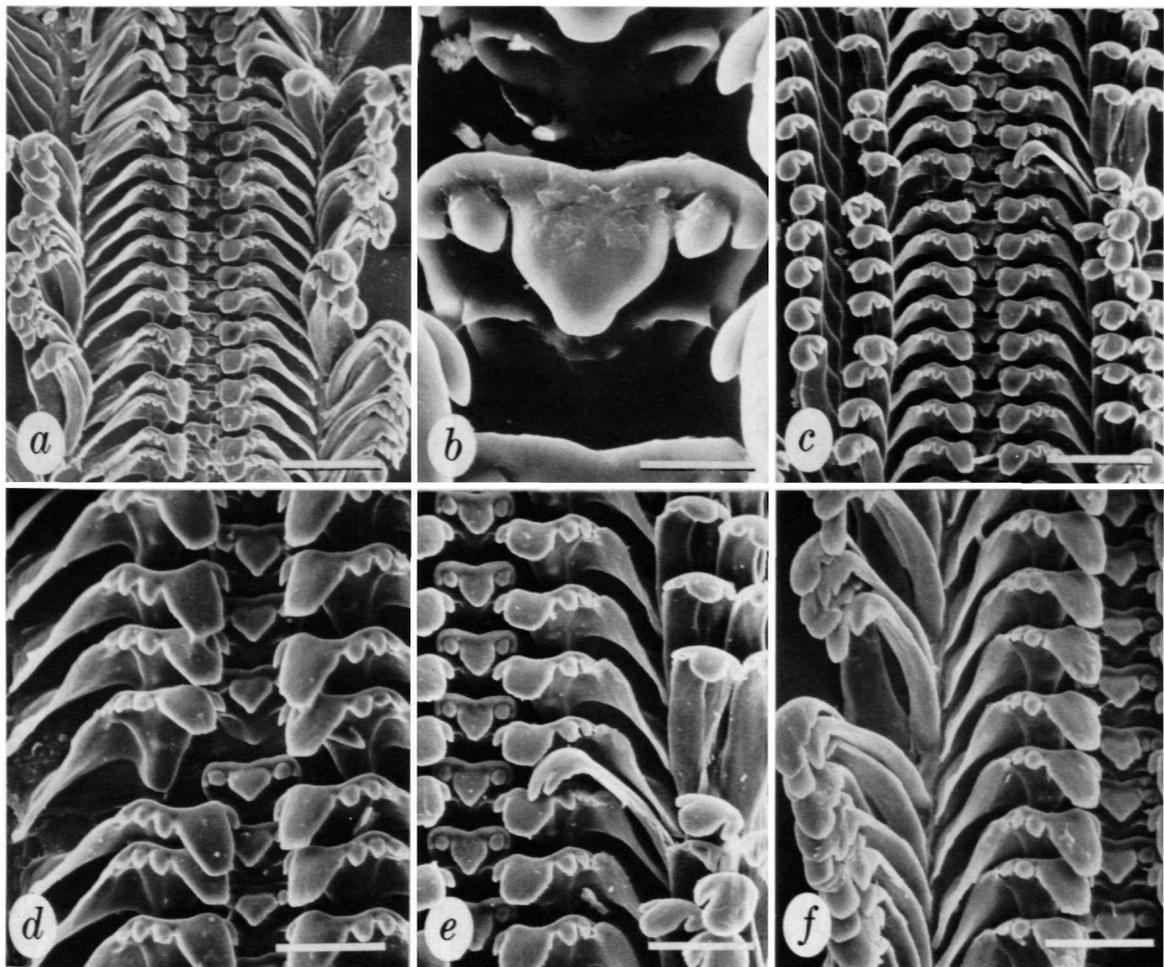


FIGURE 25.—SEM micrographs of radula of *Clypeomorus batillariaeformis*: *a*, radular ribbon, marginal teeth folded back, Eman Point, Marong, Bataan, Luzon, Philippines, USNM 774752 (bar = 150 μ m); *b*, rachidian tooth (bar = 20 μ m); *c*, radular ribbon, marginal teeth upright showing spatulate cusps (bar = 150 μ m); *d*, detail of lateral teeth showing basal plate (bar = 75 μ m); *e*, half row (bar = 75 μ m); *f*, half row, specimen from Bonagao Channel, SW Sanga, Sanga Island, Sulu Archipelago, Philippines, showing insertion of lateral and marginal teeth onto basal membrane, ANSP 230637 (bar = 75 μ m).

TABLE 13.—Analysis of radular parameters of *Clypeomorus batillariaeformis* (measurements in mm).

Character (n=12)	\bar{x}	sd	Range
Radula length	4.31	0.39	3.61–4.80
Rows of teeth	85.50	10.10	72–104
Shell length	25.14	3.94	21.13–32.48

Shell length/radula length index: 5.83

trophic, with short free-swimming demersal phase.

REMARKS.—The synonymic history of this species equals in complexity that of *Clypeomorus bifasciata* (Sowerby), a taxon with which it is frequently confused (see synonymy of *Clypeomorus bifasciata* and discussion on p. 35 for comments on this).

As can be seen in the above synonymy, other authors have proposed a number of names for this species, but most of them are unavailable. The earliest available name is *batillariaeformis*, proposed for a slender morph of this species by Habe and Kosuge (1966). I have examined the holotype of this taxon (Figure 26a) and find it to be identical with the *moniliferum* Kiener of authors. Although this species is best known as *Cerithium moniliferum* Kiener, 1841, this name has frequently been applied to other taxa, such as *Clypeomorus bifasciata*, *Clypeomorus petrosa*, *Cerithium zonatum* (Wood, 1828) or to mixtures of these species. The earliest name for the species is *Cerithium moniliferum* Kiener, but that name is a primary junior homonym of a fossil species, *Cerithium moniliferum* Deshayes, 1833. It cannot be ascertained with certainty that Kiener's taxon was not based on a mixture of specimens that also included *Clypeomorus bifasciata*. Kiener's illustration of *Cerithium moniliferum* (1841, pl. 16: fig. 3) looks like *Clypeomorus bifasciata* because it does not have the distinctive dorsal varix on the body whorl and appears to have an aperture more like *Clypeomorus bifasciata*. The questionable type in the Geneva Museum is an immature specimen without a fully developed outer lip, but it appears to be *Clypeomorus batillariaeformis*.

Since the name *moniliferum* is preoccupied and the identity of Kiener's taxon is doubtful, *moniliferum* of Kiener is best regarded as a nomen dubium.

The types of *Cerithium obscurum* (Figure 23c) and *Cerithium baccatum* (Figure 23d), both of Hombron and Jacquinot, 1852, are conspecific with *Clypeomorus batillariaeformis*, but they are both junior primary homonyms and are unavailable.

I have established that the lectotype of *Cerithium gemmulatum* Hombron and Jacquinot from Torres Strait (Figure 23a) is conspecific with *Clypeomorus bifasciata*. The former name was based on a mixture of that taxon and *Clypeomorus batillariaeformis*. Of the five paratypes of *Cerithium gemmulatum*, the two from Vavau (Figure 23b) are *Clypeomorus batillariaeformis* (see discussion of synonymy under *Clypeomorus bifasciata*, p. 29).

Cernohorsky's figures of *Clypeomorus batillariaeformis* (cited as *Clypeomorus moniliferus*; 1972:70, pl. 16: figs. 3–5) are a mixture of two species. Only figures 3 and 4 are *Clypeomorus batillariaeformis*.

Examination of the fossils that Ladd (1972:37, 40) cited as *Cerithium wainigoli* Ladd and *Cerithium alveolus* Hombron and Jacquinot convinces me that they are conspecific with *Clypeomorus batillariaeformis*.

The foregoing discussion clearly shows that this taxon has been confused with *Clypeomorus bifasciata*. Biologists consulting the literature about *Clypeomorus batillariaeformis* should be aware of this composite concept and exercise caution with published experimental results unless voucher specimens can be obtained.

ECOLOGY.—This species is an epifaunal inhabitant of the upper midtidal zone and usually occurs in dense populations on hard substrate, where it frequently clusters at low tide. I have seen *Clypeomorus batillariaeformis* living in this habitat in numerous localities in the western Pacific, and data from museum collections indicate a similar ecological distribution throughout its geographic range. Occasional populations may

be found on a softer substratum, but this is uncommon. *Clypeomorus batillariaeformis* is usually found with *Clypeomorus bifasciata*, which lives on the same substratum but at the high tide mark. As in the case of *Clypeomorus bifasciata*, the literature about *Clypeomorus batillariaeformis* (usually cited as *Cerithium moniliferum*) is frequently unreliable because of the lack of voucher specimens and the likelihood of misidentification due to mixing of similar species.

A number of papers have been written about the clustering behavior of this species and several theories put forth to explain the phenomenon (Cannon, 1979; P.H. Fischer, 1966; Rhode and Sandland, 1975; Underwood, 1979). Clustering is attributed to individuals seeking a suitable substratum (Fischer, 1966) or to avoidance of desiccation (Cannon, 1979), but as Underwood (1979:149) noted, no hard experimental evidence exists to support these theories.

The reproductive biology of *Clypeomorus batillariaeformis* has been presented by Cannon (1975; cited as *Cerithium moniliferum*), who described the anatomy, spawn, and larvae. Spawn masses are attached to the undersurfaces of rocks and are formed into flattened clusters, each about 10 mm across. A cluster is made of a broad ribbon, 4–6 eggs across, that is wound back and forth on itself several times and contains 1500–2000 eggs, each egg about 0.15 mm in diameter. Cannon noted an incubation period of 16 days and subsequent hatching of advanced veligers, which quickly metamorphosed into crawling young snails after 24 hours; thus, a brief demersal larval stage occurs. Cannon's (1975) paper, may have been based upon mixed lots of *Clypeomorus batillariaeformis* and *Clypeomorus bifasciata*. Voucher specimens that he sent to me comprised mixtures of these two species; nevertheless, my correspondence with him leads me to believe that most of the animals used in his study were indeed *Clypeomorus batillariaeformis*. All were obtained from a single intertidal station well within the tidal zone normally occupied by *Clypeomorus batillariaeformis*. In contrast, Cannon's (1979) paper on the ecology of *Clypeomorus batillariaeformis*

(cited as *Cerithium moniliferum*) is more likely to contain errors because specimens were collected from many stations, and populations were noted to consist of several "morphs." It is probable that he regarded the two species as conspecific. Cannon's (1979) and Rhode's (1981) observations on trematode parasites of *Clypeomorus* are also likely to have been based on parasites taken from two species rather than from one.

DISCUSSION.—This species is distinguished by the large varix on the right dorsal side of the body whorl and by the smooth outer lip that is drawn out to extend slightly below the level of the anterior siphonal canal.

Clypeomorus batillariaeformis is frequently confused with *Clypeomorus bifasciata* but differs from it by ecology and several distinctive shell characters, notably the placement of the major varix on the body whorl (see remarks under *Clypeomorus bifasciata*, p. 35; Figure 16).

Another similar species, *Clypeomorus inflata* Quoy and Gaimard, has a more restricted geographic range than *Clypeomorus batillariaeformis* and may be distinguished from it by a larger size and more robust shell, which is sculptured with numerous incised spiral lines and has a thicker, more crenulated outer lip.

Members of the *Clypeomorus petrosa* (Wood) complex, including *Clypeomorus purpurastoma*, new species, are sympatric with *Clypeomorus batillariaeformis* throughout most of its geographic range and are frequently confused with it. *Clypeomorus petrosa* usually lives in the lower midtidal zone and its shell is generally larger, more colorful, and more elongate than those of *Clypeomorus batillariaeformis*. It also has a sculpture of large nodules that are spirally extended. *Clypeomorus purpurastoma* may be distinguished from *Clypeomorus batillariaeformis* by its pupiform shape, purple aperture, and sharply pointed apex that is frequently concave in outline. The former lives at the upper part of the low tidal zone and is never found in microsympatry with *Clypeomorus batillariaeformis*. *Clypeomorus batillariaeformis* is highly sculptured and very colorful in the eastern part of its range, where it is difficult to

distinguish it from *Clypeomorus petrosa* (Wood). Individuals from this region and in particular populations from New Caledonia, the New Hebrides, and the Fiji Islands display a mixture of characters and are difficult to determine.

Clypeomorus batillariaeformis displays considerable variation in size and sculpture and may vary greatly in length/width ratio. Strong selection differences between morphs within different habitats may account for the high intraspecific variability. Individual snails are frequently badly eroded and lack protoconchs.

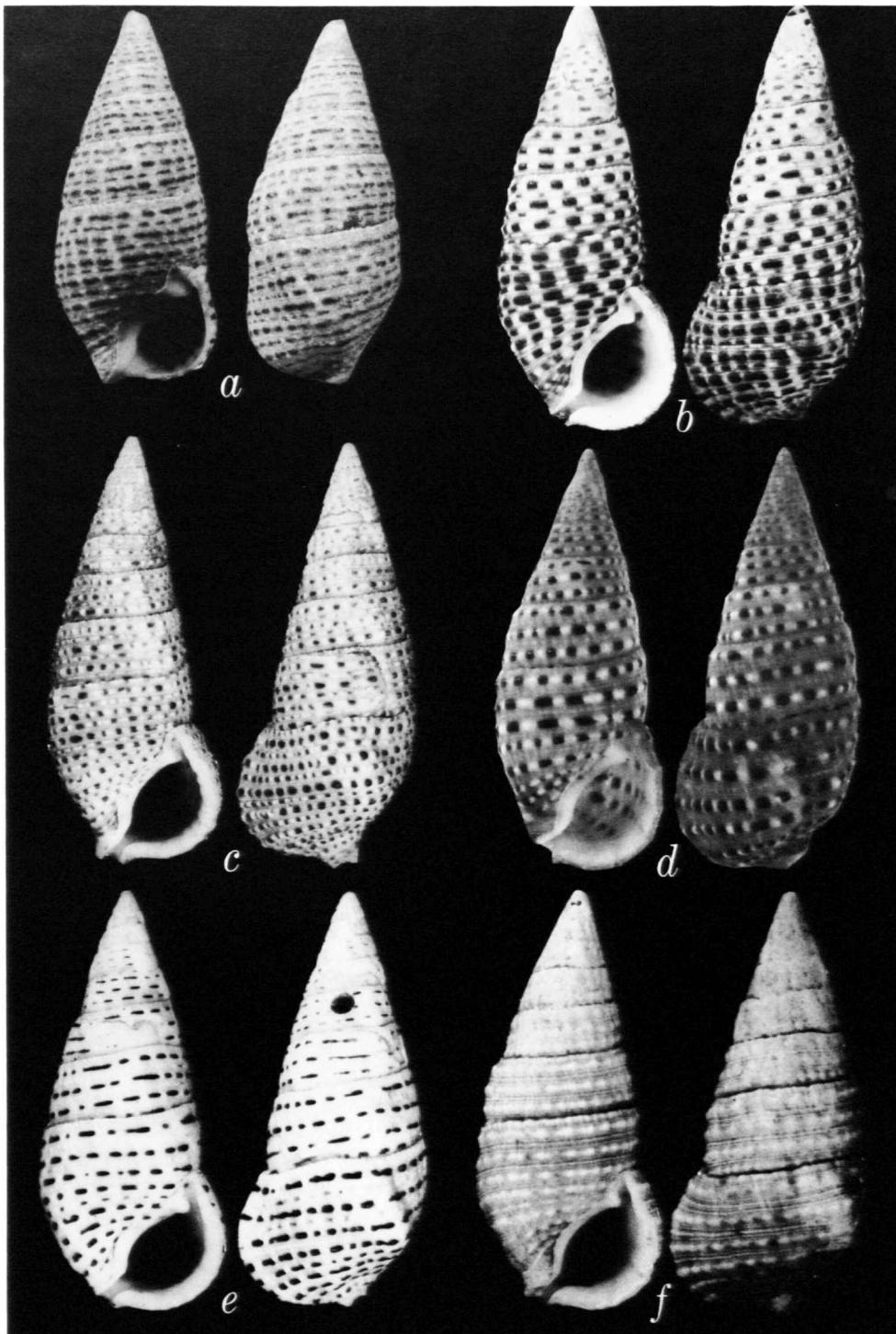
Populations of small individuals of *Clypeomorus batillariaeformis* sometime occur in northwestern Australia (USNM 691866). I have examined similar populations from Shimoni, Kenya (BMNH, not registered).

Some specimens of *Clypeomorus batillariaeformis* from northwestern Australia, the Arafura Sea, and coastal regions of southern New Guinea differ from the typical form in having longer, more slender, colorful shells, a larger shell length/aperture length index and are sculptured with more beads per whorl (Figure 26). Some are brightly colored (Figure 26*b,d*). These shells were named *Clypeomorus batillariaeformis* by Habe and Kosuge (1966:328), who believed their taxon was separate from other *Clypeomorus* species. Collection data show that these morphs live on an intertidal sandy substrate, which probably explains the elongate shell morphology. The presence of distinct, elongate morphs in these localities may be explained by the paleogeography of northern Australia. Much of the region was land during the Tertiary and only became a shallow sea in the Pleistocene (Doutch, 1972:1). The elongate shells may be due to recent dispersal of this species into these shallow, low energy habitats followed by subsequent shell modification. A comparison of shell characters and radular morphology between typical *Clypeomorus batillariaeformis* and these local morphs shows overlap in all characters, although the latter are consistently more slender. However, these morphs cannot be regarded as subspecies, because populations of similar morphs occur in Zanzibar

(ANSP 214371) (Figure 24*c*), the Caroline Islands (USNM 77668; 636170), and in New Caledonia (DMNH 117148), demonstrating that they are not geographically distinct. In Western Australia, where there is more rocky substrata, these slender forms merge into more typical *C. batillariaeformis* morphs. Some populations from coral reef regions in Queensland, Australia, NE New Guinea, the New Hebrides, and Fiji are brightly colored (Figure 24*a*).

Populations of modified forms of *Clypeomorus batillariaeformis* occur on Aitutaki, N. Cook Islands (USNM 725623), and on Rapa, Austral Islands (USNM 708783, 725398). Some of these populations from Rapa live on mud flats (USNM 725354). Cernohorsky has figured a typical specimen from Aitutaki (1972, pl. 16: fig. 5) under the name *Cerithium moniliferum*. These snails are difficult to place, differing from typical *Clypeomorus batillariaeformis* in having moderately slender, darkly pigmented shells that are sometimes thin. They are sculptured with weak spiral cords on which the beads are aligned axially to form about 14 strong ribs per whorl. The distinctive dorsal hump of *Clypeomorus batillariaeformis*, formed by a former growth varix, is much reduced or even lacking in these morphs; moreover, the body whorl is lightly swollen and the aperture wide and somewhat flaring, about one-third the shell length. The periostracum is thin giving the shell a silky aspect under magnification. As can be seen on Figure 27, these populations are relatively isolated slightly beyond the southeast range of typical *Clypeomorus batillariaeformis*. Aside from Aitutaki and Rapa, no samples of these morphs have been collected from other islands in the Cook group or in the Austral

FIGURE 26.—*Clypeomorus batillariaeformis* from Australia showing shell variability: *a*, holotype, Arafura Sea, Northern Territory (NSMT 38574; 26.4 × 12.0 mm); *b*, North Australia (USNM 304639; 31.5 × 12.4 mm); *c*, Fannie Bay, Darwin, Northern Territory (AMNH 100336; 31.5 × 11.9 mm); *d*, Taipang Bay, Northern Territory (AMNH 181519; 28 × 11 mm); *e*, Fannie Bay, Darwin, Northern Territory (AMNH 100336; 30.5 × 12.5 mm); *f*, Northern Territory (NSNM 304639; 30.8 × 13 mm).



Islands. The morphology of these morphs falls well within the range of variation that limits *Clypeomorus batillariaeformis* and does not justify taxonomic recognition, even at the subspecific level. Nevertheless, I call attention to the unusual distribution of these populations, point out that they may be somewhat isolated from the *Clypeomorus batillariaeformis* gene pool, and suggest they may be undergoing incipient speciation.

Specimens from the Caroline Islands (USNM 774567, 774579) sometimes have purple apertures and may be confused with *Clypeomorus purpurastoma*, new species. This is the only locality that I know where *Clypeomorus batillariaeformis* may have a purple aperture.

I examined a large series of unusually tiny morphs comprising a population from Lae Island, Lae Atoll, Marshall Islands (USNM 614990) (Figure 24g). Another similar population occurs on Likiep Atoll, Marshall Islands (USNM 596139). These populations are at the edge of the geographic range of *Clypeomorus batillariaeformis* and may be existing at the ecological limits of the species. In contrast to these populations, groups of extremely large morphs occur at Upolu Island, Western Samoa (ANSP 198481), at the edge of the geographic range.

FOSSIL RECORDS.—Specimens recorded from the Pliocene of Fiji by Ladd (1972:40), cited as *Cerithium wainigoli* Ladd, 1972, and from the upper Pliocene of the Philippines by Shuto (1969:67–68), cited as *Clypeomorus tuberculatus* (Linnaeus), appear to be conspecific with *Clypeomorus batillariaeformis*. *Clypeomorus batillariaeformis* also occurs in Pleistocene formations on Saipan and as a Holocene fossil on Enewetak Atoll, Marshall Islands (Ladd, 1972:37, cited as *Cerithium alveolus* Hombron and Jacquinot).

GEOGRAPHIC DISTRIBUTION (Figure 27).—*Clypeomorus batillariaeformis* has a wide Indo-Pacific distribution. Isolated from other populations, it occurs in the Austral and Cook Islands of the central South Pacific. It also occurs throughout the western Pacific where it is most common around high islands and continental shores. It ranges from the Ryukyu Islands in the north, south to the Tropic of Capricorn. It is also found along the continental margins of the Indian Ocean.

MATERIAL EXAMINED.—EAST AFRICA: grass flats, Isla di Serpenti, Chisimais, Somalia (AMNH 146219); Twiga, 12 mi (19 km) S of Mombassa, Kenya (ANSP 287346); S Wasin, Shimon, Kenya (BMNH); Vasco di Gama Pt, Mal-

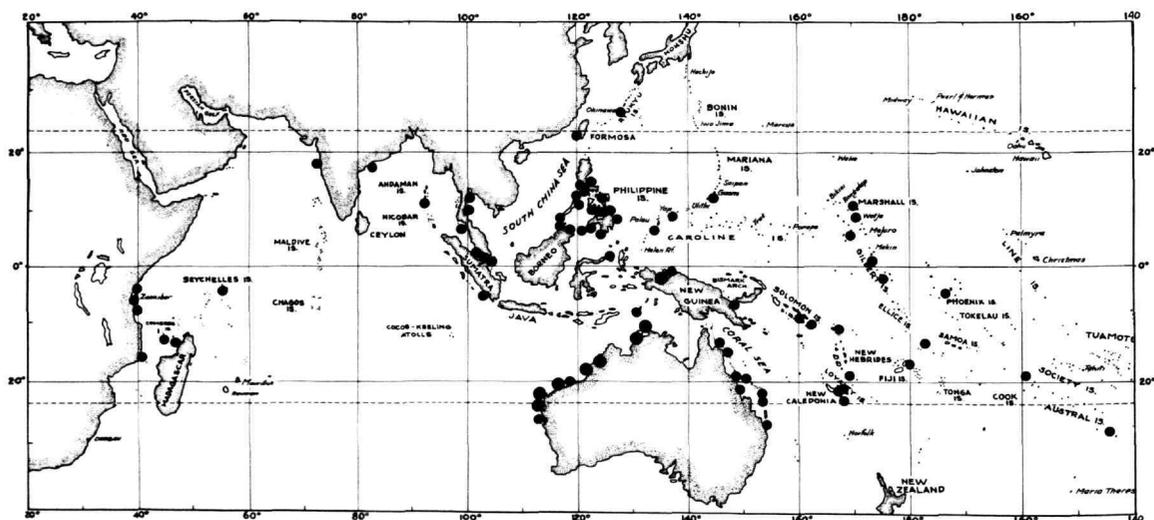


FIGURE 27.—Geographic distribution of *Clypeomorus batillariaeformis* Habe and Kosuge, 1966.

indi, Kenya (ZMA); Ras Anznani, Shimoni, Kenya (BMNH 22.11.71); Puopu, E side of Tumbabu Id, W Zanzibar (ANSP 21300); Mazizini, W Zanzibar (ANSP 214730); Chango, (Prison) Id, W Zanzibar (ANSP 214371); Bagamoyo, E Prov, Tanzania (USNM 703988); Mboa Maji, Tanzania (USNM 774547); Ras Chokir, Dar es Salaam, Tanzania (USNM 786798); NW of Choca, SW Conducia Bay, Mozambique (NM H1887). MADAGASCAR: station Jr-11, Pt Fièvre, Nossi-Bé (USNM 744504). INDIAN OCEAN: Andaman Ids (USNM 173054); Baie Ternay, Mahé, Seychelles (BMNH). CEYLON: Trincomalee, Dutch Bay, Sri Lanka (CAS); Kankasanturai, N Sri Lanka (ANSP 210976). PERSIAN GULF: Djask(LACM). INDIA: Bombay (BMNH 1838); Chanpati Beach, Bombay (USNM 701803); Waltair (USNM 622110); Bombay (ANSP 231921); Bandra, N of Bombay (USNM 443607); W of Mandapam, Gulf of Mannar (ANSP 302541); Rameswaram, Pamtan (= Rameswaram) Id, Palk Strait (ANSP 301094). SOUTHEAST ASIA: Cape Ricardo, Malacca Straits, Malaysia, IIOE Mo 8, Te Vega "A" (USNM 660996); Pulau Besar, SE of town of Malacca, Malaysia (USNM 774513); Negril Sembilan, Port Dickerson, W Malaysia (USNM 778475); Kampong, Loyang, near Chang, NE Singapore, IIOE Mo 1 (USNM 774506); Laam Son, W Phuket Id, Thailand (ANSP 286013); Pulau Hanta, SW of Singapore, IIOE, Te Vega, sta. 65 (USNM 774582); Ackam, S end of Phuket Id, Thailand (ANSP 286924); Pulau Tanga, Butang Group, Thailand (USNM 776721); Laam Yamu, E Phuket Id, Thailand (ANSP 285906); Koh Tao, Thailand (USNM 419697); Siracha, Gulf of Siam (USNM 774565). INDONESIA: Benkoelen, Sumatra (USNM 774559, 776667); Djakarta Bay, Java (ZMA 10446); W side of Mitak Id, Jamdena Straits, Tanimbar, Moluccas (USNM 774487); Gomomo Id, Pitt Pass, Celebes (USNM 233069); Look, near Mangarai Prov, Flores (UF, no number); Huron Gulf, New Guinea (USNM 487891); 0.5 mi (0.8 km) SSW of Soweik, Soepiori Id, Schouten Ids, New Guinea (ANSP 207945); NE end of Noekori Id, E Paddaido Id, New Guinea (ANSP 205942); 1 mi (1.6

km) NW Ambai Id, Japen Id, New Guinea (ANSP 207188); N shore of Maroepe Id, Ambai, Japen Id, New Guinea (ANSP 272414). N BORNEO: Pertawan Id, E Banggi (USNM 632205); W Marudu Bay, (USNM 632203); Berhala Ids, Sandakan (USNM 232865, 658121, 658155). WESTERN AUSTRALIA: NE end Rosemary Id, Dampier Archipelago (WAM 880-76); Cockatoo Id (WAM); Pt Samson (WAM 885-76); King Sound (USNM 618160); MacGregor Point, Admiralty Gulf (WAM); Troughton Ids (WAM 875-76); Ningaloo Reef, 15 mi (24 km) N of Ningaloo (WAM 884-76); S of Willy Creek, 17 mi (27 km) N of Broome (ANSP 233503); Buccaneer Rock, Broome (ANSP 232911); Entrance Pt, Broome (ANSP 232998); 2 mi (3 km) SW of Jetty, Broome (ANSP 233087; WAM 866.76); Black Ledge, 4 mi (6.4 km) E by S of Broome (ANSP 233656); 12 mi (19 km) N of Cardabia Homestead (WAM 873-76); Bill Bay, 2 mi (3 km) S of Point Maud, Cardabia (WAM); 1 mi (1.6 km) SE of False Cape Bossut, La Grange Bay (ANSP 233323); between Cape Dupuy and Cape Melovet, Barrow Id (USNM 691866); Cape Leveque (ANSP 336648); Useless Loop, Shark Bay (USNM 790691); SE side of Dirk Hartog Id, Shark Bay (WAM 876-76); Freyeinet Beach ¼ mi (0.4 km) S of Shark Bay (WAM); Tidal Creek at Little Lagoon near Denham, Shark Bay (WAM); Surf Point, Dirk Hartog Id, Shark Bay (WAM); Malumba (AMNH 181512); Port Hedland (NM G4934); Exmouth Gulf (NM G2786). NORTH AUSTRALIA: Fannie Bay, Darwin (AMNH 100336); Nightcliff Pt, Darwin (USNM 602155); Trepang Bay (AMNH 181519). RYUKYU ISLANDS: Near Ora Wau, Okinawa, Ryukyu Ids (USNM 593674); Naha, Okinawa, Ryukyu Ids (USNM 632446); Yonabaru, Okinawa, Ryukyu Ids (USNM 363737); Ukibara-Shima, E of Okinawa, Ryukyu Ids (USNM 670490); Kadena Circle, Okinawa, Ryukyu Ids (USNM 664638); Shioya, Sharawan Bay, Okinawa, Ryukyu Ids (USNM 489139); North side of Naha, Okinawa, Ryukyu Ids (ANSP 302846); Batan Bay, Okinawa, Ryukyu Ids (LACM 29256); Meta-saki Reef, Okinawa, Ryukyu Ids (LACM 29976). PHILIPPINES: Eman Pt, Morong, Ba-

taan (USNM 774755); Looc Bay, Bagac, Bataan (USNM 243725, 244031); Subic Bay, Luzon (USNM 232891); Port Binang, Subic Bay, Luzon (USNM 243847); Olongapo, Luzon (USNM 243616a, 774499); Port Matalvi, Luzon (USNM 774476); Nasugbu, Luzon (USNM 243762); Ligpo Pt, Balayan Bay, Luzon (USNM 233047, 233049, 774491); Basus River, E Luzon (USNM 774575); Jamelo Bay, Luzon (USNM 232877); Bacoor, Manila Bay (USNM no number); River at Port Galera, Mindoro (USNM 243849, 775148); Port Galera, Mindoro (USNM 244012); San Pascual, Burias (USNM 243649); Dumurug Pt, Masbati (USNM 243842); Cataingan Bay, Dumurug Pt, Masbate (USNM 243864, 243866); San Juanico Strait, Leyte (USNM 232949, 243729, 744503); Catbalogan, Samar (USNM 774480); W of Catbalogan, Samar (USNM 774490, 775144); Port Naso, Panay (USNM 232972, 232973, 232974, 774466, 774467); Opol, Mindanao (USNM 243817); Panabutan Bay, Mindanao (USNM 244032, 310237); Zamboanga, Mindanao (USNM 774494); Zamboanga, Mindanao (USNM 619847); Great Santa Cruz Id, Mindanao (USNM 232999); Panalintan Bay, Mindanao (USNM 233089); Lianga Bay, Mindanao (USNM 243892); Capunuyupugan Pt, Mindanao (USNM 774496); Palawan (USNM 239903); Ulangan Bay, near Caiholo River, Palawan (USNM 233046); Oyster Bay, Palawan (USNM 243875, 243876); Port Langcan, Dumaran Id, Palawan (USNM 233032, 244196, 774479); Tagbayag Bay, Palawan (USNM 244038, 774508); Mactan Id, Cebu (USNM 233178); Cebu (USNM 243795, 243796, 243798); Reef opposite Cebu (USNM 232871, 323873); Jolo (USNM 232984, 232985, 232987); Simaluc Id, Tawi Tawi (USNM 239625, 243706, 243708); Tabataan, Simaluc Id, Tawi Tawi (USNM 244025); Papatag Id, Tawi Tawi (USNM 233209); Id off of Tibuan, Tawi Tawi (USNM 232956, 232959); Port Ciego, Balabac (USNM 243851, 243856, 243860); Malchochin Harbor, Linapacan (USNM 233192); Lampinegan Id, off Basilan (USNM 244040); Guijulugan, Negros (USNM 243933); Lubang Id, (USNM 243777) Id ¼ mi

(0.4 km) W of Tara Id (USNM 236434); NE of Simonor Id (USNM 306294); Engano (USNM 313888); between Siasi and Bongo Ids (USNM 232879); Cabugao River, Catanduanes (USNM 232879). MARIANAS ISLANDS: Apra Bay, Guam (USNM 232943, 774571). TAIWAN: N Hoko Id (USNM 563841); Tung Lian Beach, Makung, Pescadores Ids (AMNH 130679). QUEENSLAND: Green Id (AMNH 181518); Yule Pt, N of Cairns (NM G4939); Cairns (AMNH 181491); Yule Pt, N of Cairns (BMNH); Double Heads, Yeppoon (LACM 66-219), Caloundra (LACM 35450); Kepple Id (LACM); Lizard Id (USNM); W side Lizard Id, (USNM 704746); Thursday Id (LACM); Lady Elliot Id (ANSP 267513); W end Heron Id (USNM 704889); S Molle Id (LACM 29255); Port Douglas (USNM 770611); Finlayson Pt, Mackay (BMNH 2036); Flat Top Id, near Mackay (USNM 774489); N Dunwich, Stradbroke Id (USNM 704988, WAM 881-76); near jetty, Hayman Id (USNM 704898); Low Isles (USNM 623070). NEW CALEDONIA: W end Baie des Canards, Anse Vata, Nouméa (ANSP 247561); Nouville, N part of Nouméa (USNM 806088); Point Magin, near Nouméa (USNM 774560); Pointe aux Long Cous, Nouméa (USNM 724213, 774456); Magenta Estuary, E of Nouméa (USNM 724294, 774520); Anse Vata, near Nouméa (USNM 724062); 2 km S of Conception (USNM 724530, 724532, 724535); Récif Ricaudy, S of Nouméa (USNM 784317); W side, S shore, Mt l'Or, near Nouméa (ANSP 237859); Lighthouse Id, opposite Nouméa (USNM 724423); Toaourou (USNM 774459, 774529, 774556); N end, Kouekum Id (USNM 693768); SE side of bay, Touho (ANSP 270352); Kuto Bay, Isle of Pines (DMNH 117148); N side of N'Go Bay (USNM 774457); shore, Hienghene (USNM 666083); Redika Id, 18 mi (29 km) SE of Nouméa (USNM 724130); reef E of Nau Id (USNM 693800); Bay de Prony (USNM 724820, 774510); Thio (ANSP 238385); SE side of bay, Touho (ANSP 270352); Atera Id (USNM 724186); S of Yate, Touaourou (USNM 801415). LOYALTY ISLANDS: N side of inlet at Cape Lekin, Atoll, Uvea (USNM 692815);

Lifu (USNM 423322). NEW HEBRIDES: Vanikoro Id, Santa Cruz Ids (USNM 701023); reef S of Utja, Aneityum (USNM 692124); SW Éfate Id (USNM 787978); Pointe d'Arbel, Éfate Id (USNM 787535, 787537); Takara, NE part of Éfate Id (LACM 77-42). SOLOMON ISLANDS: Pt Purris, Florida Id (USNM 432436); Choiseul Bay, Ugi Id (USNM 600409); Buraku Id, Russell Group (LACM). CAROLINE ISLANDS: Tomil Harbor, Yap (USNM 774567, 774579, 776665); Koror, Palau Ids (USNM 621155, 636170, 636198, 636209, 776668). MARSHALL ISLANDS: Nado Id, Likiep Atoll (USNM 596139, 615323); Lae Id, Lae Atoll (USNM 614990); Uterik Id, Uterik Atoll (USNM 615603, 615654); Enybor Id, Jaliuit Atoll (USNM 659322); S of Lelul, Long Id, Jaluit Atoll (USNM 659706); north point of Enybor Id, Jaliuit Atoll (USNM 659333); W side, Elizabeth Id, Jaluit Atoll (USNM 659212); Kwajalein Atoll (USNM 774448). RAPA: Ahurei (USNM 658857); S side Ahurei Bay (USNM 725592); S of Bare Pake, E coast Rapa (USNM 725398); NE corner of head of Ahurei Bay (USNM 725644); N side of Ahurei Bay (USNM 725354); Ahurei Bay (USNM 658886); FIJI: S of Waikama, Ngau (USNM 68686); NW side Ovalau Id (USNM 694258); Cuvu Id, Nandronga, Viti Levu (USNM 616871); Suva Pt, Viti Levu (USNM 532425); 8 mi (12.8 km) W of Suva, Viti Levu (USNM 723843); S of Ongea, Ongea Levu, Lau Group (USNM 531662); Curvu Id, Nandronga, Viti Levu (USNM 774549); SE side, Tavutha, Viti Levu (USNM 694397); S side Verevere Id, Vanua Levu (USNM 694900); Lebuvia Id, Mbua, Viti Levu (USNM 666385); Laucala Bay, Suva, Viti Levu (USNM 794742, 794744); S side Mathuata Id, Viti Levu (USNM 774584); Nananu-i-Ra (USNM 638525); Vanua Levu (USNM 774546); SW side Ovatoa, NW Vanua Levu (USNM 694757); Daumba Reef, S coast, Viti Levu (USNM 794732). SAMOA: (ANSP 198481); Ana Area, Tutuila (ex USNM 699399). WALLIS ISLAND: between Luanna and Fungalei Ids (USNM 676450, 676472); Wallis Id (MNHNP). PHOENIX ISLANDS: Hull's Island (USNM

13339, 513296). GILBERT ISLANDS: Lagoon of Apamama (USNM 433855, 433994); Onotoa Atoll (USNM 607498). COOK ISLANDS: W side Akitua, NE Aitutaki (ANSP 278158); jetty near Airport, Aitutaki (USNM 684959, 708783); near Arutanga Passage, Aitutaki (USNM 684791); Arutanga Village, Aitutaki (USNM 732524; 725623).

