

Review of the Deep-Sea Genus
Argyropeza (Gastropoda:
Prosobranchia: Cerithiidae)

RICHARD S. HOUBRICK

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ABSTRACT

Houbrick, Richard S. Review of the Deep-Sea Genus *Argyropeza* (Gastropoda: Prosobranchia: Cerithiidae). *Smithsonian Contributions to Zoology*, number 321, 30 pages, 12 figures, 8 tables, 1980.—An historical review of the genus *Argyropeza* is presented. The assignment of the genus within the Cerithiidae is clarified. A close relationship between *Argyropeza* and *Bittium* is suggested. *Argyropeza* species live on soft sediments of continental slopes and island groups in the Indo-Pacific and occur most frequently at bathyal depths. They have pelagic larvae and are sediment feeders. Five nominal species are recognized: *Argyropeza divina*, *A. izekiana*, *A. schepmaniana*, *A. verecunda*, and *A. leucocephala*. An appendix with species frequently assigned to or easily confused with *Argyropeza* is included.

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Review of the Deep-Sea Genus *Argyropeza* (Gastropoda: Prosobranchia: Cerithiidae)

Richard S. Houbrick

Introduction

The genus *Argyropeza* comprises five bathyal species of small, vitreous-shelled cerithids and is not well known. The systematic position of the genus within the Cerithiacea has been uncertain since *Argyropeza* was first proposed and described by Melvill and Standen (1901:372). The taxonomy of *Argyropeza* species has also been poorly understood due to the scattered literature, lack of specimens, and inadequate analysis of shell characters. Virtually nothing has been written about radulae, opercula, or internal anatomy and no attention has been given to the ecology and zoogeography of the genus.

Numerous specimens of *Argyropeza* species were dredged by the U.S. Fisheries steamer *Albatross* in the western Pacific (1907-1910) and were deposited in the National Museum of Natural History. Ecological and bathymetric data were provided with each lot. I examined these specimens and additional material from other museums that provided adequate material for statistical analysis of each species. All measurements were made on adult specimens. The number of whorls on each shell were counted after the sharp transition be-

tween protoconch and teleoconch. No preserved animals were available for dissection or sectioning. Several shells of a few species contained dried animals from which radulae and opercula were extracted and some anatomical features were studied. In this revision I have used scanning electron micrographs of radulae, protoconchs, shell sculpture, and opercula for character analysis.

ABBREVIATIONS.—

AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences of Philadelphia
BM(NH)	British Museum (Natural History)
MNHN	Museum National d'Histoire Naturelle, Paris
NSMT	National Science Museum, Tokyo
SEM	Scanning electron micrograph
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution

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tionships of some higher Cerithiacean taxa. I also thank him for critically reading an early draft of this paper. Dr. John Taylor, of the British Museum (Natural History) kindly sent photographs of some of the types. Dr. Philippe Bouchet, of the Museum d'Histoire Naturelle, Paris, kindly allowed me to examine specimens in his charge. For assistance with the SEM and preparation of the photomicrographs I thank Ms. Susanne Braden, Scanning Electron Microscope Laboratory and Mr. Victor Krantz, Photographic Services, of the National Museum of Natural History, Smithsonian Institution. Technical assistance was kindly given by Miss Cathy Lamb and Miss Cindy Gust, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution.

Historical Review

Melville and Standen (1901:372) were unsure about the taxonomic allocation of *Argyropeza* when they originally proposed it and provisionally assigned it "as an outlying form of Cerithiidae or Litiopidae." Schepman (1909:170) considered the genus related to *Cerithiopsis* and *Litiopa* because of some similarities of the radulae but noted that the operculum of *Argyropeza* was different. Although unsure of its relationships, he regarded *Argyropeza* to be a valid genus. Thiele (1918:120) observed that the radula and operculum of *Argyropeza* were similar to those of *Bittium* and he later regarded it as a subgenus of *Bittium* (Thiele, 1931:212). Hornung and Mermod (1926:207; 1928:115) referred *Argyropeza* to the Litiopidae and described two new species. Kuroda (1949:79) thought that *A. izekiana* was a deep sea representative of *Bittium*. *Argyropeza* was also assigned next to *Bittium* by Shuto (1969:64). Nothing substantial has been written about *Argyropeza* until recently when it was reviewed by Gründel (1976), who considered the systematic position of the genus and assigned it to the Procerithiidae Cossmann, 1905.

Superfamily CERITHIACEA Fleming, 1822

Family CERITHIIDAE Fleming, 1822

Subfamily CERITHIINAE Fleming, 1822

Genus *Argyropeza* Melville and Standen, 1901

Argyropeza Melville and Standen, 1901:371-372 [type-species, by monotypy, *Argyropeza divina* Melville and Standen, 1901].—Schepman, 1909:169.—Hornung and Mermod, 1926:207.—Thiele, 1931:212.—Wenz, 1940:757.—Kuroda, 1949:76.—MacNeil, 1960:40.—Franc, 1968:281.—Götting, 1974:130.—Gründel, 1976:40.—Ladd, 1977:15. *Argyropeza* [sic] Shuto, 1969:63-65.

DESCRIPTION.—Shell small, 6-8 mm in length, thin and vitreous, turreted and with 9-12 whorls sculptured with weak axial riblets and with two spiral cords bearing sharp nodules where crossed by axial riblets. Sinusigera protoconch of about three and a half whorls, sculptured with two spiral lirae and spiral band of pustules adjacent to suture. Tip of protoconch smooth, dome-shaped, white, remainder chestnut in color. Protoconch sculpture sharply separated from adult sculpture of teleoconch. Former varices present on shell, with prominent varix opposite outer lip of aperture. Suture deeply impressed, set off with inferior and superior sutural ramps. Aperture ovate with short but distinct anterior siphonal canal and weak anal canal. Outer lip thin, columella concave. Operculum thin, corneous, subcircular, and multispiral with subcentral nucleus. Animal has large snout and broad cephalic tentacles with large eyes at their bases. Mouth with triangular jaws and taenioglossate (2+1+1+1+2) radular ribbon. Radula with quadrate rachidian tooth and trapezoidal lateral tooth that is laterally elongate and is serrated with small denticles along its cutting edge. Marginal teeth long and slender and serrated, pointed tips.

REMARKS.—The name *Argyropeza* is derived from the Greek feminine noun *arguropeza* ("silver foot"), the Homeric epithet of Thetis. The genus comprises five living shelf species, *A. divina*, *A.*

izekiana, *A. verecunda*, *A. schepmaniana*, and *A. leucocephala*. They occur throughout the tropical shelf regions of the western Pacific, southeast Asia, and the Indian Ocean. The genus may be traced back to the Pliocene in the geological record.

There have been a number of species erroneously assigned to the genus *Argyropeza*. Two of these, *Argyropeza melvilli* Schepman, 1909, from the Sulu Sea, and *Argyropeza suwaensis* Ladd, 1977, from Fiji, should be referred to the genus *Abyssochrysos* Tomlin, 1927, family Abyssochrysidae Tomlin, 1927. As Barnard (1963:144) noted, Schepman (1909:170) was doubtful about the generic assignment of *A. melvilli* Schepman, but at Melvill's suggestion, referred it to *Argyropeza*. The anatomy, shell, and radula of *A. melvilli* unequivocally confirm Barnard's (1963:144) transfer of *Argyropeza melvilli* to *Abyssochrysos* (Houbrick, 1979:12).

Ladd (1977:15) described *Argyropeza suwaensis*, a fossil from early Miocene of Fiji, but only tentatively assigned it to the genus *Argyropeza*. He suggested that his fossil specimens were conspecific with *Argyropeza melvilli* Schepman, which I have shown is an *Abyssochrysos* species (Houbrick, 1979). Ladd (1977:15) noted that MacNeil (1960:43) believed that Schepman's specimen was an *Alipta* Finlay, 1926, family Cerithiopsidae. This is clearly an erroneous assignment because the protoconch and radula of *Alipta* are very different from those of *Argyropeza* or *Abyssochrysos* (see Marshall, 1978:62–63, fig. 6, a-c). I have examined Ladd's type-material of *Argyropeza suwaensis* and believe that this species is probably conspecific with *Abyssochrysos melvilli* (Schepman).

Argyropeza involuta, described by Thiele (1918:120) from two immature specimens and fragments of a third without a complete outer lip, was erroneously assigned to the genus *Argyropeza*. Both the description and examination of the holotype convince me that this species is conspecific with *Cerithium bicanaliferum* Brazier, 1877, a species that is clearly unrelated to the *Argyropeza* group.

The species described by Hornung and Mermod (1926:208) as *Argyropeza doriae* is not a member of this genus. The protoconch, shell sculpture and aperture do not fit the limits of *Argyropeza*.

I regard *Argyropeza* as a valid genus for a number of reasons. (1) The shells of the five species have distinct anterior siphonal canals and deeply impressed sutures that are set off by sloping inferior and superior sutural ramps. The shells are vitreous, sculptured similarly with weak axial riblets and spiral cords set with small, sharp nodules. All *Argyropeza* species have small shells that are vitreous, thin and bear several randomly placed varices, the most prominent one being opposite the outer lip of the aperture. (2) They share identical protoconchs suggesting that all have similar developmental modes and planktonic larvae. (3) Although the radulae of only two species are known, they are virtually identical and indicate a homologous feeding function; moreover, the fecal pellets of these species are also identical and composed of fine sediment. (4) The two species from which animals are known have similar external anatomical features. (5) All known species live in deep water environments and are found on the same kind of fine sand and mud substrata.

PHYLETIC RELATIONSHIPS.—*Argyropeza* has been assigned by various workers to the families Diastomidae Deshayes, Litiopidae H. and A. Adams, Dialidae A. Adams, and Cerithiidae Fleming. The characters, limits, and taxonomic positions of the first three families are problematic because they have been proposed on shell characters alone. For instance, *Diastoma* Deshayes, 1850, of the Diastomidae, is based upon an Eocene species, *Diastoma costellata* (Lamarck), from the Paris Basin and comprises mostly fossil species. Ludbrook (1941) recently reviewed this group. The only living species, *Diastoma melanoides* (Reeve, 1849), is found in a restricted area in southwestern Australia and its anatomy and radula are unknown. The operculum is cerithioid. The shells of all *Diastoma* species are relatively large and have

smooth outer lips that lack anterior siphonal canals. I thus exclude *Argyropeza* from this group.

The Litiopidae, as exemplified by *Litiopa*, which lives on pelagic algae, bears little resemblance to *Argyropeza* in shell characters, radula, or ecology. Moreover, *Litiopa* has opercular and epipodial tentacles (pers. observ.) not seen in *Argyropeza*. I thus dismiss the family Litiopidae as a correct assignment for *Argyropeza*.

The Dialidae are an unlikely family in which to place *Argyropeza*. Although *Diala* has been referred to the Diastomidae and the Cerithiidae by various workers, *Diala* species lack an anterior canal, a feature always present in members of the Cerithiidae; moreover, they tend to have thin, squat shells, smooth protoconchs, flatter whorls, and a lower aperture-length to shell-length ratio than do *Argyropeza* species. They also lack former varices and axial ribs. Living *Diala* snails have epipodial tentacles, an anatomical feature not present in the Cerithiidae. I thus consider this group totally unrelated to *Argyropeza*.

The relationship of *Argyropeza* to other supra-specific taxonomic groups in the Cerithiidae is difficult to assess because many of the smaller shelled genera in the family are not sharply defined and are either artificial or parochial in scope. Moreover, there is little known about the anatomy, radulae, or biology of these taxa (see Houbrick, 1975; 1977). Although some anatomical features of *Argyropeza* species are described in this paper, the detailed anatomy of the open pallial gonoducts remains unknown because the material I examined was too poorly preserved for critical study of internal ducts. It is thus impossible to make reliable anatomical comparisons with other groups.

Argyropeza is frequently confused with the genus *Fenella* A. Adams, 1860 (= *Obtortio* Hedly, 1899; = *Eufenella* Kuroda and Habe, 1952), but true *Fenella* species all lack an anterior canal and should probably be considered members of the families Dialidae or Diastomidae. There is also some confusion about the status of the genus *Alaba*. *Alaba* species have epipodial tentacles and their shells lack an anterior canal; thus, they too

should be assigned to the Dialidae or Diastomidae.

There are a number of small cerithid-like snails lacking epipodial tentacles and with slight anterior canals that are frequently placed in the genus *Fenella*. These are probably members of the genus *Alabina* (W. F. Ponder, pers. comm., 1979). Although *Alabina* has been considered a synonym of *Fenella*, it is obviously better referred to the Cerithiidae and is probably close to *Bittium*. More anatomical information and radular studies are needed to assess the relationship of *Alabina* to *Bittium* and *Argyropeza*.

Hornung and Mermod (1926:207) considered *Argyropeza* to be closely related to, or synonymous with, the genus *Glosia* Cossmann, 1921, which they placed in the family Litiopidae. *Glosia* species do not have an anterior siphonal canal and are here regarded as members of the Diastomidae. Hornung and Mermod also believed that *Alabina* Dall 1902 was a synonym of *Argyropeza*. As noted above, there is not enough data to justify this conclusion.

Gründel (1976:40) noted a morphological similarity between *Argyropeza* and the Jurassic genus *Cryptaulax* (*Xystrella*), which he referred to the family Procerithiidae. He (1976:44) thus assigned *Argyropeza* to the family Procerithiidae Cossmann, 1906, subfamily Cryptaulinae Gründel, 1976, and placed *Bittium* in the same family, subfamily Procerithiinae Cossmann, 1905. I find Gründel's (1976) revision of the "Bittium Group" unsatisfactory for a number of reasons. Although his classification is based on fossils and a few living species, his analysis employed shell characters alone and ignored biological data. Gründel (1976) placed undue emphasis on protoconch morphology in developing a phylogeny for this group. It has been shown that protoconchs differ according to the mode of larval development (direct or indirect) and that developmental modes frequently vary between species within the same genus and sometimes within a single species (see Robertson, 1976:227-232, for an excellent review). I have shown two kinds of development occur in *Cerithium* species (Houbrick, 1970; 1974a;

1974b) and the same phenomenon has been cited for the Cerithiopsidae (Marshall, 1978). Thus, a classification of supraspecific taxa based upon protoconch morphology does not necessarily reflect phylogeny and may be misleading. Gründel (1976:40) mistakenly interpreted the sinusigera notch of the protoconch as a varix, whereas it indicates a dramatic change in environment and the beginning of new growth and shell sculpture. It is thus not exactly the same as a typical growth varix. He also stated that the aperture of *Argyropeza* lacked a clear canal. This is incorrect, as a cursory glance at the plates in this paper will show. As a result of the undue emphasis on differences in shell sculpture, Gründel's (1976) classification is artificial and topheavy with supraspecific taxa. I prefer to disregard the higher taxonomic categories used by Gründel (1976) and consider *Argyropeza* and *Bittium* to be closely related genera in the family Cerithiidae.

Gründel (1976:46) proposed a new genus, *Varicopeza*, for a living species from the South China Sea that he named *Varicopeza varicopeza*. He believed *Varicopeza* was closely related to *Argyropeza* and *Cryptaulax*. His plates indicate that the specimens he used had missing apertures. Gründel's species, *Varicopeza varicopeza*, is a synonym of *Cerithium bicanaliferum* Brazier, 1877 (also known as *Cerithium trigonostomum* Melvill, 1910). I have examined numerous specimens and the embryonic whorls, radula, shell, distinctive aperture, and anal canal of *Cerithium bicanaliferum* are different from those of *Argyropeza* species.

The evidence derived from analysis of adult shell physiognomies, protoconchs, radulae, and opercula indicates that *Argyropeza* should be referred to the family Cerithiidae Fleming. Adult *Argyropeza* shells are much thinner and vitreous than those of *Bittium* but both genera are alike in having shells with distinct former varices present, the strongest one being opposite the outer lip of the aperture. Their general shell physiognomies are also similar but the suture of *Argyropeza* species is more deeply impressed. The larval shells or protoconchs of *Argyropeza* are distinctive due to a single spiral row of pustules adjacent to the suture

but are otherwise similar to those of some *Cerithium* species or somewhat like those depicted for *Bittium* by Gründel (1976:41, figs. 9–12) and Richter and Thorson (1975:166, pls. 3–4). The protoconchs of species in both genera consist of about three and a half whorls and are sculptured with two spiral lirae that begin to appear on the third whorl. They also have a deep sinusigera notch. Some *Bittium* and *Cerithium* species have tiny pustules covering the third whorl of the protoconch. Thus, although *Argyropeza* protoconchs are distinctive, they share some characters with those of *Bittium* and *Cerithium*.

Both *Bittium* and *Argyropeza* species have similar radulae. The radula of *Bittium* differs in having marginal teeth with more spatulate tips and lateral teeth that have long vertical extensions on the lower plate of the tooth. The cutting edge of the lateral teeth is also serrated with fewer denticles than *Argyropeza*.

The opercula of species in both genera are cerithioid, but there are more spirals in *Argyropeza*.

Although these similarities may be due to convergence, they are the only lines of evidence now available for phyletic speculation and, taken in their totality, are probably reliable. I thus concur with the opinion of previous authors, as outlined above, that *Argyropeza* is probably closely related to the genus *Bittium*. Although *Bittium* is sometimes placed in the subfamily Bittinae, I prefer not to recognize this subfamily or other higher categories proposed for the *Bittium* group because our present state of knowledge lends no biological or phyletic significance to them. My views on this subject have been discussed in more detail elsewhere (Houbrick, 1977).

INTERSPECIFIC RELATIONSHIPS.—Due to the lack of anatomical characters, any remarks about interspecific phylogeny of the five *Argyropeza* species are of necessity largely speculative. The only consistent characters available for all species are those derived from the shell. I have used a multi-character analysis to express phylogeny by seeking to determine the primitive or derived state of each character. Evidence from ontogeny, stratigraphic position, and outgroup comparison has been used

to determine the state of a character. Ontogeny assumes that a character state appearing first in development is more generalized than one appearing later; in other words, ontogeny recapitulates phylogeny often enough that it can help to determine polarity. Stratigraphic position is a useful criterion because the earlier the first appearance of a character, the more likely it is to be primitive. Outgroup comparison determines the occurrence of the characters in a related group.

While I realize that this method is unsatisfactory in many respects, it utilizes the only available information about this deep-sea group. A cladogram showing inferred relationships is presented below in Figure 1. The character states chosen for analysis are presented in Table 1. Of the five species, *Argyropeza divina* is unique in physiognomy, simple in shell sculpture, and attains the largest size. It has the widest geographic distribution and occurs in the greatest concentrations. This species has been recorded from the Pliocene to the Recent and is thus the oldest known *Argy-*

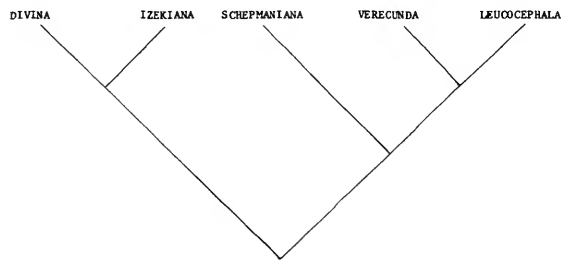


FIGURE 1.—Inferred phylogeny of *Argyropeza* species.

TABLE 2.—Comparison of *Argyropeza* species, using shell characters (measurements in mm; based on mean values)

species	no.	length	width	aperture length	$\frac{\text{aper. length}}{\text{aper. width}}$	no. whorls	no. spiral cords	no. ribs	apical angle
<i>divina</i>	20	6.96	2.21	1.85	3.80	9	2	12.5	35°
<i>izekiana</i>	20	4.63	1.53	1.09	4.27	8	2	12.5	35°
<i>schepmaniana</i>	20	4.14	1.28	0.77	5.40	8	3	13.5	32°
<i>leucocephala</i>	10	3.88	1.20	0.76	5.10	7	3	16.5	22°
<i>verecunda</i>	5	2.77	0.98	0.55	5.04	8	4	14.5	32°

TABLE 1.—Character states used in the construction of a phylogeny for *Argyropeza* species

character	primitive	derived
shell length	high	low
shell width	high	low
aperture length	high	low
$\frac{\text{aperture length}}{\text{shell length}}$	low	high
number of whorls	high	low
spiral cords	few	many
axial riblets	few	many
apical angle	high	low

ropeza taxon. The shell characters of this species are thus assumed to be the most primitive of the group. It is interesting to note that all species begin growth with two spiral cords per whorl. *Argyropeza izekiana* shares with *A. divina* large size, a simple shell sculpture of two spiral cords, sharp nodules, and 12.5 axial riblets. *Argyropeza schepmaniana* is known as a fossil from the Pleistocene, has three spiral cords and 13.5 axial riblets and appears to be related to *A. leucocephala*. Both of these species share sculptural similarities with *A. verecunda*, the smallest and most elaborately sculptured species of the group. Table 2 presents a comparative list of shell characters.

ECOLOGY.—All specimens of *Argyropeza* have been dredged from deep-sea shelves or slopes on muddy or fine grained substrata where they frequently occur in large populations. Table 3 shows the depth ranges of different species. All live in

the bathyal zone as defined by Hedgpeth (1957: 18) where they appear to be confined to continental slopes.

The stomach contents and fecal pellets of *A. divina* and *A. izekiana* contain fine particles of sand, detritus, and a few foraminifer tests. This evidence and radular morphology indicate that *Argyropeza* species are probably detritivores that eat the sediments on which they live.

Although the spawn of *Argyropeza* species is not known, the protoconchs of all species bear distinctive sculpture and have a clear sinusigera notch, indicative of a planktotrophic larval phase. This may account for the wide, but sometimes spotty distribution of most species and indicates that genetic exchanges can occur between populations, a fact well documented by Bouchet (1976) and Bouchet and Wařen (1979) for other deep-sea prosobranchs.

TABLE 3.—Bathymetric distribution of *Argyropeza* species

species	no. of stations	depth range (meters)	mean depth	sd
<i>divina</i>	75	58–923	356	196.04
<i>izekiana</i>	70	49–914	307	159.83
<i>schepmaniana</i>	44	33–914	145	176.00
<i>verecunda</i>	3	39–285	162	123.00
<i>leucocephala</i>	1	133	—	—

Argyropeza divina Melvill and Standen

FIGURES 2–4

Argyropeza divina Melvill and Standen, 1901:371–372, pl. 21: fig. 3 [holotype: BM(NH) Reg. No. 1887.2.9.1749, type-locality: 24°05'N, 57°35'E., Gulf of Oman, 375 m].—Schepman, 1909:169–170, pl. 21: fig. 3.—Melvill, 1912:246–247, pl. 12: fig. 10.—Gründel, 1976:44, pl. 1: figs. 7, 9–10.—Thiele, 1918:373.—MacNeil 1960:40, pl. 11: fig. 19.

Argyropeda [sic] *divina* Melvill and Standen.—Shuto, 1969:64–65, pl. 2: figs. 7–11.

Cerithium (s. str.) *spinigerum* Martin, 1884:156, pl. 8: fig. 152.

Potamides spiniger (Martin).—Tesch, 1920:58, pl. 131: fig. 185.

Potamides (*Tympanotonus*) *spiniger* (Martin).—Martin, 1899:208.

Argyropeda [sic] *spinigera* (Martin).—Shuto, 1969:64, pl. 2: figs. 7–11.

DESCRIPTION.—*Shell*: small, about 7 mm long, thin, elongate, turreted, and consisting of 9 adult whorls with apical angle of 35°. Whorls convex, angulate, and deeply impressed suturally. Adult whorls sculptured with two primary spiral cords, one weaker spiral cord adjacent to suture on upper portion of whorl, and with 12–13 weak, transverse axial ribs that form sharp nodes where they cross the two marginal major spiral cords. Axial ribs and nodes stronger on earlier whorls, nearly absent on penultimate and body whorls. Suture deep and distinct. Protoconch I smooth, one and one-half whorls; protoconch II, two whorls, sculptured with spiral band of axially elongated pustules adjacent to suture and with two spiral cords near mid-portion of whorl. Spiral cords sometimes weakly pustulate. Sinusigera sinus deep and narrow. Transition from protoconch to teleoconch sharply defined. Body whorl inflated, sometimes with varix opposite outer lip, especially in older shells. Sculpture on body whorl frequently diminished, and below the two primary cords there are 5–6 smooth spiral cords that become thinner as they progress to siphonal canal. Aperture ovate, close to one-fourth the length of the shell. Anterior siphonal canal short and broad, slightly curved to left. Small, indistinct anal canal present. Outer lip thin, smooth, and sinuous in outline. Columella slightly concave to straight with thin shiny callus. Shell covered with thin, light tan periostracum, and is shiny and vitreous in recently dead specimens, chalky in older ones. Shell frequently pigmented with light tan flammules that run transversely between axial ribs. Portions of spiral cords between axial ribs usually darker tan creating light spiral spots.