***Clypeomorus pellucida* (Hombron and Jacquinot), new combination**

FIGURES 28–31

- Cerithium pellucidum* Hombron and Jacquinot, 1852, pl. 23: figs. 24, 25 [holotype: MNHNP, no number; type-locality: Solomons]; 1854:101–102.—Tryon, 1887:133, pl. 24: fig. 22.—Oostingh, 1925:44.
- Cerithium patulum* Sowerby, 1855:871–872, pl. 179; fig. 74 [lectotype: here selected, BMNH, not registered; type-locality: Ilo Ilo, Panay, Philippines]; 1865, pl. 5: fig. 33.—Tyron, 1887:133, pl. 24: figs. 20–22.—Martens, 1897:170.—Tesch, 1920:53, pl. 130: fig. 174.
- Cerithium patulum* var. *depauperata* Dautzenberg and Fischer, 1905:126.
- Cerithium gibberosum* Frauenfeld, 1867:7–8, pl. 1: fig. 7 [holotype: Vienna Museum; type-locality: Nicobar Islands; not *Cerithium gibberosum* Grateloup, 1832].
- Cerithium gibberulum* Frauenfeld [sic].—Tyron, 1887:133.
- Cerithium echinatiformis* K. Martin, 1884:153–154, pl. 8: fig. 150 [holotype: RGM 12000; type-locality: Fatu Lilib, Timor, Pliocene].
- Cerithium patulum* (Sowerby).—Shirai, 1977:275.

DESCRIPTION.—*Shell* (Figures 28, 30; Table 14): Adult shell elongate, turritid, reaching 16.5 mm in length and having teleoconch of about 10 whorls with apical angle of 30 degrees.

TABLE 14.—Analysis of shell parameters of *Clypeomorus pellucida* (measurements in mm).

Character (n=25)	\bar{x}	sd	Range
Shell length	22.65	4.16	16.31–30.06
Shell width	10.33	1.85	7.01–14
Aperture length	6.32	1.15	4.33–9.02
Aperture width	4.93	1.00	3.36–6.97
No. axial ribs per whorl	11.76	1.13	10–14

Length/width index: 2.19

Shell length/aperture length index: 3.58

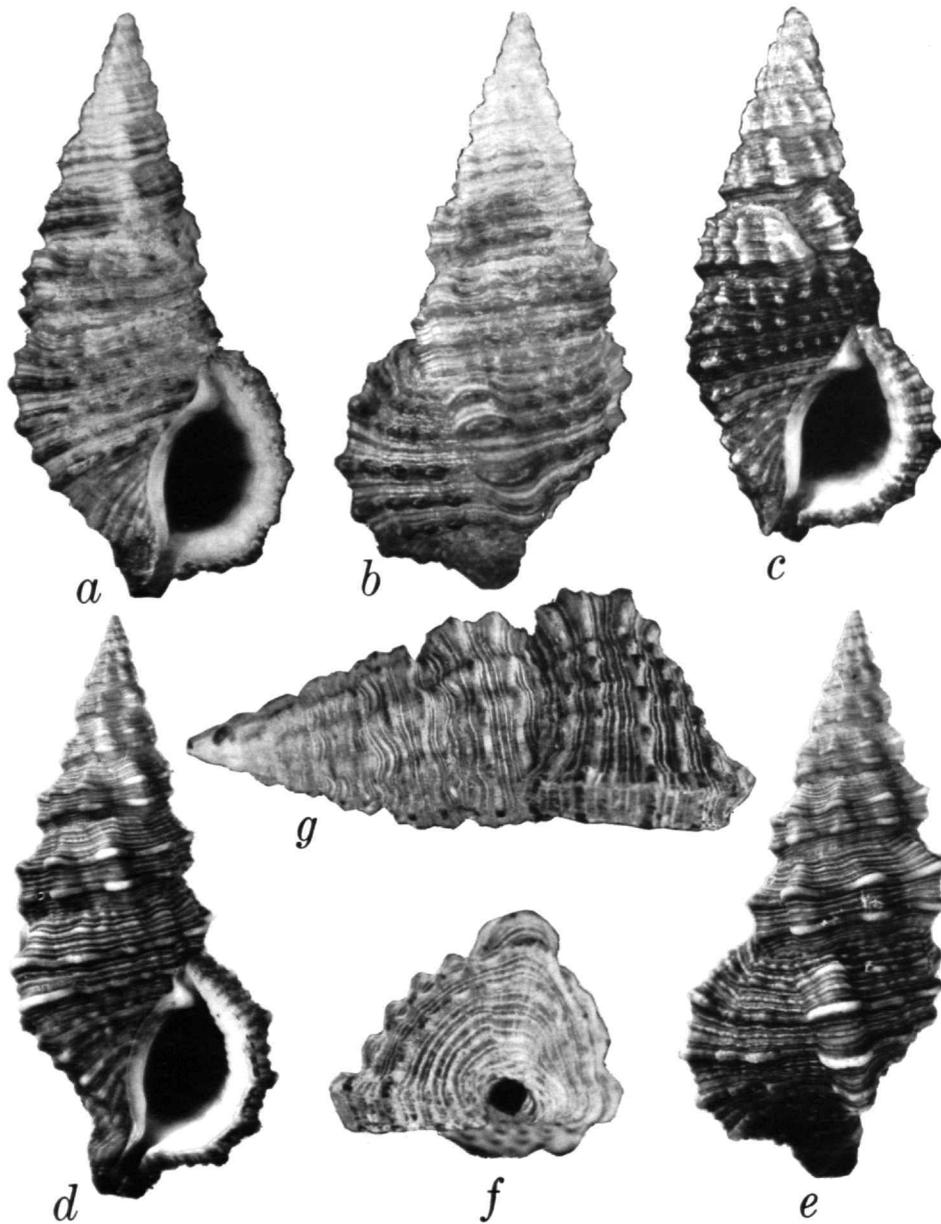


FIGURE 28.—*Clypeomorus pellucida* (Hombron and Jacquinot, 1852): *a, b*, lectotype of *Cerithium patulum* Sowerby, 1855, BMNH, no registry number (26.2 × 11.6 mm), Ilo Ilo, Panay, Philippines; *c*, holotype of *Cerithium pellucidum* Hombron and Jacquinot, 1852, Solomon Islands, MNHNP, no number (25 × 10.7 mm); *d, e*, Malcochin Harbor, Linapacan Island, Philippines, USNM 243850; *f, g*, anterior and side views showing dorsal varix, placement of anterior canal, and outer lip of peristome; same data as in *d* and *e*.

Whorls angular, moderately inflated, nearly straight-sided at apex. Upper portion of each whorl slopes broadly toward suture while adapical part more sharply impressed toward suture. Suture distinct, impressed, wavy. Each adult whorl sculptured with 2 dominant, nodose spiral cords and 1 weaker, spiral nodose cord on upper slope of whorl. Adult whorls sculptured with numerous, deeply incised, spiral lines. Nodes arranged axially to form strong axial ribs, about 12 per whorl. Former varices are present. Early postnuclear whorls sculptured with 2 distinct, smooth, spiral cords. Protoconch unknown, always eroded in adults. Body whorl large, inflated, sculptured with 8 or 9 beaded spiral cords and constricted at base. Large, angular varix on dorsal part of body whorl at 90 degree angle to plane of aperture. Second large angular varix on body whorl opposite outer lip, nearly joining it at anterior siphon. Apertural surface of body whorl concave. Aperture large, flaring, about one-third the length of shell, circular-ovate with concave columella, and moderate columellar callus. Anterior siphonal canal nearly straight, somewhat in line with shell axis. Anal canal deeply incised, bordered with parietal columellar plait and extending well into shell aperture. Crenulate outer lip of aperture expanded and thickened to form heavy varix. Upper edge of outer lip extends up to median part of penultimate whorl. Inner surface of outer lip beveled, weakly toothed in older specimens. When viewed laterally, plane of aperture in line with shell axis. Periostracum thin, tan, frequently eroded on apical portion of shell. Shell color brown, usually with fine, white, spiral lines. Nodes usually lighter than rest of shell. Operculum ovate, thin, corneous, paucispiral with nucleus near edge. Attachment scar ovate, on bottom third of operculum.

Radula (Figure 29; Table 15): Radular ribbon moderately long, about 3.3 mm in length and comprising 63 rows of teeth in animal 20 mm long. Shell length/radula length index 4.91. Rachidian tooth (Figure 29d) pentagonal, about 65 μ m wide. Basal plate of rachidian with broad

TABLE 15.—Analysis of radular parameters of *Clypeomorus pellucida* (measurements in mm).

Character (n=7)	\bar{x}	sd	Range
Radula length	4.88	0.68	4.38–6.31
Rows of teeth	87.71	10.05	79–107
Shell length	23.96	2.31	20.09–26.41

Shell length/radula length index: 4.91

basomedial projection flanked on each side with pit-like depression and with shorter basolateral projection. Top of rachidian deeply concave in center forming V shape. Cutting edge of rachidian tooth with large, pointed, spade-shaped, central cusp flanked by 2 sharp denticles on each side. Lateral tooth (Figure 29b,d) rhomboidal, with long twisted basolateral projection that inserts onto radular membrane. Basal plate of lateral tooth has long, median, buttress-like projection directed downward. A small rounded bump is at center of buttress and articulates with next row of teeth. Top of lateral tooth slightly concave, serrated with small pointed inner denticle, large spade-shaped cusp, and 2 (sometimes 3) smaller pointed denticles. Marginal teeth (Figure 29b,c) wide, slightly constricted at bases, sinuous at outer margins, wide at center of tooth shaft, curved and broadly spatulate at tips. Tip of inner marginal tooth has 2 rounded inner cusps, a larger rounded central cusp, and 1 outer rounded cusp. Outer marginal tooth identical but lacking outer cusp.

Animal: Anatomy as in *Clypeomorus bifasciata*. Preserved animal light brown with transverse lines and flecks of darker brown. Snout broad, tentacles thick at penduncular base, narrowing distally. Eyes large. Foot large with white sole. Propodium has thick anterior pedal mucous gland that extends deeply into foot and secretes copious amounts of mucus. Mantle edge papillae long, thicker, wider, and darker at inhalant and exhalant siphons. Bipectinate osphradium and narrow ctenidium extending length of mantle cavity. Hypobranchial gland comprised of thick transverse folds of glandular tissue. Jaws large,

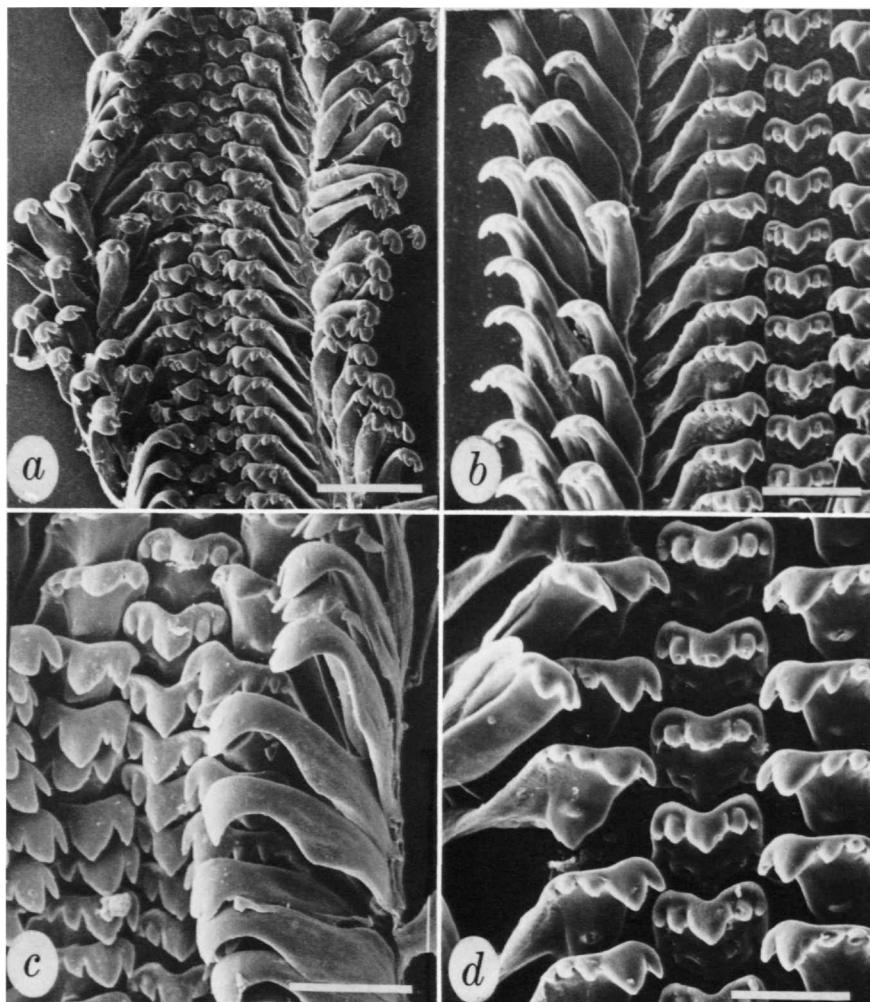


FIGURE 29.—SEM micrographs of *Clypeomorus pellucida*: *a*, general view of radular ribbon (bar = 150 μ m); *b*, half row with marginal teeth folded back showing lateral teeth (bar = 150 μ m); *c*, half row with marginal teeth folded over ribbon showing wide buttress at base of marginals (bar = 75 μ m); *d*, detail of rachidian and lateral teeth (bar = 75 μ m).

oval, and about 0.7 mm long. Salivary glands are thick flat tubules lying mostly anterior to nerve ring but extend partially through it.

REMARKS.—This species is not commonly known in popular shell books and is usually cited as *Cerithium patulum* Sowerby, 1855 (Figure 28*a,b*) in the scientific literature. The earliest valid name is *Cerithium pellucidum* Hombron and Jacquinot, 1852 (Figure 28*c*). *Cerithium gibbero-*

sum Frauenfeld, 1867, is another rarely used name that is also synonymous with *Clypeomorus pellucida*. The Pliocene fossil described by K. Martin (1884), *Cerithium echinatiformis* (Figure 30*a-c*), is merely a specimen of *Clypeomorus pellucida* with a broken or immature outer lip. The anterior canal is twisted sharply to the left as in Recent immature specimens.

ECOLOGY.—*Clypeomorus pellucida* normally

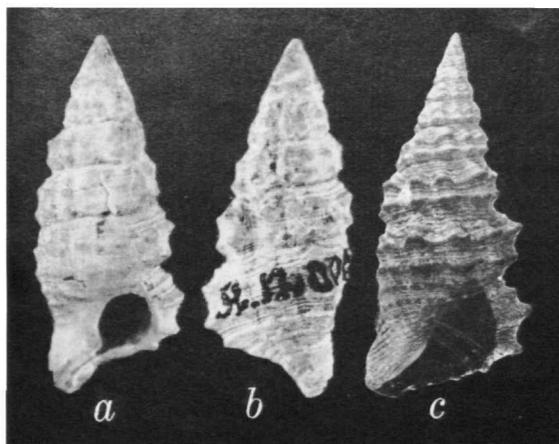


FIGURE 30.—*Cerithium echinatiformis* K. Martin, 1884: *a*, *b*, holotype, Pliocene of Fatu Lilib, Timor, RGM 12000 (18.2 mm long); *c*, immature specimen, Malcochin Harbor, Lina-pacan, Philippines, USNM 243850 (28.5 × 12.3 mm).

lives on the aerial roots of mangroves slightly above the high tide mark. The shell morphology of this estuarine species is admirably suited for clinging to roots. The large anterior pedal mucous gland probably enhances crawling on the dry surface of mangrove roots. The plane of the aperture is tangential to the shell surface and passes through the apex allowing the entire shell to clamp against the root surface. Little is known of the biology of this species, but its unusual mangrove habitat suggests a different ecology from the high energy rocky substrates of most other *Clypeomorus* species. The protoconch and early whorls are always eroded and the spawn and larvae unknown; consequently, it is not possible to deduce the mode of development. *Clypeomorus pellucida* presumably grazes on microalgae associated with mangrove aerial roots. The stomach of preserved specimens is filled with filamentous green algae and detritus, and the ovate fecal pellets are comprised of sand grains and detrital particles.

DISCUSSION.—The pronounced spiral and axial sculpture, dark brown color, large angular former varices, the humped lateral aspect, and flattened concave apertural plane are all distinctive characters that make *Clypeomorus pellucida*

unlikely to be confused with most other *Clypeomorus* species. It approaches *Clypeomorus batillariaeformis* Habe and Kosuge in general shell physiognomy and may be confused with some morphs of that species. There is also some resemblance to *Clypeomorus bifasciata*. Immature specimens of *Clypeomorus pellucida* do not have the angular look of adults, but they are smoother and look more like other young cerithiids. Early postnuclear whorls are tapered and sculptured with two spiral cords. Subadults and snails in the process of adding a new whorl are remarkably distorted when viewed aperturally (Figure 30): the anterior siphonal canal is sharply twisted almost 90 degrees to the left due to the concavity of the aperture and large varix opposite the outer lip. Young snails are extremely asymmetrical and it is difficult to imagine how they are able to crawl or attach themselves to mangrove roots during this growth stage.

Plaziat (1977:38–39, pl. 1: figs. 1–4) considered *Clypeomorus pellucida* (cited as *Cerithium patulum*) to be an ecophenotype of *Clypeomorus batillariaeformis* (cited as *Clypeomorus moniliferum*) and believed that the distinctive shape of *Clypeomorus pellucida* morphs was correlated with their habit of living on aerial mangrove roots. He illustrated specimens of several other *Clypeomorus* species that he thought were transitional morphs between *Clypeomorus batillariaeformis* and *Clypeomorus pellucida*. Plaziat (1977) was not familiar with the *Clypeomorus* complex on a worldwide basis and has mistakenly illustrated three different species instead of one very variable species. Plaziat's (1977, pl. 1: figs. 1–4) illustrations, while said to represent transitional morphs, actually depict specimens from three different geographic localities and do not show an ecological transition or ecocline. His figures 1 and 2 are both *Clypeomorus pellucida* taken from mangrove roots. Figure 3 is *Clypeomorus batillariaeformis* from a rocky beach and figure 4 is *Clypeomorus bifasciata* from a sandy habitat bordering mangroves. *Clypeomorus pellucida* may be distinguished from these two other species by its straight-sided whorls, a large dorsal varix on the body whorl that is at a 90 degree angle to the

apertural plane, the concave surface of the ventral part of the body whorl, an anterior siphonal canal in line with the shell axis, by two prominent spiral cords, and large former varices on each whorl. In contrast, both *Clypeomorus batillariaeformis* and *Clypeomorus bifasciata* have more inflated whorls, siphonal canals directed 45 degrees to the left of the shell axis, and three spiral whorl cords per whorl. In *Clypeomorus batillariaeformis*, the dorsal varix of the body whorl is at a 120 degree angle to the apertural plane while *Clypeomorus bifasciata* lacks a dorsal varix altogether but has a thick varix on the body whorl opposite the outer lip. All of these features may be seen in Plaziat's figures (1977:38). Besides these differences, the radula of *Clypeomorus pellucida* is longer and more robust, with the cusps less spatulate than those of *Clypeomorus batillariaeformis* and *Clypeomorus bifasciata*.

Fossil RECORDS.—*Clypeomorus pellucida* is recorded from the Pliocene of Timor by K. Martin (1884:153), who named the fossil *Cerithium echinatiformis* (Figure 30). Martin noted its similarity to *Cerithium patulum* (= *Clypeomorus pellucida*) but believed that it differed enough to be considered a separate species. The minor sculptural differences in the fossil easily fall within the range of sculptural variation seen in many specimens of the Recent species. Considering that so many living *Clypeomorus* and cerithiid species are represented in the fossil record, it is not unreasonable to consider Martin's fossil species conspecific with *Clypeomorus pellucida*.

GEOGRAPHIC DISTRIBUTION (Figure 31).—This species is confined mainly to the western Pacific where, it lives from the Ryukyu Islands south throughout the Philippine and Indonesian archipelagos. It is also found to the east in the

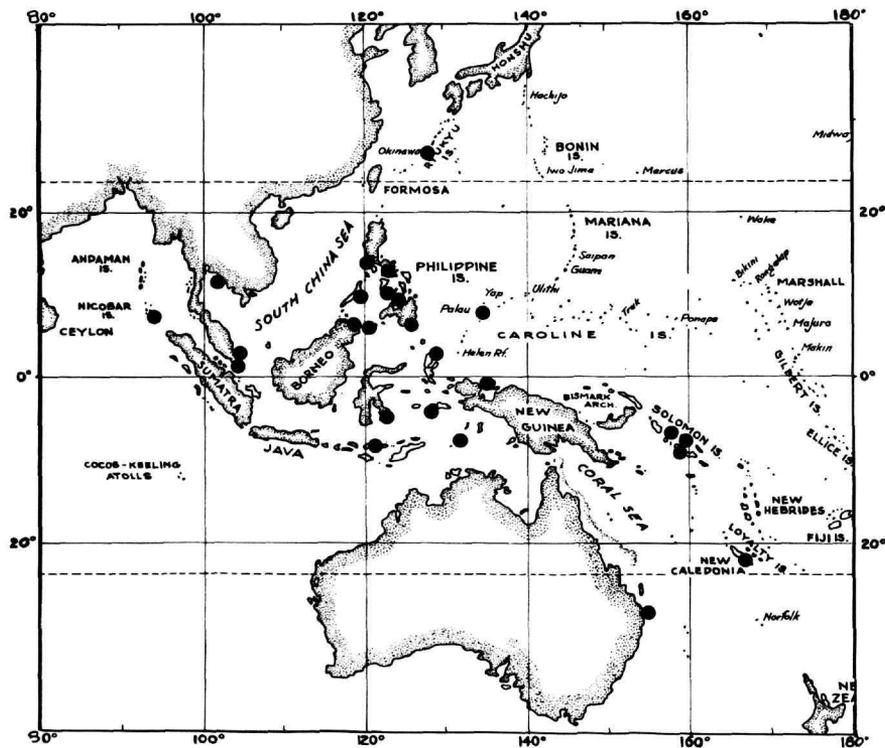


FIGURE 31.—Geographical distribution of *Clypeomorus pellucida* (Hombron and Jacquinot, 1852).

Solomons and the Loyalty Islands and has been collected as far south as lower Queensland. Museum specimens from the Andaman Islands in the eastern Indian Ocean indicate that it most likely occurs in other areas of the Andaman Sea where there is suitable mangrove habitat.

MATERIAL EXAMINED. — **SOUTHEAST ASIA:** Singapore (USNM 18620, 48011); Palau Sudong, Singapore (USNM 631939); Krangi, Singapore (ANSP); Cape Rachardo, Malacca Strait (USNM 660997, 660996); Koh Kut, Gulf of Siam (USNM 405832); Mersing, SE Malaya (WAM). **INDONESIA:** Sumatra (ZMA, Siboga Expedition); Menschenetei Id, Java (ANSP); Labuan Blanda Id, Butung Strait, Celebes (USNM 233040); Cape Tandjung, Ndorotai, 3 km NNE Reo, Flores (UF 24771); W side Mitak Id, Jamolena Straits, Tanimbar, Moluccas (USNM 774400); S side of Morotai, E of Gila Peninsula Halmahera Group (USNM 542549); Kg Said, NW coast of Ambon Id, Moluccas (WAM). **NEW GUINEA:** Sorendidori, E side of Soepiori Id, Schouten Ids, West Irian (ANSP); 1½ mi (2.4 km) SW Mansoten, Sorendidori, Biak, Schouten Ids (both ANSP); Joyce Bay, Port Moresby, Papua (DMNH). **N BORENO:** Po Bui Id, Sandakan (USNM 243694, 232865); Batu Sapi, Sandakan (USNM 666860); Kudat Bay (USNM 632200, ANSP). **PHILIPPINES:** mouth of small stream, Canmahala Bay, Ragay Group, Luzon (USNM 239730); Basus River, E Luzon (USNM 774473); Balayan Bay, mouth of Santiago River, Luzon (USNM 233057); Basud River, Luzon (USNM 239884); Ragay River, Ragay Group, Luzon (USNM 240173); S end of Matbunkay Cove, 14 km S of Nasugbu, Batangas (ANSP); Viejo Victorias, Negros Occidental (USNM 313296); Siaton, Tambobo, S Negros Oriental (USNM 808387); S Bias Bay, W Daco Id, Negros Oriental (USNM 808027); mouth of Mangnanad River, Victorias, Negros (USNM 419386); Malcochin Harbor, Linapacan Id (USNM 243850); near Cebu City, Cebu (USNM 243795, 543722); Puerto Princesa, Palawan (USNM 303688); Puerto Galera, Mindoro Oriental (USNM 777292, 777281); Bongabon, Mindoro (USNM 239841); W side, Hadayan Id, NW Bohol

(ANSP); San Juanico Strait, Samar, Leyte (USNM 243864); Opol, Mindanao (USNM 774524, 232975); Davao, Mindanao (UF 24765); Engans (USNM 306294); Bongao Channel, SW end Sanga Sanga Id, Sulu Archipelago (ANSP); Dos Amigos Bay, Tawi Tawi (USNM 243904). **RYUKYU ISLANDS:** Naha, Okinawa (USNM 633812). **PALAU ISLANDS:** Arakitaoch stream, Palau (USNM 656510); 1 mi (1.6 km) SE of main dock, Koror Id (ANSP); entrance to Garumisukan River, Karamando Bay, Babelthaupt Id (ANSP). **SOLOMON ISLANDS:** Pavuvu Id, Russel Id Group (USNM 488306); Santa Isabel Id (AMNH); Choiseul Bay, Choiseul Id (ANSP). **AUSTRALIA:** Cooktown, Queensland (DMNH 32750); Cockle Bay, Magnetic Id, Queensland (USNM, no number); between Dunwich and Myora, N Dunwich, Stradbroke Id, Queensland (USNM 705006). **NEW CALEDONIA:** 2 mi (3 km) S of Conception (USNM 724531, 724535).

***Clypeomorus petrosa* (Wood),
new combination**

Although *Clypeomorus petrosa* has a wide Indo-Pacific distribution, close examination of numerous samples from throughout its range reveals three allopatric geographical varieties. Populations from continental regions in the Indian Ocean are quite distinct from those in the western South Pacific while those from the Ryukyus, and the Philippine and Indonesian Archipelagos are morphologically different from those indicated above. The Indian Ocean morphs were considered to be varieties of *Clypeomorus petrosa* and given the varietal name *gennesi* Fischer and Vignal in P.H. Fischer, 1901; those from the Philippines were recognized as a separate taxon and named *Cerithium chemnitzianum* by Pilsbry (1901).

I initially considered each of the three groups as a separate species, but in areas of parapatry there are intergrades that indicate the *petrosa* complex is best regarded as a superspecies, sensu Mayr (1969:52–53). According to this concept, the component species of a superspecies are des-

TABLE 16.—Summary of ANOVA and Student-Neuman-Keuls Post Hoc Comparison for three subspecies of *C. petrosa* complex (df = 2.87; species names with same letter after mean do not significantly differ).

Subspecies	Shell length (F=9.56) \bar{x}	Shell width (F=5.38) \bar{x}	Aperture length (F=64.94) \bar{x}	Aperture width (F=14.44) \bar{x}
<i>C. p. gennesi</i>	24.36 b	11.93 b	6.74 a	5.31 a
<i>C. p. petrosa</i>	27.03 a	12.73 a	7.73 b	5.89 b
<i>C. p. chemnitziana</i>	27.52 a	13.11 a	9.61 c	6.34 c

ignated as semispecies, a term used to include borderline cases of speciation. The morphologies of these three taxa were compared with each other and the discriminating characters for each taxon are presented in each respective subspecific discussion. Statistical analyses of shell length, shell width, aperture length and aperture width were also made among the three taxa. A one way Analysis of Variance (ANOVA) shows all F values are highly significant. Paired comparisons were made using Student-Neuman-Keuls Post Hoc Comparison. The results are presented in Table 16. All comparisons are significant except for shell length and shell width between *Clypeomorus petrosa petrosa* and *C. petrosa chemnitziana*. *Clypeomorus petrosa gennesi* differs significantly from these two taxa in all characters and may be sufficiently distinct to warrant specific recognition. I have not seen *C. p. gennesi* alive and do not know its anatomy well. There is a lack of sufficient comparative material from the western Indian Ocean and the presence of intergrades in areas of parapatry is uncertain. For practical purposes I shall follow Mayr's (1969:197) advice and treat these allopatric populations of doubtful rank as subspecies. It is obvious that more careful work is needed on the *petrosa* complex by local workers. For the present, I feel justified in regarding these taxa as subspecies and alert future workers about the possible problems to be investigated in this group.

***Clypeomorus petrosa petrosa* (Wood),
new combination, new status**

FIGURES 32, 33*b,d*, 34, 35

?*Strombus tuberculatus* Linnaeus, 1767:1213, no. 514 [type: not found, see Dodge, 1956:289; type-locality: "In

Mare Mediterraneo"; not *Strombus tuberculatus* Born, 1778; nomen dubium].

Strombus petrosus Wood, 1828:13, 34 [cited as *Cerithium* on p. 34], pl. 4: fig. 9 [holotype: BMNH, no number; type-locality: "East Indies," here restricted to Suva, Viti Levu, Fiji].

Cerithium janellii Hombron and Jacquinot, 1852, pl. 24: figs. 19–22 [holotype: MNHNP, no number; type-locality: "Vavao"]; 1854:104.

Cerithium petrosus (Wood).—Sowerby, 1855:871, pl. 182: figs. 171–172; 1865, pl. 7: fig. 43a,b.—Fischer and Vignal in P.H. Fischer, 1901:111.—Kobelt, 1890:83–84, pl. 16: figs. 2–3.

Cerithium variegatum Quoy and Gaimard.—Sowerby, 1865: pl. 7: figs. 41a,b,c [not *Cerithium variegatum* Quoy and Gaimard, 1834: is *Clypeomorus petrosa* (Wood, 1828)].

Clypeomorus tuberculatus (Linnaeus).—Cernohorsky, 1972: 70, pl. 16: fig. 2 [not *Strombus tuberculatus* Linnaeus, 1767: is *Clypeomorus petrosa* (Wood, 1828)].

Cerithium bifasciatum Sowerby.—Dance, 1974:66, text fig. [not *Cerithium bifasciatum* Sowerby, 1855: is *Clypeomorus petrosa* (Wood, 1828)].

Cerithium petrosus (Wood).—Shirai, 1977:275 [not *Clypeomorus petrosa* (Wood, 1828): is *Clypeomorus bifasciata* (Sowerby, 1855)].

DESCRIPTION.—*Shell* (Figure 32; Table 17): Adult shell obese, angular in outline, with mod-

TABLE 17.—Analysis of shell parameters of *Clypeomorus petrosa petrosa* (measurements in mm).

Character (n=30)	\bar{x}	sd	Range
Shell length	27.03	2.81	18.07–30.45
Shell width	13.11	1.43	8.42–15.3
Aperture length	7.73	0.93	4.95–9.35
Aperture width	5.89	0.69	3.62–7.05
No. beads on penultimate whorl	13.9	2.15	11–19

Shell length/shell width index: 2.06

Shell length/aperture length index: 3.50

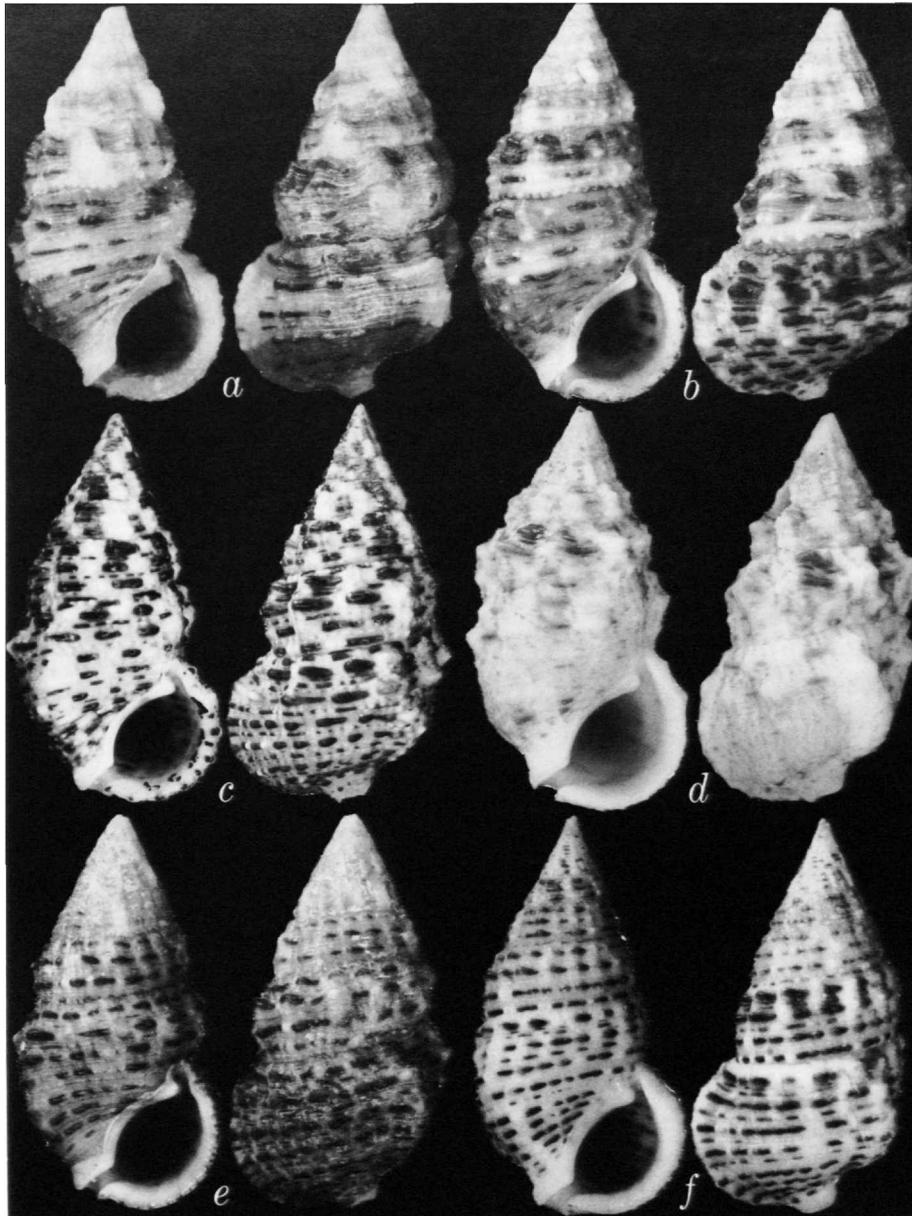


FIGURE 32.—*Clypeomorus petrosa petrosa* (Wood, 1828), showing variation in shell form, sculpture, and color: *a*, holotype of *Strombus petrosus* Wood, 1828, BMNH no number, locality cited as "East Indies" (25.6 × 13.9 mm); *b*, Fiji, USNM 76677 (27.4 × 13.7 mm); *c*, Wakaya Island, Fiji, USNM 666294 (28.2 × 14.1 mm); *d*, Koh Tao, Thailand, USNM 405956 (20.4 × 10.5 mm); *e*, Fiji, USNM 76677 (27.4 × 13.9 mm); *f*, Russell Island, Queensland, Australia, USNM 623082 (27.4 × 13.1 mm).

erately elongate teleoconch comprising 9 or 10 inflated, nodulose whorls having an apical angle of 38 degrees. Shell reaching 30.5 mm in length. Outline of shell pupiform due to concave aspect of early whorls and inflation of later whorls. Whorls sculptured with three major nodulose spiral cords and numerous smooth fine spiral striae. Inflated penultimate whorl has a fourth nodulose spiral cord at base of whorl adjacent to suture. Nodes frequently spinose on penultimate and body whorls and drawn out spirally. Nodes aligned to form about 14 axial ribs on penultimate whorl. Former varices present forming larger axial ribs, the largest being on body whorl. Early whorls each with 3 beaded spiral cords and distinct axial riblets formed by alignment of beads. Postnuclear whorls each with 3 smooth spiral cords. Protoconch unknown. Body whorl large, inflated, sculptured with numerous fine spiral threads and 8 or 9 beaded spiral cords, the most prominent being on the upper portion of the whorl. Base of body whorl moderately constricted; slight siphonal fasciole present. Large angular dorsal varix on body whorls about 45 degrees left of the plane of the aperture when shell viewed anteriorly. Suture distinct, slightly wavy. Aperture ovate, a little less than one-fourth the length of the shell. Anterior siphonal canal short, distinct, moderately reflexed, and with directed axis. Anal canal distinct, deeply incised, and bordered by parietal columellar plait that extends well into shell aperture. Columella concave with slight columellar parietal callus. Outer lip thin, slightly thickened at edge, and moderately crenulate. Parietal part of outer lip extends slightly onto penultimate whorl. Plane of outer lip in line with shell axis. Bottom portion of outer lip pendant, curving around to siphonal canal and when the shell is viewed anteriorly, appears to extend slightly over siphonal opening. Shell color normally white, sometimes cream, light yellow or brown. Nodes usually dark brown or black, presenting overall pattern of dashed spiral lines and spots. Shell occasionally pigmented with alternating, thick bands of brown and white. Aperture and colu-

mella white; darker spots on shell surface showing through inner wall of aperture. Periostracum light brown, usually eroded on earlier whorls. Operculum thin, tan, ovate, corneous, paucispiral with nucleus near inner edge. Attachment scar on lower third of obverse of operculum has raised spiral threads originating from nucleus.