Animal: Head and foot pigmented with dark brown, especially on snout and tentacles. Tentacles large, broad, and with large dark eyes at their bases. Snout broad, bilobed at tip, and with relatively large buccal mass. Mouth with pair of jaws about 0.25 mm long, triangular in shape, comprised of 55–60 rows of hexagonal plates that become quadrate at the cutting edge. Stomach filled with fine sand, foraminifera, and detrital

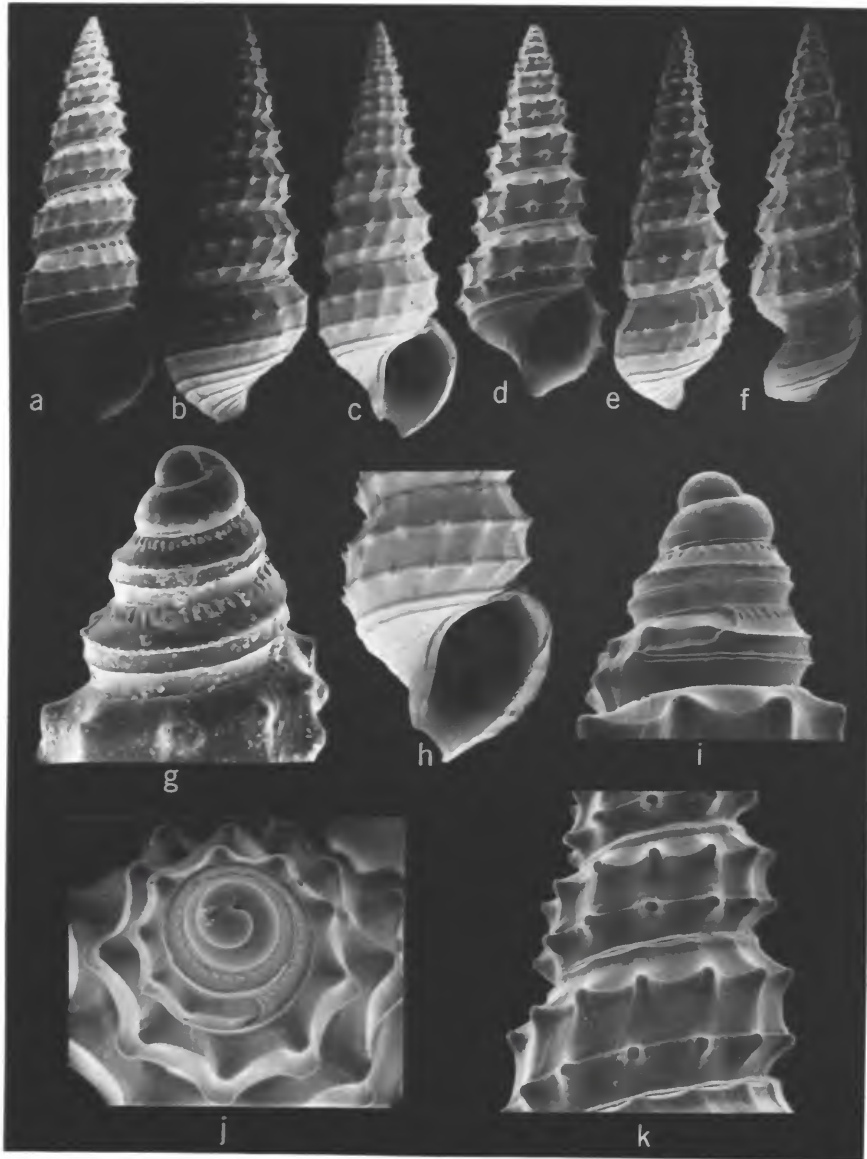


FIGURE 2.—*Argyropeza divina* Melvill and Standen: *a, b*, typical adult specimens showing overall sculptural pattern (USNM 238517, USBF Sta 5450, off Batan Id, Lagonoy Gulf, E Luzon, Philippines, 746m); *c–e* adult specimens (USNM 276553, USBF Sta 5242, Pujada Bay, E Mindanao, Philippines, 349m; *c* and *e*, 14 \times ; *d*, 28 \times); *f*, side view of adult shell showing sinuous outer lip. (USNM 302513, USBF Sta 5191, Tanon Str, off Refugio Id, Philippines, 258 m, 14 \times); *g*, protoconch showing larval shell sculpture (USNM 238513, locality same as in *a, b*); *h*, detail of aperture showing anterior siphonal canal and sculpture of body whorl (USNM 276553, locality same as in *c–e*); *i*, protoconch showing sinusigera notch and larval shell sculpture, 200 \times (USNM 238517, locality same as in *c–e*); *j*, top view of protoconch showing change between larval and adult sculpture (USNM 238517, 200 \times , locality same as in *c–e*); *k*, detail of adult whorls showing two spiral cords and nodules (USNM 276350, USBF Sta 5247, off Davao, Mindanao, Philippines, 40 \times).

TABLE 4.—*Argyropeza divina*, measurements of shell characters (in mm)

character	number	mean	range	sd
length	20	6.96	6.0–7.58	0.44
width	20	2.21	1.91–2.66	0.18
aperture length	20	1.85	1.33–2.16	0.20
shell length aper. length	20	3.80	3.41–4.51	0.38
# whorls	20	9.00	—	—
# spiral cords	20	2.00	—	—
# ribs	20	12.5	12–13	—
apical angle	20	35°	—	—

particles. Intestine large, filled with many ovate fecal pellets about 0.2 mm in diameter. Mantle edge papillate and slightly flaring at anterior siphon. Pallial gonoducts open. Other pallial organs not observed. Foot large, and with groove at anterior of propodium. Operculum thin, corneous, tan, nearly circular, and multispiral with subcentral nucleus. Operculum large in relation to foot, slightly concave and bent at circumference to fit aperture snugly. Attachment scar on reverse of operculum ovate. Eggs and larvae unknown.

Radula (Figure 3): Radular ribbon taenioglossate, about one-eleventh the length of the shell, comprising 50 rows of teeth. Rachidian tooth quadrate, somewhat concave at sides. Cutting edge of rachidian with sharply pointed central cusp flanked with two, sometimes three smaller cusps on each side. Base of rachidian tooth flat with slight lateral projections at each end. Lateral tooth trapezoidal, laterally elongate and with slightly curved top. There are seven cusps, the first small, the second large and sharply pointed, and the remaining cusps becoming smaller toward the lateral portion of the cutting edge of the tooth. A blunt longitudinal projection extends from the lower mid-portion of the basal plate. Base of lateral tooth straight. Inner marginal tooth long, slender, and curved, pointed at tip and serrated with 4–6 sharp denticles on inner side and with 5–6 denticles on outer side. Outer

marginal tooth same as inner but lacking denticles on outer surface.

ETYMOLOGY.—Latin *divinus* (“divine”).

COMPARATIVE REMARKS.—*Argyropeza divina* is distinguished from its congeners by a generally larger size, a deep sutural impression, sharply sloped whorls adjacent to the suture, and by sculpture of two strong spiral cords that are set with sharp nodes. The aperture length to shell length ratio is lower than in the other species and the aperture is decidedly more ovate. Although not noted in the original description, it is the only *Argyropeza* species that is pigmented with brown blotches. The rachidian tooth of the radula usually has two small denticles adjacent to each side of the central cusp whereas in *A. izekiana*, there are normally three denticles on each side of the central cusp. *Argyropeza divina* is the type-species of the genus and appears to be the most common and abundant species in the group. Melvill and Standen (1901:872) compared it with *Royella sinon* Bayle (cited as *Cerithiopsis sinon*), but the sculptural resemblance is only superficial for *Royella* is a monotypic genus in the Potamididae H. and A. Adams, having a round, multispiral operculum with a central nucleus and a large shell, and is phylogenetically far-removed from *Argyropeza*.

Schepman (1909:61) noted that the operculum is multispiral. Although there are numerous spirals, the nucleus is subcentral and cerithioid; consequently, the operculum should not be construed to be multispiral in the sense of a potamidid operculum. The radula of this species was crudely illustrated by Schepman (1909, pl. 21: fig. 3), who found it too small to accurately describe. The radular ribbon is very small: It averaged 0.9 mm in length and 0.18 mm in width and comprised 50 rows of teeth in two specimens from which I was able to extract it undamaged. Although Schepman (1909:169) said there were three smaller cusps adjacent to each side of the central cusp of the rachidian tooth, scanning electron micrographs show that there is variation in the number of cusps and that there are usually only two cusps present (see Figure 3). The inner and outer marginals are serrated with tiny cusps along their cutting edges.

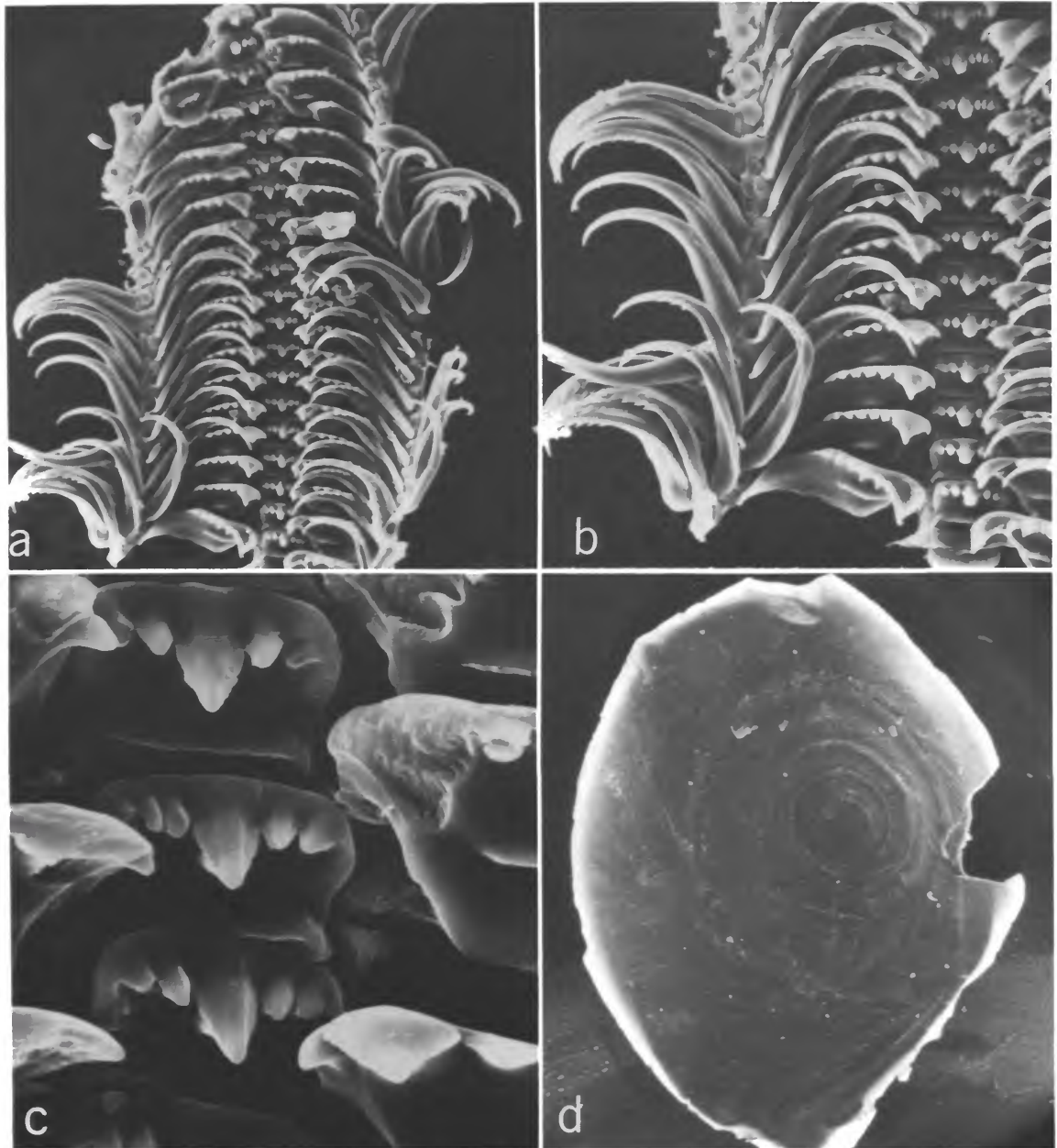


FIGURE 3.—SEM micrographs of radula and operculum of *Argyropeza divina* (USNM 276350, USBF Sta 5247, off Davao, Mindanao, Philippines, 247m): *a*, portion of radular ribbon, 260 \times ; *b*, close-up of half row of teeth showing tiny cusps on sickle-like marginal teeth, 420 \times ; *c*, detail of rachidian tooth, 1600 \times ; *d*, view of free surface of operculum showing spiral growth lines and eccentric nucleus, 50 \times .