Radula (Figure 33*b,d*; Table 18): Radular ribbon short, about one-sixth the length of the shell and comprising about 80 rows of teeth. Shell length/radula length index 5.32. Rachidian tooth (Figure 33*e*) pentagonal, about 75 μm wide. Basal plate of rachidian tooth pointed at base and with slight lateral depression midway on each side. Sides of rachidian tooth convex, top straight or slightly convex. Cutting edge with large, chisel-shaped central cusp flanked by 1 or 2 tiny blunt denticles on each side. Lateral tooth (Figure 33*c*) rhomboidal with long twisted lateral extension that inserts onto basal radular membrane. Basal plate of lateral tooth with large, medianly placed butress, directed downward. Cutting edge of lateral tooth with large, chisel-shaped median cusp flanked on inner side by single small pointed denticle and on outer side by 2 (sometimes 3), small pointed denticles. Slight flange on basal plate is directly adjacent to cutting edge of lateral tooth. Marginal teeth (Figure 33*b,d,f*) long, curving, slightly swollen in center of tooth shaft, and pointed where attached to radular membrane. Tips of marginal teeth sharply curved and spatulate. Inner marginal tooth with two small blunt inner denticles and a large spoon-shaped central cusp and single, tiny, pointed, outer denticle that is nearly fused to

TABLE 18.—Analysis of radular parameters of *Clypeomorus petrosa petrosa* (measurements in mm).

Character (n=5)	\bar{x}	sd	Range
Radula length	4.85	0.32	4.35–5.19
Rows of teeth	83.40	5.32	78–91
Shell length	25.82	1.34	23.8–27.55

Shell length/radula length index: 5.32

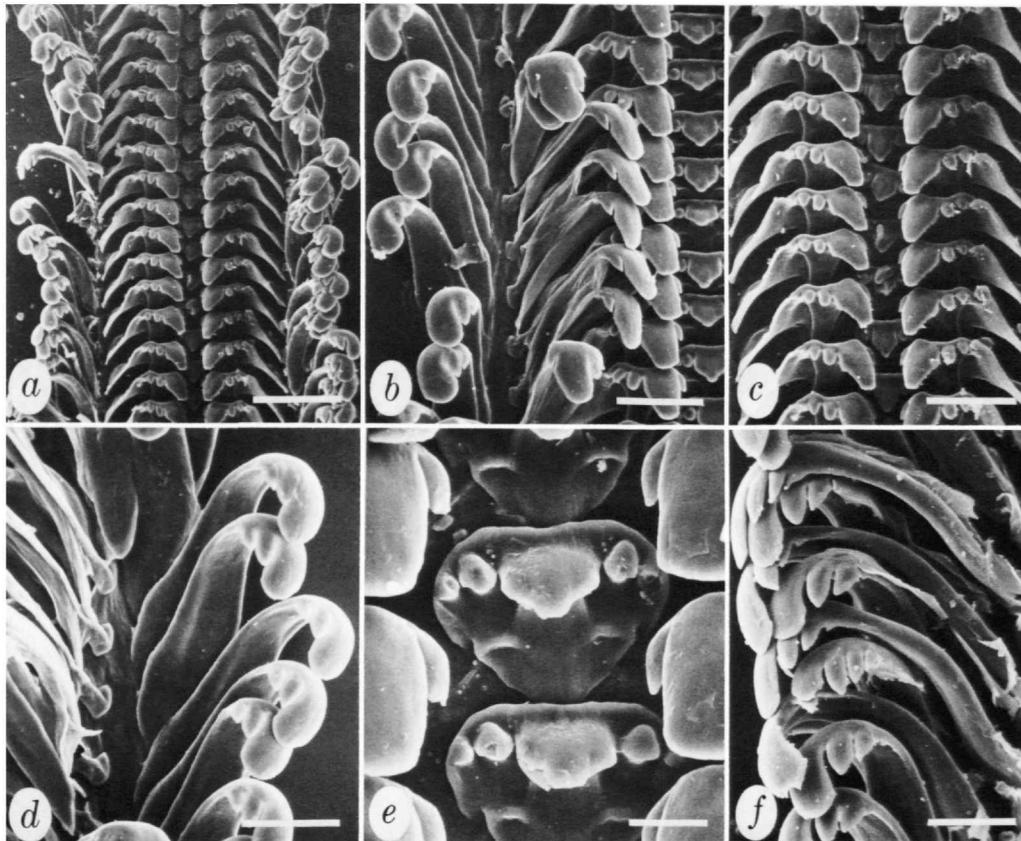


FIGURE 33.—SEM micrographs of radula of *Clypeomorus petrosa* and subspecies: *a*, radular ribbon from *C. p. chemnitziana*, Looc Bay, Bagac, Bataan, Luzon, Philippines, USNM 774750 (bar = 150 μ m); *b*, detail of marginal teeth of *C. p. petrosa* from Yate, New Caledonia, ANSP 238300 (bar = 100 μ m); *c*, detail of lateral and marginal teeth of *C. p. chemnitziana* from Looc Bay, Bagac, Bataan, Luzon, Philippines, USNM 774750 (bar = 180 μ m); *d*, detail of marginal teeth showing cusp structure of nominate subspecies (note attachment of lateral teeth to radular membrane), Yate, New Caledonia, ANSP 238300 (bar = 75 μ m); *e*, detail of rachidian tooth, *C. p. gennesii* from Ma'Agana, Gulf of Aqaba, Israel, USNM 798125 (bar = 25 μ m); *f*, detail of tips of marginal teeth showing inner cusp structure, *C. p. chemnitziana*, USNM 774750, from Looc Bay, Bagac, Bataan, Luzon, Philippines (bar = 50 μ m).

large cusp. Outer marginal tooth same, only lacking outer denticle.

Animal (Figure 34): Head-foot tan and covered with tiny white dots and larger black blotches. Mantle edge bifurcated into outer smooth fold and inner papillate one. Papillae at dorsal mantle edge numerous, moderately long. Right side of foot has deep ciliated groove that runs from exhalant siphon to sole of foot. No

ovipositor seen. Pallial complex as described in *Clypeomorus bifasciata*. Pair of salivary glands present, two thirds of which lie anterior to nerve ring. Midesophagus enlarges to form large crop. Pallial oviduct differs from that of *Clypeomorus bifasciata* in having a heavily ciliated worm-like ridge (Figure 34A, *r*) along the edge of the lateral lamina, which is fused to the mantle wall. It is particularly well developed adjacent to the open-

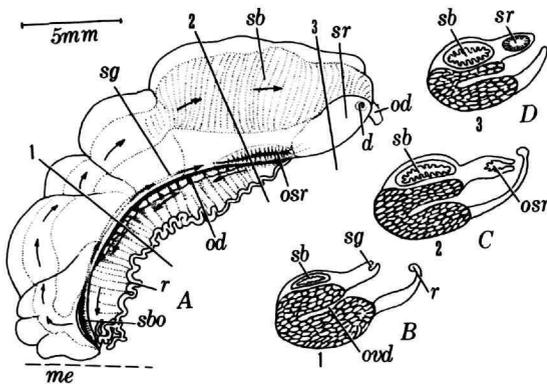


FIGURE 34.—*Clypeomorus petrosa petrosa*: A, pallial oviduct showing general configuration of open duct dissected out from mantle cavity (distal end of duct at bottom); B–D, sections through pallial oviduct correspond to lines 1, 2, 3, in drawing A. (ABBREVIATIONS: *d* = duct from seminal receptacle to oviduct; *me* = mantle edge; *od* = oviduct; *osr* = opening of sperm gutter into seminal receptacle; *ovd* = oviducal groove; *r* = ciliated ridge at edge of lateral lamina; *sb* = spermatophore bursa; *sbo* = opening of sperm gutter into spermatophore bursa; *sg* = sperm gutter at edge of medial lamina; *sr* = seminal receptacle.)

ing of the spermatophore bursa (Figure 34A, *sbo*). The sperm gutter (Figure 34A,B, *sg*) is wide and spacious at its distal end (Figure 34A, *sbo*) but becomes shallow in the midportion of the edge of the medial lamina and opens into a deep duct (Figure 34A,C, *osr*) that leads into the seminal receptacle (Figure 34A,D, *sr*). This arrangement differs from that of *Clypeomorus bifasciata*, *C. brevis*, and *C. batillariaeformis*. A duct (Figure 34A, *d*) lies on the inner surface of the seminal receptacle, opening into the oviducal groove (Figure 34A,B *ovd*). The spermatophore bursa opening (Figure 34A, *sbo*) is wide and spacious at the distal end of the medial lamina but narrows and becomes a tube leading into a spacious spermatophore bursa located in the proximal portion of the lamina (Figure 34A,C,D, *sb*). The spermatophore bursa (Figure 34A-D, *sb*) opens into the seminal receptacle (Figure 34A,C, *osr*). Under the seminal receptacle (Figure 34A,D, *sr*) on the proximal side of the medial lamina, there is a small duct (Figure 34A, *d*) that leads into the proximal

oviducal groove, presumably the site of fertilization. Males not observed.

REMARKS.—Wood's (1828) holotype is shown in Figure 32a. Dodge (1956:290) considered *Cerithium petrosus* (= *Strombus petrosus*) to be a synonym of *Cerithium tuberculatum*, but I regard *Strombus tuberculatus* of Linnaeus as a nomen dubium. As Hanley (1855:276) stated, "... much uncertainty has accrued as to the shell intended ... because it was inadequately described by Linnaeus and ... unillustrated by any pictorial synonym." Hanley (1855, pl. 4: fig. 4) illustrated a shell from the Linnaean collection that he believed was the *Strombus tuberculatus* of Linnaeus. In contrast to Dodge's (1956:290) opinion, however, I believe there is no way to ascertain the shell Linnaeus had in mind when he described *Strombus tuberculatus* in the 12th edition (1767) of the *Systema*. I have previously indicated that *Cerithium tuberculatum* (Linnaeus) has a complex taxonomic history and that it should not be confused with the *Strombus tuberculatus* of Born, 1778 (Houbrick, 1978b:645), which is a synonym of *Batillaria sordida* (Gmelin in Linnaeus, 1791).

Examination of the holotype of *Cerithium janelii* Hombron and Jacquinot confirms that it is conspecific with *Clypeomorus petrosa* (Wood). Dance (1974:66) erroneously called the latter *Cerithium bifasciatum* Sowerby, while Shirai (1977:275) wrongly applied the name *Cerithium petrosus* to *Cerithium bifasciatum* Sowerby (= *Clypeomorus bifasciata* (Sowerby)). Cernohorsky (1972:70) used the name *Clypeomorus tuberculatus* (Linnaeus) for *Strombus petrosus* (= *Clypeomorus petrosa petrosa*).

ECOLOGY.—At Lizard Island, Queensland, Australia, this species lives among rocks, usually in sand and rubble-filled crevices between boulders, from the low to midtidal zones. Although some specimens occasionally burrow into sand adjacent to rocks, *Clypeomorus petrosa* is not an infaunal, sand-dwelling species. At Dumba Reef, Viti Levu, Fiji, I found it to be abundant at the midtide zone where it occurred in crevices, between rocks on an algal covered rocky bench. In

Nouméa, New Caledonia, it lived slightly above the midtide zone in a similar habitat. Museum records from other locations indicate similar habitats. When several congeners occur along a rocky shore, *Clypeomorus petrosa* is always found in the mid to lower tidal zones, but it may undergo ecological release when it is the only *Clypeomorus* species at a given locality.

This species probably eats the microalgae and/or detritus covering its rocky habitat. The radular ribbon, about one-sixth the length of the shell, is shorter than those of the *Clypeomorus* species living higher in the intertidal zone, suggesting that *Clypeomorus petrosa* eats algae of smaller particle size.

Shells of this species are frequently badly eroded and covered with crustose coralline algae. In New Caledonia, *Hipponix conicus* (Schumacher), is commonly found on the shell and forms deep erosion pits on the last two whorls where it is attached. Shells with chipped apertures indicate crab attacks.

DISCUSSION.—The major discriminating characters of this subspecies are the fat, rounded, obese whorls and the large, angulate penultimate and body whorls. Shells are sculptured with large, spinose, spirally arranged nodes, which are normally dark colored, presenting an overall spotted appearance. *Clypeomorus petrosa petrosa* is one of the more highly sculptured *Clypeomorus* species, approaching *Clypeomorus pellucida* and *Clypeomorus admirabilis* in this respect. *Clypeomorus pellucida*, although sympatric with *Clypeomorus petrosa petrosa*, lives in mangrove habitats and has a dark colored shell not likely to be confused with that of the latter. *Clypeomorus admirabilis* is allopatric to *Clypeomorus petrosa petrosa*. The congener with which this subspecies may be most easily confused is *Clypeomorus batillariaeformis* (formerly known as *Clypeomorus moniliferum*). The latter species lives higher in the intertidal zone and is usually a smaller, less attenuate, and colorless species than *Clypeomorus petrosa petrosa*. The latter is distinguished from these morphs by its spirally elongate shell, rounded angulate whorls, spinose nodes, and by a more deeply

impressed suture. *Cerithium zonatum* (Wood) may also be confused with this subspecies, but the former species has smaller, more pointed nodes and always lacks the large dorsal varix on the body whorl. Another species with which *Clypeomorus petrosa petrosa* may be confused is *Cerithium caeruleum* Sowerby, 1855, from the western Indian Ocean. It too is a stocky, spinose species but is allopatric to this subspecies and is not easily confounded with the Indian Ocean subspecies, *Clypeomorus petrosa gennesi*.

Clypeomorus petrosa petrosa is variable in both sculpture and color and appears to attain its greatest size in Queensland, Australia (Figure 32f), Fiji (Figure 32b,c,e) and a few Melanesian island groups. Some populations contain individuals with more elongate shells than normal and these are easiest to confuse with slender morphs of *Clypeomorus batillariaeformis*. Close examination of the sculpture is necessary to separate the two. Color pattern varies: individuals may be pigmented with broad, tan-brown, spiral bands (Figure 32a,b), scattered brown blotches (Figure 32d), or spiral bands of dark brown spots (Figure 32c,e,f).

Intergrades between this subspecies and *Clypeomorus petrosa chemnitziana* occur in the Philippines and in Southeast Asia that are difficult to assign to a given subspecific taxon.

FOSSIL RECORD.—This subspecies has been recorded from the upper Pliocene deposits at Port Hawannah, Éfate, New Hebrides (Abrard, 1946:56; cited as *Cerithium* (*Pithocerithium*) *petrosium*).

GEOGRAPHIC DISTRIBUTION (Figure 35).—This subspecies is generally confined to the southwestern Pacific where it is most common in Melanesia. Some populations also occur in SE Asia and the Philippines but are uncommon. Although the subspecies has been found in Guam, no specimens from the Caroline Islands were available. It probably occurs there, but this region is the edge of the range for the subspecies.

MATERIAL EXAMINED.—SOUTHEAST ASIA: NE coast, E of St. John's Id, Singapore (USNM 660811); Koh Tao Id, Gulf of Siam,

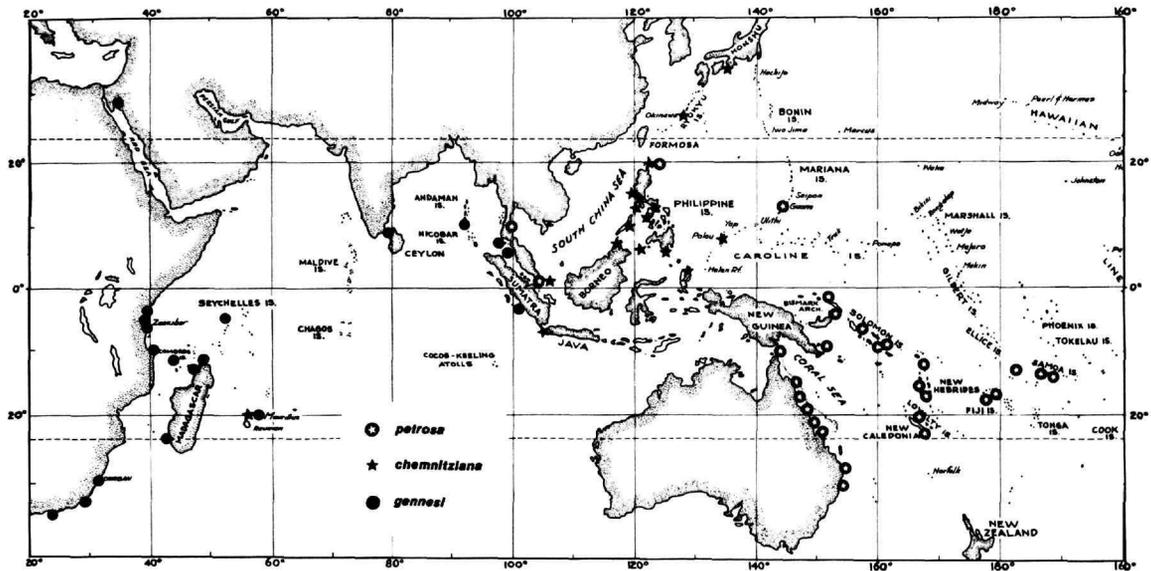


FIGURE 35.—Geographic distribution of the subspecies of *Clypeomorus petrosa* (Wood, 1828).

Thailand (USNM 405956). GUAM: At'n beach (USNM 670052); Apra Bay (USNM 232943). RYUKYU ISLANDS: Chinen, Okinawa (LACM 272270). QUEENSLAND, AUSTRALIA: Murray Id, Torres Strait (AMS); Stover Bay, Somerset, Cape York Peninsula (AMS); Lizard Id (USNM 794872, 794874); Hope Ids, S of Cooktown (AMS); Low Ids, Port Douglas (AMS, USNM 704070, 770612); Russell Id (USNM 623082); Michaelmas Cay, NE of Cairns (AMS); Green Id (AMS); Geoffrey Bay, Magnetic Ids, off Townsville (AMS); Palm Ids, N of Townsville (AMS); Hollbourne Id, N of Bowen (AMS); Lindeman Id, Cumberland Group (AMS); Hook Id, Whitsunday Group (AMS); Hayman Id, Whitsunday Group (USNM 704905); Mackay (AMS); Yeppon (AMS); Facing Id, N of Gladstone (AMS); N Keppel Id, off Rockhampton (AMS); Girt Id, Keppel Bay (WAM 886-76); Shelly Beach, Caloundra (AMS). NEW SOUTH WALES, AUSTRALIA: Wooli, SE of Grafton (AMS); Wodgodga (AMS); Angousie (AMS); Minnie Wakers (AMS).

BISMARK ARCHIPELAGO: Duke of York

Ids, New Britain (AMS); Mongop, S of Kavieng, New Ireland (AMS); Kuia Id, Lusancay Ids, Trobriand Group (AMS). SOLOMON ISLANDS: Choiseul Id (ANSP 185356); Lunga, Guadalcanal (AMNH 129751); Laulasi Id, S of Aoki, W coast of Malaita Id (AMS). SANTA CRUZ ISLANDS: Santa Cruz Id (AMS); Vanikoro Id (AMS); Reef Id (AMS). NEW HERBIDES: N end, Black Beach, Tana (USNM 692455, 692574); Palikulo Bay, Espirito Santo (USNM 686275, 686276); Killi Killi, Little Malo (USNM 686297, 686307); Vir, NE of Santa Maria Id, Banks Group (USNM 686249); lagoon of Efate (AMS); Efate Id (AMS, USNM 787650); NW Efate (USNM 787727); Pointe d'Arbel, Efate (USNM 787504, 787508); Takara, NE part of Efate Id (LACM77-42); SE coast of Santos Id (USNM 787214). LOYALTY ISLANDS: We, Lifu (USNM 784177); Lifu (USNM 423311). NEW CALEDONIA: Hienghene (USNM 666088); N end, Kouebuni Id (USNM 693757); SE end, Nau Id (USNM 693802, 693803); Redika Id, 18 mi (29 km) SE Nouméa (USNM 724131); Pt Magnin, near Nouméa (USNM

724089); N part of Nouméa (USNM 801417); Touaurou (USNM 724611, 784362, 784391, 784402); San Gabriel, 8 km S of Touaurou (USNM 784358); S of Yate, Touaurou (USNM 801415); Yate (ANSP 238300); Baie de Prony (USNM 724817).

FIJI: (USNM 76677); W side of Mali pass, N coast, Vanua Levu (USNM 694856); Rambi Id, Georgia Cave, W coast of Vanua Levu (USNM 695394); N side of Verevere Id, N coast of Vanua Levu (USNM 694995); SW side of Ovatoa, Vanua Levu (USNM 694758); S of Wai-kama, Ngau (USNM 686685); S of Harold Bay, Ngau (USNM 686624, 686642); W side of Waya Id, Kandavu (USNM 692242); Yawiavu Point, S tip, Kandavu (USNM 697062); Daumba Reef, S coast of Viti Levu (USNM 794734); Nandi Bay, Viti Levu (ANSP 255355); W side Malake Id, Viti Levu (USNM 694569); Cuvu Id, Nandronga, Viti Levu (USNM 616871); Yakuilau Id, off Nandi Bay, Viti Levu (USNM 658772); Suva, Viti Levu (USNM 532090); Leleuvia Id, Mbau, Viti Levu (USNM 666406); w side Malake Id, Viti Levu (USNM 694500); Makuluva, Viti Levu (USNM 531854); NW side Ovalau Id (USNM 694256); Felialupo Road, W side of Savai (USNM 675953); NE side Wakaya Id (USNM 666353, 666294); Matruku (USNM 686517); N side of Totoya Id (USNM 686547). SAMOA: Pago Pago, Tutuila (USNM 574040) Airport Reef, Tutuila (USNM 699472, 699474, 699475); Leone Bay, Tutuila (USNM 699337); Asili area, Tutuila (USNM 699355); Fagasa Bay, Tutuila (USNM 699385); Vatia Cove, Tutuila (USNM 699277); Fagaitua Bay, Tutuila (USNM 704691); Fagaalu, Tutuila (USNM 699021, 699025); W side of Ofu, Manua Ids, Tutuila (USNM 699422); Mulinuu Point, Upolu (USNM 698820); Apra (USNM 573865, 573878). WALLIS AND FUTUNA: Pointe d'Alo to Sigave bay, Futuna, Horn Ids (USNM 676656); NW of Mira, Alofi, Horn Ids (USNM 676657); E side of Anse de Sigave, Futuna, Horn Ids (USNM 676498); N coast of Faioa, Wallis Id (USNM 676243); shore of Faioa, Wallis Id (USNM 676100). RAPA: (USNM, no number).

Clypeomorus petrosa chemnitziana (Pilsbry),
new status

FIGURES 33a,c,f, 35, 36

Cerithium variegatum Quoy and Giamard.—Sowerby, 1865, pl. 7: figs. 41a,b,c, [in part, fig. 41c is not *Cerithium variegatum* Quoy and Gaimard, 1834: is *Clypeomorus petrosa chemnitziana* (Pilsbry, 1901)].

Cerithium chemnitzianum Pilsbry, 1901:393, text fig. [holotype: ANSP 247576; type-locality: Loo Choo Islands].—Dance, 1974:66, text fig.

Clypeomorus chemnitzianus (Pilsbry).—Shirai, 1977:27.

DESCRIPTION.—*Shell* (Figure 36; Table 19): Adult shell turreted, pupiform having teleoconch of 10 whorls and apical angle of 38 degrees. Length/width index 2.16. Shell reaching 32 mm in length. Early whorls concave but most adult whorls are inflated. Postnuclear whorls and early whorls sculptured with 3 spiral beaded cords on which beads aligned to form axial riblets, presenting cancellate appearance. Adult whorls sculptured with 3 major, granose, spiral cords and numerous finer spiral lirae. Numerous tiny beads on spiral cords, about 23 per whorl, tend to coalesce. Beads on adult whorls not aligned to form axial riblets. Penultimate whorl sculptured with 3 or 4 major spiral, beaded cords and numerous finer spiral lirae. Early whorls usually eroded, protoconch unknown. Body whorl weakly sculptured with numerous finely beaded spiral cords, the 2 nearest the suture having the largest beads. Large dorsal varix of body whorl at a 45-degree angle to plane of

TABLE 19.—Analysis of shell parameters of *Clypeomorus petrosa chemnitziana* (measurements in mm).

Character (n=30)	\bar{x}	sd	Range
Shell length	27.52	2.53	22.55–32.19
Shell width	12.73	1.10	10.42–15.39
Aperture length	9.61	1.09	7.29–12.43
Aperture width	6.34	0.73	4.95–8.09
No. beads on penultimate whorl	23	0	0

Shell length/shell width index: 2.16

Shell length/aperture length index: 2.86

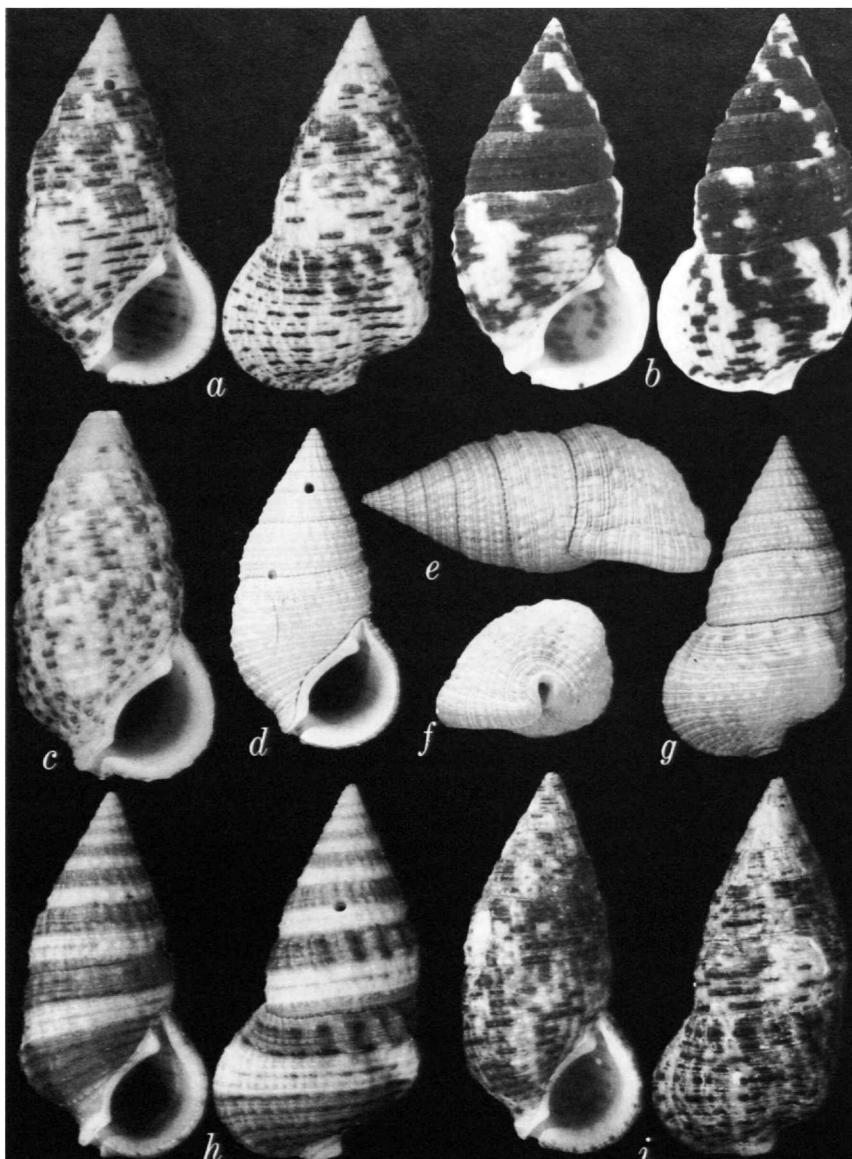


FIGURE 36.—*Clypeomorus petrosa chemnitziana* Pilsbry, 1901) showing variation in shell form, sculpture, and color: *a*, Kadena Circle, Okinawa, USNM 669652 (30.4 × 16 mm); *b*, Kadena Circle, Okinawa, USNM 669652 (28.6 × 14.6 mm); *c*, holotype of *Cerithium chemnitzianum* Pilsbry, 1901, from Loo Choo Islands (Ryukyus), ANSP 247576 (27 × 13.5 mm); *d-g*, apertural, dorsal, lateral, and anterior views (shell whitened with ammonium chloride to enhance sculptural pattern; note placement of penultimate varix on body whorl); *h*, Onna Flats, S. Kunigami-Gun, Okinawa, USNM 670667 (29.8 × 15.1 mm); *i*, Looc Bay, Bagac Bataan, Luzon, Philippines, USNM 774750 (27.9 × 13.3 mm).

aperture when shell viewed anteriorly. Suture deeply incised, somewhat wavy. Aperture ovate, a little less than one-third the shell length. Apertural characters similar to those of nominate subspecies, but outer lip more rounded, smoother, and less angulate where it joins penultimate whorl. Shell color white to yellow, densely dotted with rich brown spots or lines on the spiral cords. Larger maculations of brown or tan or wide brown bands may be present. Aperture and columella white. Periostracum light brown. Operculum as in nominate subspecies.

Radula (Figure 33a,c,f; Table 20): *Radula* essentially like that of typical subspecies. Radular ribbon a little over one-sixth the shell length, with approximately 65 rows of teeth. Shell length/radula length index 5.90.

Animal: Color of head and foot whitish, with pink and black dots and larger pink maculations. Mantle edge bright yellow.

DISCUSSION.—The holotype is shown in Figure 36b. This subspecies is easily separated from the other two in the *Clypeomorus petrosa* complex by its pupiform shape, numerous grooved spiral lines, and relatively smooth sculpture (Figure 36a-g). It lacks tubercles and prominent beads and has a lower shell length/aperture length index than its other close relatives. *Clypeomorus petrosa chemnitziana* also tends to be highly colored, may be spotted (Figure 36a,c), and is frequently banded or blotched with dark brown to yellowish brown pigment (Figure 36b,h).

ECOLOGY.—I observed this subspecies at Morong, Bataan, Luzon, Philippines, where it lives in the lower subtidal zone and just below the low tide mark. It occurs in sand filled crevices and

around the bases of rocks and stones. Although it is frequently found partially buried in the sand, it is not an infaunal species and is commonly seen on rocky surfaces where it is an active crawler. I observed a *Morula* species feeding on an immature specimen of this subspecies. The eggs, larvae, and protoconch are unknown.

FOSSIL RECORD.—No fossils of this subspecies have been recorded.

GEOGRAPHIC DISTRIBUTION (Figure 35).—*Clypeomorus petrosa chemnitziana* occurs in southern Japan and the Ryukyus, and extends south to the Philippines and Indonesia where it is most common. It appears to be confined to the continental portions of the western Pacific. The one record from Mauritius is doubtful and needs reconfirmation.

MATERIAL EXAMINED.—MAURITIUS: (USNM 26768). SOUTHEAST ASIA: NE coast, E of St John's Id, S of Singapore (USNM 660798); Raffles Light, Singapore (ANSP 245495, 245689). INDONESIA: S shore of Morotai, E of Gila Peninsula, Halmahera Group, Moluccas (USNM 542548); W Marudu Bay, N Borneo (USNM 632197, 632198); Sibuan Id, N Borneo (ANSP 295334); S shore, palau Peutjang, Udjong Kulon, W Java (WAM). PHILIPPINES: Saban Id, Batanes Group (USNM 243915, 243920, 243922); Matabungkay, 115 km SSW of Manila, Luzon (AMS); Looc Bay, Bagac, Bataan, Luzon (USNM 774750, 744977); Eman Pt, Morong, Bataan, Luzon (USNM 774751); Wawa, Nasugbu, Batangas Prov. Luzon (WAM); Camp Wallace, La Union, Luzon (USNM 233101); Besogo, Luzon (USNM 232909); Maricaban Id, Luzon (USNM 232939, 232942); Nasugbu, Luzon (USNM 232863, 232864, 233087); Ligpo Pt, Balayan Bay, Luzon (USNM 243764, 243766); Port Binang, Subic Bay, Luzon (USNM 243685); Tagbayag Bay, Palawan (USNM 244190, 244191, 244192); Puerto Princesa, Palawan (USNM 311326); Port Langcan, Dumaran Id, Palawan (USNM 243873); Cataingan Bay, Dumurug Pt, Masbate (USNM 243835, 243841); Pt Naso, Panay (USNM 243896); Polloc, Mindanao (USNM

TABLE 20.—Analysis of radular parameters of *Clypeomorus petrosa chemnitziana* (measurements in mm).

Character (n=6)	\bar{x}	sd	Range
Radula length	4.63	0.3	4.50–5.23
Rows of teeth	77.33	5.32	72–84
Shell length	27.33	2.07	27.41–31.32

Shell length/radula length index: 5.90

232910); Baluk Id, Sarangani Group, Mindanao (USNM 244006); Jolo Id (USNM 233107); Tivinao Id (USNM 244009). JAPAN: Kii, Honshu (LACM). RYUKYU ISLANDS: Buckner Bay, Okinawa (LACM); Smuggler's Cove, Okinawa (LACM); beach, Naha Air Force base, Okinawa (LACM); Ogimi, Okinawa (USNM 488132); Ngao, Okinawa (USNM 363718, 613749); 5 mi (8 km) WNW Port Naha, Sand and Kirni Ids, Okinawa (USNM 632522); Onna flats, S of Kunigami-Gun, Okinawa (USNM 670667); Kadena Circle, Okinawa (USNM 664652, 669652); E of Ukibara-Shima, Okinawa (USNM 670491); Aguni Shima (LACM). TAIWAN: Now Wow (USNM 243879, 243881). PALAU: SE corner of Eil Malk, Palau (ANSP 200368).

***Clypeomorus petrosa gennesi* (Fischer and Vignal), new combination, new status**

FIGURES 33e, 35, 37

Cerithium petrosom var. *gennesi* Fischer and Vignal in P.H. Fischer, 1901:111, pl. 4: fig. 7 [holotype: MNHNP, no number; type-locality: Djibouti].

DESCRIPTION.—*Shell* (Figure 37; Table 21): Shell and operculum similar to those of *Clypeomorus petrosa petrosa*. Adult shell thick, moderately elongate and pupiform with teleoconch comprising 9 or 10 inflated nodulose whorls having an apical angle of 33 degrees. Length/width index 2.04. Shell smaller than *Clypeomorus petrosa petrosa*, reaching 30 mm in length. Outline of shell pupiform due to concave appearance of early whorls and inflation of later whorls. Sculpture of whorls same as in nominate subspecies, only beads smaller and more numerous. Beads aligned to form weak axial ribs, about 17 per whorl. Largest beads or nodes appear on second spiral cord. Specimens with more spinose nodes tend to have fewer but better defined axial ribs. Postnuclear whorls or early whorls sculptured with 3 spiral cords crossed by thin axial riblets to form overall cancellate sculpture. Early whorls usually eroded; protoconch unknown. Body whorls sculptured same as in nominate

subspecies; large varix present on dorsolateral surface of body whorl about 25–30 degree angle to plane of aperture when shell viewed anteriorly. Suture distinct, moderately impressed. Aperture ovate, a little less than one-fourth shell length. Apertural characters similar to those of nominate subspecies. Lower part of outer lip pendant, extending slightly below the anterior siphonal canal. Shell color whitish, with spirally elongate spots and maculations of gray to dark brown pigment. Nodes and beads tend to be dark in color. Aperture white.

Animal: Poorly preserved specimens were not significantly different in anatomy from the nominate subspecies.

Radula (Figure 33; Table 22): Radula essentially identical to that described for nominate subspecies. Radular ribbon a little less than one-sixth the shell length and with about 16 rows of teeth per mm. Shell length/radula length index 5.41.

REMARKS.—This subspecies was originally proposed for East African populations of *Ceri-*

TABLE 21.—Analysis of shell parameters of *Clypeomorus petrosa gennesi* (measurements in mm).

Character (n=30)	\bar{x}	sd	Range
Shell length	24.36	3.60	19.89–30.04
Shell width	11.93	1.68	9.20–14.70
Aperture length	6.74	0.96	5.31–8.50
Aperture width	5.31	0.81	3.57–6.80
No. beads on penultimate whorl	17	5.55	10–29

Shell length/shell width index: 2.04

Shell length/aperture length index: 3.61

TABLE 22.—Analysis of radular parameters of *Clypeomorus petrosa gennesi* (measurements in mm).

Character (n=2)	\bar{x}	sd	Range
Radula length	4.00	0	4
Rows of teeth	66.00	2.83	64–68
Shell length	21.65	3.61	19.1–24.2

Shell length/radula length index: 5.41

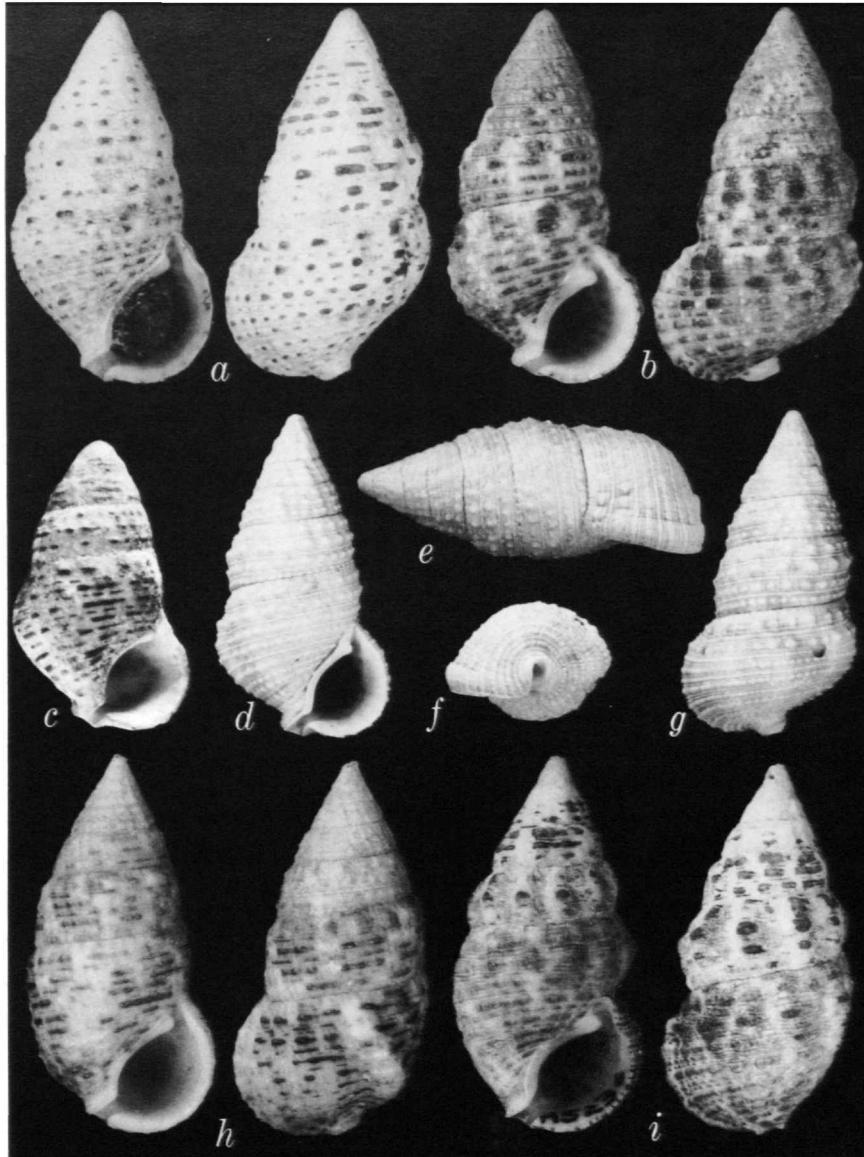


FIGURE 37.—*Clypeomorus petrosa gennesi* (Fischer and Vignal, 1901), showing variation in shell form, sculpture, and color: *a*, Dahab, Gulf of Aqaba, Israel, USNM 794183 (24.1 × 12.1 mm); *b*, Tuléar, Madagascar MNHNP, no number (29.6 × 15.2 mm); *c*, holotype of *Cerithium petrosus* var. *gennesi* Fischer and Vignal, 1901, from Djibouti, MNHNP, no number (29.6 × 15.2 mm); *d-g*, apertural, dorsal, lateral, and anterior views (shell whitened with ammonium chloride to enhance sculptural pattern; note placement of major varix on body whorl); *h*, Mauritius, USNM 26768, an intermediate form between *C. p. gennesi* and *C. p. chemnitiziana*; Pondoland, Natal, South Africa, NM A5236 (28.2 × 14.3 mm).

thium petrosum by Fischer and Vignal (in P.H. Fischer, 1901:111). Although attributed to both authors, the name appears in a publication by P.H. Fischer (1901), who included Vignal as coauthor. The name *gennesi* has been overlooked by workers since its proposal. Fischer's type is shown in Figure 37c.

ECOLOGY.—*Clypeomorus petrosa gennesi* lives on hard substratum in the intertidal zone and appears to be similar in ecology to the nominate subspecies. No accurate records indicate its exact placement in the intertidal zone, but shells of this subspecies are frequently badly eroded, indicating a high energy environment. Thomassin and Galenon (1977:248) recorded it (cited as *Clypeomorus moniliferus*) from the boulder rampart area and the rampart of the Soradrano fringing reef of the southern Grand Récif at Tuléar, Madagascar.

DISCUSSION.—*Clypeomorus petrosa gennesi* is distinguished from the other subspecies by its generally smaller shape, lower apical angle, higher aperture length/shell length ratio, less angular whorls, and by numerous spiral beads, which are larger than those of *C. p. chemnitziana*. Its sculpture is seldom as tubercular as is characteristic of the typical subspecies and the dull gray-white color and dark spots easily separate it from the other two subspecies. The most discriminating character is the large varix on the dorsolateral portion of the body whorl (Figure 37f). In the other two subspecies, the varix is more dorsally placed. Analysis of Variance and comparisons (Table 16) between the taxa showed that *C. p. gennesi* differs significantly from the other two subspecies in length, width, aperture length, and aperture width.

Specimens from some populations such as those from localities in East Africa (USNM 380890, 604530, 703828, NM A5236) (Figure 37b,i) and from the Red Sea (USNM 794180, 798125) may be more nodulose than normal but seldom become as tuberculated as the nominate subspecies. These morphs may be confused with *Cerithium caeruleum* Sowerby, with which they are sympatric; however, the latter species is larger,

not pupiform, lacks the three spiral beaded cords, and is distinctly more spinose in outline. The radula of *Cerithium caeruleum* is also very different from that of *Clypeomorus petrosa gennesi*.

I have examined samples from a population of dwarf individuals sculptured with very fine beads from Eilat, Gulf of Aqaba (USNM 672286). Specimens from SE Asia, Mauritius (Figure 37h), and Indonesia grade into *C. p. chemnitziana* and *C. p. petrosa* and have the major varix more dorsally placed on the body whorl. Specimens I examined from northern Ceylon (ANSP 210985) had an interesting mixture of shell characters between *C. p. gennesi* and *C. p. petrosa* forms.

FOSSIL RECORD.—This subspecies has been recorded by Abrard (1942:60, pl. 6: fig. 26; cited as *Cerithium petrosum*) from the Pleistocene of Ras Doumeira, French Somalia.

GEOGRAPHIC DISTRIBUTION (Figure 35).—This subspecies is confined to the Indian Ocean where it is most common along shores of large mountainous islands and continental regions.

MATERIAL EXAMINED.—RED SEA: Eilat, Gulf of Aqaba, Israel (USNM 672286); Marsa, El Eit, Gulf of Aqaba (USNM 794180); Ras Abu Galum, Gulf of Aqaba (USNM 794177); Ma'Agana, Gulf of Aqaba (USNM 798125); Dahab, Gulf of Aqaba (USNM 794183). EAST AFRICA: (USNM 604530); Shimoni, Kenya (BMNH); Ras Mjimwema, magogoni, Tanzania (USNM 703882); 9 mi (14.5 km) S of Dar es Salaam, Mboa Mogi, Tanzania (USNM 703828); Porto Amelia, Mozambique (USNM 634080). SOUTH AFRICA: Mbotyi East, Pondoland, Natal (NM A5236); Durban, Natal (USNM 380890); Algoa Bay (AMS). MADAGASCAR: New Delta, Fisherena, Tuléar (USNM 771431, 771432, 774469); numerous localities (Thomassin collection, MNHNP); Baie d' Ambre (USNM 719518); Ambatomboka, Nossi Bé (USNM 776722); Ambariobe Bay, Nossi Bé (USNM 719804); Pt Fièvre, Nossi Bé (USNM 719294). INDIAN OCEAN: Mayotte, Comoros (NM G3522); Seychelles (USNM 634727); Baie Ternay, Mahé, Seychelles (BMNH); Belle Ombre, NW Mahé, Seychelles (ANSP 311294); NW Bay, Mahé, Seychelles

(ANSP 297747; Mahé, Victoria, Seychelles (LACM 31617); Mauritius (USNM 26768, 774552); E of E Point Village, Diego Garcia, Chagos Archipelago (USNM 702145); Port Blair, Andaman Ids (BMNH). CEYLON: Kan Kesantuari (ANSP 210985). SOUTHEAST ASIA: Goh Huyong, Similian Ids, Thailand (USNM 661183); Pualu Tanga, Butang Group, Thailand (USNM 776666); S side Ao Pa Tong, Ko Phuket, Thailand (USNM 661776); E side Ko Bon Id, off S Phuket Id, Thailand (ANSP 286139, 287226); Laam Son, W Phuket Id, Thailand (ANSP 296013). INDONESIA: Benkoelen, Sumatra (USNM 774558).

Clypeomorus purpurastoma, new species

FIGURES 38–40

DESCRIPTION.—*Shell* (Figure 38; Table 23): Adult shell turreted, fusiform, reaching 26.8 mm in length and having teleoconch of 10–12 whorls with an apical angle of about 40 degrees. Whorls moderately inflated; upper whorls attenuate, concave in outline but becoming larger and more globose in last three whorls giving entire shell a pupiform outline. Protoconch unknown. Whorls sculptured with 3 (rarely 4) major spiral beaded cords and two spiral lirae, which may also bear tiny beads. Numerous fine spiral incised lines present. Each spiral cord bears about 19 beads per whorl. Beads aligned to form axial ribs only on first 4 whorls. Later whorls have dominant spiral sculpture and an occasional former varix. Suture straight, somewhat indistinct. Body whorl large, a little over one-half shell length and nearly circular in cross section. Body whorl sculptured with 8 spiral beaded cords, the largest one being subsutural. Large varix on right dorsal surface of body whorl at 65 degree angle to plane of aperture. Very weak, barely discernible varix present opposite outer lip. Aperture oval, small, about one-third the shell length. Columella concave with narrow parietal callus and distinct columellar lip. Anterior siphonal canal short, slightly reflected and bent to left at 45 degree

TABLE 23.—Analysis of shell parameters of *Clypeomorus purpurastoma*, new species (measurements in mm).

Character (n=30)	\bar{x}	sd	Range
Shell length	21.16	4.33	12.81–26.80
Shell width	9.41	1.35	6.40–11.90
Aperture length	5.49	0.86	3.63–6.55
Aperture width	3.99	0.78	2.28–5.55
No. beads per spiral cord on penultimate whorl	19.30	4.05	14–31

Length/width index: 2.25

Shell length/aperture length index: 3.85

angle to shell axis. Anterior siphonal canal well developed, bordered with columellar fold that extends well within shell aperture. Outer lip of aperture curved, semicircular, smooth, and thin, except for thick varix on outer surface of lip. Inner surface of lip relatively smooth or with weak spiral lirae. Bottom of outer lip partially crosses over anterior siphonal canal. Parietal portion of outer lip extends slightly onto penultimate whorl. Plane of outer lip parallel with shell axis. When shell viewed anteriorly, siphonal canal opening is at center. Periostracum thin, brownish. Shell color variable, usually white with brown blotches and spiral brown spots and streaks. Beads usually dark brown, sometimes white. Shell occasionally banded with brown or entirely melanistic. Aperture and columella purple. Operculum, thin, tan, ovate, and corneous with eccentric nucleus near columellar edge. Attachment scar oval and on lower obverse half of operculum.

Radula (Figure 39; Table 24): Radular ribbon short, about one-seventh the shell length, comprised of about 83 rows of teeth. Shell length/radula length index 6.9. Rachidian tooth (Figure 39e) pentagonal, about 50 μ m wide. Top of rachidian tooth slightly concave, rounded at sides and bearing 1 central spade-shaped cusp flanked by 2 (sometimes 1) tiny blunt denticles on each side. Sides of rachidian tooth rounded, terminating in a point midway along basal plate of tooth. Basal plate of rachidian tooth a rounded

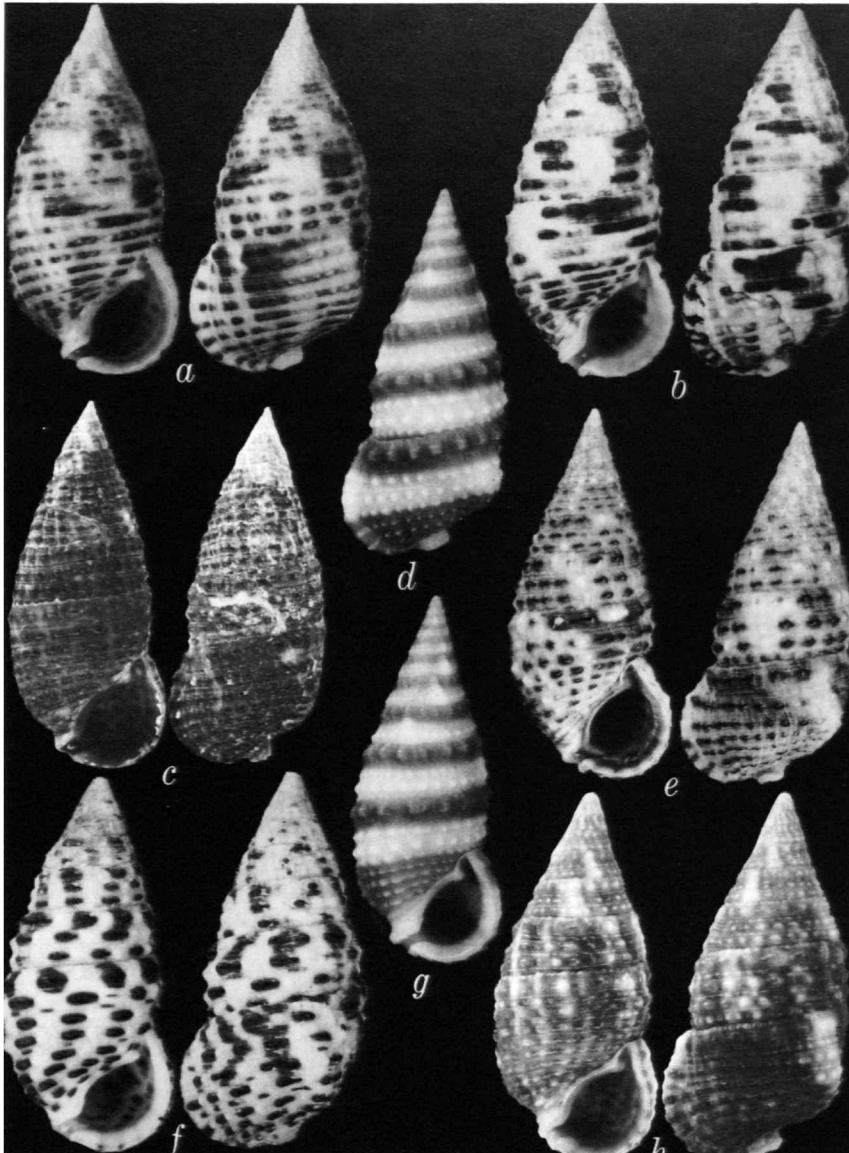


FIGURE 38.—*Clypeomorus purpurastoma*, new species, from different geographical areas showing variation in shell form, sculpture, and color (all specimens shown at the same size): *a*, typical eastern Indian Ocean morph from Grande Récif, Tuléar, Madagascar, MNHNP no number (23.5 × 10.7 mm); *b*, SW Lunga Bay, South Africa, NM H1895 (25.5 × 10.7 mm); *c*, Amamioshima, Ryukyu Islands, Japan, USNM 774581 (21.8 × 8.9 mm); *d*, Maricaban Island, Luzon, Philippines, USNM 232979 (20.5 × 8.2 mm); *e*, holotype, Napot Pt, Morong, Bataan, Luzon, Philippines, USNM 774749 (26 × 10.5 mm); *f*, Pulau Siburu, N of Sipora Island, SW Sumatra, Indonesia, USNM 654725 (22.9 × 10.9 mm); *g*, Maricaban Island, Luzon, Philippines, USNM 232979 (20.5 × 8.2 mm); *h*, Jolo Jolo, Sulu Archipelago, Philippines, USNM 233097 (21.5 × 10.2 mm).

triangle that has tiny, elevated ridge medianly placed on each side. Lateral tooth (Figure 39*b,c,f*) rhomboidal with long lateral extension of basal plate that tapers and twists where it is inserted on radular membrane. Basal plate of lateral tooth with large pointed median buttress, directed downward. Center of buttress has tiny raised pustule. Top of lateral tooth concave with cutting

TABLE 24.—Analysis of radular parameters of *Clypeomorus purpurastoma* (measurements in mm).

Character (n=9)	\bar{x}	sd	Range
Radular length	3.3	0.58	2.8–4.5
Rows of teeth	82.6	13.43	65–112
Shell length	22.4	1.69	21.2–25.5

Shell length/radula length index: 6.91

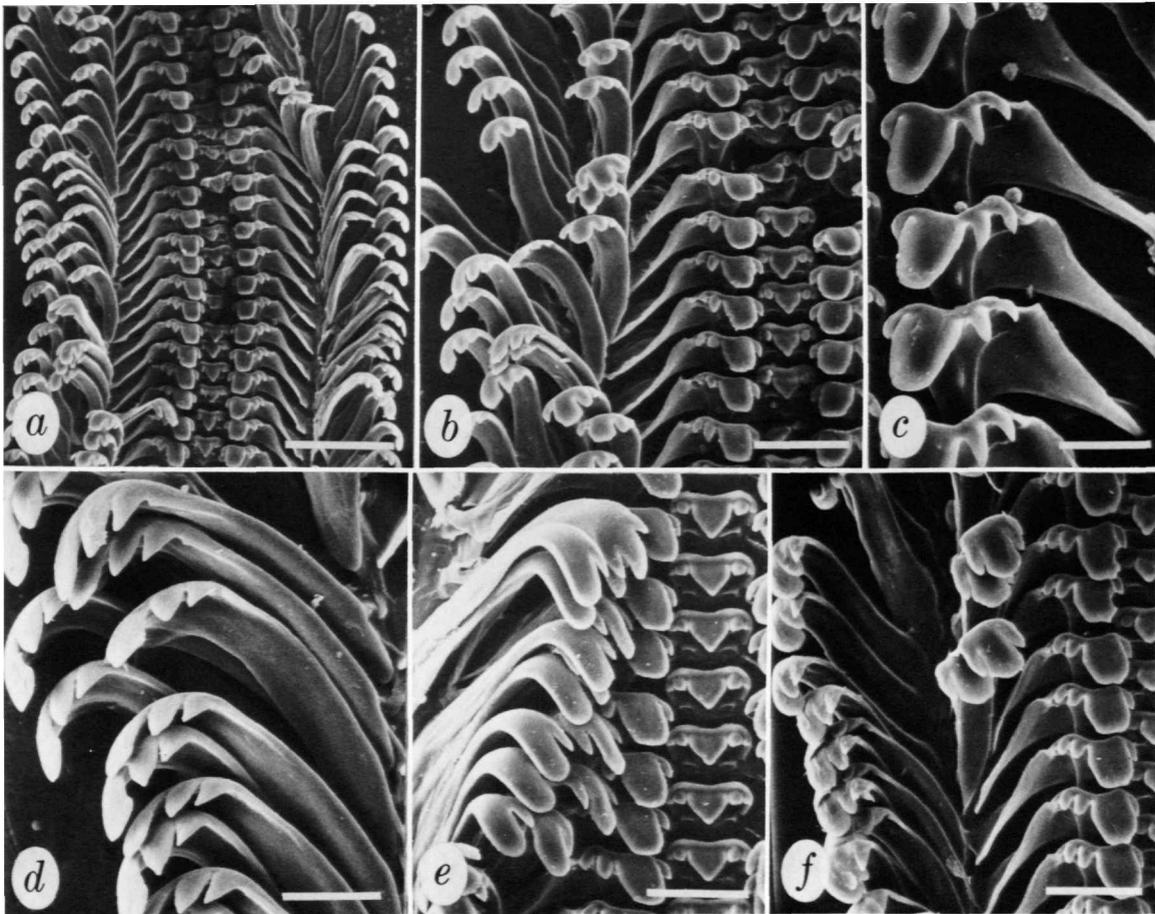


FIGURE 39.—SEM micrographs of radula of *Clypeomorus purpurastoma*, new species: *a*, general view of radular ribbon of specimen from Napot Point, Morong, Bataan, Luzon, Philippines, USNM 774749 (bar = 150 μ m); *b*, close-up of radula showing half rows of teeth, Napot Point, Morong, Bataan, Luzon, Philippines, USNM 774749 (bar = 75 μ m); *c*, detail of lateral teeth of specimen from Pointe Fièvre, S Nossi-Bé, NW Madagascar, ANSP 258528 (bar = 40 μ m); *d*, detail of cusp structure of tips of marginal teeth, Eman Point, Morong, Bataan, Luzon, Philippines, USNM 774770 (bar = 40 μ m); *e*, marginal teeth folded over lateral and rachidian teeth, Laam Son, W Phuket Island, Adaman Sea, Thailand, ANSP 286011 (bar = 60 μ m); *f*, detail showing insertion of lateral and marginal teeth onto radular membrane, Bongao Channel, SW end of Sanga Sanga, Sulu Archipelago, Philippines, ANSP 230638 (bar = 75 μ m).

edge bearing large broad chisel-like median cusp flanked on inner side by small pointed denticle and on outer side by 2 widely separated pointed denticles. Lateral extension of basal plate with slight flange directly adjacent to cutting edge of lateral tooth. Marginal teeth (Figure 39*d,e*) long and sinuous, with moderately wide shafts and pointed bases where they are inserted onto radular membrane. Tips of marginal teeth spatulate and sharply curved. Inner marginal tooth with broad chisel-shaped central denticle flanked on inner side by 2 nearly fused pointed denticles and by 1 outer pointed denticle. Outer marginal tooth same only lacking outer denticle.

Animal: Head-foot color dusky, blotched with black, orange, and white. Snout darkly pigmented in center. Tentacles anterior to eyes, darkly pigmented. Inner edge of inhalant siphon has large yellow siphonal spot. Other anatomical systems as described in *Clypeomorus bifasciata*.

HOLOTYPE.—USNM 774749, 26 mm in length, 10.5 mm in width (Figure 38*e*).

PARATYPES.—USNM 784650, 16 specimens.

TYPE-LOCALITY.—In sandy areas around boulders just below low tide mark, Napot Pt, Morong, Bataan, Luzon, Philippines.

ETYMOLOGY.—From the Latin *purpura* (purple) and the Greek *stoma* (mouth), referring to the purple aperture.

REMARKS.—This species, although common throughout its range, has never been recognized as a distinct taxon. It has been figured frequently as a variation of other species and is most usually "lumped" with *Cerithium sejunctum* Iredale or *Cerithium moniliferum* of authors (= *Clypeomorus batillariaeformis* Habe and Kosuge, 1966). For example, two of the shells figured in Sowerby's *Thesaurus* (1855, pl. 182: figs. 167, 168) as *Cerithium variegatum* Quoy and Gaimard are *Clypeomorus purpurastoma*, and plate 7: figure 41a of Sowerby (1865), cited as *Cerithium variegatum* Quoy and Gaimard, is also *Clypeomorus purpurastoma*. Cernohorsky (1972:70), in his treatment of *Clypeomorus batillariaeformis* (cited as *Clypeomorus moniliferus*), has undoubtedly included *C. purpurastoma* in his concept of that taxon because

he mentions that some specimens have purple apertures.

ECOLOGY.—Throughout its geographic range, this species lives in the low intertidal zone on a hard substrate. Although it frequently occurs in geographic sympatry with *Clypeomorus petrosa* (Wood), *Clypeomorus batillariaeformis* Habe and Kosuge, and *Clypeomorus bifasciata* (Sowerby), it is ecologically separated from them. I have observed *Clypeomorus purpurastoma* at Morong, Bataan, Luzon, Philippines, living at the low tide mark on a hard substratum where it occurs on boulders and large cobbles. It occurs in moderately sized populations and is an active crawler that does not avoid the light. Few individuals are found under rocks. I observed another population in Dumbea, Viti Levu, Fiji, at the midtide mark on a rocky bench adjacent to a fringing reef. The ecological pattern is similar for populations from East Africa and other western Pacific regions, because records of identical substrata preferences and intertidal zonation are cited on labels accompanying museum collections of this species.

Although other congeners are geographically sympatric with this species, microsympatry does not occur: *Clypeomorus batillariaeformis* and *Clypeomorus petrosa* live higher in the intertidal zone than *Clypeomorus purpurastoma*. The latter, however, appears to exhibit ecological release when these co-occurring congeners are absent and will then expand into other parts of the intertidal zone although never to the high tide zone.

The short radula suggests that this species grazes on algae or detritus of small particle size. Many shells were found with peeled apertures indicating crab predation and with bore holes indicative of muricid snail predators. Nothing is known of the reproductive biology or life history of this species, and since the protoconch is unknown, the developmental mode cannot be ascertained.

DISCUSSION.—The most salient characters of this species are its pupiform shell and purple aperture. The only other shallow water cerithiid with a pupiform shell and purple aperture is

Clypeomorus nympa, new name (previously known as *Cerithium sejunctum* Iredale) (Figure 56), which it closely resembles. *Clypeomorus nympa* tends to live around low lying, oceanic island groups and atolls and is particularly abundant in Micronesia and Polynesia, whereas *Clypeomorus purpurastoma* lives along continental shores and archipelagos associated with continents. Thus the two species, while overlapping in some parts of their ranges, are mostly allopatric. *Clypeomorus purpurastoma* is a larger, less globose, more attenuate species and differs in sculpture from *Clypeomorus nympa* in having smaller, more numerous beads on spiral cords and a tendency to have smaller spiral lirae. It also has a more weakly defined suture. Other species with which *Clypeomorus purpurastoma* may be confused are *Clypeomorus batillariaeformis* (previously known as *Cerithium moniliferum*), *Clypeomorus petrosa* (Wood), and *Cerithium zonatum* Wood. Some morphs of these species are very difficult to separate from *Clypeomorus purpurastoma* without careful examination. The easiest way to recognize *C. purpurastoma* is by examining the lower lip of the aperture, which is always pendant. When the shell is viewed dorsally, the margin of the lower lip extends below the end of the anterior siphonal canal, whereas in the other species, the siphonal canal is slightly longer than the lower lip.

The only species that has a dorsal varix on the body whorl similar to that of *Clypeomorus purpurastoma* is *Clypeomorus batillariaeformis*, but this species lacks a purple aperture. Nevertheless, slender morphs of *Clypeomorus batillariaeformis* closely resemble *Clypeomorus purpurastoma* and identification of these species should be made carefully.

There is a great deal of variability in color within populations, but no geographic or ecological color clines are apparent. In some specimens the purple aperture is very pale. Some populations have more pupiform shells (Figure 38*a,d,g,h*) than others and this trait does not vary within populations. Specimens from western Africa and Madagascar tend to be obese and larger with flatter, smoother beads than those from the

western Pacific (Figure 38*a,d,g,h*).

The radula of *Clypeomorus purpurastoma* resembles those of the *Clypeomorus bifasciata* species group, the *Clypeomorus batillariaeformis* group and the *Clypeomorus petrosa* group, all of which have similar radular configurations. The rachidian tooth of *Clypeomorus purpurastoma*, however, has a slightly longer extension to the point of the triangular base of the basal plate.

FOSSIL RECORDS.—Not known in the fossil record.

GEOGRAPHIC DISTRIBUTION (Figure 40).—Most records are from the western Pacific, from the Ryukyu Islands south to Indonesia and east to Fiji and Tonga. This species also occurs in the eastern Indian Ocean and is common in East Africa and Madagascar. It probably exists in suitable habitats in India and Ceylon. Although specimens from Fiji and Tonga are common, I have not seen any from the New Hebrides, Solomons, or New Caledonia; but the species most likely occurs throughout Melanesia.

MATERIAL EXAMINED.—EAST AFRICA: Isla di Serpenti, Chisimaio, Somalia (AMNH 146219); Kichangani Kenya (BMNH); NW of Choca, SW Conducia Bay, Mozambique (NM H1893); Ras Chokir, Dar es Salaam, Tanzania (USNM 786797); Mombassa Id, Tanzania (ANSP 272424); Mangapwani, NW Zanzibar (ANSP 212969); Pange Id, W Zanzibar (ANSP 214275). MADAGASCAR: Pt Fièvre, Nossi-Bé, (ANSP 258528, USNM 719218, 719456, 774505); N of Sarodrano Pt, Tuléar (USNM 771433); Ambariobe, South Rock, Nossi-Bé (USNM 720105); Crater Pt, Ambatomboka, Nossi-Bé (USNM 285585); Sarodrano, Tuléar; Sarodrano, N Point, Tuléar; Grand Récif, Tuléar (MNHNP). INDIAN OCEAN: Baie Ternay, Mahé, Seychelles (BMNH); Port Blair, Andaman Ids (BMNH).

SOUTHEAST ASIA: Goh Sindarar Nua (Chance Id), Thailand (USNM 661431); Laam Son, W Phuket Id, Andaman Sea, Thailand (ANSP 286011, 286013); Laam Seng, 1 mi (1.6 km) S of Laam Son, W Phuket Id, Andaman Sea, Thailand (ANSP 285853); N end Bangtan Bay,

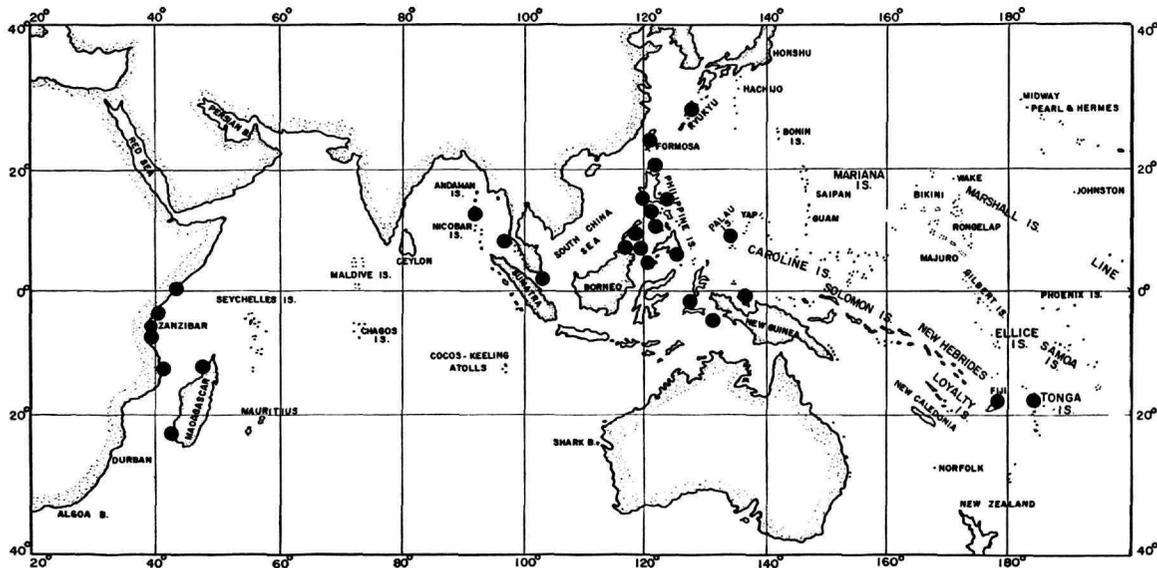


FIGURE 40.—Geographic distribution of *Clypeomorus purpurastoma*, new species.

W side of Phuket Id, Thailand (ANSP 285927); Raffles Light, Singapore (ANSP 272425); Labrador, Singapore (ANSP 245688); off Mersing, E coast of Malaysia (WAM). INDONESIA: S coast Gomumu Id, S of Obi Id, Moluccas (WAM); Waratneu Id, Tajundu, Kai Ids, Moluccas (USNM 746762); Pombo Id, Haruku Strait, E of Ambon (USNM 746563); Teloc Slawi, Komodo, Lesser Sundas (UF, no number); Pulau Siburu, N of Sipora Id, SW Sumatra (USNM 654725). N. BORNEO: Kudat (USNM 666749); Sibuan Id (ANSP 295334); Taganak Id (USNM 243942). RYUKYU ISLANDS: Amamioshima (USNM 774581). TAIWAN: (ANSP 243475).