ECOLOGY.—Museum records indicate that *A. divina* normally occurs on muddy bottom throughout its range. It is occasionally found on very fluid mud or on fine sand substratum. Station data from 75 samples indicate a bathymetric range of 58–923 meters and a mean depth range of 356 meters. Specimens from the western Pacific tend to be larger than those from the western Indian Ocean. The stomachs of several specimens from the Philippines were filled with fine sand, detritus, and a few foraminifer tests. Fecal pellets were ovoid, about 0.2 mm in length and comprised fine sand and detritus. The small radula and scythe-like lateral teeth indicate that *A. divina* ingests the sediment on which it lives and is probably a detritivore.

GEOGRAPHIC DISTRIBUTION.—(Figure 4). This species occurs throughout the Philippines and the

Indonesian Archipelago, including New Guinea. It is also found in Madagascar and in eastern Africa, from Zanzibar to Durban, South Africa. Originally collected in the Gulf of Oman, it probably occurs in suitable habitats throughout the Indian Ocean. *Argyropeza divina* is geographically sympatric with *A. izekiana* and *A. schepmaniana* in the Philippines and occurs with *A. izekiana* in New Guinea and in eastern Africa. All three species probably occur throughout the Indian Ocean and western Indo-Pacific Oceans.

Fossil RECORDS.—*Argyropeza divina* has been recorded as a fossil from the Pliocene of Okinawa (MacNeil, 1960:40, pl. 11: fig. 9). MacNeil remarked that the fossils did not appear to be separable from living *A. divina*. I have examined his specimens and concur that the fossils are conspecific with *A. divina*. I have also seen Pleis-

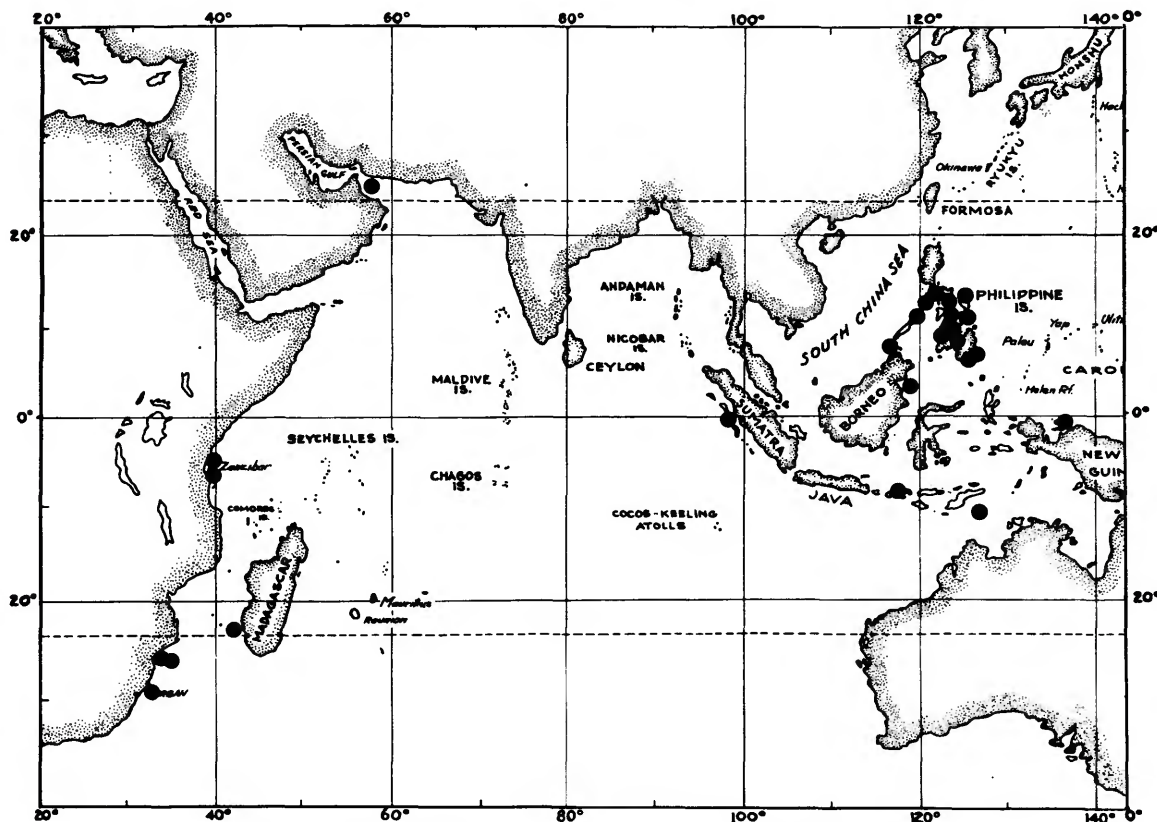


FIGURE 4.—Geographic distribution of *Argyropeza divina* Melvill and Standen.

tocene fossils deposited in the Australian Museum, Sydney, from the NW bank of the Kavavas River, near Riet, Gazelle Peninsula, New Britain, Papua.

Although Shuto (1969:65) noted that fossils he identified as *A. divina* from the Tertiary of Panay Id, Philippines differed slightly from typical *A. divina* in having a weakly granulated subsutural thread, I concur with him that they are probably conspecific. I believe Shuto (1969:65) was wrong in considering *A. spinigera* to be a valid species because examination of many specimens of *A. divina* shows that the arrangement of the basal spiral cords of *A. spinigera* falls within the range of variation of *A. divina*. I thus regard *A. spinigera* to be conspecific with *A. divina*.

A fossil species from the Pliocene of Java, described by K. Martin (1884:156, pl. 8: fig. 152) as *Cerithium spinigerum*, appears to be conspecific with *A. divina*. Tesch (1920:58, pl. 31: fig. 185) erroneously transferred *C. spinigerum* to the genus *Potamides* Brongniart, family Potamididae. His figures of the fossil specimens unequivocally depict *Argyropeza divina*.

SPECIMENS EXAMINED.—ARABIAN SEA: Gulf of Oman, 285 m (USNM 424891). EASTERN AFRICA: Baia de Laurencos Marques, Mozambique, 450 m (USNM 718491); near Inhaca, Baia de Laurencos Marques, Mozambique, 366 m (USNM 717907); 60 mi (96.0 km) NE of Durban, South Africa, 366 m (USNM 717246); 30 mi (48.0 km) NE of Durban, South Africa, 77 m (USNM 718107). MADAGASCAR: 40 mi (64.0 km) WSW off Tulear, 82 m (USNM 717535; 717516; 717613); Tulear (coll. B. Thomassin). PHILIPPINES: Tayabas Bay, off Tayabas Lt, Luzon, 347 m (USNM 285464); Tayabas Bay, off Tayabas Lt, Luzon, 152 m (USNM 285545); Tayabas Bay, off Tayabas Lt, Luzon, 291 m (USNM 285617); Tayabas Gulf, Luzon, (USNM 301903); Balayan Bay, Luzon, 291 m (USNM 235360); Regay Gulf, off Arena Pt, Luzon, 525 m (USNM 284289); off Matocot Pt, W Luzon, 311 m (USNM 775069; USNM 775068); off Matocot Pt, W Luzon, 402 m (USNM 775036); off Malavatuan Id, W Luzon, 186 m (USNM 774765); off Cape Santiago, W Luzon, 720 m (USNM 235094); off N Cebu, 130 m (USNM 280890); off Laus Pt, E Cebu, 302 m (USNM 288515); off Laus Pt, E Cebu, 291 m (USNM 288740); off Laus Pt, E Cebu, 296 m (USNM 290490); off Laus Pt, E Cebu, 320 m (USNM 289140); off Chocolate Id, N Cebu, 271 m (USNM 280842; USNM 259603); off Batag Id, N Samar, 700 m (USNM 289381); Sogod Bay, Leyte, 918 m (USNM 277844); off Tolosa, E

Leyte (USNM 277768); off Lusaran Lt, Guimaras, 175 m (USNM 281313); off Apo Id, S Negros, 468 m (USNM 291201); off Apo Id, S Negros, 464 m (USNM 286654); off Cabilao Id, W Bohol, 318 m (USNM 259839); off Ponson Id, Camotes Id, 347 m (USNM 298383); NW off Panglao Id (USNM 246937); off Pescador Id, Tanon Strait, 419 m (USNM 3925; USNM 281154); off Pescador Id, Tanon Strait, 548 m (USNM 274927); off Refugio Id, Tanon Strait, 472 m (USNM 302513); off Observatory Id, Palawan, 84 m (USNM 282594); W of Cape Melville, Balabac, 214 m (USNM 237927); Lagonoy Gulf, E Luzon, 914 m (USNM 787685); off Pt Tuguan, S Luzon 731 m (USNM 285409); off Sombrero Id, Balayan Bay (USNM 262305); off Sombrero Id, Balayan Bay, 291 m (USNM 262280; USNM 262309); off Sombrero Id, Balayan Bay, 216 m (USNM 774763); off Balanja Pt, SE Mindoro, 428 m (USNM 276250); off Pt Origen, Tablas, 133 m (USNM 281489); Regay Gulf, off N Burias, 192 m (USNM 312689; USNM 775113; USNM 280510); off N Ticao Id, 413 m (USNM 285275); off Pt Dumurug, Masbate, 249 m (USNM 284160); off Pt Dumurug, Masbate, (USNM 274690); off Talajit Id, SE Masbate, 245 m (USNM 298258; USNM 234204); off Adyagan Id, E Masbate, 245 m (USNM 775119); off Sibugay Id, E of Masbate, 247 m (USNM 277536); off Destacado Id, E of Masbate, 146 m (USNM 280585); off Destacado Id, 216 m (USNM 298062; USNM 285349); SE off Bantayan Id, 58.5 m (USNM 775050); off Cape Melville, Balabac Strait, 271 m (USNM 234741; USNM 297522); off Davao, Mindanao, 247 m (USNM 276350); Iligan Bay, N Mindanao, 923 m (USNM 290235); Pujada Bay, E Mindanao, 398.5 m (USNM 276497); Pujada Bay, E Mindanao, 313 m (USNM 276414); Pujada Bay, E Mindanao, 349 m (USNM 255602; USNM 276553); Pujada Bay, E Mindanao, 393 m (USNM 380152; USNM 277461); E of Bongo Id, 289 m (USNM 775058). BORNEO: Off Silungan Id, 558 m (USNM 279078; USNM 774761; USNM 774759); Sibuko Bay, Sipadan Id, 759 m (USNM 278704); Sibuko Bay, off Si Amil Id, 534 m (USNM 289713); Sibuko Bay, off Mabul Id, 475 m (USNM 278824). NEW GUINEA: 2 mi (3.2 km) S Konori Id, Mios Woendi Atoll, Padaido Ids, 457 m (ANSP 025362).

Argyropeza izekiana Kuroda

FIGURES 5-7

Argyropeza izekiana Kuroda, 1949:76-79, fig. 1 [holotype: NSMT; type-locality: off Tosa, Shikoku, Japan, 100 m]. *Argyropeza izekii* [sic] Kuroda.—Habe, 1964:42, pl. 12: fig. 27 [mistakenly cited as fig. 26].

DESCRIPTION.—*Shell*: small, about 4.6 mm long, elongate, turreted, comprising 8-11 whorls about 1.53 mm wide. There are 8 flat-sided adult whorls that are impressed suturally. Apical angle of shell

35 degrees. Adult whorls with two spiral cords, one near top and the other at bottom whorl. Lower spiral cord sometimes weak. Spiral cords weakly beaded. One microscopic spiral cord on upper portion of whorl adjacent to suture. Shell sculptured with 12–14 axial ribs per whorl that form small sharp nodes where they cross spiral cords. Axial ribs strongest on first two whorls of teleoconch. Body whorl lacks axial ribs, nodes and has weak spiral sculpture. Suture well-defined, set off by sloping inferior and superior sutural ramp on each whorl. Protoconch I smooth, comprising one and one-half whorls; protoconch II, consists of two whorls, sculptured with spiral band of ovoid pustules adjacent to suture and with two spiral cords, the lower of which is formed of two fine, spiral lirae. Sinusigera sinus deep and narrow. Abrupt transition from protoconch to teleoconch marked by distinct change in sculpture. Former varix normally on right dorsal side of body whorl. Sculpture of body whorl comprises two weak, widely-spaced, spiral cords below which are 4–5 spiral lirae that grow weaker as they approach the anterior siphonal canal. Aperture ovate-circular, a little more than one-fourth the length of the shell. Columella straight and with weak parietal callus. Anterior siphonal canal short and broad, opening to left about 45° from the shell axis. Outer lip convex, smooth, thin, slightly sinuous. Anal canal indistinct. Periostracum very thin, pale tan. Shell vitreous, shining, white, chalky in dead specimens. Operculum concave and with circumference slightly bent to fit snugly into aperture of shell.

Animal (preserved): Head-foot small in relation to shell, flesh colored. Snout bilobed at tip. Tentacles wide, more flat than round, and each with large black eye at outer side of tentacle base. Intestine large, filled with large ovoid fecal pellets composed of fine sand. Anus close to mantle edge. Buccal mass large, filling much of snout.