PHILIPPINES: Sabtang Id, Batanes Group (USNM 243911); Gigmoto, Cataduanes Id (ANSP 223140); Eman Pt, Morong, Bataan, Luzon (USNM 774757, 774770); Napot Pt, Morong, Bataan, Luzon (USNM 774749); Jamelo Bay, Luzon (USNM 243949, 243951); Marican Id, Luzon (USNM 232940, 232942, 232979, 232977); Lippo Pt, Balayan Bay, Luzon (USNM 243764); Besogo, Luzon (USNM 232908); Laguna de Bay, Luzon (USNM 283324); Butananan Id, E Luzon (USNM

233003); Santa Cruz Harbor, Marinduque (USNM 243826); Laylay, Marinduque; Puerto Galero, Mindoro (USNM 774481); Hill, W side of Mansaloy Bay, Mindoro (USNM 243818); Salpa Id, 2 km S of Olango Id, E Cebu (ANSP 230447); Pt Naso, Panay (USNM 243898, 243901); Enrique Villaneuva, Siquijon, off Negros (USNM 774493); Palawan (USNM 283308); Port Langcan, Dumaran Id, Palawan (USNM 243878); Puerto Princesa, Palawan (USNM 224615); Cataingan Bay, Dumurug Pt, Masbate (USNM 243834); Malcochin Harbor, Linpacan (USNM 243861); Davao, Mindanao (USNM 233139, LACM 25160); Opol, Mindanao (USNM 232974); Capunuygan Pt, Mindanao (USNM 243888); Polloc, Mindanao (USNM 232912, 232913); Little Santa Cruz Id, Zamboanga, Mindanao (USNM 244032); Baluk Id, Sarangani Group (USNM 244006); Lampinagan Id, off Basilan (USNM 233193); Bubuan Id, Jolo (USNM 233097, 243644); Jolo Jolo, Sulu Archipelago (USNM 232869, 232870, 233097, 233109); W of Caluman Id, SW of Siasi Id, Sulu Archipelago (ANSP 318816); Sitanki, Sitanki, Tawi Tawi Group (USNM 243638);

Similuc Id, Tataan Id, Tawi Tawi Group (USNM 239707); small island, 0.5 mi (0.8 km) W of Tara Id, Tapul Id, Sulu Archipelago (USNM 243775, 243789); Bongao Channel, SW end of Sanga Sanga Id, Sulu Archipelago (ANSP 230638); Gagayan Sulu (USNM 233226). PALAU: Kayangel Id, Kayangel Atoll (USNM 489001, 616929); SW Rattakadokoru Id (ANSP 201617); Anguar Id (USNM 616980, 786918).

NEW GUINEA: reef, 1 mi (1.6 km) NE Mios Woendi Id, Padaido Ids, West Irian (ANSP 205771); SSW of Soweck, Soepiori Id, Schouten Group, West Irian (ANSP 207937); Wandamin Bay, West Irian (ZMA). FIJI: Daumba Reef, S coast of Viti Levu (USNM 794733); Daumba Reef, Nauva, Viti Levu (USNM 790683); Nandi Bay, Viti Levu (ANSP 255355); Tavua, Viti Levu (LACM 77-35); inlet by Yanuca Id, Viti Levu (FSM 24772); Suva, Viti Levu (USNM 532104). TONGA: Sopa Reef, Tongatapu (USNM 654210).

***Clypeomorus inflata* (Quoy and Gaimard),
new combination**

FIGURES 41–43

Cerithium inflatum Quoy and Gaimard, 1834:130, pl. 55: fig. 10 [holotype: MNHNP, no number; type-locality: Île de Vanikoro].—Kiener, 1841: 41–42, pl. 7: fig. 1—Deshayes in Lamarck, 1843:319–320.—Sowerby, 1855:871, pl. 182: fig. 170; Sowerby 1865, pl. 9: fig. 60.—Tyron, 1887:132, pl. 23: fig. 16 [not figs. 17, 18 or pl. 34: fig. 7].—Martens, 1897:174–175.—Kobelt, 1898:185–186, pl. 34: fig. 7.—Tesch, 1920:55–56, pl. 131: fig. 180.—Oostingh, 1925:4.

DESCRIPTION.—*Shell* (Figure 41; Table 25): Adult shell globose with low spire and teleoconch of 7 or 8 inflated angular whorls having apical angle of 45–50 degrees. Shell reaching 26.9 mm in length. Whorls of teleoconch with broad sub-sutural ramp below, which are 2 nodose spiral cords. Whorls sculptured with numerous small spiral cords and deeply incised spiral lines crossed by tiny axial incised lines giving shell a scaly appearance. Nodes on spiral cords aligned to form about 12 axial ribs per whorl but former

TABLE 25.—Analysis of shell parameters of *Clypeomorus inflata* (measurements in mm).

Character (n=30)	\bar{x}	sd	Range
Shell length	22.49	1.92	19.21–26.9
Shell width	12.58	1.12	10.15–14.6
Aperture length	7.84	0.77	8.9–6.15
Aperture width	6.23	0.67	4.6–7.51
No. axial ribs per whorl	6.63	2.72	3–13
No. beads on penultimate whorl	11.00	1.10	8–13

Length/width index: 1.79

Shell length/aperture length index: 2.87

varices interrupt regular pattern of axial nodes. Postnuclear whorls sculptured with 3 or 4 spiral cords, usually badly eroded. Protoconch unknown. Body whorl large, highly inflated, and sculptured with 7 major spiral cords, numerous fine spiral threads, and incised spiral lines. Major spiral cords are thickest at center and base of body whorl. Large, angular dorsal varix and varix opposite outer lip present on body whorl. Base of body whorl constricted, with thick siphonal fasciole, and apertural side somewhat flattened. Suture deeply impressed, wavy. Aperture large, round, flaring, a little less than half the shell length. Anterior siphonal canal short but distinct, about 45 degrees to the left of the shell axis. Anal canal distinct, bordered by parietal columellar plait, which extends well within shell aperture. Columella concave with thickened parietal callus. Outer lip thick, rounded, and crenulate, having numerous spiral plications on its inner surface. Parietal part of outer lip extends slightly onto penultimate whorl. Plane of outer lip parallel to shell axis. Shell color ranges from dark brown to cream, occasionally spiral tan bands present. Aperture and columella white. Periostracum thin, light brown, usually eroded. Operculum unknown.

Animal: Not known.

Radula (Figure 42): Radular ribbon long, a little over one-third the shell length. Radular ribbon 9 mm long, comprising 153 rows of teeth

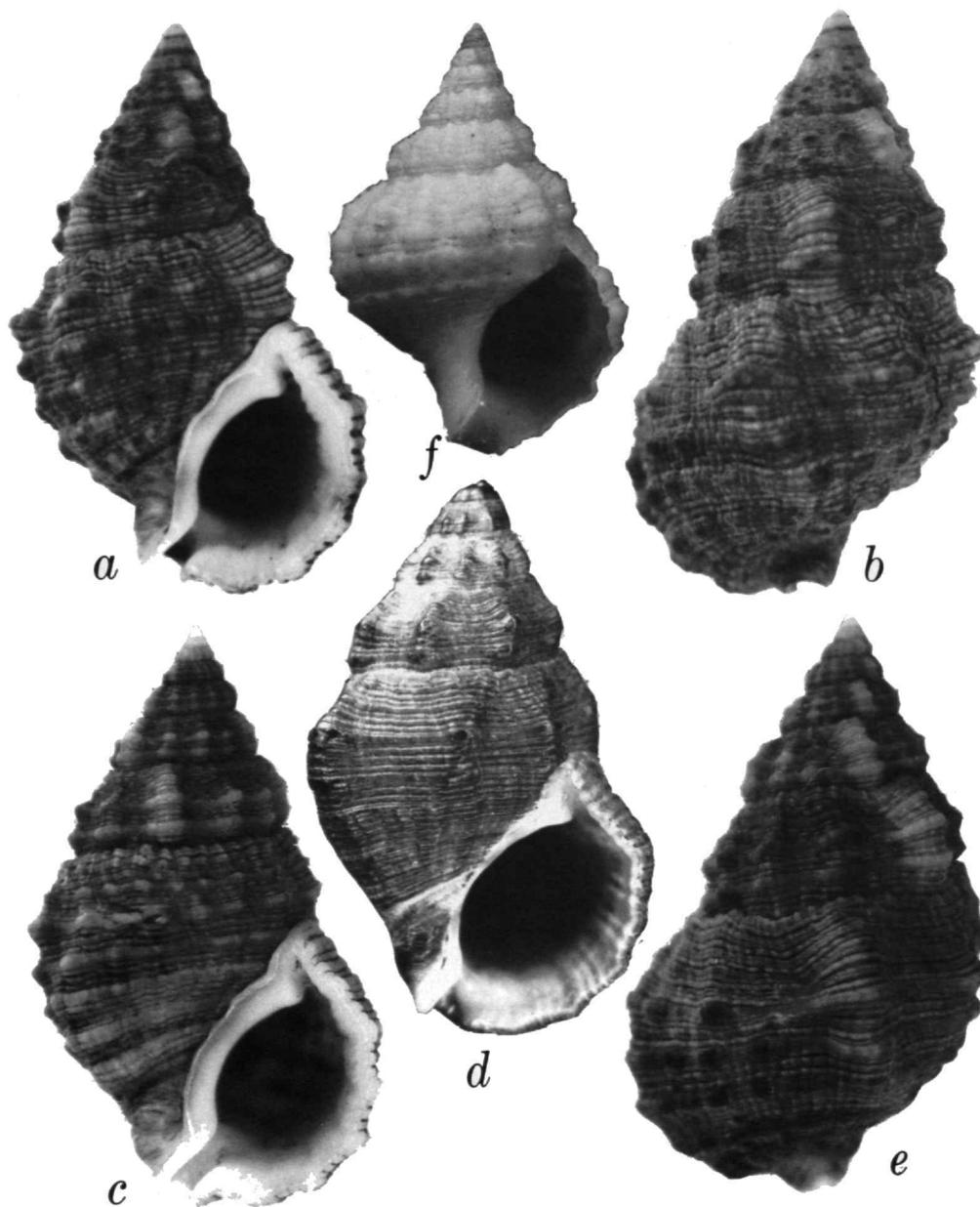


FIGURE 41.—*Clypeomorus inflata* (Quoy and Gaimard, 1834), showing variation in shell form and sculpture: *a, b*, Malabuyac, Cebu, Philippines, USNM 774584 (27 × 14.5 mm); *c, d*, Malabuyac, Cebu, Philippines USNM 774585 (24.4 × 13.4 mm); *e*, holotype of *Cerithium inflatum* Quoy and Gaimard, 1834, from Vanikoro, Santa Cruz Islands, MNHNP no number (19.9 × 11.5 mm); *f*, immature specimen from Guiljungan, Negros, Philippines, USNM 232852 (14 × 9.5 mm).

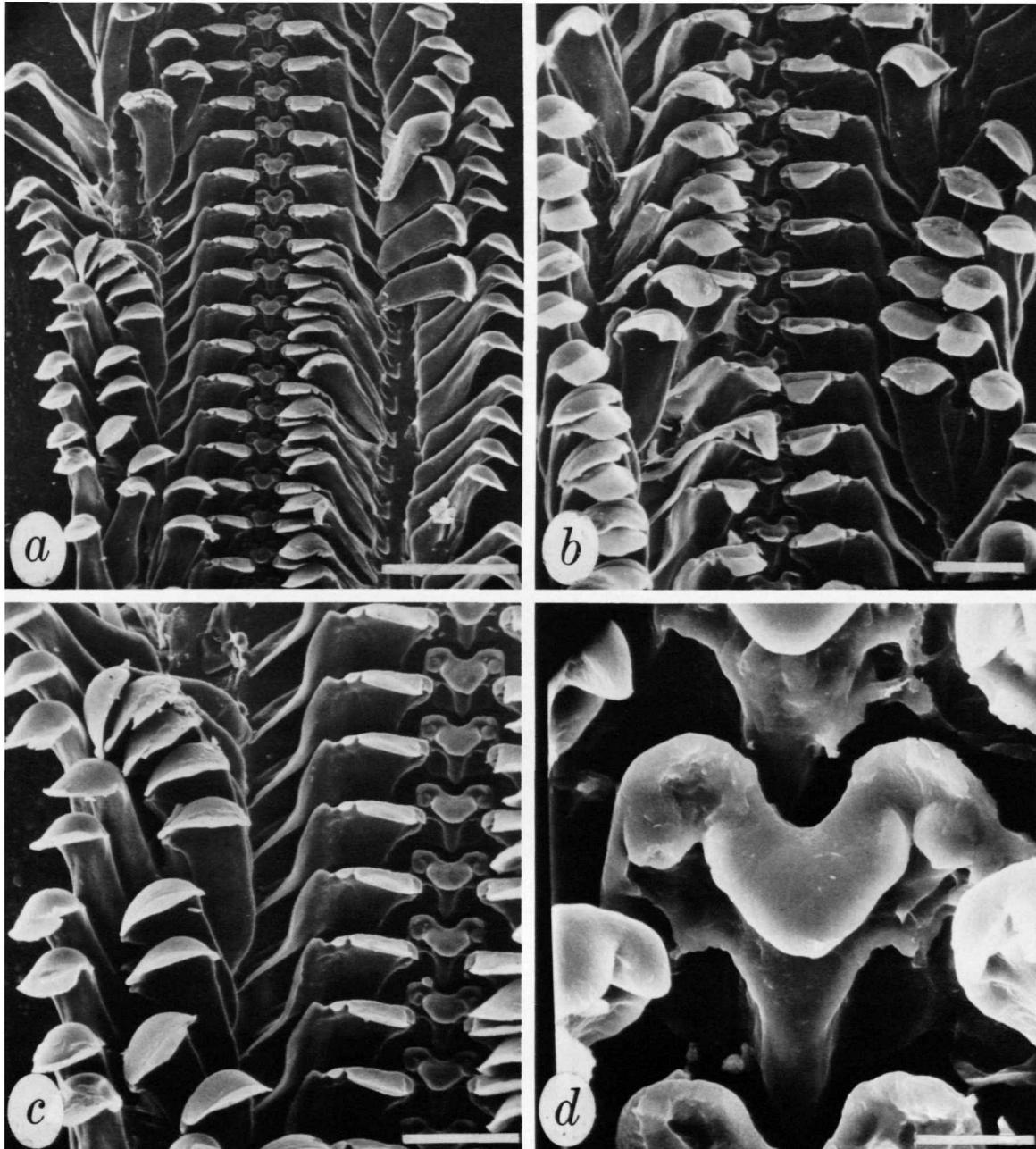


FIGURE 42.—SEM micrographs of radular ribbon of *Clypeomorus inflata* from Tanjung Cape, Flores, Indonesia: *a, b*, general aspect of radular ribbon, marginal teeth folded back, UF 24770 (bars = 200 μm and 100 μm , respectively); *c*, half-row (bar = 100 μm); *d*, detail of rachidian tooth (bar = 20 μm).

in snail 25 mm long. Shell length/radula length index 2.7. Rachidian tooth (Figure 42*d*) pentagonal, about 60 μ m wide. Basal plate of rachidian tooth flat with median narrow buttress that projects slightly over median base of plate. Top of buttress extends laterally to sides of basal plate. Top of rachidian tooth concave, forming deep V-shaped depression in center. Cutting edge of rachidian tooth has broad central rounded spade-shaped cusp flanked on each side with single tiny rounded denticle. Lateral tooth (Figure 42*b,c*) rhomboidal with long twisted basolateral projection that inserts onto radular membrane. Basal plate of lateral tooth with long semimedial buttress-like projection directed downward. Top of lateral tooth straight with broad chisel-like central cusp flanked on each side with single tiny denticle. Where outer denticle ends on top of lateral tooth, upper basal plate has flange before extending basolaterally. Marginal teeth (Figure 42*b,c*) long and wide, curving at tips and narrow at base where inserted onto radular membrane. Curved tips of marginal teeth broadly spatulate, forming large spoon-shaped central cusp with rounded edge. Inner marginal tooth with tiny single sharp denticle nearly fused to each side of cusp. Outer marginal tooth same, lacking outer denticle.

REMARKS.—This taxon, cited by many earlier authors, is not well known in the recent literature. It is unusual for a cerithiid species proposed in the early nineteenth century to have no synonyms. The holotype (Figure 41*e*) is a beachworn specimen from Vanikoro, Santa Cruz Islands, the edge of the species' geographic range.

ECOLOGY.—Very little is known about the habitat of this species. The stocky shell and large aperture indicate an intertidal habitat on a hard substratum, such as cobbles and rocks. The protoconch is unknown and no information exists about the spawn, eggs, or developmental biology. The long radula suggests that coarse substrata are grazed.

DISCUSSION.—The distinguishing characters of *Clypeomorus inflata* are its fat stocky shape, large angular body whorl and aperture, a deeply

impressed suture, broad subsutural ramp, sculpture of two dominant spiral nodose cords per whorl, angular former varices and axial ribs, and the presence of a siphonal fasciole. The obese shell of this species is closest to that of *Clypeomorus subbrevicula*. Tesch (1920:55) regarded *Clypeomorus subbrevicula* (cited as *Cerithium breviculum* Sowerby) as a synonym of *Clypeomorus inflata*, but the two taxa are distinct species. The former is generally a more obese shell. *Clypeomorus inflata* is easily separated from *Clypeomorus subbrevicula* by its more angular whorls, fewer beaded spiral cords, large varices, and raised parietal outer lip that extends onto penultimate whorl. In addition, *Clypeomorus subbrevicula* has more spiral beaded cords per whorl and has an overall rounded shape. Some squat morphs of *Clypeomorus batillariaeformis* Habe and Kosuge, may be confused with *Clypeomorus inflata*, but the former species lacks the anal fasciole and broad subsutural ramp, and has more spiral cords and nodulose beads per whorl.

In general, this species does not display a great deal of variability in shell sculpture, even in immature specimens (Figure 41*f*). Color variations are more common and alternate between dark brown (Figure 41*c,d*) and cream colored individuals (Figure 41*f*). Specimens with light brown spiral bands are occasionally seen.

The radula most closely resembles that of *Clypeomorus irrorata* (Gould) and *Clypeomorus subbrevicula* (Oostingh) (Figure 2*c*). There is also some resemblance to the radulae of *Clypeomorus admirabilis*, new species, and *Clypeomorus adunca* (Gould). These five species may share a common lineage.

FOSSIL RECORDS.—Not recorded as a fossil in the literature.

GEOGRAPHIC DISTRIBUTION (Figure 43).—Found throughout the Philippines and eastern Indonesia. The record from Guam needs to be reconfirmed.

MATERIAL EXAMINED.—INDONESIA: Bawean Id, Java Sea (ZMA); Amurang, Celebes (ZMA); Lintido, Celebes (ZMA); Baie Taimanoek, Sumba (ZMA); Ndorota, 3 mi NNE Reo,

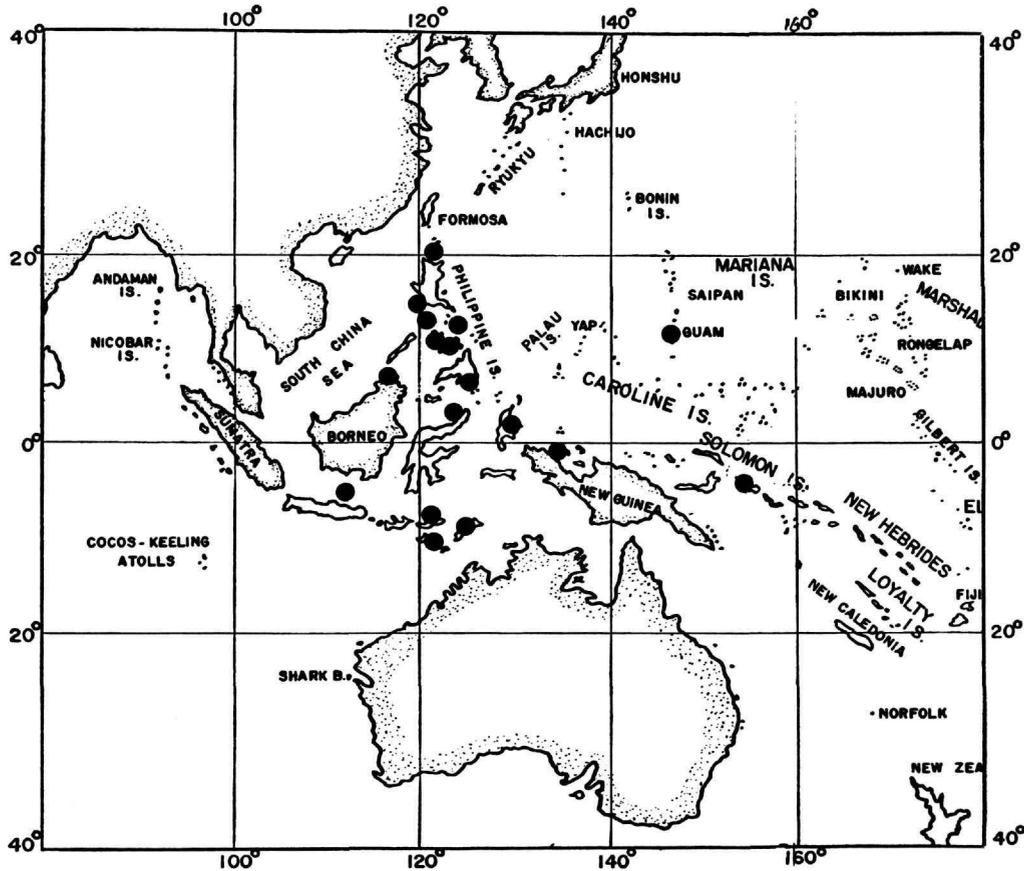
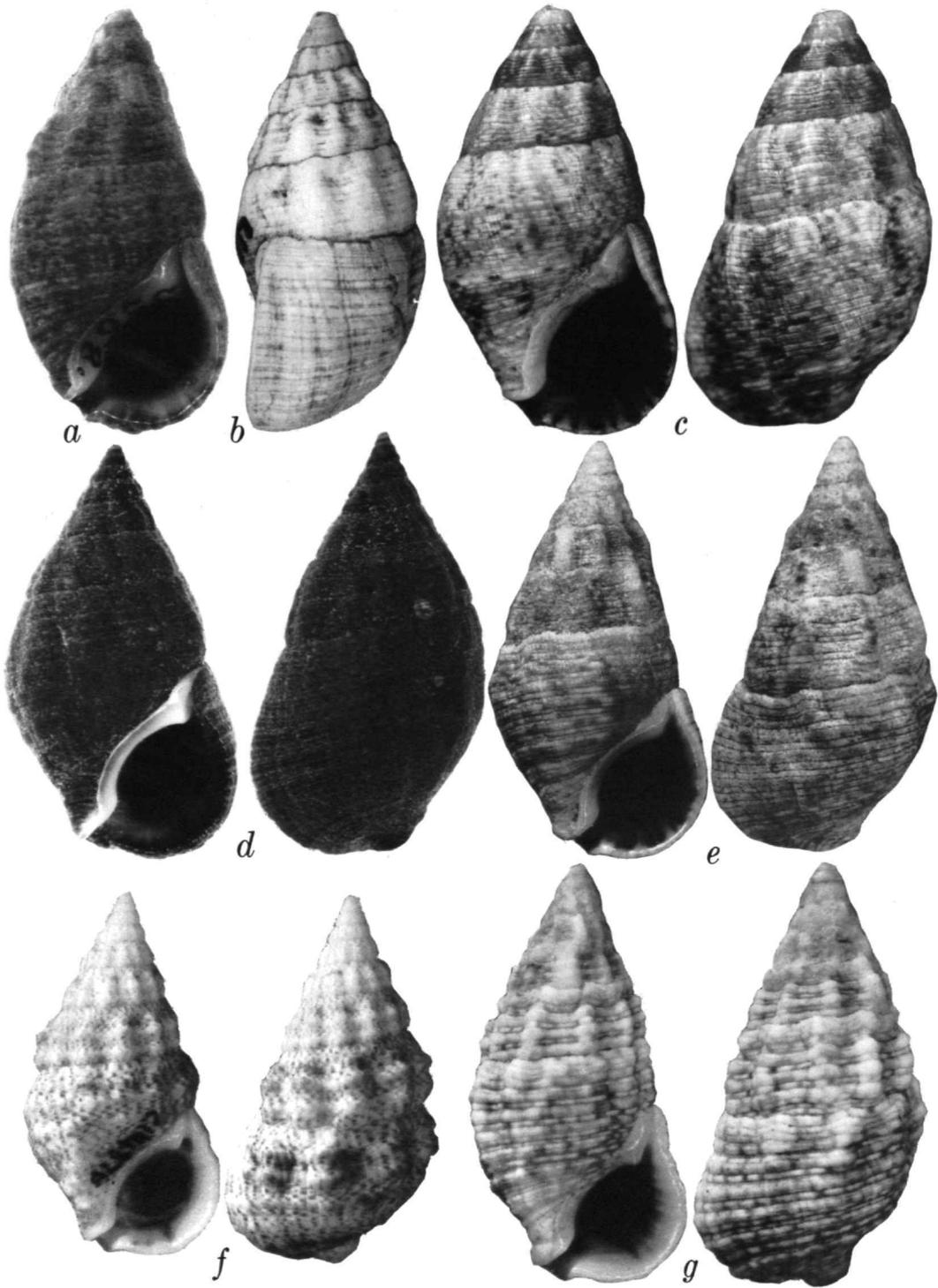


FIGURE 43.—Geographical distribution of *Clypeomorus inflata* (Quoy and Gaimard, 1834).

Tandjung Cape, Flores (UF 24770); 2 km W Wae Radja, Flores, Lesser Sundas (UF 1660); Timor (ZMA); Kudat Bay, Kudat, N Borneo (USNM 632229). NEW GUINEA: Manokwari, NW end of West Irian (ANSP 249640). MARIANA ISLANDS: Apra Bay, Guam (USNM 774572). PHILIPPINES: Mahinog, Camiguin Id, Babuyan Group (USNM 233039); Mariveles, Luzon (USNM 303653); Atimonan, Tayabas Prov, Luzon (USNM 310338); Subic Bay, Luzon (USNM 774569); mouth of small stream, Canmahala Bay, Ragay Group, Luzon (USNM 239718); Jamelo Bay, Luzon (USNM 243952, 774578); Nasugbu, Luzon (USNM 232862); W coast, Palau Id, Luzon (USNM 774577); Napot

Pt, Morong, Bataan, Luzon (USNM 776662); Cabago Pt, Looc Bay, Bataan, Luzon (USNM 774754); Palawan (LACM 35445); Bolalo Bay, Palawan (USNM 243690); Mansalay River, Mindoro (MCZ); Guiljungan, Negros (USNM 232849, 232852, 244081); Malabuyac, Cebu (AMNH 121934, USNM 774570, 774584, 774585); Compostela, Cebu (USNM 233232); Balabac (USNM 303674); Pt Naso, Panay (USNM 243897); W of Cabbalogan, Samar (USNM 243821); Balbut Id, Savangani Group (USNM 233188); small stream near Mali, Pujada Bay, Mindanao (USNM 243902); Capumuypu-gan Pt., Mindanao (USNM 233239); Davao, Mindanao (USNM 233136).



Clypeomorus irrorata (Gould),
new combination

FIGURES 44–46

Cerithium irrorata Gould, 1849:119 [holotype: USNM5568; paratype: MCZ 169206; type-locality, here designated: Looc Bay, Bataan, Luzon, Philippines; not *Cerithium irrorata* C.B. Adams, 1852]; 1852:148; 1856, pl. 10: fig. 168.—Johnson, 1964:94.

Cerithium obesum Sowerby, 1855:868, pl. 181: figs. 141–142 [lectotype: BMNH, not registered; type-locality: Bohol, Philippines; not *Cerithium obesum* Deshayes, 1834; nor Gabb, 1873 (in part); nor Guppy, 1876]; 1865: pl. 9: fig. 62.—Martens, 1897:175.—Tesch, 1920:56, pl. 131: fig. 181.—Oostingh, 1925:45.

Cerithium repletulum Bayle, 1880:248 [new name for *Cerithium obesum* Sowerby, 1855].—Tryon, 1887:139, pl. 26: fig. 92.—Kobelt, 1895:186–187, pl. 34: fig. 9.

DESCRIPTION.—*Shell* (Figure 44; Table 26): Shell thick, having teleoconch of 8 or 9 whorls, apical angle of 45 degrees, and reaching 15.5 mm in length. Early juvenile whorls and protoconch usually eroded or decollate. Length/width index of 2.27. Whorls sculptured with 9–15 broad wavy axial ribs, and with many fine flattened spiral threads and numerous, spiral microscopic incised lines. Body whorl wide, inflated, about one-half the length of the shell. Axial ribs on body whorl plicate, and limited to upper third of whorl adjacent to suture. Shell depressed between axial plications on body whorl. Lower two-thirds of body whorl lack axial sculpture, having only spiral elements present. Body whorl slightly constricted at base. Aperture ovate, about one-third the shell length. Anterior

FIGURE 44.—*Clypeomorus irrorata* (Gould, 1849) from various geographical areas showing variation in shell form, sculpture, and color: *a*, holotype of *Cerithium irroratum* Gould, 1849, no locality cited, USNM 5568 (21 × 12 mm); *b*, lateral view of specimen from Malabuyoc, Cebu, Philippines, USNM 774586 (23.5 × 12.1 mm); *c*, lectotype of *Cerithium obesum* Sowerby, 1855, from Bohol Island, Philippines, BMNH, no number (20.7 × 10.77 mm); *d*, Malabuyoc, Cebu, Philippines, USNM 774586 (23.1 × 11.7 mm); *e*, Osima, Osumi, Ryukyu Islands, USNM 343866 (14.5 × 7 mm); *f*, Low Isles, NE of Port Douglas, Queensland, Australia, AMS C114876 (21.9 × 11 mm); *g*, Shioya, Shanawan Bay, Okinawa, USNM 774500 (19.5 × 10 mm).

TABLE 26.—Analysis of shell parameters of *Clypeomorus irrorata* (measurements in mm).

Character (n=30)	\bar{x}	sd	Range
Shell length (last 3 whorls)	19.24	1.65	15.46–24.34
Shell width	9.37	1.65	7.47–12.17
Aperture length	5.76	1.04	3.08–8.15
Aperture width	4.66	0.79	2.95–6.05
No. axial ribs	11.20	1.41	9–15

Length/width index: 2.27

Length/aperture length index: 3.69

TABLE 27.—Analysis of radular parameters of *Clypeomorus irrorata* (measurements in mm).

Character (n=5)	\bar{x}	sd	Range
Radula length	7.44	1.87	5.5–9.7
Rows of teeth	139	30.20	105–175
Shell length	18.10	2.30	15.3–21.7

Shell length/radula length index: 2.54

siphonal canal short, deep, slightly turned at a 45 degree angle to shell axis. Anal canal deep, extending into shell aperture, bordered by posterior columellar tooth. Columella concave with thickened callus extending at parietal area onto lower fourth of penultimate whorl. Outer lip rounded, smooth, thick, and interiorly lirate. Thick varix along edge of outer lip. Upper edge of outer lip partially extends onto penultimate whorl. Plane of outer lip parallel to shell axis. Entire aperture heavily enameled. Suture incised, wavy. Protoconch unknown. Shell color variable, normally white, brown, or gray, overlain by numerous thin spiral dotted lines of brown and black. Entire shell sometimes black. Periostracum thin, light brown, frequently eroded on most of shell. Operculum thin, corneous, ovate, and paucispiral with subcentral nucleus adjacent to anterior siphonal canal.

Radula (Figure 45; Table 27): Radular ribbon long, about 7.5 mm in length and having 139 rows of teeth. Shell length/radula length index 2.54. Rachdian tooth (Figure 45*d*) squar-

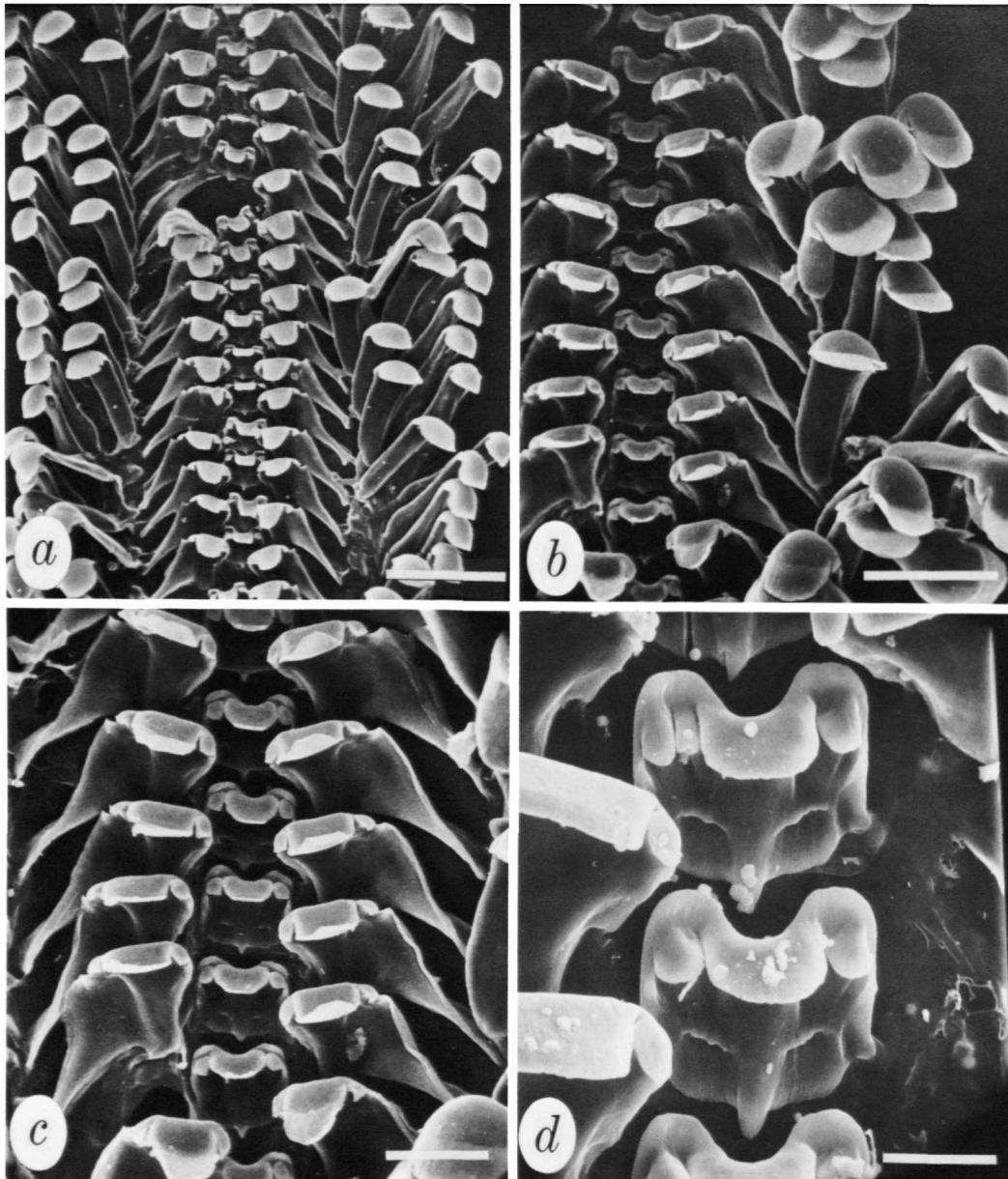


FIGURE 45.—SEM micrographs of radular ribbon of *Clypeomorus irrorata* from Eman Point, Morong, Bataan, Luzon, Philippines, USNM 774753: *a*, general aspect of radular ribbon, marginal teeth folded back (bar = 150 μm); *b*, *c*, detail of marginal and lateral teeth, note spoon-like tips of marginals and long, twisted basolateral extensions of lateral teeth (bars = 150 μm and 50 μm , respectively); *d*, detail of rachidian tooth, note deep depression on top of tooth (bar = 25 μm).

ish, about 55 μm wide, with deep dorsal median depression. Cutting edge of rachidian tooth bears large flat chisel-like medial cusp flanked on each side by small peg-like denticle. Basal plate of rachidian tooth flat, with long pointed central glabella originating at its center and extending, buttress-like, below base. Base of rachidian tooth slightly convex with 2 small pointed lateral ends. Lateral tooth (Figure 45c) trapezoidal having dorsal moderately convex, cutting edge bearing large shovel-like cusp flanked on each side with small pointed denticle. Basal plate of lateral tooth with long tapering basolateral projection, which twists where it is inserted onto radular membrane. Blunt basolateral median projection extends ventrally to cutting edge. Marginal teeth (Figure 45b) long, wide, curved, spatulate, and wide at tips. Tip of inner marginal tooth bears median wide scoop-like cusp flanked on each side with small pointed denticle. Outer marginal tooth identical, only lacking outer denticle.