Radula (Figure 6): Radular ribbon long, taenioglossate. Rachidian tooth quadrate in shape, concave at sides, slightly convex at tip. Cutting edge of rachidian tooth serrated with long, sharply pointed central cusp that has a tiny lat-

TABLE 5.—*Argyropeza izekiana*, measurements of shell characters (in mm)

character	number	mean	range	sd
length	20	4.63	4.17–5.25	0.29
width	20	1.53	1.42–1.75	0.12
aperture length	20	1.09	1.0–1.25	0.84
shell length aper. length	20	4.27	3.86–4.67	0.23
# whorls	20	8.00	—	—
# spiral cords	20	2.00	—	—
# ribs	20	12.5	12–13	—
apical angle	20	35°	—	—

eral denticle on each side of the median portion of cusp. Base of rachidian tooth slightly convex with sharp lateral projection at each side. Basal plate of rachidian tooth thick. Lateral tooth trapezoidal, laterally elongate and with slightly curved top that is serrated with 7–8 pointed cusps. First cusp small, second large, wide, and pointed, and remainder small and decreasing in size toward the lateral portion of tooth. Blunt longitudinal projection extends from lower mid-portion of basal plate. Base of lateral tooth slightly concave. Inner marginal tooth long, slender, curved, sharply pointed at tip, and serrated with 5–6 sharp denticles on inner side and 5 denticles on outer side. Outer marginal tooth same as inner marginal, but lacking denticles on outer surface.

ETYMOLOGY.—Named in honor of Mr. Izeki.

COMPARATIVE REMARKS.—This species is distinguished from its congeners by 9.5 flat-sided, spinose whorls and by the presence of predominant transverse axial ribs that cross two weak spiral cords on each whorl. It is closest in sculpture to *Argyropeza divina*, which also has only two spiral cords per whorl and which is similarly spinose. *Argyropeza izekiana* is smaller and less attenuate than *A. divina* and has a shorter anterior siphonal canal than the latter species. The sutural ramp of *A. izekiana* is less pronounced than in *A. divina*.

It should be noted that Habe (1964:42, pl. 12: fig. 27) mistakenly cited fig. 26 of his plate in reference to *A. izekiana*. He also erroneously as-

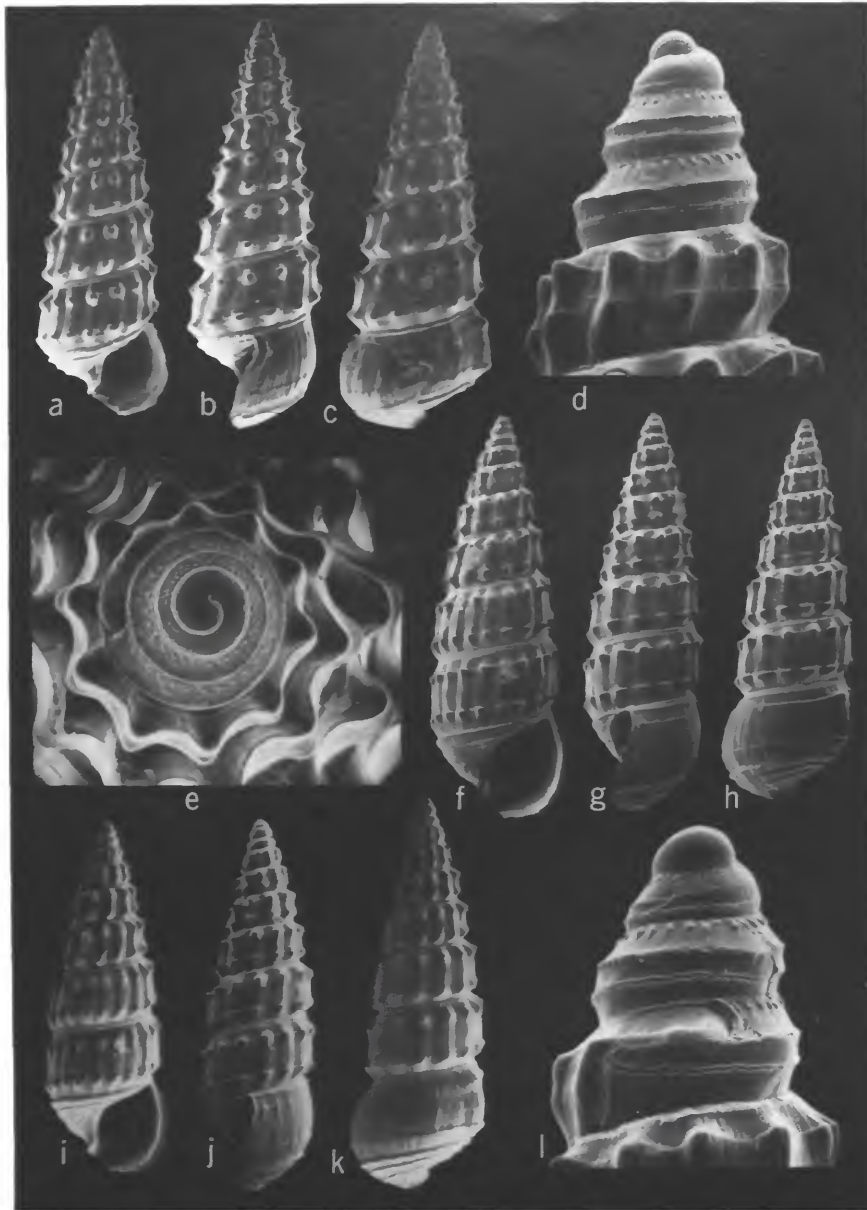


FIGURE 5.—*Argyropeza izekiana* Kuroda, showing variability in shell form and sculpture: *a-c*, apertural, side, and dorsal views of adult shells (note sinuous outer lip), 25 \times ; *d*, protoconch showing larval shell sculpture, 170 \times ; *e*, top view of protoconch showing disparity between larval and adult sculpture, 175 \times ; *f-h*, apertural, side, and dorsal views of adult shells: note stronger axial riblets in contrast to *a-c*; 30 \times ; *i-k*, apertural, side and dorsal views of adult shells with strong axial ribs (USNM 262893, USBF 5131, off Panabutan Pt, W Mindanao, Philippines, 49m, 24 \times); *l*, protoconch showing sinusigera notch, 215 \times . (*a-h* and *l* all USNM 774591, USBF Sta 5398, off Gigantangan Id, NW Leyte, Philippines.)

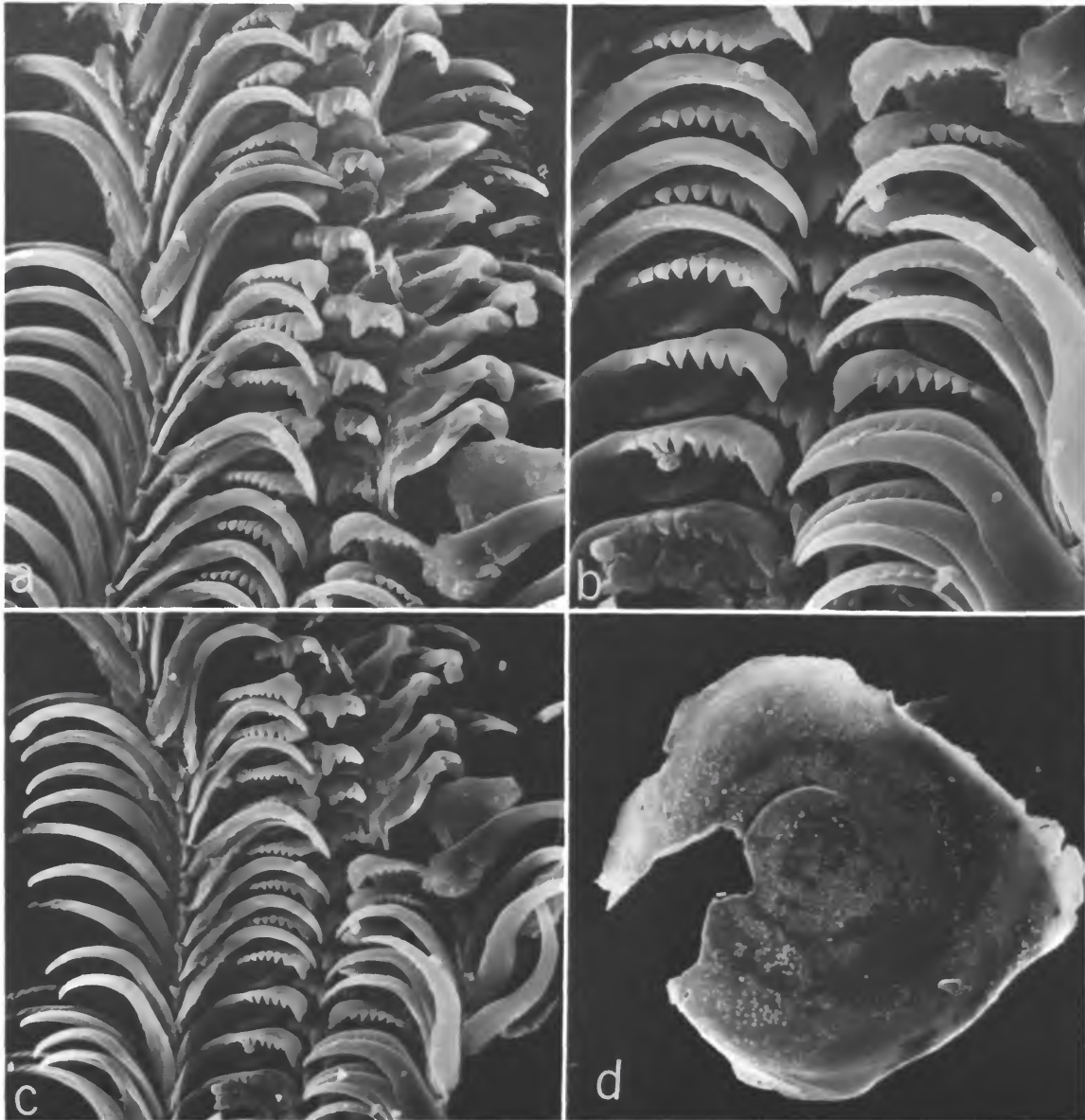


FIGURE 6.—SEM micrographs of radula and operculum of *Argyropeza izekiana* Kuroda (USNM 281893, USBF Sta 5392, off Adyagan Id, E Masbate, Philippines, 247m): a, worn portion of radular ribbon, 1000X; b, close-up of lateral and marginal teeth, 1500X; c, portion of radular ribbon, 650X; d, view of free portion of operculum, 100X.

signed it to the family Cerithiopsidae H. and A. Adams. Shuto's (1969:64) statement that *A. izekiana* is readily distinguished from other *Argyropeza* species in having the upper row of pustules much

closer to the suture is erroneous.

Bittium porcellanum Watson, 1886 is similar to this species. It looks very much like those morphs of *A. izekiana* that have prominent axial ribs, but

having examined the type-specimen, I regard *B. porcellanum* as distinct from *A. izekiana*. Moreover, the glossy shell with brown-tipped protoconch, and the depth at which it was collected (283 meters) indicate an assignment to a genus other than to *Bittium*. Watson (1886:559) was obviously uncomfortable in referring *B. porcellanum* to *Bittium* because he noted that it was an "aberrant form of *Bittium*."

ECOLOGY.—This species lives at depths ranging from 49 to 914 meters and has a mean bathymetric distribution of 307 meters (Table 3). Station data show that it is usually found on sediments comprised of mud or finegrained sand. The small radula and fecal pellets that consist of fine sediment and detritus point to a macrophagous feeding habit. Many specimens from the Philippines had drill holes that were moderately large and of the kind made by naticid snails (see Carriker and Yochelson, 1968).

GEOGRAPHIC DISTRIBUTION (Figure 7).—Most records of *A. izekiana* are from the western central Pacific where it is found from southern Japan

south to Indonesia, New Guinea, Australia, and east to New Caledonia and the New Hebrides. There is also a single record from Mozambique, in the western Indian Ocean. I have examined this material, which comprises three specimens, and find no essential differences in shell physiognomy between these specimens and those collected in the Philippines. Other *Argyropeza* species have a similar range and when more deep sea dredging occurs in the Indian Ocean it is probable that *A. izekiana* will be found in other localities. To my knowledge, no fossil records of this species exist.

SPECIMENS EXAMINED.—PHILIPPINES: off Matocot Pt, W Luzon, 384 m (USNM 277379); off Matocot Pt, W Luzon, 311 m (USNM 275955; USNM 278514); off Matocot Pt, W Luzon, 402 m (USNM 774607; USNM 278474); off Matocot Pt, W Luzon, 314 m (USNM 277982); off Matocot Pt, W Luzon, 362 m (USNM 276725); off Matocot Pt, W Luzon, 247 m (USNM 276060); off Malavatuán Id, W Luzon, 186 m (USNM 258402; USNM 775111); off Laus Pt, W Luzon, 296 m (USNM 774605); SW, off Corregidor Lt Luzon, 247 m (USNM 294331); SW, off Corregidor Lt Luzon, 216 m (USNM 278316); Lagonoy Gulf, E Luzon,

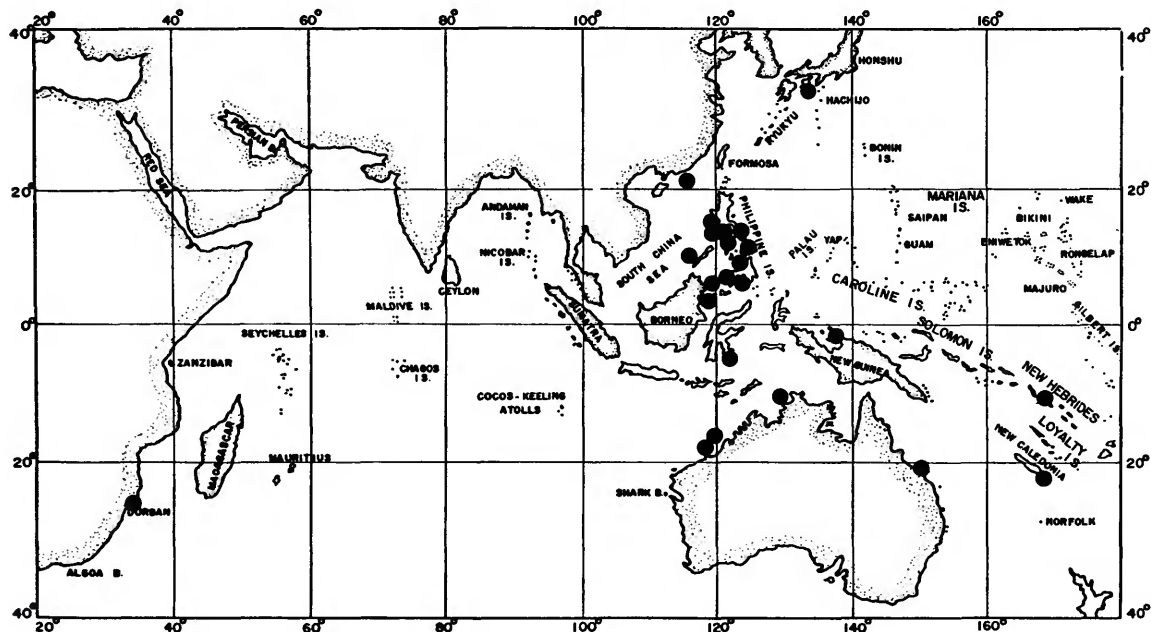


FIGURE 7.—Geographic distribution of *Argyropeza izekiana* Kuroda. The disjunct distribution may be due to poor sampling in other areas of the Indian Ocean.

914 m (USNM 282979; USNM 787684); Laguna de Bay, Luzon (USNM 283322); off Sombrero Id, Balayan Bay, 291 m (USNM 262299; USNM 787470); off Subaango, Mindoro, 296 m (USNM 244140); off Balanja Pt, SE Mindoro, 265 m (USNM 276212); off Pt Origen, Tablas, 133 m (USNM 281521); off Sibugay Id, E of Masbate, 197 m (USNM 774602); off Adyagan Id, E Masbate, 247 m (USNM 281893); off Destacado Id, E of Masbate, 146 m (USNM 775046); off Gigantangan Id, NW Leyte, 208 m (USNM 291296; USNM 774591); off Lauis Pt, E Cebu, 265 m (USNM 290603); off Lauis Pt, E Cebu, 302 m (USNM 775123); Cebu (USNM 235036); off Capitancillo Id, N Cebu, 333 m (USNM 287810); off Capitancillo Id, N Cebu, 345 m (USNM 289158); off Cabilao Id, W Bohol, 318 m (USNM 775116); off Ponson Id, Camotes Id, 347 m (USNM 775061); off Observatory Id, Palawan Pass, 79 m (USNM 775060); off Observatory Id, Palawan Pass, 84 m (USNM 775054); NE off Balabac Id, 124 m (USNM 787134); off Panabutan Pt, W Mindanao, 49 m (USNM 262865; USNM 262893); off Tagolo Pt, N Mindanao, 400 m (USNM 286753); E of Bongo Id, 289 m (USNM 230199); Port Pio V, Camiquin Id, (USNM 301346); off Dammi Id, Sulu Arch, 490 m (USNM 286270); off Dammi Id, Sulu Arch, 444 m (USNM 286468); N off Sibutu Id, Sulu Arch, 320 m (USNM 287330). CHINA SEA: Off Pratas Id, 274 m (USNM 290767; USNM 309210); off Pratas Id, 161 m (USNM 285042); off Pratas Id, 622 m (USNM 284343); off Pratas Id, 420 m (USNM 284687; USNM 312743; USNM 296999); off Pratas Id, 256 m (USNM 285101); off Pratas Id, 274 m (USNM 274663; USNM 259537; USNM 284958); off Pratas Id, 380 m (USNM 277295); off Pratas Id, 223 m (USNM 284561). BORNEO: Off Silungan Id, 558 m (USNM 774760; USNM 775120); Darvel Bay, off Sibutu Id, 296 m (USNM 287020). CELEBES: Buton Strait, 68 m (USNM 279847). MOZAMBIQUE: Near Inhaca Id, 366 m (USNM 775063). NEW CALEDONIA: Off S New Caledonia, 22° 17'S, 167° 14'E, 425-430 m (MNHN). JAPAN: Tosa Bay, Shikoku, 80-150 m (AMS). NEW HEBRIDES: Espirito Santo (AMS). AUSTRALIA: 150 mi (240.0 km) W of Cape Leveque, WA, 16° 16'S, 120° 45'E, 330 m (AMS); N of Cape Leveque, WA, 14° 07'S, 122° 52'E, 256 m (AMS); 210 mi (336.0 km) N of Broome, WA, 14° 50'S, 121° 45'E, 230 m (AMS); 150 km NW of Melville Id, NT, 9° 53'S, 130° 2'E, 205 m (AMS); 386 km N of Goulburn Id, NT, 8° 02'S, 133° 50'E, 108 m (AMS); NE of Lady Musgrave Id, Qld, 23° 38.8'S, 152° 45.5'E, 365 m, HMAS *Kimbla*, Stn 24 (AMS); 25 mi (40.0 km) E of Lady Musgrave Id, Qld, 22° 44'S, 152° 49'E, 357 m (AMS); E of Lady Elliott Id, Qld, 24° 00'S, 153° 06.5'E, 531-476 m (AMS).

Argyropeza schepmaniana Melvill

FIGURES 8-9

Argyropeza schepmaniana Melvill, 1912:246-247, pl. 12: fig. 11 [holotype: BM(NH) Reg. No. 1912.9.17.42; type-locality:

Merkan Coast, Charbar, Persian Gulf, Iran, 73 m].—Thiele, 1918:120.—Hornung and Mermod, 1926:207-208.—Kuroda, 1949:78.—MacNeil, 1960:40, pl. 2: fig. 1.

DESCRIPTION.—*Shell*: Small, about 4.14 mm long, 1.28 mm wide, elongate, turreted, consisting of 8 adult whorls and having apical angle of 32°. Whorls convex and impressed suturally. Adult whorls sculptured with three primary spiral cords and a fourth very thin spiral cord on the upper portion of the whorl adjacent to suture. First two primary spiral cords closer to each other than to third, which is lower on whorl. Axial ribs that are slightly transverse, about 13-14 per whorl, form small, sharp nodules or spines where they cross the spiral cords creating an overall spinose reticulate effect. Suture deep and distinct. First two whorls of teleoconch have only two spiral cords. Sculpture less distinct on body whorl. Protoconch I smooth, one and a half whorls; protoconch II two whorls, sculptured with a spiral band of ovoid pustules adjacent to suture and with two equidistant spiral cords at mid-portion of whorl. Spiral cords sometimes weakly pustulate and bottom one consisting of two fine spiral lirae. Sinusigera sinus moderately deep and narrow. Sharp transition from protoconch to teleoconch marked by sinuous growth scar. Several former varices usually present on penultimate and body whorl opposite outer lip. Sculpture of body whorls same as other whorls except for 5-6 thin spiral cords at base of whorl, becoming weaker at anterior siphonal canal. Aperture ovate, a little over one-

TABLE 6.—*Argyropeza schepmaniana*, measurements of shell characters (in mm)

character	number	mean	range	sd
length	20	4.14	4.58-3.75	0.27
width	20	1.28	1.17-1.42	0.08
aperture length	20	0.77	0.67-0.92	0.07
shell length aper. length	20	5.40	4.91-6.09	0.38
# whorls	20	8.00	—	—
# spiral cords	20	2.00	—	—
# ribs	20	13.5	13-14	—
apical angle	20	32.0	—	—

fifth the length of the shell. Columella smooth, straight with thin, shiny callus. Outer lip thin, smooth, and slightly curved at edge. Anterior siphonal canal short, broad, and slightly curved

to left. Anal canal indistinct. Shell shiny, white, chalky in dead specimens. No periostracum observed. Animal, operculum, radula, eggs and larvae unknown.

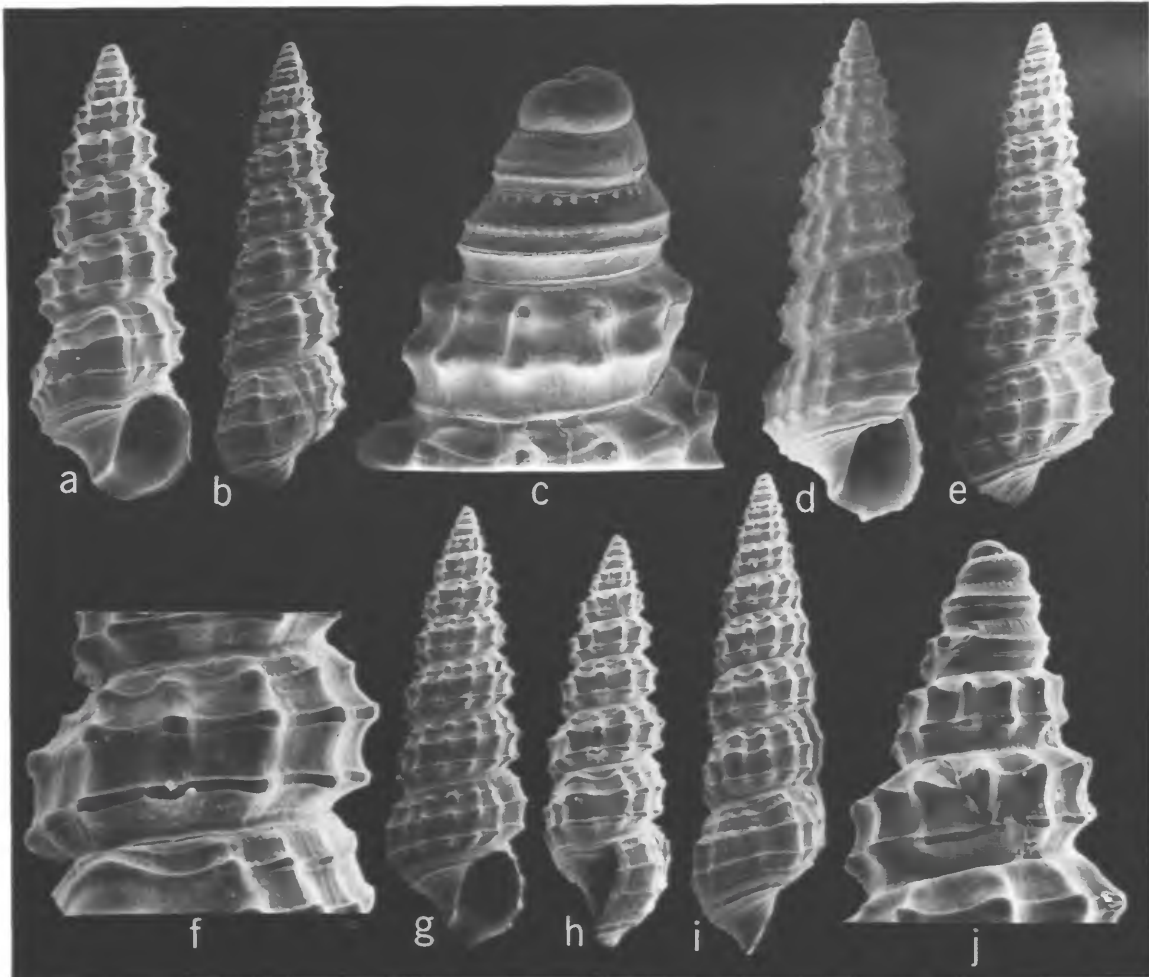


FIGURE 8.—*Argyropeza schepmaniana* Melvill: *a, b*, typical adult shells showing overall sculpture and varices (USNM 288300, USBF Sta 5426, off Mantaquina Id, E Palawan, Philippines, 49m, *a*, 34 \times ; *b*, 26 \times); *c*, protoconch showing details of larval shell sculpture, USNM 285913, USBF Sta 5348, Palawan Pass, Philippines, 30 \times ; *d, e*, adult shells (USNM 285913, locality data as in *c*; *d*, 30 \times ; *e*, 32 \times); *f*, detail of sculpture on adult whorl showing three spiral cords and nodules (USNM 263526, Sta 5097, off Corregidor Id, Luzon, Philippines 55m, 75 \times); *g-i*, adult shells, apertural, side and dorsal views showing former varices (USNM 263526, locality data is in *f*; *g*, 22 \times ; *h* and *i*, 26 \times); *j*, detail of protoconch and early whorls showing sculptural disparity between larval and adult shell (USNM 263526, locality data as in *f*; 100 \times).