Animal: Head-foot and short snout dark colored, lined with numerous fine transverse dark lines. Tentacles dark brown, each with large eye at base of peduncular stalk. Sole of foot cream colored. Mantle edge cream colored, with fine transparent papillae separated from each other by yellow pigmented area. Interior of inhalant siphon bright yellow, divided longitudinally with thin septum attached to mantle roof, but free distally. Ctenidium pink-brown, bipectinate osphradium dark brown and thick hypobranchial gland whitish. Kidney bright purple, stomach yellow, digestive gland brown and gonads yellow or cream. Pallial oviduct has long shallow sperm gutter beginning at distal end of medial lamina and ending postmedianly in large spermatophore bursa located in proximal half of the lamina. No seminal receptacle seen. Stomach large, long crystalline style present.

REMARKS.—This species, rarely mentioned in the literature, is usually cited as *Cerithium obesum* Sowerby (lectotype, Figure 44c), but the name *C. obesum* is preoccupied and was given a replacement name, *C. repletulum*, by Bayle (1880:248). This was unnecessary because Gould (1849:119)

had previously described this species. The name, *Cerithium irrorata*, however, was overlooked by most subsequent authors. Gould did not cite a type-locality. The holotype of *Cerithium irrorata* is shown in Figure 44a. Kobelt (1895:97) mistakenly considered *Cerithium irrorata* Gould to be a synonym of *Cerithium ocellatus* Bruguière (= *Cerithium stercusmuscarum* Valenciennes, 1833), an eastern Pacific species. Examination of the types of *Cerithium irrorata* shows that it is a distinct species restricted to the Indo-West-Pacific and in no way related to *Cerithium stercusmuscarum*.

I herein designate Looc Bay, Bataan, Luzon, Philippines as the type-locality of *Clypeomorus irrorata*.

ECOLOGY.—This species lives in the mid to high tide zones where it is found among rocks and stones. In the Philippines, I observed a large population at Looc Bay, Bagac, Bataan, Luzon, during the month of October. The majority of this population lived at the midtidal zone among cobbles and gravel mixed with coarse sand. At low tide the snails were partially buried in the sand at the bases of the cobbles and stones and were difficult to detect. Although no juvenile snails were found, many individuals were in the process of adding new whorls and had incomplete outer apertural lips. The spawn and type of development are unknown, but the limited geographic range of this species suggests a lecithotrophic kind of development.

This species grazes on microalgae that cover rocks. The long radula indicates that coarse substrata is ingested. Stomach contents consist of red algae and numerous fine sand grains.

Oostingh (1925:45) reported this species from Ternate, Halmahera, Indonesia, indicating that it was collected on mangrove trees by Martens. This seems an odd habitat and suggests that Oostingh may have misidentified his specimens.

Predation was not observed, but some specimens have been seen with drill holes made by naticid snails. No shells with peeled apertures were found, and as the shell is very thick, crab attacks do not appear to be common.

DISCUSSION.—This is an easy species to rec-

ognize because, exclusive of the early whorls, most specimens have an overall smooth stubby appearance and are sculptured with numerous spirally incised lines and very broad axial ribs (Figure 44*b-e*). The wide axial ribs are more defined on the upper two-thirds of each whorl and may be very pronounced in some specimens. Individuals from some localities are more rugose due to stronger spiral and axial sculpture: Puerto Princessa, Palawan, Philippines (ANSP 224591); Enrique Villanueva, Siquijor Island, off Negros, Philippines (USNM 774492); Malcochin Harbor, Linapacan Id., Palawan, Philippines (USNM 243857); Shioya, Shanawan Bay, Okinawa (USNM 774500) (Figure 44*g*). In these specimens the spiral lines are more deeply incised and the axial ribs more numerous (up to 11 per whorl). Specimens from Djakarta Bay, Java (ZMA) and Port Douglas, Queensland, Australia (AMS C114876) (Figure 44*f*) have prominent, nodose axial ribs. Individuals from Indonesian populations tend to have more prominent knobbed axial ribs that are at a 45 degree angle to the shell axis. They are sculptured with deeper incised lines, but younger specimens are more like those from Philippine populations. Shells of *Clypeomorus irrorata* that have more rugose sculpture (Figure 44*f*) somewhat resemble those of *Clypeomorus admirabilis*; but the latter species has thicker spiral cords and more nodulose axial ribs. I am unable to discern a geographic pattern in the distribution of the more highly sculptured specimens and regard them as local ecomorphs or genetic races. The colors of individual snails from a single population may vary: a population from Looc Bay, Bataan, Luzon, Philippine (USNM 774748) exhibits a spectrum of dark brown to cream-colored individuals. Other populations examined are uniformly pigmented. Populations from the Ryukyu Islands (USNM 343866) tend to have smaller, narrower shells with well-developed axial sculpture.

Among its congeners, *Clypeomorus irrorata* has one of the longest radular ribbons. It is closest to that of *Clypeomorus inflata* (Quoy and Gaimard) indicating that the two may be closely related. I suggest that *Clypeomorus irrorata*, *Clypeomorus in-*

flata, and *Clypeomorus subbrevicula* comprise a species-group of similar origin. The radula of *Clypeomorus adunca* also bears some resemblance to *Clypeomorus irrorata*. From the cladistic analysis of *Clypeomorus* species a cladogram (Figure 1) was generated that supports this concept. None of these species are geographically widespread.

FOSSIL RECORD.—*Clypeomorus irrorata* has been recorded from the Pliocene of Timor by Tesch (1920:56), who cited it as *Cerithium obesum* Sowerby. Tesch's figure leaves no doubt that his specimen is *Clypeomorus irrorata*. This species has lived in the same geographic region since the Pliocene and does not appear to have changed appreciably in shell morphology since that time.

GEOGRAPHIC DISTRIBUTION (Figure 46).—The range of *Clypeomorus irrorata* is limited to the Indo-West Pacific where it appears to be most common in the Philippines and in the Indonesian Archipelago. The record from Ceylon indicates that this species may also occur in suitable habitats along the western Malay Peninsula and on islands of the Andaman Sea.

MATERIAL EXAMINED.—**CEYLON:** (ANSP 247909). **SINGAPORE:** Tanjong Gulf (USNM 631931, ANSP 239554). **THAILAND:** Si Racha, Gulf of Siam (USNM 774501). **INDONESIA:** Batavia Bay, Java (ZMA); Amsterdam, Middelburg, Leiden and Hoorn Ids, Djakarta Bay, Java (ZMA); Bali (AMS); Kudat Bay, N. Borneo (USNM 632239); Telok Slawi, Komodo Id, Lesser Sunda Islands (UF 24760). **AUSTRALIA:** Low Isles, NE of Port Douglas, Queensland (AMS C114876; AMS 117188). **NEW GUINEA:** Wandamen Bay, West Irian (ZMA); Japen Id, Schouten Ids, West Irian (AMS); N shore of Maroepe Id, Ambai Ids, West Irian (ANSP 208535). **PHILIPPINES:** Matabungbay, 115 km SSW of Manila, Luzon (AMS); Eman Pt, Morong, Bataan, Luzon (USNM 774753); Eman Pt, Morong, Bataan, Luzon (USNM 774753); Jamelo Bay, Luzon (USNM 243948); Butananan Id, E. Luzon (USNM 233004); Palaui Id, W coast, Luzon (USNM 232925); coast of Mariveles, Luzon (USNM 303681); Canmahana Bay, Ragay Gulf, Luzon (USNM 239731); Luzon (USNM 243616); Bus-

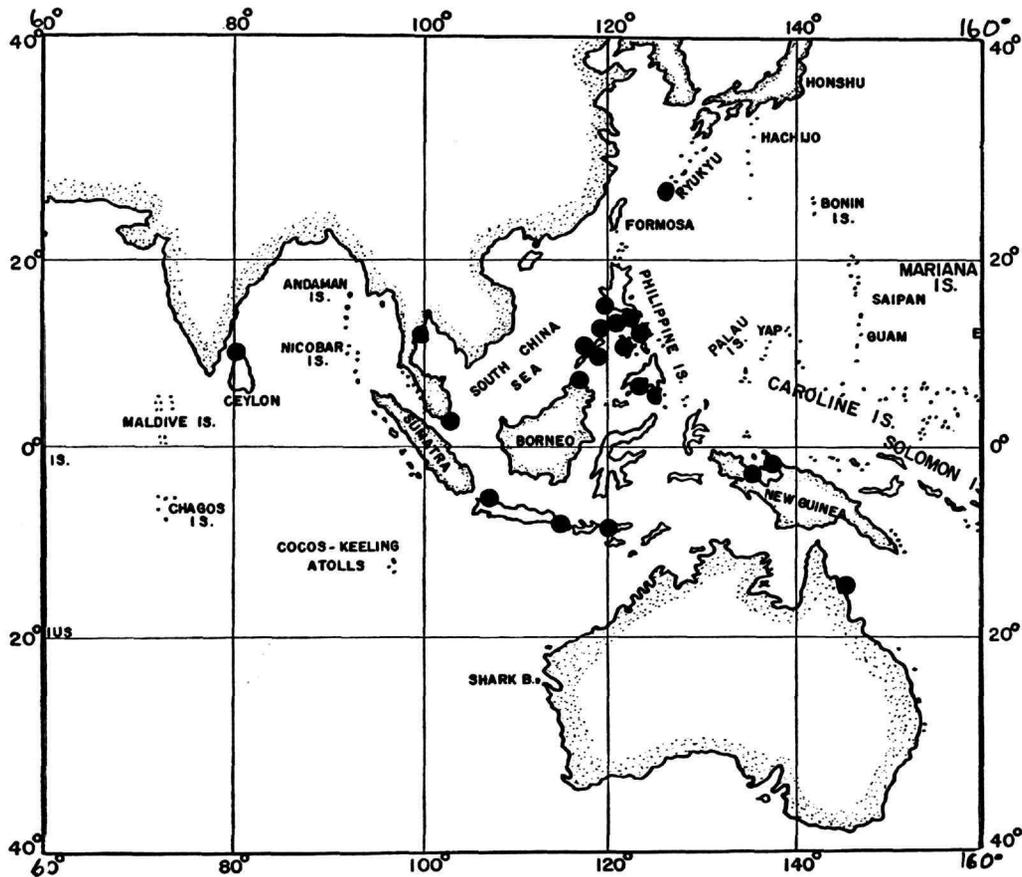


FIGURE 46.—Geographic distribution of *Clypeomorus irrorata* (Gould, 1849), new combination.

uanga, Bintnan Id, Calamian Gp (USNM 233014); Coron, Bintuan Id, Calamian Gp (USNM); Puerto Princessa, Palawan (ANSP 224591, 272422); Bolalo Bay, Palawan (USNM 243689, 243692); Tagbayug Bay, Palawan (USNM 244186, 244189); Ulugan Bay near Caiholo River, Palawan (USNM 239915, 243945); Malcochin Harbor, Linapacan Id, Palawan (USNM 243857, 243858); Estero Pt, Sablayan Bay, Mindoro (USNM 232839); Tilik, Lubang Id (USNM 229917); Catbalogan, Samar (USNM 232951); San Pascual, Burias (USNM 239950); Guiljungan, Negros (USNM 232854, 24405); Enrique Villanueva, Siquijor Id (USNM 774492); Mactan Id, Cebu (USNM 244038); Malabayoc, Cebu (USNM 774586, AMNH

121935, CAS 39494); 12 km N Cebu at Tayud, Cebu (UF 30347); Sarangani Id, Sarangani Bay, Mindanao (USNM 233131); 22 km N Lupou, Tagdado, Banay, Banay Dist, Mangapa Bay, Davao, Mindanao (UF 30567); Malabang, Mindanao (USNM 233143); Tictauan Id, Mindanao (USNM 243829). RYUKYU ISLANDS: Shioya, Shanawan Bay, Okinawa (USNM 774500); Oshima, Osumi (USNM 343866).

Clypeomorus admirabilis, new species

FIGURES 47-49

DESCRIPTION.—*Shell* (Figure 47; Table 28): Shell turreted, moderately elongate with teleoconch of 8 or 9 angulate, inflated whorls having

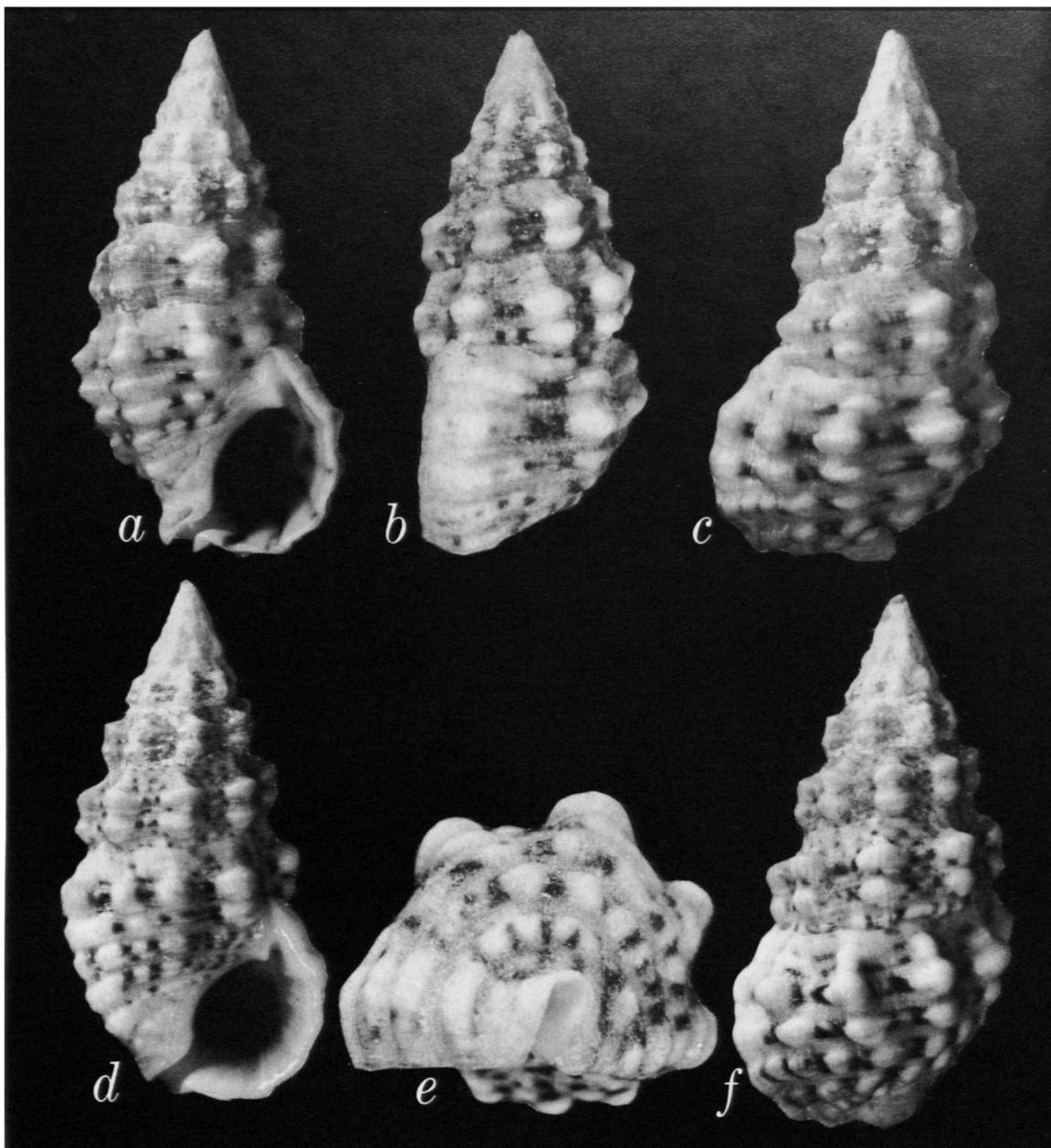


FIGURE 47.—*Clypeomorus admirabilis*, new species, showing variation in shell sculpture (all specimens from type lot, False Cape Creek, 100 mi (161 km) S of Broome, Western Australia): *a-c, e*, ANSP 233431 (20 × 11 mm); *d, f*, holotype, WAM 3346-83 (24.4 × 11.7 mm); *b, e*, ANSP 233431, lateral and anterior views (20 × 11 mm).

TABLE 28.—Analysis of shell parameters of *Clypeomorus admirabilis*, new species (measurements in mm).

Character (n=25)	\bar{x}	sd	Range
Shell length	22.03	2.76	16.40–26.25
Shell width	10.93	1.47	7.95–12.78
Aperture length	6.34	0.65	5.2–7.6
Aperture width	5.02	0.54	3.95–5.95
No. axial ribs on penultimate whorl	8.88	0.97	7–10

Length/width index: 2.02

Shell length/aperture length index: 3.47

an apical angle of 40 degrees. Shell reaching 26.3 mm in length (not on Table 28). Teleoconch whorls have broad subsutural ramp below which are 2 (rarely 3) distinct, thickened, nodose spiral cords. Nodes somewhat spinose, sometimes reduced and blunt, aligned to form about 9 distinct axial ribs per whorl. Entire shell covered with fine microscopic spiral threads and weak, broad, axial ribs that are absent on earliest whorls. Early whorls usually badly eroded, even in immature specimens. Suture distinct, wavy. Body whorl large, angulate, sculptured with 5 or 6 nodose spiral cords and 8 or 9 angulate, axial ribs. Large varix present opposite outer lip and at edge of outer lip of aperture. Ventral side of body whorl flattened and base constricted at siphon. Slight siphonal fasciole present. Aperture ovate, a little less than one-third the shell length. Anterior siphonal canal short, deep, and deflected to left at a 45 degree angle to shell axis. Anal canal distinct, bordered with columellar fold that extends well within shell aperture. Columella concave with moderate parietal callus. Outer lip weakly crenulate, thick, bearing varix. Inner surface of outer lip beveled and with four pairs of spiral plications. Outer lip extends slightly onto penultimate whorl. Plane of outer lip parallel to shell axis. Periostracum thin, yellowish, usually eroded on upper whorls. Shell color white to yellow-tan and usually with spiral bands of brown quadrate spots between nodes. Shell sometimes lacking spots, nodes usually white or light colored. Operculum thin, tan,

corneous, ovate and with nucleus near edge. Attachment scar elongate, on lower half of obverse of operculum.

Radula (Figure 48): Radular ribbon long, a little less than one-third the shell length and comprising 126 rows of teeth in shell 25 mm long. Shell length/radula length index 2.8. Rachidian tooth (Figure 48d) pentagonal, about 64 μm wide and as high as wide. Basal plate of rachidian tooth flat, slightly pointed at base; sides straight with thin lateral buttresses on each side. Top of rachidian tooth straight, cutting edge with broad, chisel-shaped, straight-edged central cusp flanked on each side by single blunt tiny denticle. Basal plate of lateral tooth (Figure 48c) has long, twisted, lateral projection that inserts onto radular membrane and large, downward directed median buttress. Cutting edge of lateral tooth has single large, wide, spoon-shaped cusp flanked by a tiny blunt denticle on each side; denticles nearly fused to large central cusp. Lateral extension of basal plate with slight baffle directly adjacent to cutting edge of lateral tooth. Marginal teeth (Figure 48a,b) long, having wide shafts and spatulate curved tips; narrow at bases where inserted onto radular membrane. Tips of marginal teeth with large spoon-shaped cusps having single tiny inner denticles. Outer edges of marginal teeth smooth.

Animal: Not known.

HOLOTYPE.—WAM 3346-83, 24.4 mm length, 11.7 mm width (Figure 47d,f).

PARATYPES.—USNM 784652, 7 specimens; ANSP 233431, 38 specimens; AMS 139779, 3 specimens.

TYPE-LOCALITY.—In sand and rock, 182 meters up False Cape Creek, 100 mi (161 km) S of Broome, Western Australia, 16 Sep 1958, Virginia Orr, coll.

ETYMOLOGY.—From the Latin adjective *admirabilis*, -e (wonderful, admirable), referring to the beautiful sculpture and color.

ECOLOGY.—There is virtually no ecological data accompanying museum specimens of this species. Field records from the Broome area indicate that *Clypeomorus admirabilis* lives on

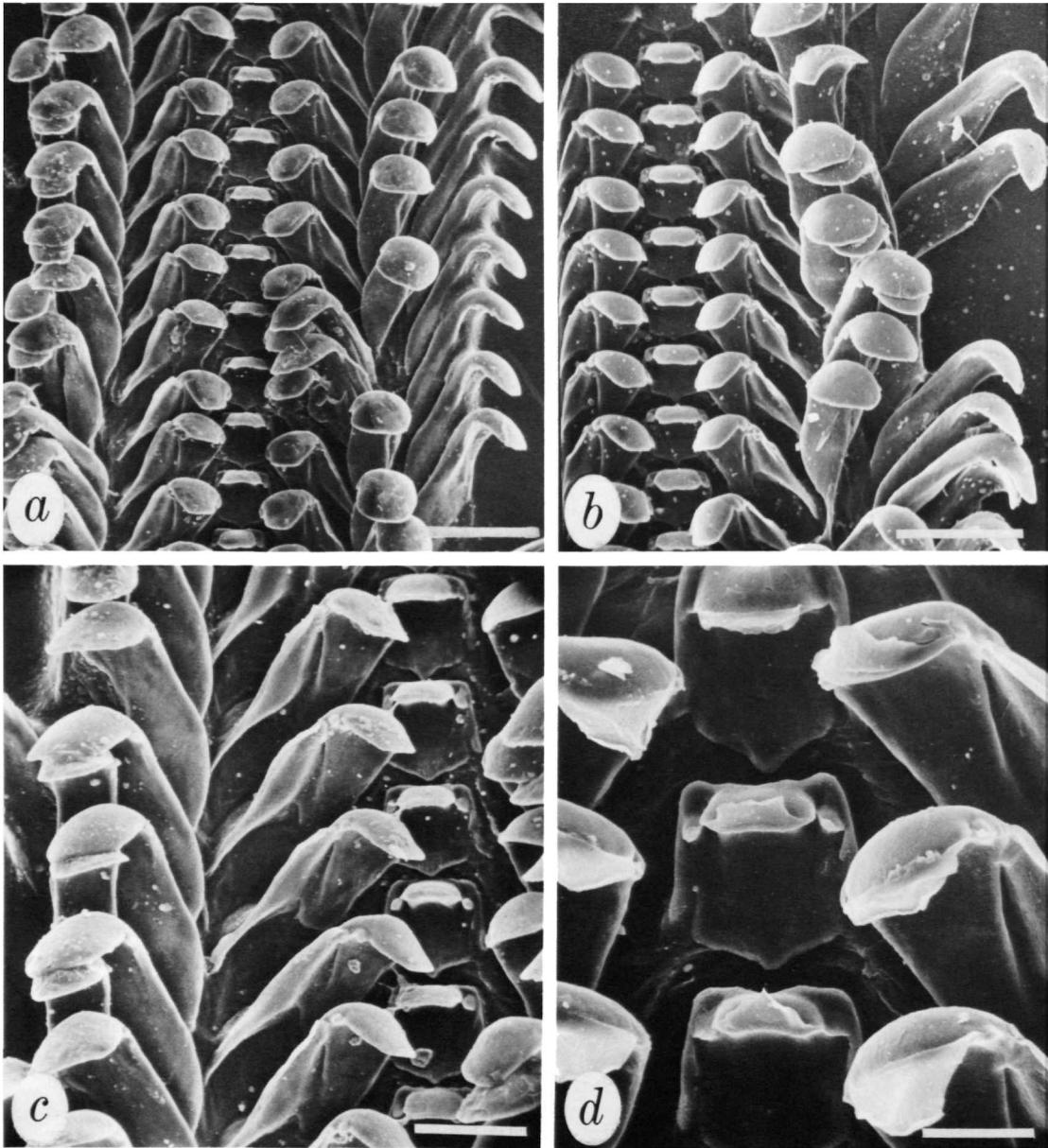


FIGURE 48.—SEM micrographs of radula of *Clypeomorus admirabilis*, new species, from False Cape Creek, 100 mi (161 km) S of Broome, Western Australia, ANSP 233431: *a*, radular ribbon with marginal teeth folded back revealing general aspect of radular teeth (bar = 150 μm); *b*, *c*, detail of half-row of teeth showing cusps on rachidian and lateral teeth; note spoon-like cusps and near lack of denticles on tips of marginal teeth (bars = 150 μm and 75 μm , respectively); *d*, detail of rachidian tooth showing elongate basal plate (bar = 40 μm).

sandy rubble in intertidal flats near mangroves, on muddy flats around Buccaneer Rock, and at the mouth of tidal creeks. This kind of intertidal habitat is typical for most *Clypeomorus* species. Eggs and larvae are unknown, but the limited geographic range suggests lecithotrophic development.

The spoon-shaped cusps on the lateral and marginal teeth may indicate a scraping, shoveling function on soft substrate.

DISCUSSION.—This unusually knobby species occurs within a limited range in northwestern Australia. It is easily recognized by distinctive sculpture of two large spiral cords bearing large nodes that form distinct axial ribs and by its color pattern of brown quadrate spiral spots on a white-yellow background. Color is variable, some morphs being nearly devoid of brown spots. In immature specimens, the early whorls are sculptured with spiral incised lines and threads and the axial ribs usually do not appear until the fifth whorl. In some specimens, the large nodes are reduced. The color pattern of some sympatric morphs of *Clypeomorus bifasciata* (Figure 11j,l,n) closely resembles that of *Clypeomorus admirabilis*. *Clypeomorus bifasciata*, however, differs in having three spiral beaded cords and more axial ribs per whorl. It is easily distinguished from *Clypeomorus admirabilis* by its overall beaded aspect. Some morphs of *Clypeomorus irrorata*, in which the normally broad smooth axial ribs are more fully plicate and smoothly nodose (Figure 44f), may also be confused with *Clypeomorus admirabilis*, but the former generally have more axial ribs per whorl.

The sculpture and color pattern of *Clypeomorus admirabilis* closely resemble those of the more rugose morphs of *Clypeomorus brevis* (Quoy and Gaimard), but the former species differs in having more nodose cords per whorl and a sub-sutural ramp. Moreover, these two species are allopatric in their distributions and have radulae that are quite different from one another.

The radula of *Clypeomorus admirabilis* is distinctive in that the large spoon-shaped cusps on the lateral and marginal teeth are developed to such

a degree that they nearly obliterate the smaller denticles on those teeth. The rachidian tooth is distinguished by its length and squarish shape due to the flat upper surface and very flat basal plate. The radula most closely resembles that of *Clypeomorus irrorata*, but differs from that species chiefly by the lack of a deep concave depression on the top of the tooth. The radula of *Clypeomorus admirabilis* also bears some similarity to that of *Clypeomorus subbrevicula* and less so to *Clypeomorus adunca*. The shell, sculpture, and radula suggest a close relationship between *Clypeomorus admirabilis* and *Clypeomorus irrorata*. The two species are geographically separated, the former being confined to northwestern Australia.

FOSSIL RECORD.—No fossils are known.

GEOGRAPHIC DISTRIBUTION (Figure 49).—*Clypeomorus admirabilis* is confined mainly to the northwest coast of Western Australia, but it is also known from the Northern Territory. It has one of the most restricted ranges of any *Clypeomorus* species.

MATERIAL EXAMINED.—WESTERN AUSTRALIA: Malay Bay (AMS); Swan Id (AMS); Balgin Creek, Cape Leveque (NMV); 182 m up False Cape Creek, 100 mi (161 km) S of Broome (ANSP 233431); Willy Creek, Broome (NMV); Buccaneer Rock, Broome (ANSP 232850, 232939); Roebourne (NM G4935); 7 mi S of

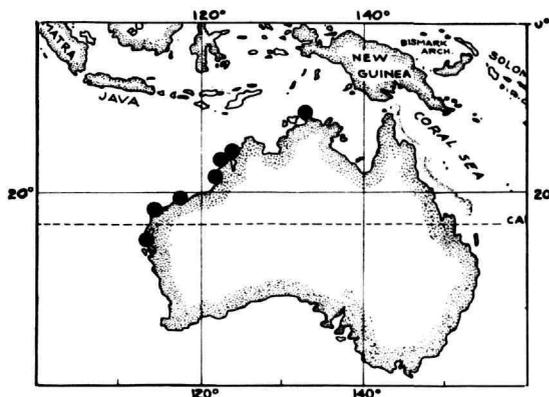


FIGURE 49.—Geographic distribution of *Clypeomorus admirabilis*, new species, in Australia.

Exmouth, Exmouth Gulf (AMS); Carnarvon (NM G3880). NORTHERN TERRITORY: Malay Bay (AMS).

Clypeomorus subbrevicula (Oostingh)

FIGURES 50–52

Cerithium breviculum Sowerby, 1834:213, unnumbered pl. fig. 1 [type material not found, Sowerby's fig. 1 here selected to represent lectotype; type-locality: Philippines; not *Cerithium breviculum* Deshayes, 1833].—Kiener, 1841–1842:53–54, pl. 15: fig. 4.—Sowerby, 1855:869, pl. 181: fig. 143; 1865, pl. 7: fig. 46.—Tryon, 1887:132, pl. 23: fig. 18.—Martens, 1897:174.—Kobelt, 1898:245, pl. 42: fig. 18.

Cerithium humile Dunker, varietas [sic].—Lischke, 1875:50, pl. 3: figs 19, 20 [in part].

Cerithium subbreviculum Oostingh, 1925:45 [new name for *Cerithium breviculum* Sowerby, 1834].

Clypeomorus subbreviculus (Oostingh).—Shirai, 1977:275.

DESCRIPTION.—*Shell* (Figure 50; Table 29): Adult shell stocky, short, and thick with overall rounded ovate shape, and reaching 28 mm in length (not included in Table 29). Teleoconch comprising 8 or 9 inflated whorls that have an apical angle of about 50 degrees. Length/width index 1.72. Whorls rounded, with subsutural ramp below, which consists of 2 major beaded spiral cords. Whorls sculptured with numerous incised spiral lines and smaller spiral cords that are usually beaded. Subsutural spiral cord has many small axial plications. Fine axial incised lines give overall scaly appearance to shell. Beads of 2 major spiral cords elevated, sometimes pointed, and aligned to form 12 or 13 axial ribs limited to lower part of each whorl. No varices present. Suture deeply impressed, wavy. Protoconch unknown. Early postnuclear whorls usually badly eroded or missing. When present, early whorls sharply tapered, straight-sided, presenting concave appearance and sculptured with 2 smooth spiral cords. Body whorl very large, inflated and rounded, constricted at base and with slight siphonal fasciole. Apertural side of body whorl rounded. Body whorl sculptured with 6 or 7 beaded spiral cords. Beads drawn out spirally and aligned to form axial ribs. Aperture large,

TABLE 29.—Analysis of shell parameters of *Clypeomorus subbrevicula* (measurements in mm).

Character (n=31)	\bar{x}	sd	Range
Shell length	20.25	3.13	14.52–25.61
Shell width	11.77	1.57	9.14–14.95
Aperture length	8.00	1.28	6.05–10.65
Aperture width	6.00	0.91	4.57–7.55
No. beads on spiral cord of penultimate whorl	13.10	2.20	10–16

Length/width index: 1.72

Shell length/aperture length index: 2.53

ovate, a little less than half the shell length. Shell length/aperture length index 2.53. Anterior siphonal canal short, deep, and at 65 degrees angle to left of shell axis. Anal canal deeply incised, bordered with columellar fold that extends well into shell aperture. Columella concave with thick parietal callus and distinct columellar lip. Outer lip rounded, thick, moderately crenulate, with beveled inner surface bearing numerous spiral plications. Parietal portion of outer lip in line with suture, not extending onto penultimate whorl. Plane of outer lip parallel to shell axis. Periostracum thin, usually eroded. Shell color dirty gray or brown with black or brown beads. Aperture and columella white. Operculum sub-circular, thin, corneous, and paucispiral with eccentric nucleus near opercular edge. Attachment scar elongate, limited to bottom portion of operculum.

Radula (Figure 51; Table 30): Radular ribbon long, a little less than one-third the shell length, comprising 140 rows of teeth in snail 21 mm long. Shell length/radula length index 2.94. Rachidian tooth (Figure 51c) pentagonal, about 33 μ m wide. Base of rachidian tooth triangular with central pointed buttress that slightly overhangs tooth base. Central buttress with a tiny pointed projection flanking each side. Sides of rachidian tooth straight, top concave. Cutting edge of rachidian tooth has large spade-shaped central cusp flanked on each side by one tiny blunt denticle. Lateral tooth (Figure 51b,c) large, rhomboidal, with long twisted basolateral projec-

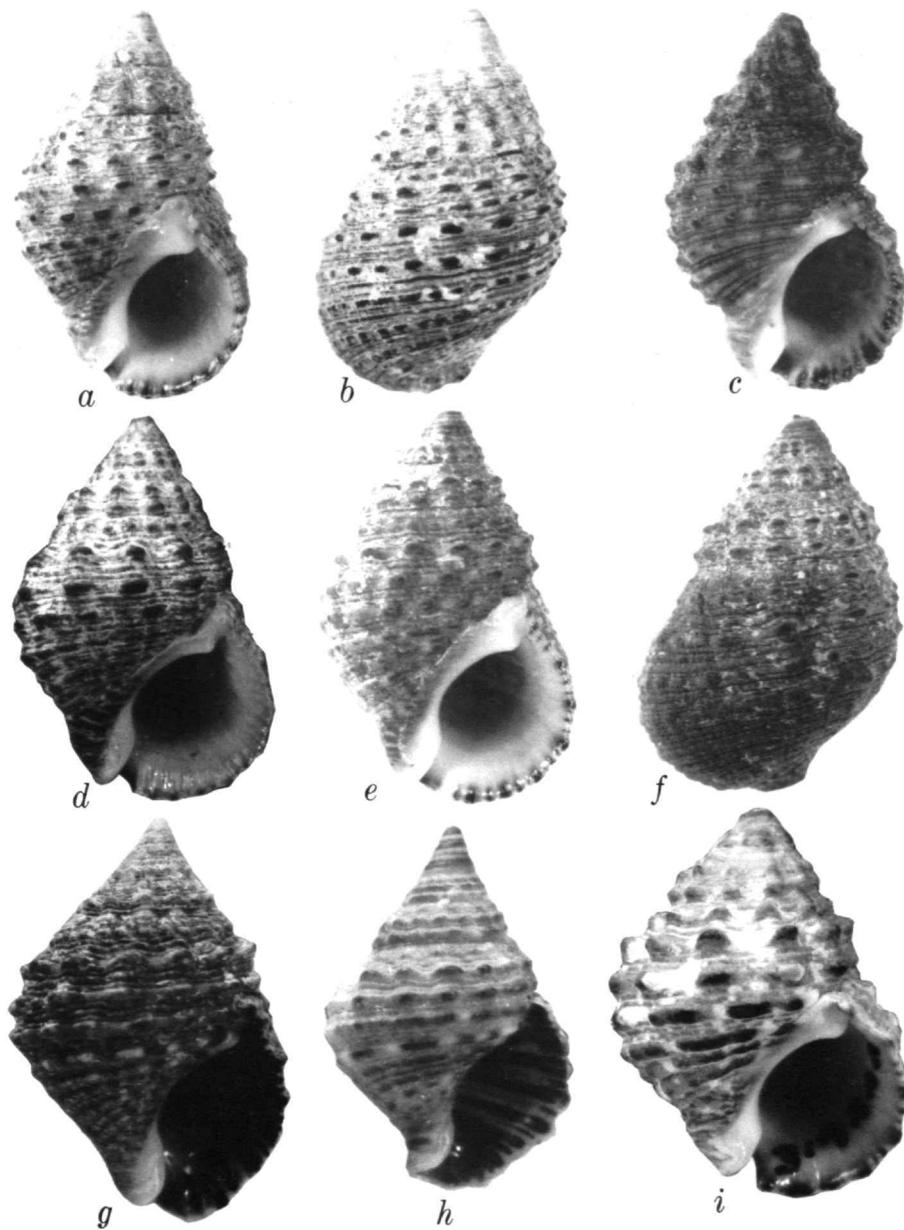


FIGURE 50.—*Clypeomorus subbrevicula* (Oostingh, 1925), showing variation in shell form and sculpture: *a, b*, Mansalay River, Mindoro, Philippines, MCZ no number (24.2×13.5 mm); *c, d*, same locality as above (22.9×3.4 mm); *e, f*, lectotype of *Cerithium breviculum* Sowerby, 1834, BMNH 1904.10.28.152 (24.2×13.9 mm); *g, h*, immature specimens from Cabcaben, SE Bataan, Luzon, Philippines, ANSP 229745 (16.5×10.5 mm; 7.6×4.5 mm, respectively); *i*, stocky morph from Indonesia, ANSP 319225 (20×13.5 mm).