ETYMOLOGY.—Named after M. A. Schepman, who described the mollusks of the *Siboga* Expedition.

COMPARATIVE REMARKS.—This species is distinguished from its congeners by a slender shape, small aperture, and a high aperture-length to shell-length ratio. It is distinctive in that the first two whorls of the teleoconch bear two spiral cords while the remaining whorls each have three nodulose spiral cords. Numerous sharp nodules on the spiral cords give the shell a distinctive spiny look.

Argyropeza schepmaniana resembles *A. verecunda* Melvill and Standen 1903 in sculpture, but the former is much larger and does not have four spiral cords on most of the whorls of the teleoconch. *Argyropeza verecunda* is not well known and when more comparative material is available it may prove to be a subspecies of *A. schepmaniana*.

The sculpture and form of *Scala nodifera* Thiele, from the western Indian Ocean, looks very much like that of *A. schepmaniana* except that the upper teleoconch has only axial sculpture present. The shell of *Scala nodifera*, as depicted by Thiele (1918, pl. 11: fig. 6), is missing the aperture, but the marginal tooth of the radula as depicted in Thiele's (1918: pl. 34: fig. 20) illustration, is very different from those of *Argyropeza* species.

I have included MacNeil's (1960:40) citation of *A. schepmaniana* in the synonymy, but like MacNeil, have some doubt about the identity of the specimen he figured. Although it looks like *A. schepmaniana*, the length (9.1 mm) of the specimen is far beyond the range of numerous samples I have examined (2.3–5.9 mm). For this reason, I am hesitant to regard it as being conspecific with *A. schepmaniana* and am inclined to consider it as a closely related fossil species of *Argyropeza*.

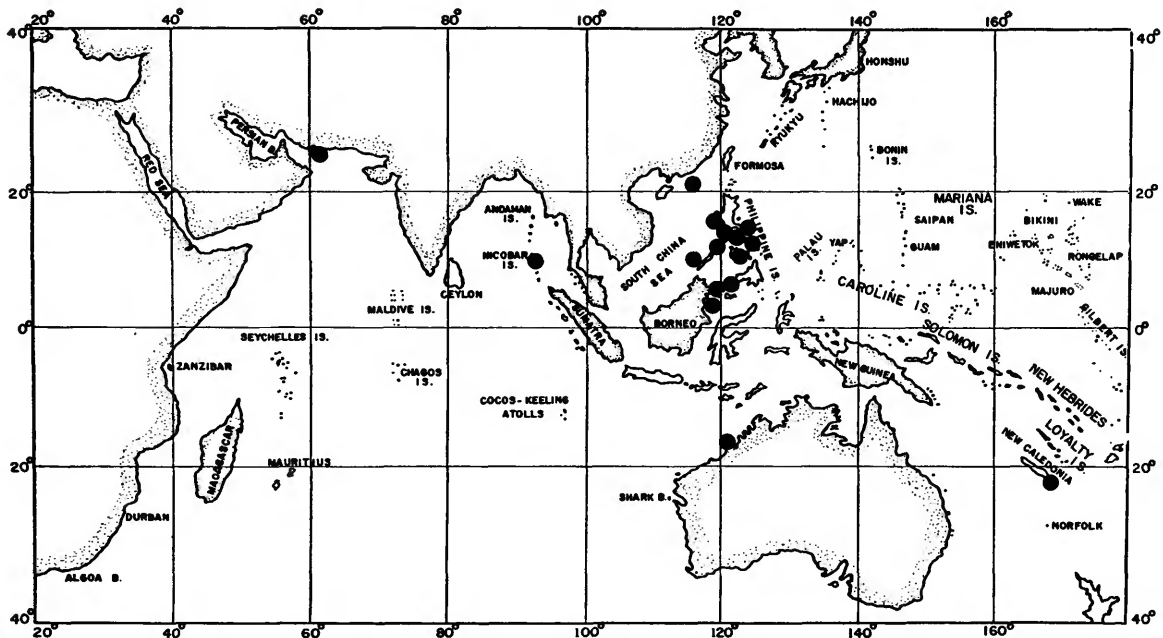
ECOLOGY.—*Argyropeza schepmaniana* has a bathymetric range of 33–914 meters and a mean depth range of 145 meters. It lives on muddy bottom and is sometimes found with *A. divina* or *A. izekiana*. Although nothing is known of the animal, it presumably has a radula similar to the other species of *Argyropeza* and is probably a detritivore. The protoconch and the sinusigera notch indicate

a pelagic larval phase and a mode of development identical to those of its congeners.

GEOGRAPHIC DISTRIBUTION (Figure 9).—Originally described as an uncommon species from the Arabian Sea, *A. schepmaniana* is abundant in the Philippines and South China Sea where it is sympatric with *A. divina* and *A. izekiana*. Specimens I examined from New Caledonia were typical. This species probably has a wider distribution in the Western Pacific.

FOSSIL RECORD.—MacNeil (1960:40) cited a single specimen from the Miocene of Okinawa as a possible fossil record of *A. schepmaniana*, but this is not enough material upon which to base a final decision (see discussion above under "Systematic Remarks"). I have examined Pleistocene fossils of *A. schepmaniana* deposited in the Australian Museum, Sydney, from the NW bank of the Kavavas River, near Riet, Gazelle Peninsula, New Britain, Papua.

SPECIMENS EXAMINED.—AUSTRALIA: 100 mi (160.0 km) NW of Broome, WA, 16°58'S, 120°47'E, 194 m (AMS). PHILIPPINES: Lagonoy Gulf, E Luzon, 914 m (USNM 289593); Lagonoy Gulf, E Luzon, 86 m (USNM 219366); off Sueste Pt, W Luzon, 46 m (USNM 774606); off Malavatuan Id, W Luzon, 33 m (USNM 278182); off Matocot Pt, W Luzon, 402 m (USNM 775039); off Arena Pt, Ragay Gulf, Luzon, 525 m (USNM 787469); NW off Corregidor Lt, 68 m (USNM 262440); USNM 262158); S off Corregidor Lt, 55 m (USNM 263526; USNM 291474); S off Corregidor Lt, 69 m (USNM 262777); S off Corregidor Lt, 64 m (USNM 291566); USNM 257320; USNM 257223; USNM 257224); SW off Corregidor Lt, 247 m (USNM 294299); off Sombrero Id, Balayan Bay, 216 m (USNM 262034); N off Marinduque, 353 m (USNM 277067); SE off Bantayan Id, 58.5 m (USNM 775051); N off Marinduque, 91 m (USNM 276097); Daram Channel, W Samar, 58.5 m (USNM 280754); off N Badian Id, W Samar, 64 m (USNM 258062); off Linbancauyan Id, W Samar, 91 m (USNM 277684); off Batag Id, N Samar, 548 m (USNM 289074); off Sibugay Id, E of Masbate (USNM 291740); off Balabac (USNM 787134); Linapacan Strait, off Observatory Id, Palawan, 84 m (USNM 282846; USNM 291658); Palawan Pass, (USNM 285913); off Observatory Id, Palawan Pass, 84 m (USNM 787681; USNM 775053; USNM 291619); off Observatory Id, Palawan Pass, 79 m (USNM 775045); off Tocihi Pt, Tawi-tawi, 90 m (USNM 274417); off Panabutan Pt, W Mindanao, 48 m (USNM 293359; USNM 282126; USNM 255745); off Panabutan Pt, W Mindanao, 49 m (USNM 262898; USNM 262892; USNM 262893; USNM 262869;

FIGURE 9.—Geographic distribution of *Argyropeza schepmaniana* Melvill.

USNM 262896); off Panabutan Pt, W Mindanao, 69 m (USNM 293562; USNM 787682); E of Burias, 192 m (USNM 244143). CHINA SEA: Off Pratas Id, 161 m (USNM 284988). NEW CALEDONIA: Off S New Caledonia; 22°17'S; 167°14'E, 425–530 m (MNHN).

Argyropeza leucocephala (Watson)

FIGURE 10

Brittium leucocephalum Watson, 1886:558–559, pl. 38: fig. 7 [holotype: BM(NH) Reg. No. 1887.2.9.1749; type-locality: reefs off Honolulu, Hawaii, 73 m].—Tryon, 1887:157, pl. 31: fig. 31.

Cerithium (Brittium) leucocephalum (Watson).—Kobelt, 1898: 259, pl. 44: fig. 9.

DESCRIPTION.—Shell small, about 3.88 mm long and 1.20 mm wide, white, porcellaneous, elongate, turreted, with a length-width index of 5.10 and comprising 7 convex adult whorls with an apical angle of 22°. Each adult whorl sculptured with three spiral cords crossed by 16–17 weak, axial riblets forming sharp nodules at intersections. Apical angle of Protoconch I consists of 1.5 smooth whorls except for weak spiral line of

TABLE 7.—*Argyropeza leucocephala*, measurements of shell characters (in mm)

character	number	mean	range	sd
length	10	3.88	3.60–4.36	0.248
width	10	1.20	1.08–1.28	0.076
aperture length	10	0.76	0.64–0.88	0.082
shell length aper. length	10	5.10	—	—
# whorls	10	7.00	—	—
# spiral cords	10	3.00	—	—
# ribs	10	16.5	16–17	—
apical angle	1–	—	—	—

pustules at base of suture. Protoconch II with two distinct spiral cords on mid-portion of whorls and a spiral row of elongate but small pustules at base of suture. Numerous microscopic pustules cover lower two-thirds of whorl. Protoconch terminated by distinct sinusigera sinus. Transition from protoconch to teleoconch sharply defined. First three

juvenile whorls sculptured with two spiral cords adorned with sharp nodules and weak axial riblets. Body whorl inflated, sculptured with three spiral nodulose cords and very weak axial riblets.