TABLE 30.—Analysis of radular parameters of *Clypeomorus subbrevicula* (measurements in mm).

Character (n=10)	\bar{x}	sd	Range
Radula length	7.00	0.55	6.15–7.81
No. of teeth	139.90	7.78	125–153
Shell length	20.61	1.91	16.73–23.49

Shell length/radula length index: 2.94

tion that inserts onto radular membrane. Basal plate of lateral tooth has long semimedial buttress-like projection that extends ventrally. Top of lateral tooth straight, bearing broad, chisel-like central cusp that is flanked on inner side by single tiny pointed denticle and on outer side by 2 small pointed denticles. Where outer denticle ends, basal plate extends dorsally and is slightly reflected to form large flange. Marginal teeth (Figure 51*d*) long, curved, having broad shafts with tapered bases, and curved spatulate tips. Tip of inner marginal tooth bearing wide central cusp flanked on each side by single tiny pointed denticle that is almost fused to central cusp. Outer marginal tooth same, only lacking outer denticle.

Animal: Preserved animal gray with black spots and lines. Mantle edge has thick white papillae. Semicircular jaws about 0.5 mm long. Buccal mass large. Internal anatomy unknown.

REMARKS.—This species is best known as *Cerithium breviculum* Sowerby, 1834 (Figure 50*e*), but that name is unavailable as Deshayes (1833) had earlier used it for a fossil species. Oostingh (1925) proposed a new name, *Cerithium subbreviculum*, for Sowerby's taxon, and Shirai (1977: 275) was the first to refer the species to *Clypeomorus*. A manuscript name of Pilsbry, "*oshimanum*," appears on labels of some museum specimens, but this name was never published and is not listed in the catalogue of Pilsbry's taxa published by Clench and Turner (1962). Lischke's (1875:50) plate 3: figures 19, 20 are not varieties of *Cerithium humile* Dunker but represent *Clypeomorus subbrevicula*.

ECOLOGY.—This species lives on hard substra-

tum in the intertidal zone. The obese thick shell with large aperture is well suited to high energy habitats and exposure at low tides when the animal clings tightly to rocks. Although it appears to be common, little is known about its biology. The protoconch is unknown and no information exists about spawn, eggs, or developmental biology. The long radular ribbon suggests that it grazes on coarse substrata. Fecal pellets from preserved animals comprise small detrital particles and sand grains. Several specimens examined had drill holes on their upper whorls of the kind produced by muricid gastropods (Yochelson and Carriker, 1968).

DISCUSSION.—*Clypeomorus subbrevicula* is easily recognized by its stocky obese shape, lack of varices, sculpture of spiral beaded whorls, and wide aperture (Figure 50). It has one of the longest radulae of all *Clypeomorus* species, although the shell length/radula length index is low due to the short shell. It closely resembles *Clypeomorus inflata* in obesity but that species is much more angular in appearance due to its varices (see remarks under *Clypeomorus inflata* for a more detailed comparison, p. 92). The only other species with which *Clypeomorus subbrevicula* may be confused is *Clypeomorus bifasciata* (Sowerby). Although these two species are sympatric, *Clypeomorus subbrevicula* differs in having more inflated rounded whorls, a subsutural ramp, and two dominant spiral beaded cords per whorl. It also lacks the two prominent varices present on the right and left sides of the shell of *Clypeomorus bifasciata*.

This species varies considerably in shell sculpture. Although the general pattern of sculpture remains the same, in some populations, certain sculptural elements are more emphasized than others, and these appear to correlate with geography. For instance, most specimens from the Philippines have a low relief sculpture of weak axial ribs and narrow spiral cords bearing many small beads. Some specimens from this area have more stronger spiral cords with spiny beads, and the axial ribs on the body whorl are more prominent (USNM 233073, 243709, 243902). Spec-

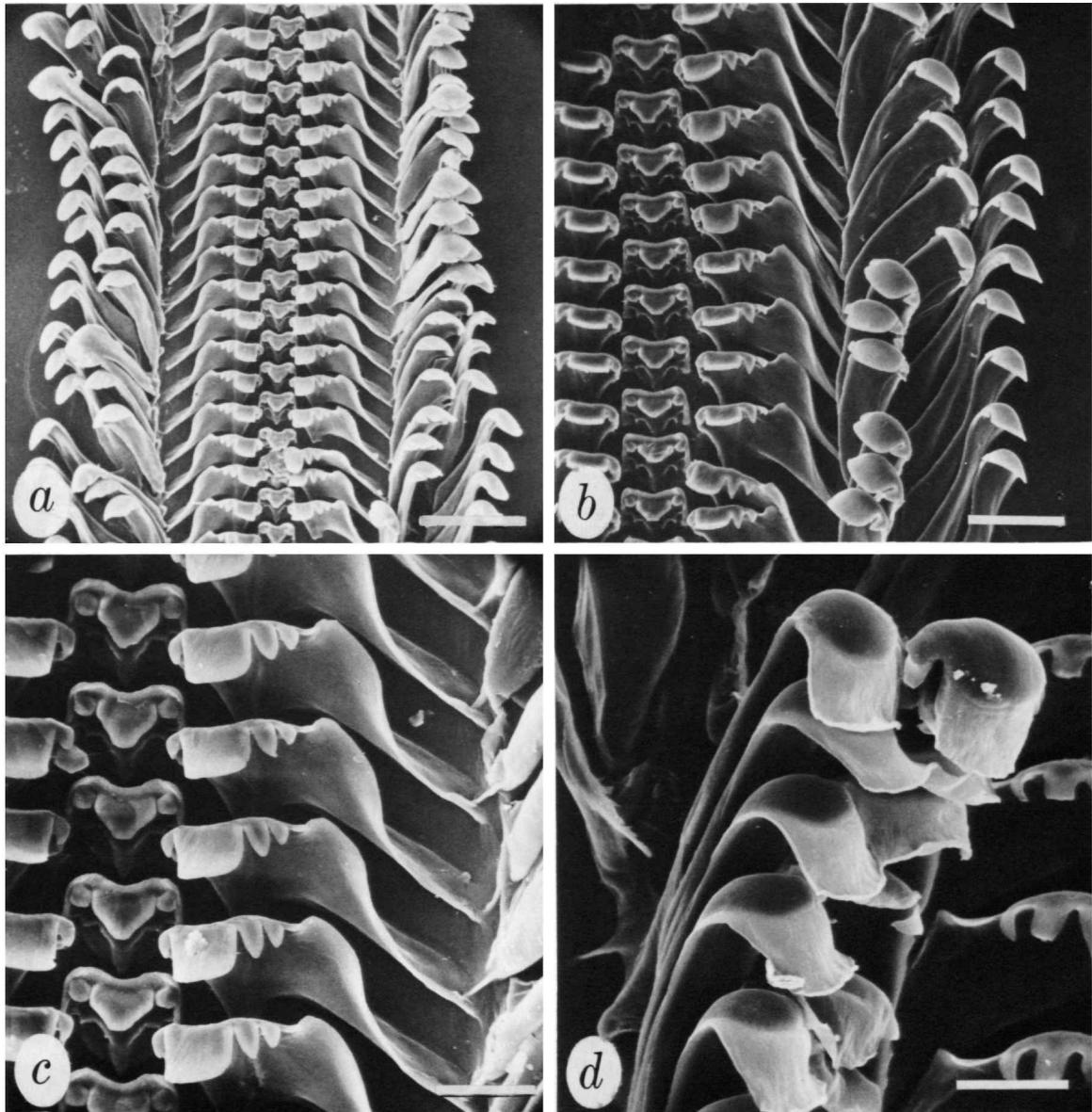


FIGURE 51.—SEM micrographs of radula of *Clypeomorus subbrevicula* from 18 km N of Touho, New Caledonia, ANSP 270416: *a*, radular ribbon with marginal teeth folded back to expose lateral and rachidian teeth (bar = 104 μm); *b*, half-row of radula showing inner and outer marginals (bar = 61 μm); *c*, detail of rachidian and lateral teeth showing basal plate of rachidian and basolateral extension of lateral teeth (bar = 29 μm); *d*, view of marginal teeth showing broad spoon-like tips (bar = 25 μm).

mens from Indonesia have fewer beads and are extremely stocky (USNM 233015; ANSP 319225) (Figure 50i). Populations from New Caledonia comprise individuals that have strong axial ribs and the beads on the spiral cords tend to be drawn out spirally. These specimens (USNM 664677, 724822) have a more sharply defined subsutural ramp. Specimens from Japanese Islands have weak sculpture and tend to be more elongate. These are general geographic trends and are based on qualitative observations. More material is needed for analysis before the trends described above may be called clinal.

FOSSIL RECORD.—To my knowledge, this species has not been recorded as a fossil.

GEOGRAPHIC DISTRIBUTION (Figure 52).—*Clypeomorus subbrevicula* appears to be confined to the western Pacific where it ranges from south-

ern Japan south to New Caledonia and the New Hebrides. It is most common in the Philippines and the Indonesian archipelago. The one record from India appears to be reliable, but more specimens from this area need to be examined to confirm its presence in the eastern Indian Ocean.

MATERIAL EXAMINED.—INDIA: Waltair (USNM). INDONESIA: (ANSP 319225); Keledjitan, Bantam, Java (USNM 260543); Wynkoopsbaai, Java (ZMA); Bali (AMS); Uki, Buru Id, Moluccas (USNM 233015); Morotai, Halmahera Group, Moluccas (USNM 542545, 542541); Gulf of Ende, Flores (ZMA); Maumere, Flores (UF 24766); Timor (ZMA); Taganac Id, Borneo (USNM 243940, 243944). NEW GUINEA: Huron Gulf (USNM 487915); Dogura, near Milne Bay (AMS); Rabaul, New Britain, Bismark Archipelago (AMS); Kavieng, lower archipelago,

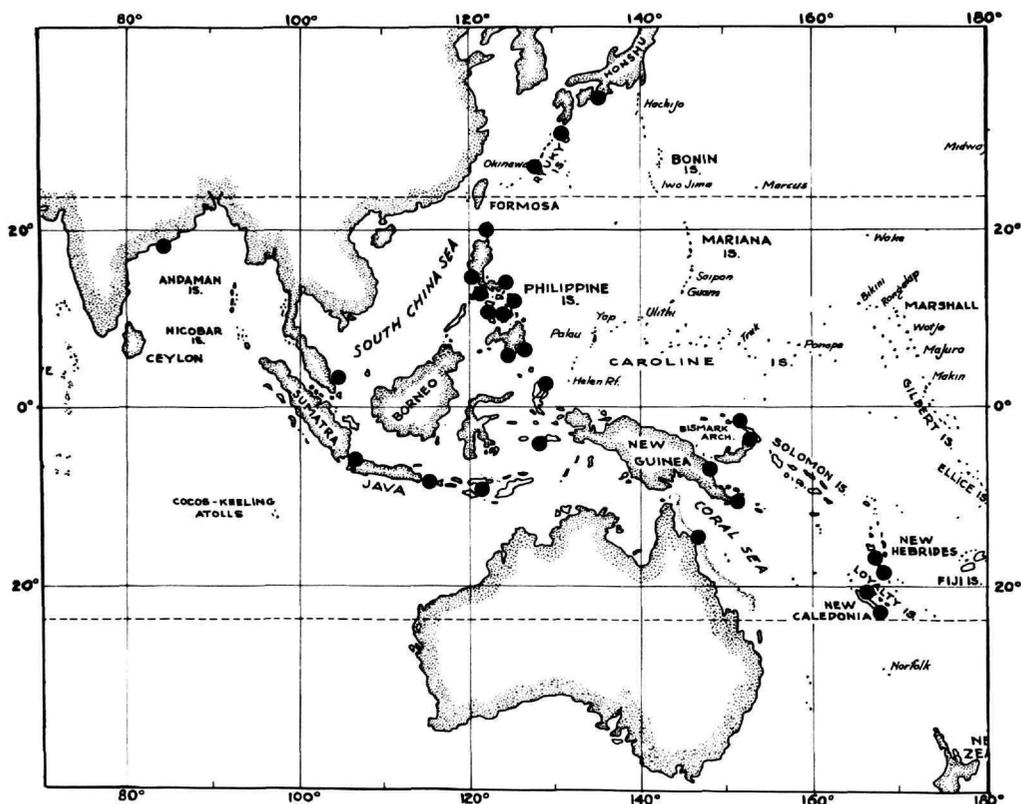


FIGURE 52.—Geographic distribution of *Clypeomorus subbrevicula* (Oostingh, 1925).

New Ireland (ANSP 185279). NEW HEBRIDES: Eromanga (AMS); N coast, Efate (AMS). AUSTRALIA: Hartley's Creek, N Queensland (AMS). NEW CALEDONIA: Poindimie (AMS); near Kunie, Port Kuto, Île des Pins (AMS); E of Prony Village, Prony Bay, (USNM 724822, 724865); SW of old mine wharf, N side N'go Bay (USNM 664678, 664677); Thio (ANSP 238385); 18 km N of Touho (ANSP 270416); Port Ngea, Magenta Station, Nouméa (ANSP 271133). RYUKYU ISLANDS: Osima, Osumi (USNM 343868, 488034); Okinawa (USNM 774531, 671091); Metasaki Bay, Okinawa (LACM 7332, 27653, 29937); Amamioshima (USNM 669825); Nase, Oshima Id (ANSP 363740); Metasaki Reef, Okinawa (ZMA; LACM 72023; Gushiken-wan, 3½ mi (5.6 km) E Bisezaki, Okinawa (LACM 77-58). PHILIPPINES: Sabtang Id, Batanes Group (USNM 243917); Port Pio V., Camiguin Id, Babuyan Group (USNM 233073, 233074, 243709, 243710); Subic Bay, Luzon (USNM 593855); W shore, Subic Bay, Luzon (USNM 543334); Port Binang, Subic Bay, Luzon (USNM 243717); Jamilo Bay, Luzon (USNM 243950, 243952, 774574); Mariveles Bay, Luzon (USNM 239784); W coast Palaui Id, Luzon (USNM 232923, 243711); Nasugbu, Luzon (USNM 232859); Besogo, Luzon (USNM 232907); Dagupan, Luzon (USNM 232843); Eman Pt, Morong, Bataan, Luzon (USNM 774758); Napot Pt, Bataan, Luzon (USNM 774680); Cabcaben, SE Bataan, Luzon (ANSP 229745, DMNH 2719); N shore, Ft Mills, Cavite, Luzon (USNM 472941); Villa Carmen, Bataan, Luzon (LACM 89036); Tabgayag Bay, Luzon (USNM 244192); Mansalay River, Mindoro (MCZ); Gigmoto, Catanduanes Id (ANSP 223149); Cabugao River (USNM 232880); Guiulugan, Negros (USNM 232853, 232856, 244055, 44047); mouth of Siaton River, Siaton, Negros Oriental (USNM 598124); E side Jagbolaran Strait, Bohol (USNM 244084); Gajoagan Id, off N Samar (USNM 233203); Taliray, Cebu (USNM 774563); N Cebu at Tayud, Cebu (UF 30348); Capanuyugan Pt, Mindanao (USNM 243890); Bali, Pujado Bay, Mindanao (USNM

243902); Sarangani Bay, Mindanao (USNM 233128).

***Clypeomorus adunca* (Gould),
new combination**

FIGURES 53–55

Cerithium aduncum Gould, 1849:119 [holotype: USNM 5567; type-locality: Mindanao, Philippines]; 1852:147; 1856, pl. 10: fig. 167a,b; 1862:61, 245.—Sowerby, 1865, pl. 9: fig. 57.—Tryon, 1887:139, pl. 26: figs. 96, 97.—Kobelt, 1895:186, pl. 34: fig. 8.—Schepman, 1909: 162.—Johnson, 1964:38.

Cerithium dorsuosum A. Adams in Sowerby, 1855:867, pl. 181: figs. 130–140 [lectotype, here selected, BMNH, not registered; type-locality: Misamis, Mindanao, Philippines; not *Cerithium dorsuosum* Menke, 1828]; 1865, pl. 9: fig. 56a,b.—Tryon, 1887:139, pl. 26: fig. 97.—Kobelt, 1893: 103–104, pl. 20: figs. 9–10.

DESCRIPTION.—*Shell* (Figure 53; Table 31): Adult shell thick, turreted, moderately elongate, reaching 17.5 mm in length, with teleoconch of 6 or 7 whorls having apical angle of 30 degrees. Length/width index 2.01. Adult whorls nearly straight sided, smooth overall, but incised with numerous fine spiral lines. Former varices present, prominent varix on dorsal surface of body whorl. Body whorl inflated, flattened on aperture side. Aperture ovate, nearly one-fourth the length of the shell. Anterior siphonal canal short, straight, and deep. Columella concave with slight callus. Anal canal deep, defined by posterior columellar plait, and extending posteriorly onto penultimate whorl. Outer lip thick and smooth,

TABLE 31.—Analysis of shell parameters of *Clypeomorus adunca* (measurements in mm).

Character (n=15)	\bar{x}	sd	Range
Shell length (last 3 whorls)	15.4	2.05	11.01–19.90
Shell width	8.67	0.93	6.67–10.05
Aperture length	8.38	1.03	5.65–9.75
Aperture width	3.93	0.59	2.75–4.65

Length/width index: 2.01

Length/aperture length index: 2.09

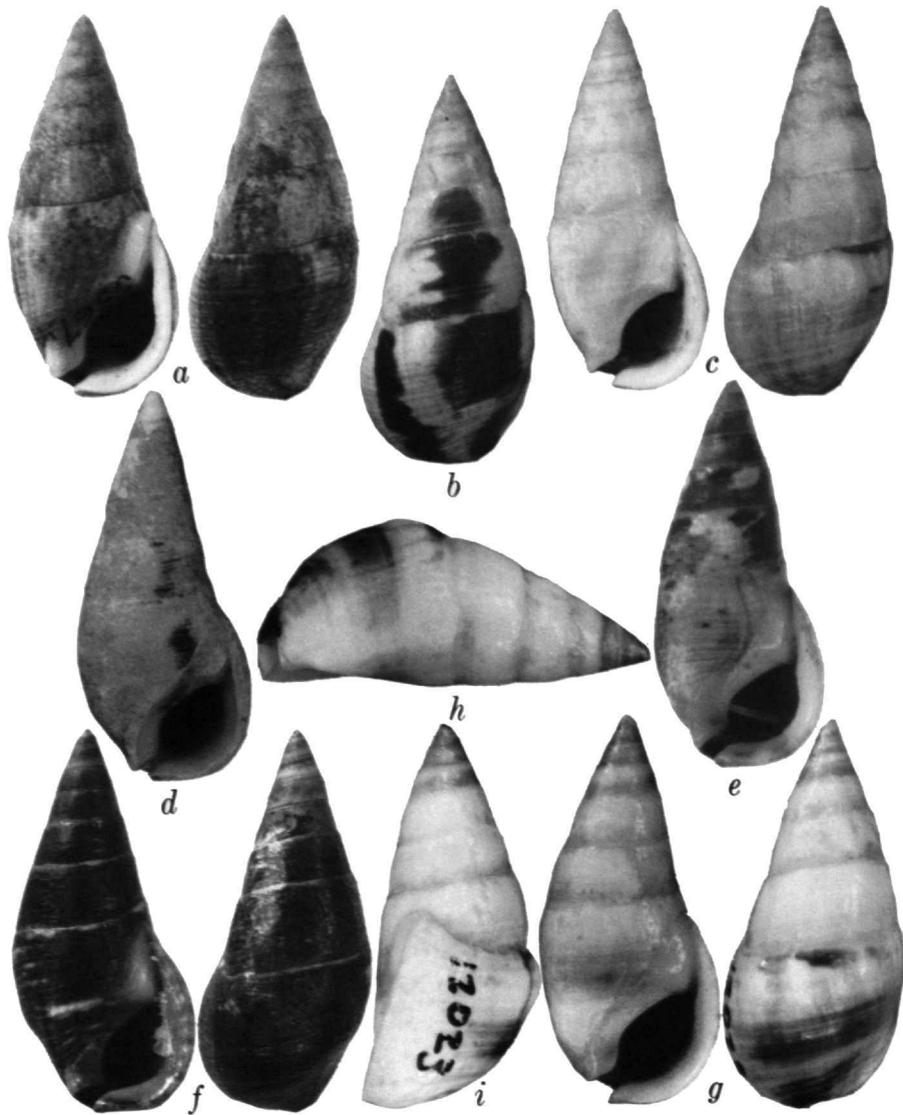


FIGURE 53.—*Clypeomorus adunca* (Gould, 1849) showing types of taxa synonymous with it and variation in form and sculpture of shells from different localities: *a*, holotype of *Cerithium aduncum* Gould, 1849, USNM 5567, Mindanao, Philippines (24.3 × 10.4 mm); *b*, lectotype of *Cerithium dorsuosum* A. Adams, 1855, BMNH, no number, figured by Sowerby (1855, pl. 181: fig. 140), from Corregidor, Manila Bay, Luzon, Philippines; *c*, paratype of *Cerithium dorsuosum* A. Adams, 1855, BMNH, no number, figured in Sowerby (1855, pl. 181: fig. 139); *d*, *e*, specimens from Siboga Expedition, Sta 50, Badjo Bay, Flores, Indonesia, ZMA, no number (27 × 10 mm; 24 × 9.7 mm, respectively); *f*, paratype of *Cerithium dorsuosum* A. Adams, 1855, BMNH, no number, figured in Sowerby (1855, pl. 181: fig. 38); *g*–*i*, specimen from Philippines showing various views of shell (17.5 × 7.9 mm).

but interiorly lirate. Outer lip extends nearly two-thirds over side of penultimate whorl. Plane of aperture tangential with shell and passes through the apex, giving shell distorted look and causing it to "bend" ventrally. Suture incised, distinct, and straight. Shell color white, variably blotched or striped with brown or gray; sometimes completely brown. Aperture normally white. Protoconch unknown. Periostracum not seen. Operculum thick, corneous, tan, ovate, and paucispiral with eccentric nucleus. Rugose attachment scar on lower half of obverse of operculum.

Radula (Figure 54): Radular ribbon tiny, fragile, and with 90 rows of teeth, in animal with shell length of 22 mm. Shell length/radula length index 5.81. Rachidian tooth (Figure 54*b,c*) pentagonal, about 30 μm wide. Top of rachidian tooth with sharp concave depression. Cutting edge has 1 large pointed median cusp flanked on each side with 2 blunt denticles. Basal plate of rachidian tooth flat with thin horizontal ridge at its center and with a small median pointed projection at its base. Lateral tooth (Figure 54*b,c*) rhomboidal with extremely long basolateral projection that tapers where it is inserted onto radular membrane. Top of lateral tooth flat, bearing large rounded central cusp flanked on each side by smaller pointed denticle. Basal plate of lateral tooth bearing median pointed projection. Marginal teeth (Figure 54*d*) long, spatulate with curved tips. Tip of inner marginal has a large spoon-shaped central median cusp flanked on inside by 2 smaller blunt denticles and on outside by single small denticle. Outer marginal identical but lacking outer denticle.

Animal: (This description is based on one poorly preserved animal and is not complete.) Animal cream colored except for dark brown snout and tentacles. Mantle papillae at inhalant siphon longer and darker. Under surface of inhalant siphon dark colored and wrinkled with longitudinal folds. Osphradium prominent. Ctenidium and hypobranchial gland brown. Kidney appears to consist of a single lobe. Buccal mass moderately large. Salivary glands not seen. Esophagus widens behind nerve ring to form

midesophageal gland that is lined with numerous thin finger-like lamellae. Stomach large, typically cerithioid, about 1.5 whorls in length. Fecal pellets ovate, arranged in transverse clusters in rectum and comprised of coarse sand grains and detrital particles. Distal two-thirds of medial lamina of pallial oviduct has shallow sperm gutter along its edge, which empties into a deep complex receptacle lying in the proximal half of the medial lamina. Receptacle walls have numerous longitudinal fine folds and the chamber is divided longitudinally by a thin wall of tissue that is free at one end and overlaps with another smaller longitudinal partition. This bifurcated arrangement is similar to that of other *Clypeomorus* species. Half of the chamber is probably the spermatophore receptacle and the other half the seminal receptacle. No duct leading from the chamber to the oviducal groove was seen. The bifurcation does not continue as the receptacle becomes a single chamber at its proximal end.

REMARKS.—The species was called *Cerithium dorsuosum* A. Adams (Figure 53*b,c*) by many early authors, but Tryon (1887), Kobelt (1895) and Schepman (1909) all considered that name to be synonymous with *Cerithium aduncum* Gould. After examination of the types, I concur with them.

ECOLOGY.—The only preserved specimens of this species I could obtain were those taken by the *Siboga* expedition. The shape of the shell seems to indicate that the animal lives on a hard substratum, perhaps on cobbles. The shell has a "bent" appearance when viewed laterally and would fit the contours of a rounded rock or cobble. The *Siboga* specimens were taken in Badjo Bay, but Schepman (1909:162) did not give exact ecological data. His statement, "up to 40 M. Mud, sand and shells," indicates that they were recovered in a dredge haul. I believe, however, that this species probably lives in the intertidal or shallow subtidal zone on a relatively hard substratum. The short radula would indicate that it eats fine particles, but coarse sand grains and large forams found in the gut indicate otherwise. The eggs and larvae are unknown.

DISCUSSION.—*Clypeomorus adunca* has a

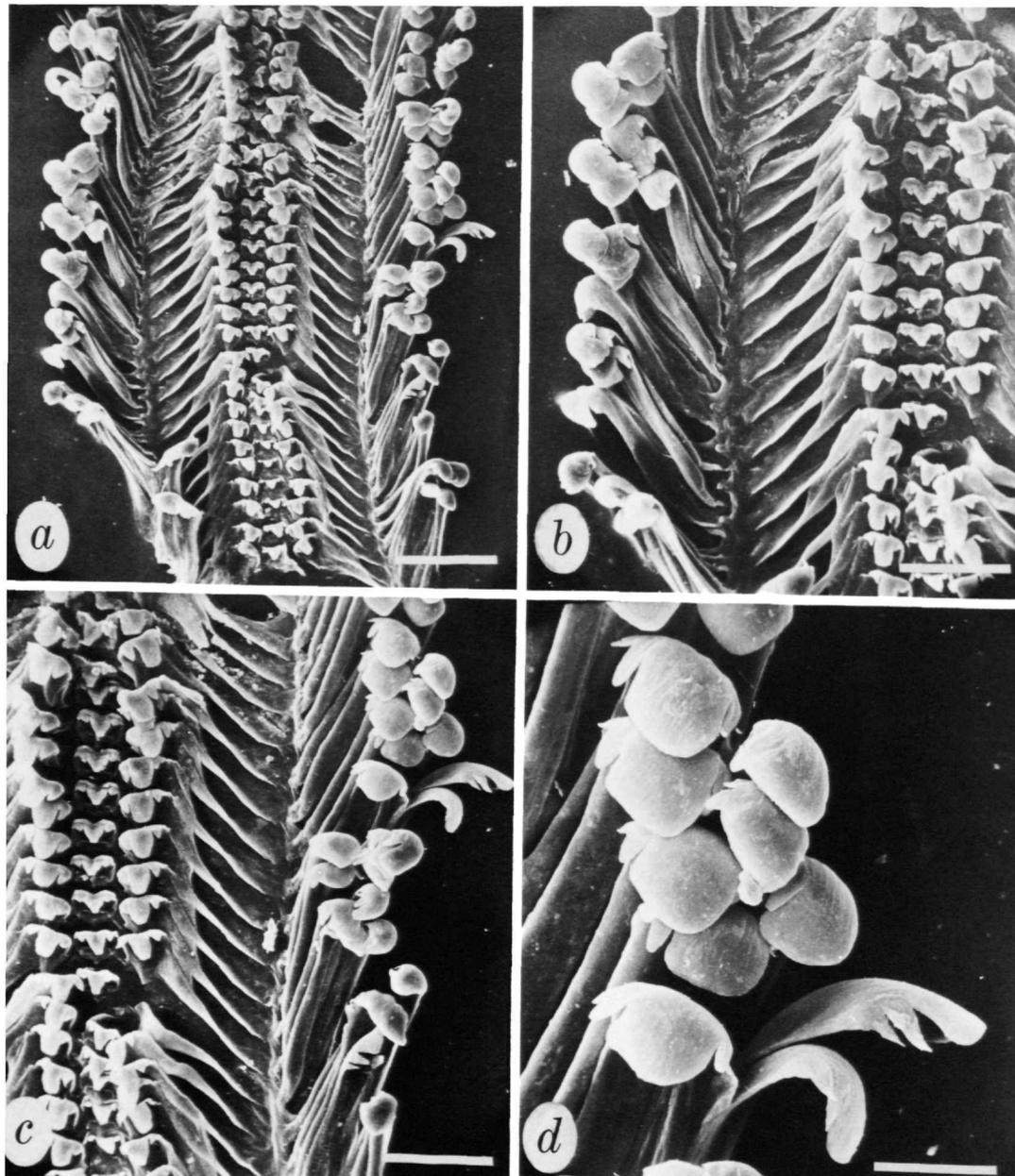


FIGURE 54.—SEM micrographs of the radula of *Clypeomorus adunca* from Badjo Bay, Flores, Siboga Sta 50, Indonesia (ZMA): *a*, radular ribbon with marginal teeth folded back exposing lateral and rachidian teeth (bar = 150 μ m); *b*, *c*, detailed views of half-row of teeth showing details of lateral and rachidian teeth; note long basolateral projections on lateral teeth (each bar = 100 μ m); *d*, detail of cusps on marginal teeth showing spoon-like tips (bar = 40 μ m).

unique shell morphology and is not likely to be confused with any other species. Its long tapering apex, thickened aperture, long anal canal, humped lateral aspect, and smooth sculpture are all distinctive characters (Figure 53). The relative lack of sculpture is similar to some forms of *Clypeomorus irrorata* (Gould). The short radula, although quite distinctive, resembles those of *Clypeomorus irrorata* (Gould) and *Clypeomorus admirabilis*, new species, in the spatulate aspect of the marginal teeth and suggests that these three species may share a common lineage. This hypothesis was not born out by the cladistic analysis of *Clypeomorus* species; however, the generated cladogram placed *Clypeomorus adunca* on a stem that was part of an unresolved polychotomy and showed numerous changes in character states. The relationship of this species to other *Clypeomorus* species is unresolved.

Clypeomorus adunca is the rarest of all *Clypeomorus* species, at least in museum collections. I have seen very few specimens, but it may be common in local populations within its limited range.

FOSSIL RECORD.—Not cited as a fossil in the literature.

GEOGRAPHIC DISTRIBUTION (Figure 55).—This species appears to be confined to the Philippines and the Lesser Sunda Islands, Indonesia, but may occur throughout the Moluccas.

MATERIAL EXAMINED.—PHILIPPINES: Luzon (CAS); Puerto Princessa, Palawan (ex ANSP 224591); Canmahana Bay, Ragay Gulf, Luzon (USNM 239716); Cebu (LACM HH-4377); Santa Cruz, Tiglawigan, Negros (USNM 313387); Jolo, Jolo (USNM 232874); "Philippine Islands" (AMNH 110667). INDONESIA: Badjo Bay, Flores Siboga Sta 50 (ZMA).

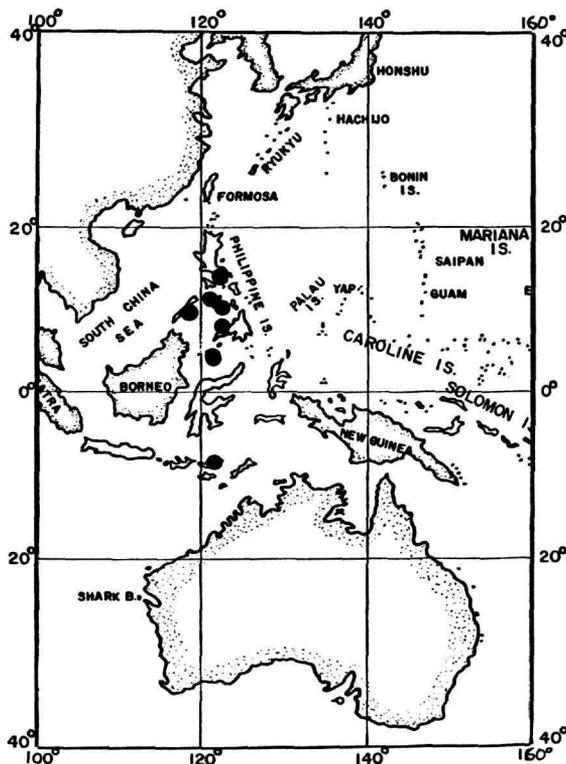


FIGURE 55.—Geographic distribution of *Clypeomorus adunca* (Gould, 1849).

Clypeomorus nymphe, new name

FIGURES 56–59

Cerithium variegatum Quoy and Gaimard, 1834:129, pl. 55: fig. 17 [lectotype, here selected: MNHNP, no number; type-locality: Tongatapu; 2 paralectotypes, largest selected as lectotype, smaller specimen is not *Cerithium variegatum*; not *C. variegatum* Fischer, 1807, nor Menke, 1829, nor Folin, 1869].—Sowerby, 1855:870–871, pl. 182: figs. 166–169 [in part]; 1865, pl. 7: fig. 41 [in part].—Tryon, 1887:134, pl. 24: figs. 41, 43, 45, pl. 25: figs. 65, 66 [pl. 25: figures not *C. variegatum* Quoy and Gaimard, 1834].—Kobelt, 1893:120–122, pl. 23: figs. 4, 5, pl. 27: figs. 8, 9.

Cerithium zonale Quoy and Gaimard, 1834:133, pl. 55: fig. 9 [holotype: MNHNP, no number; type-locality: not given; not *C. zonale* Bruguière, 1792].

Cerithium pupa Sowerby, 1865, pl. 12: fig. 84 [lectotype: BMNH, no number; type-locality: Capul, Philippines; not *C. pupa* J. Martin, 1863].—Sowerby, 1855, pl. 12 [1866] fig. 308.—Tryon, 1887:133, pl. 24: fig. 28.—Kobelt, 1898:235, pl. 41: fig. 12.

Cerithium tuberculatum var. *variegatum*.—E.A. Smith, 1884: 63–64.—Schepman, 1909:161.

Cerithium sejunctum Iredale, 1929:278 [new name for *Cerithium variegatum* Quoy and Gaimard, 1834; not *Cerithium sejunctum* Zekeli, 1852].—Demond, 1957:293, fig. 10.

DESCRIPTION.—Shell (Figure 56; Table 32): Adult shell pupiform, reaching 21 mm in length and having teleoconch of 9 whorls with an apical

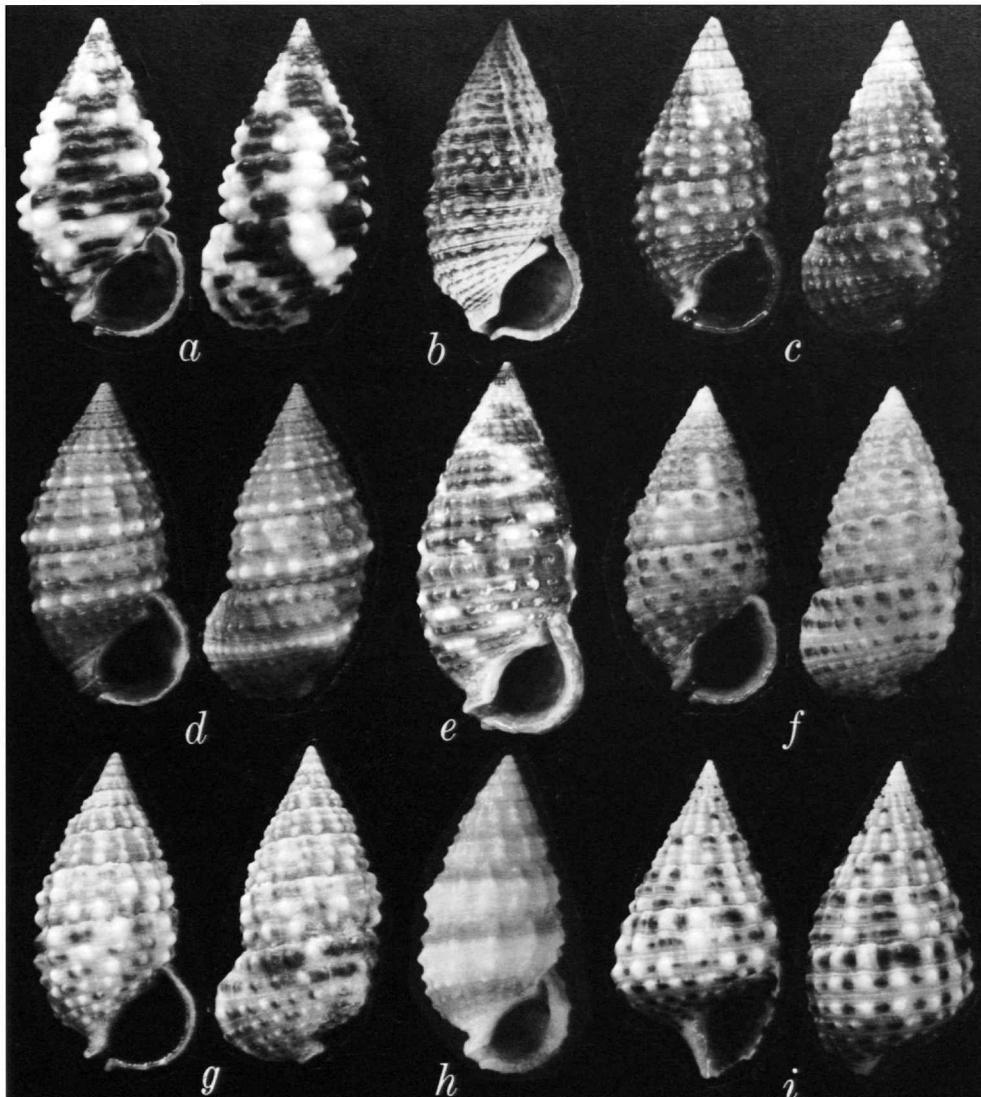


FIGURE 56.—*Clypeomorus nympha*, new name, showing variation in shell sculpture and color of synonymous taxa: *a*, knobby morph from Anchorage Island, Suvarev, Cook Islands, USNM 704446 (13.8×7 mm); *b*, holotype of *Cerithium zonale* Quoy and Gaimard, 1834, MNHNP, no number; *c*, melanistic morph from Enewetak Atoll, Marshall Islands, USNM 581788 (11×5 mm); *d*, banded morph from Apamama, Gilbert Islands, USNM 434004 (15×7 mm); *e*, lectotype of *Cerithium variegatum* Quoy and Gaimard, 1834, MNHNP, no number, from Tongatapu, Tonga (19×8.2 mm); *f*, Diego Garcia, Chagos Archipelago, Indian Ocean, USNM 702162 (13×6.1 mm); *g*, Enewetak Island, Enewetak Atoll, Marshall Islands, USNM 803196 (15×8 mm); *h*, lectotype of *Cerithium pupa* Sowerby, 1865, from Capul, Philippines, BMNH, no number (17.8×8.3 mm); *i*, immature specimen lacking outer lip from Enewetak Island, Enewetak Atoll, Marshall Islands, USNM 803196 (13×6 mm).

TABLE 32.—Analysis of shell parameters of *Clypeomorus nympha* (measurements in mm).

Character (n=28)	\bar{x}	sd	Range
Shell length	14.10	2.68	9.43–21.29
Shell width	6.78	1.10	4.62–9.38
Aperture length	3.07	0.45	2.33–4.27
Aperture width	2.90	0.47	2.14–3.86
No. of beads on penultimate whorl	15.07	3.16	11–22
No. whorls	10.18	0.90	9–12

Shell length/shell width index: 2.07

Shell length/aperture length index: 4.59

angle of 45 degrees. Whorls inflated, upper whorls attenuate, concave in outline, becoming globose in penultimate whorl. Body whorl slightly less globose. Protoconch unknown. Early whorls sculptured with three spiral cords and axial riblets presenting an overall reticulate appearance. Adult whorls sculptured with 3 beaded spiral cords. Beads are rounded and line up to form axial ribs. There are about 14 ribs on the penultimate whorl. Axial ribs less defined or lacking on body whorl. There are several microscopic spirally incised lines between the spiral cords. Suture distinct, wavy. Former varices present; largest varix on dorsal surface of body whorl at a 45 degree angle to axis of shell when viewed anteriorly. Body whorl elongate, somewhat constricted, about one-half the shell length. Body whorl sculptured with 8 weakly beaded spiral cords; largest spiral cord with most prominent beads is subsutural. Edge of outer lip thickened. Aperture ovate, violet, a little less than one-fourth the shell length. Columella concave with distinct columellar lip. Anterior siphonal canal short, deeply incised, slightly reflected, and at a 50 degree angle to shell axis. Anal canal distinct, defined by columellar plait that extends into shell aperture. Outer lip smooth, curved, and pendent with its base lower than the anterior siphonal canal. Plane of outer lip parallel to shell axis. Periostracum not evident. Shell color variable; white with brown, tan, or orange blotches, and

spiral bands of brown spots. Brown bands sometimes present. Operculum thin, tan, corneous with eccentric nucleus.

Radula (Figure 57; Table 33): Radula ribbon about one-sixth the shell, length, comprising 13 rows of teeth. Shell length/radula length index 5.81. Rachidian tooth (Figure 57*b*) pentagonal, slightly concave on top, rounded on sides, and bearing 1 large central spade-shaped cusp flanked by 2 blunt denticles on each side. Denticle adjacent to central cusp is largest. Basal plate of rachidian tooth triangular with centrally placed extension. Lateral tooth (Figure 57*b,d*) rhomboidal with long laterobasal extension of basal plate, which twists where it is attached to radular membrane. Basal plate of lateral tooth with long median downwardly directed buttress. Center of buttress has tiny raised pustule. Top of lateral tooth concave with cutting edge bearing large spade-shaped median cusp, flanked on inner side by smaller sharp-pointed denticle and on outer side by 2 widely separated pointed denticles. Lateral extension of basal plate of lateral tooth has a flange directly adjacent to cutting edge of tooth. Marginal teeth (Figure 57*c*) long, sinuous, having moderately wide shafts. Tips of marginal teeth spatulate. Inner marginal tooth has long chisel-shaped center denticle flanked on inner side by 2 closely set pointed denticles and by 1 inner pointed denticle. Outer marginal tooth same, only lacking outer denticle.

Animal (Figure 58): Head-foot cream colored, with brown and tan maculations, and covered with tiny white spots. Tentacles striped with broken lines of black and yellow. Black eyes

TABLE 33.—Analysis of radular parameters of *Clypeomorus nympha* (measurements in mm).

Character (n=6)	\bar{x}	sd	Range
Length	2.29	0.19	2.06–2.57
No. of rows	12.67	5.50	12–17
Shell length	13.25	0.80	12.35–14.47

Shell length/radula length index: 5.81

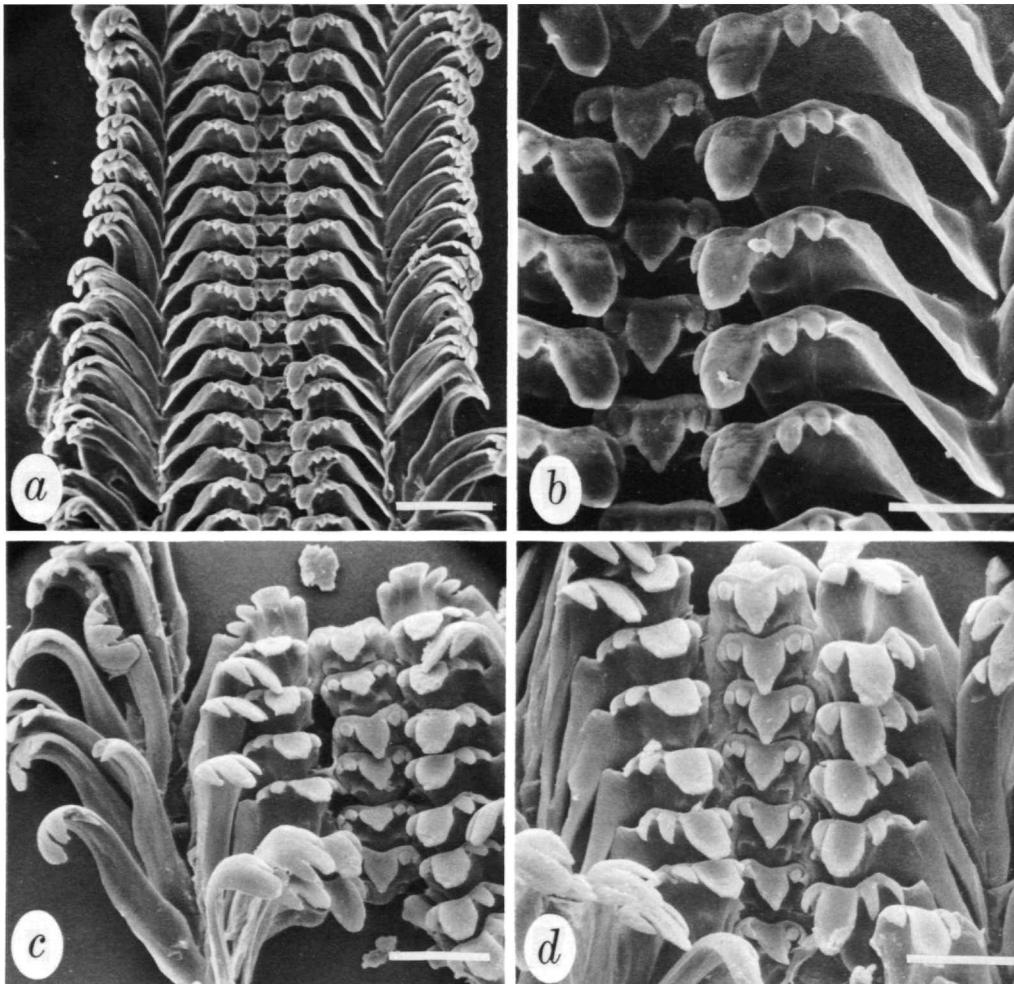


FIGURE 57.—SEM micrograph of radula of *Clypeomorus nympa*, new name: *a*, radular ribbon, marginal teeth spread back (bar = 100 μ m), Pago Bay, Guam, Mariana Islands (USNM 774769); *b*, detail of rachidian and lateral teeth, same locality as *a* (bar = 50 μ m); *c*, disarticulated radula, showing marginal teeth (bar = 50 μ m), Enewetak Island, Enewetak Atoll, Marshall Islands (USNM 803196); *d*, detail of rachidian and marginal teeth, same locality as *c* (bar = 40 μ m).

surrounded with orange pigment. Ciliated groove runs down right side of foot in females. Dorsal part of mantle edge with long transparent papillae. Mantle yellow. Kidney purple and ovary cream-yellow. Testis orange. Within mantle cavity, osphradium tan, ctenidium white, and hypo-branchial gland light yellow. Oviduct opening distal to anus. Medial lamina of female pallial

oviduct (Figure 58C, *ml*) bears a large, pouch-like ciliated sperm gutter that opens (Figure 58A,B, *sbo*) into a spacious spermatophore bursa (Figure 58A–D *sb*) that extends into the proximal portion of the lamina. Along the free edge of the medial lamina a shallow ciliated groove runs back to a deeper groove within which lies the bright orange seminal receptacle (Figure 58A,D *sr*). The

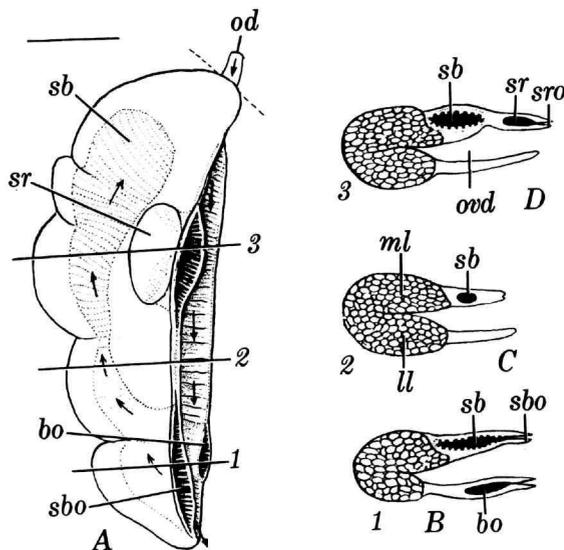


FIGURE 58.—*Clypeomorus nympha*, new name: A, pallial oviduct dissected out of mantle cavity showing relationships of structures; distal end of duct at bottom (bar = 1 mm); B–D, sections 1, 2, 3 through oviduct corresponding to lines 1, 2, 3 in drawing A. (Abbreviations: bo = ciliated bursa; ll = lateral lamina; ml = medial lamina; ov = oviduct; ovd = oviducal groove; sb = spermatophore bursa; sb0 = spermatophore bursa opening; sr = seminal receptacle; sro = seminal receptacle opening.)

seminal receptacle lies in the median portion of the pallial oviduct some distance from the oviduct entrance (Figure 58A, *od*). In the distal portion of the lateral lamina (Figure 58B, *ll*) is another ciliated pouch of unknown function (Figure 58A,B, *bo*).

REMARKS.—The earliest name for this species, *Cerithium variegatum* Quoy and Gaimard, 1834, is preoccupied. Iredale (1929:278) proposed *Cerithium sejunctum* as a replacement name but that name was previously used by Zekeli (1852) for a fossil species. The type material of *Cerithium variegatum* comprises three specimens, the largest of which (19 × 8.2 mm) I herein select as the lectotype (Figure 56e). The smallest specimen is a tiny *Clypeomorus bifasciata*. Sowerby's (1855, pl. 182: figs. 166–169) figures of *Cerithium variegatum* are a mixture: his figures 166 and 169 are *C. variegatum*, while his figures 167, 168 are

Clypeomorus pupurastoma, new species.

Tryon (1887:134) suggested that *Cerithium variegatum* was a variety of *Clypeomorus morus* (Lamarck) [= *Clypeomorus bifasciata* (Sowerby)]. None of the plate figures he cited are of *C. variegatum* sensu Sowerby. Tryon also believed that *Cerithium pupa* Sowerby was a variety of *Cerithium tuberculatum* Lamarck (= *Clypeomorus petrosa* (Wood)), but he is clearly wrong as examination of the types demonstrates.

E.A. Smith (1884:64) considered *variegatum* a variety of *Cerithium tuberculatum* (Linnaeus) and noted the violet aperture of var. *variegatum* as a distinguishing character. He "lumped" all of these species, including *Cerithium petrosus* (Wood) and *Cerithium brevis* Quoy and Gaimard, under *Cerithium morus* Lamarck (= *Clypeomorus bifasciata*). Smith obviously misunderstood the whole group and admitted that he found it "very perplexing." Schepman (1909:161) followed Smith's views, citing *C. tuberculatum* var. *variegatum* from Celebes and Obi, Indonesia. It is unclear if Schepman's specimens were really *C. tuberculatum* var. *variegatum*; consequently, I have discounted the localities cited by him.

The name, *Cerithium pupa* Sowerby, 1865, is conspecific with *C. variegatum* and is also preoccupied. There are two syntypes in the British Museum. I select the specimen (17.8 × 8.3 mm) figured by Sowerby (1865, pl. 12: fig. 84) as the lectotype (Figure 56h).

Cerithium zonale Quoy and Gaimard, a faintly banded morph, is also conspecific with *Cerithium variegatum* Quoy and Gaimard, 1834.

Since all other names are preoccupied, I propose the new specific name *nympha* (a Latin derivation of the Greek *nymphē*, a pupa, signifying the pupa-like shape of the shell) and transfer the species to the genus *Clypeomorus*.

ECOLOGY.—*Clypeomorus nympha*, new name, is a common species associated with coral islands where it lives among small rocks and on algal mats of intertidal flats and benches. I have observed this species at Enewetak Atoll, Marshall Islands, where it is common on the windward side of the island among rocks along the coral

bench at the high tide zone. In the daytime, it is usually buried in sandy pockets around rock bases, but emerges at night. At Pago Bay, Guam, I observed large populations on algal turf in the intertidal portion of a windward rocky bench. Although found around some continental and volcanic islands in the Philippine and Indonesian archipelagos, this species appears to be most common on low lying coral atolls associated with oceanic islands. Demond (1957:293) noted that in most Micronesian areas it is ordinarily found buried in sand among rocks and rocky tide pools on windward ocean reef flats. Gibbs (1975) reported it to be among the most common of gastropods in the lagoon sediments of Aitutaki Atoll, South Cook Islands. He is undoubtedly referring to shells of dead specimens, because *Clypeomorus nympha*, new name, does not live in sandy, lagoon environments. Abbott (1950:71) stated that it was plentiful in the shallow grassy parts of the lagoon of Cocos-Keeling Atoll, but it is uncertain whether or not he identified these specimens correctly. Maes (1967), in a more thorough study of the malacofauna of the islands, did not record it. Museum records all indicate an intertidal, hard substrate as the habitat.

Nothing is known about the spawn or mode of development of this species.

DISCUSSION.—*Clypeomorus nympha*, new name, is distinguished by its relatively small pupiform shape, sculpture of three spiral cords all bearing rounded, knobby beads on each whorl, and by its violet aperture. It closely resembles *Clypeomorus purpurastoma*, new species, which is the only other *Clypeomorus* species to have a purple aperture. *Clypeomorus purpurastoma*, however, is a larger, less globose species. It has smaller more numerous beads on the spiral cords and a more weakly defined suture. *Clypeomorus nympha* is more inflated and has pronounced spiral sculpture and larger beads. The two species are allopatric, except in a few limited regions (see discussion under *Clypeomorus purpurastoma*, p. 86).

I include this species in *Clypeomorus* with some hesitation. Although the shell morphology is very *Clypeomorus*-like, the layout of the pallial oviduct

and, in particular, the size and placement of the seminal receptacle (Figure 58) are more like those seen in some *Cerithium* species. I only tentatively refer this species to *Clypeomorus* and suggest that convergence in shell morphology due to similar habitat may explain the close resemblance to other *Clypeomorus* species.

Shell shape and sculpture are fairly constant throughout the range of this species but samples from Tonga (USNM 654210) and Samoa (USNM 573880, 573942, 574020) are less pupiform, have lower relief sculpture, smaller beads, and tend to be larger than average. Some specimens have prominent beads (Figure 56a,c). The color of specimens throughout the range is white with blotches and spirally arranged spots of brown. There are some melanistic forms (Figure 56c). The brown pigment ranges in color from dark brown to a light orange. Some specimens (USNM 434004) are banded (Figure 56d).

FOSSIL RECORD.—Not recorded as a fossil in the literature.

GEOGRAPHICAL DISTRIBUTION (Figure 59).—In the Indian Ocean from the Seychelles to Cocos-Keeling (Abbott, 1950), on low lying oceanic islands. No reliable records from Indonesia. In the Pacific, from the Philippines east throughout Micronesia to the South Cook Islands, Tonga, and also in eastern southern Japan and Taiwan. Dautzenberg (1929:483) cited *Cerithium variegatum* Quoy and Gaimard from Nosy Bé, Madagascar, but he probably had *Clypeomorus purpurastoma*, new species. I have not seen specimens from Madagascar.

MATERIAL EXAMINED.—INDIAN OCEAN: E of Harsburg Pt, Diego Garcia, Chagos Archipelago (USNM 702162); Bel Ombre, Mahé, Seychelles (private collection); Fadiffolu Atoll, Maldives (ANSP 253621); NW tip of Gan, Addu Atoll, Maldives (ANSP 304191); Ongu Id, N Malosmadulu Atoll, Maldives (ANSP 304409). NEW GUINEA: NW end of Manokwari, West Irian (ANSP 249623); reef, E of Pai Id, Mios Woendi Atoll, Padido Ids, West Irian (ANSP 205077); 5 mi (8 km) NW of Rani Id, Biak Id, Schouten Ids, West Irian (ANSP 207582); reef

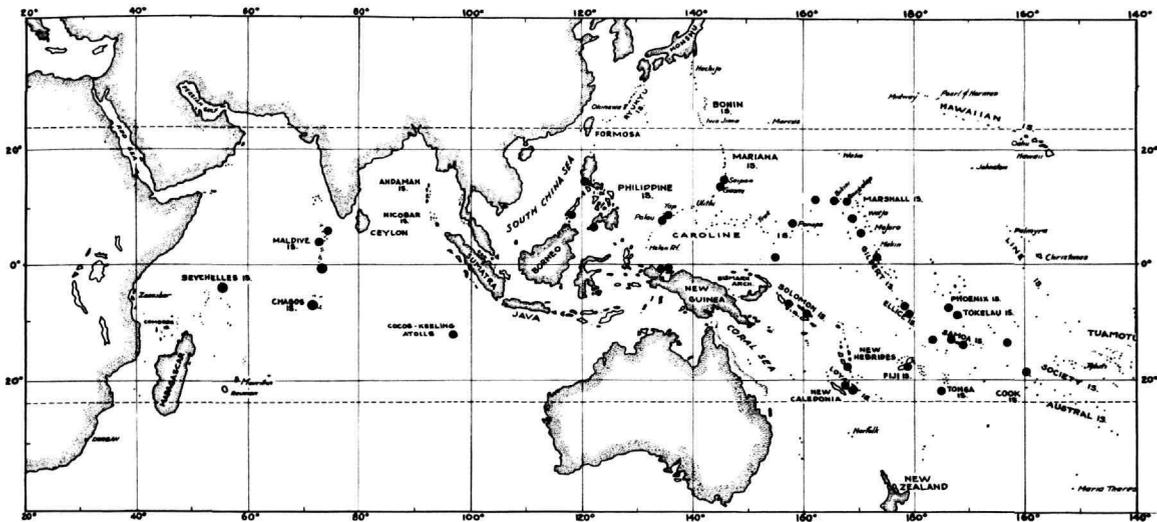


FIGURE 59.—Geographic distribution of *Clypeomorus nympha*, new name.

NE end of Noekori Id, Padido Ids, West Irian (ANSP); Mios Woendi Atoll, Padido Ids, West Irian (USNM 542657, 542730). PHILIPPINES: Sabtan Id, Batanes Group (USNM 243918, 243924); Cavite, Luzon (USNM 232955); Cabalao, Polillo Gp, Quezon Prov, Luzon (LACM 76769); Tagbayag Bay, Palawan (USNM 775150); Zamboanga, Mindanao (USNM 233160); Isle, 0.25 mi (0.4 km) N of Tara Id (USNM 243781).

MELANESIAN ISLANDS: Choiseul Bay, Choiseul, Solomon Islands (ANSP 1853550); Nudha Id, Indispensable Strait, Solomon Islands (LACM 78-69.51); ESE of Inyeng Id, Ancityum, New Hebrides (USNM 692230); Lifu, Loyalty Islands (USNM 744555); Maré, Loyalty Islands (MCZ). MARIANA ISLANDS: Apra Bay, Guam (USNM 232943, 232946, 243619); Pago Bay, Guam (USNM 774769); Saipan (USNM 602456); Rota Id (USNM 620121). FIJI: NE side, inner reef, Wakaya (USNM 666363); W side Wadiji Id (AMNH). PALAU ISLANDS: Kayangel Id, Kayangel Atoll (USNM 616928); S end Ngajangel Id, Kayangel Atoll (ANSP 616928); Rattakadokoru Id, Palau Id (ANSP); S of Koese Id, near Koror, Babelthaup Id (ANSP); E Babelthaup (USNM 620902). CAROLINE IS-

LANDS: Ponape (MCZ); Sand Id, Metalanim Harbor, Ponape (ANSP 314237); Hare, Kapin-gamarangi Atoll (USNM 610792, 611046, 611048); Asor Id, Ulithi Atoll (USNM 593210).

MARSHALL ISLANDS: Bikini and Enewetak Atolls (numerous localities throughout, USNM); Piganigaroyaro Id, Rongelap Atoll (USNM 585579); Kabelle, Rongelap Atoll (USNM 583441); Rabelle Id, Rongelap Atoll (USNM 582417); Arbar Id, Rongelap Atoll (USNM 582443); Elizabeth Id, Jaluit Atoll (USNM 659163, 659166, 659197); Sidneytown, S of Jabor, Jaluit Atoll (USNM 659568); N end of Me-jatto Id, Jaluit Atoll (USNM 660110); N end, Lijeron Id, Jaluit Atoll (USNM 660071, 660077); N part, Enybor Id, Jaluit Atoll (USNM 659327); SW of Kabbenbock Id, N of Jabor, Jaluit Atoll (USNM 659100, 659129); W side of Pinglap Id, Jaluit Atoll (USNM 756846); Likiep Atoll (USNM 596138); between Loi and S Loi Ids, Kwajalein Atoll (USNM 587349, 614138); Ailuk Id, Ailuk Atoll (USNM 615142); S side, Lae Id, Lae Atoll (USNM 614926, 614980). GILBERT ISLANDS: Apamama (USNM 434004, 434005, 434010); Onotoa Atoll (USNM 607833); Apiang Id (MCZ). ELLICE ISLANDS: main id, Vaitupu (USNM 685918,

695972); main village, Vaitupu (USNM 686053); main id, Nukulailai (USNM 685811). TOKELAU: W side, Nukunonu (USNM 786723). WALLIS: N and S sides, Nukuhifala (USNM 676337). SAMOA: Tutuila (USNM 488641, 774450); Apia (USNM 573848, 573880, 573942); Pago Pago, Tutuila (USNM 574020); airport reef, Tutuila (USNM 699470. TONGA ISLANDS: Sapu Reef, Tongtapu (USNM 654210). PHOENIX ISLANDS: "Hulls Group" (USNM 13340). COOK ISLANDS: lagoon shore, Anchorage Id, Suvarov (USNM 704455, 704446); outer side of Akaiami Id, Aitutaki (USNM 697306).

***Clypeomorus verbeekii* (H. Woodward)**

FIGURE 60

Cerithium Verbeekii H. Woodward, 1880:240, pl. 5: fig. 9a,b [holotype: RGM, no number, 21.4 mm; type-locality: Miocene of Nias Island, Sumatra].—Tesch, 1920:53, 120, pl. 130: fig. 175.

Cerithium (s. str.) *Verbeekii* Woodward [sic].—K. Martin, 1884:152, pl. 8: fig. 149; 1899:199, pl. 31: figs. 457, 457a, 458, 458a, 459; 1914:161.—Ickie and Martin, 1907:211, 215.

Cerithium (*Vulgocerithium*) *verbeekii* (Woodward).—Cossmann, 1906:80.

Cerithium (*Thericium*) *verbeekii* (Woodward).—Wissemma, 1947:62–63.

Clypeomorus verbeeki [sic] (Woodward).—Shuto, 1969:68.

DESCRIPTION (Figure 60).—Shell turreted, stocky, about 21 mm long, having teleoconch of 7 or 8 moderately inflated whorls. Protoconch and early whorls eroded. Penultimate whorl sculptured with 4 major beaded spiral cords, in between which are thinner minor beaded cords. Axial riblets cross spiral cords forming beads and are more distinct on upper whorls. Axial riblets very weak on body whorl. Former varices present, major varix on body whorl opposite outer lip. Body whorl has 3 major spiral cords and 6 or 7 thinner beaded spiral lirae at siphonal constriction. Suture impressed, distinct. Aperture ovate, columella concave with minor columellar callus. Anal canal well defined by parietal columellar fold that extends well into aperture.

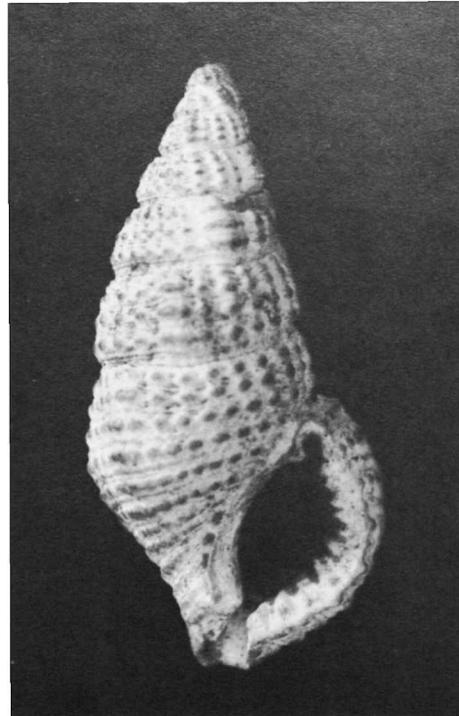


FIGURE 60.—Lectotype of *Clypeomorus verbeekii* (H. Woodward), Nias Island, Sumatra, Indonesia (Miocene), RGM, no number (21.4 mm).

Outer lip thick, slightly crenulate, beveled along inner edge, and bearing numerous teeth. Anterior canal short, well defined, projecting about 45 degrees to left of shell axis.

ETYMOLOGY.—Named after M. Verbeek.

REMARKS.—Originally referred to *Cerithium* Bruguière, 1789, and later to *Vulgocerithium* Cossmann, 1895 (a synonym of *Thericium* Monterosato, 1890; see Houbrick, 1974:38–39), by Cossmann (1906:80), this species is better placed in *Clypeomorus* on the basis of shell characters. It looks very much like *Clypeomorus bifasciata* but is distinct in a number of traits, as noted by Martin (1884:152–153) and Tesch (1920:53–54). The whorls of *Clypeomorus verbeekii* seem to be more angular, there are four major spiral cords in contrast to the three of *C. bifasciata*, the beads are finer, and the axial riblets more distinct than

in typical *C. bifasciata*. The sculpture is quite variable, especially in the number and development of axial ribs. I examined the holotype figured by Tesch (1920, pl. 130: fig. 175) and five other specimens from the three known recorded localities. The holotype is the only specimen with a complete aperture and outer lip, and it resembles *Clypeomorus bifasciata*. However, *C. verbeekii* does not have the axial rib development seen in the other specimens.

FOSSIL RECORDS.—Known from the Miocene of Nias Island, Sumatra, the early and late Miocene (Tjilanang beds) of Java, and late Miocene of East Borneo, and the Pliocene of Timor (Vlerk, 1931:250).

***Clypeomorus tjilonganensis* (K. Martin),
new combination**

FIGURE 61

Cerithium (s. str.) *tjilonganensis* [sic] K. Martin, 1899:197, pl. 31: fig. 454 [holotype: RGM 10353, 32.1 mm long; type-locality: Miocene of Selatjan, Tji Longan, Java].

Cerithium (*Vulgocerithium*) *tjilonganense*.—K. Martin, 1921:470, pl. 3: figs. 63–64.—Cossmann, 1906:80.

DESCRIPTION (Figure 61).—Shell fat, pupiform, comprising 10 inflated whorls sculptured with 2 dominant spiral cords bearing sharp nodes and numerous finer spiral lirae, the most anterior of which is beaded. The first dominant spiral cord is anterior and adjacent to the suture and the second is on the middle of the whorl. The spinose beads are not axially aligned. Former varices are present, the largest being opposite the outer lip of the aperture. Suture distinct, somewhat wavy. Protoconch unknown. Body whorl large with numerous spiral cords, some beaded and aside from the two dominant cords, more distinct at the siphonal constriction. Columella concave with distinct plait adjacent to anal canal. Moderate columellar callus present. Outer lip unknown.

ETYMOLOGY.—Named after the type-locality, Tji Longan.

REMARKS.—*Clypeomorus tjilonganensis* looks morphologically very much like *Clypeomorus pe-*



FIGURE 61.—Lectotype of *Clypeomorus tjilonganensis* (K. Martin), Selatjan, Tji Longan, Java, Indonesia (Miocene), RGM 10353 (32 mm).

trota, but the latter species does not have the sharp nodes on its early whorls as does the holotype of *Clypeomorus tjilonganensis* from Tji Longan, Java. Martin (1921:470, pl. 60; figs. 63, 64) later illustrated other specimens of this species from Kali Tjibodas, Java, which I have examined. They appear to be less spinose and look more like typical *C. petrosa* or the subspecies. *C. p. chemnitziana* and also have some resemblance to *Clypeomorus purpurastoma*, new species. Martin mentioned that this species shows considerable variation in shell sculpture. None of the type material has a complete outer lip, so details of the aperture are unknown. A paratype (RGM 10353) has larger nodes than the holotype. As I have previously suggested (Houbriek, 1978a:19), this species closely resembles *Rhinoclavis floraensis* Ladd, 1972, and may be conspecific with it. More material of *R. floraensis* is needed for comparison

in order to resolve this problem. It is probably closely related to the *Clypeomorus petrosa* complex.

FOSSIL RECORDS.—This species is known from the early to late Miocene Njalindoeng beds of Java.

***Clypeomorus alasaensis* Wissema**

FIGURE 62

Clypeomorus alasaensis Wissema, 1947:72–73, pl. 3: fig. 84 [holotype: RGM; no number, 17 mm long; type-locality: upper reaches of Alasa River, Nias Id, Sumatra loc. 42, Plio-Pleistocene].

DESCRIPTION (Figure 62).—The following is from Wissema (1947:72–73).

Shell moderate large, rather high conical, with convex whorls. The top is worn and only 7 whorls are left. The sculpture consists of sharp axial ribs and fine lines of growth, crossed by four sharp spirals and two or three spiral lirae in the interstices of the last. On the cross points small but sharp granules are formed. The hindmost spiral is slightly smaller than the others. In the forward suture a fifth spiral is visible. On the bodywhorl the axial ribs are feebler and do not reach any farther than the three hindmost spirals. The two spirals before them, to which is added a third one, are granulated finer and much denser. Still more to the front four somewhat smaller spirals occur, which are granulated irregularly. The spiral lirae are also present on the base. The aperture is missing the outer lip and the canal. The columella is convex, and the inner lip thickened. Opposite to the aperture is a heavy varix, while on the spire several varices occur, which are more numerous in the older whorls. All varices are crossed by the granulated spirals. Atl. 17.3, Diam. of the penultimate whorl 8.4 mm. The peculiar coarse sculpture caused by the about equally sharp axial ribs and spirals, which gave rise to a nice rectangular pattern on the spire; and the very strong varices, are characteristic for this species.

ETYMOLOGY.—Named after the River Alasa.

REMARKS.—This species is known only from the holotype, which is, as depicted by Wissema (1947, pl. 3: fig. 84), fragmentary and missing the outer lip. The shape and sculpture place it

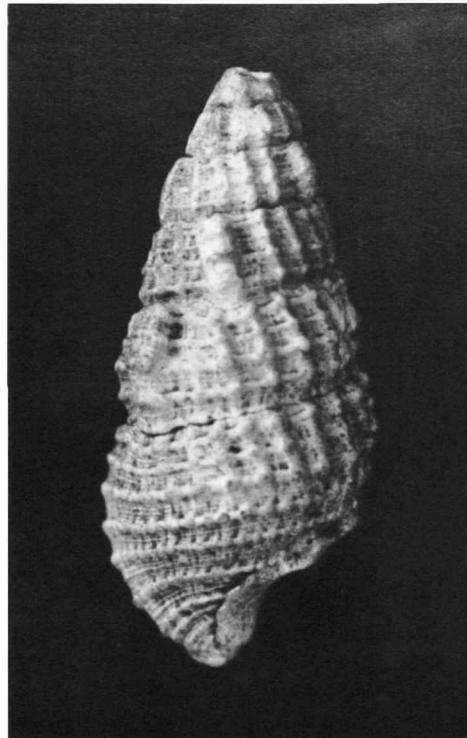


FIGURE 62.—Holotype of *Clypeomorus alasaensis* Wissema, Alasa River, Nias Island, Sumatra, Indonesia (Plio-Pleistocene), RGM, no number (17 mm).

unequivocally in *Clypeomorus*. The beaded sculpture and large varix on the body whorl opposite the outer lip closely resemble those features in *Clypeomorus bifasciata*. There are, however, four spiral cords, and the axial riblets are more sharply defined in *Clypeomorus alasaensis*, presenting a crisp, reticulate pattern. Because of the rarity of Wissema's published thesis, I have repeated his description above.

FOSSIL RECORDS.—Known only from the type-locality on Nias Island, in strata of Plio-Pleistocene age.

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Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume(number):pagination: "10(2):5-9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

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