Base of body whorl slightly concave and with three thin spiral lirae. Suture deeply impressed, forming slight sutural ramp on upper portion of each whorl. Aperture ovate, about one-fifth the

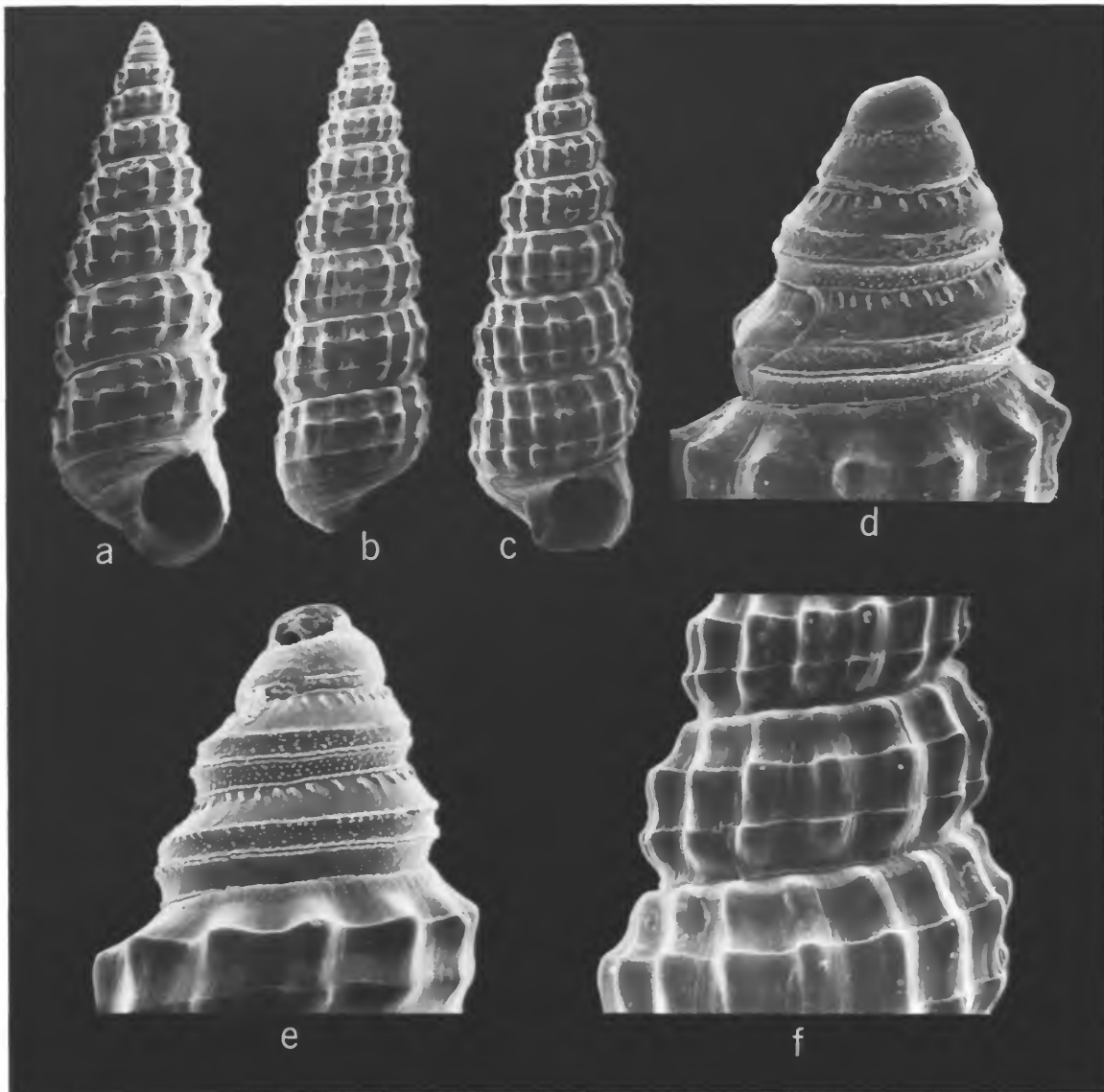


FIGURE 10.—*Argyropeza leucocephala* Watson (USNM 783499, Mamala Bay, Oahu, Hawaii, 200m): *a-c*, adult shells showing overall sculptural pattern, 30 \times ; *d*, protoconch showing sinusigera notch, 200 \times ; *e*, protoconch showing larval sculpture, 200 \times ; *f*, detail of adult whorls showing two spiral rows of nodules, 85 \times .

length of the shell. Outer lip smooth, rounded. Anterior siphonal canal shallow, but distinct. No anal canal. Columella smooth, concave, and with slight columellar lip.

ETYMOLOGY.—Greek *leukon* ("white") plus *kephale* ("a head").

COMPARATIVE REMARKS.—This species most closely resembles *A. schepmaniana* but may be distinguished from it by larger size and lack of prominent varices. I have seen *A. leucocephala* specimens only from the Hawaii area, where it was first discovered and described as a *Bittium* species by Watson (1886). It is possible that *A. leucocephala* may be a large morph of *A. schepmaniana*. Our present knowledge of *A. schepmaniana* shows that it is geographically limited to the western Pacific; however, should new specimens turn up in the area between Hawaii and the western Pacific, the status of these two species will have to be reevaluated.

Tryon (1887:157) thought this species was similar to *Bittium perparvulum* Watson, 1887 but the protoconch of the latter lacks the two spiral cords and is much different. Kobelt (1898:259) assigned it to *Cerithium*, but the size, protoconch, and overall physiognomy of *A. leucocephala* exclude it from this genus.

The holotype of *A. leucocephala* is an immature individual specimen with a slightly damaged aperture and worn protoconch but it seems to agree with specimens recently dredged in Hawaiian waters and figured in this paper (Figure 10). Watson's (1886) original description appears to closely match that of *A. schepmaniana*. The protoconch that Watson (1886) mentioned had a white tip and brownish lower part, is identical to those of other *Argyropeza* species. The general shell physiognomy and the vitreous aspect of the shells of fresh specimens would indicate that Watson's species should be more properly referred to the genus *Argyropeza* than to *Bittium*.

ECOLOGY.—Specimens of *A. leucocephala* in hand comprise only a limited sample and the radula, operculum, and soft parts are unknown. The sinusigera protoconch points to a pelagic larval phase and suggests that this species has a wider geographic range than is now known. Nothing is

known of the ecology except that Hawaiian specimens have been dredged at 200 m on a fine sandy bottom. There are no fossil records of this species and the geographical range, based upon available records, is limited to the Hawaiian Islands.

SPECIMENS EXAMINED.—Mamala Bay, Oahu, Hawaii, 200 m (USNM 783499); Reefs off Honolulu, Hawaii, 73 m (BM(NH) Reg. No. 1887.2.91749).

Argyropeza verecunda Melvill and Standen

FIGURES 11–12

Cerithium verecundum Melvill and Standen, 1903:300, pl. 21: fig. 5 [2 paratypes: BM(NH) Reg. No. 1903.12.15.90–92; 2 paratypes: ANSP 164787; type-locality: 24°58'N, 56°54'E, Gulf of Oman, 285 m].

Cerithium pervicax Melvill, 1904:161, pl. 10: fig. 7 [6 paratypes: BM(NH) Reg. No. 1905.7.14.21–26; 3 paratypes: ANSP 97739; type-locality: 24°58'N, 56°54'E, Gulf of Oman, 285 m].

?*Obolortio elongella* Melvill, 1910:6, pl. 1: fig. 14 [holotype: BM(NH) Reg. No. 1912.8.16.96, Mekran Coast, off Charbar, Pakistan].

DESCRIPTION.—Shell small, about 2.77 mm long, 0.98 mm wide, thin, moderately elongate, turreted, and consisting of 8 adult whorls that are convex and with impressed sutures. Apical angle of 32 degrees. Adult whorls each sculptured with 4 spiral cords and 14–15 axial ribs that form small nodes where they cross spiral cords giving overall nodular, cancellate appearance. Earliest whorls of teleoconch have two weak spiral cords. Re-

TABLE 8.—*Argyropeza verecunda*, measurements of shell characters (in mm)

character	number	mean	range	sd
length	5	2.77	2.42–3.08	0.29
width	5	0.98	0.91–1.08	0.07
aperture length	5	0.55	0.50–0.58	0.04
shell length aper. length	5	5.04	4.84–5.04	0.17
# whorls	5	8.00	—	—
# spiral cords	5	4.00	—	—
# ribs	5	14.5	14–15	—
apical angle	5	32°	—	—

maintaining whorls of teleoconch each with four, equidistant spiral cords that are most fully developed on the penultimate and body whorls. First spiral cord weak and on sutural ramp; remaining

spiral cords strong. Body whorl moderately inflated and with 4–5 spiral cords on base around siphonal constriction. Former varices randomly distributed but weak. Protoconch I smooth, one

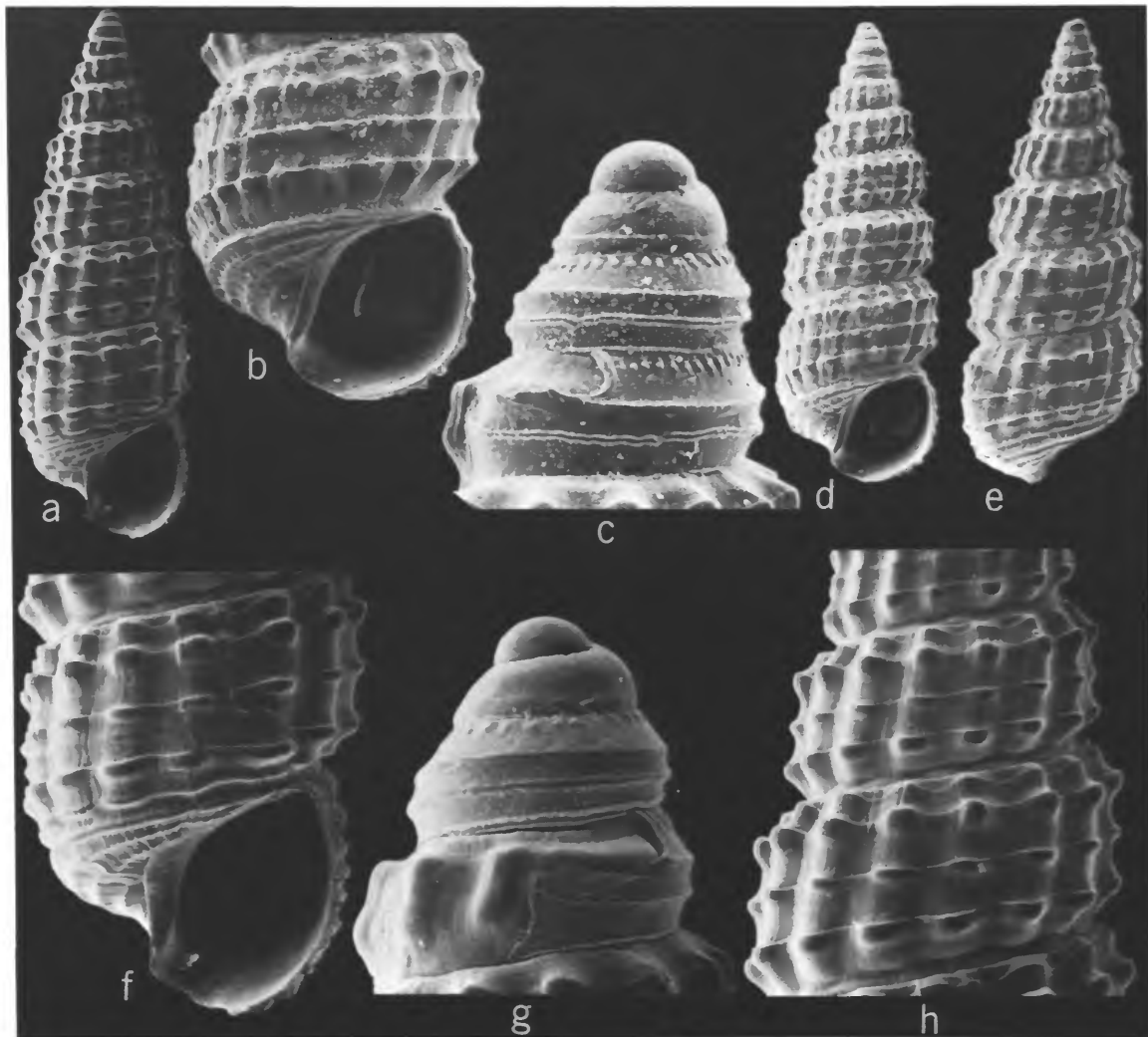


FIGURE 11.—*Argyropeza verecunda* (Melville and Standen): *a*, specimen from Gulf of Oman, showing overall sculptural pattern, 34 \times ; *b*, detail of aperture showing anterior siphonal canal, 75 \times ; *c*, protoconch, showing sinusigera notch and larval sculpture, 250 \times ; *d*, *e*, specimens from Andaman Sea showing overall sculptural pattern, 44 \times ; *f*, detail of aperture showing anterior siphonal canal, and sculptural details of body whorl, 66 \times ; *g*, protoconch showing sinusigera notch, 250 \times ; *h*, detail of adult whorls showing four spiral rows of nodules, 75 \times . (*a*, *f*–*h* all USNM 424893, Gulf of Oman, Arabian Sea 285m; *b*–*e* all ANSP 293078, *Anton Bruun* Sta 37A, IIOE, 13°28'N; 97°19'E, 91.2 km NW of Tavoy, Andaman Sea, S Burma, 39m.)

and one-half whorls; protoconch II, two whorls, sculptured with spiral band of pustules adjacent to suture and with two spiral cords on mid-portion of whorl. Sinusigera sinus deep and narrow; marked transition in sculpture from protoconch to teleoconch. Aperture ovate about one-fifth the length of the shell. Anterior siphonal canal short and broad, slightly curved to the left. No anal canal present. Columella straight with slight parietal callus. Outer lip thin, smooth, and semicircular in outline. Shell vitreous shining white; chalky in dead collected specimens. Operculum, radula, soft parts, eggs, and larvae unknown.

ETYMOLOGY.—Latin *verecundas* ("unassuming").

COMPARATIVE REMARKS.—*Argyropeza verecunda* is the smallest species in the genus and except for size, is morphologically very similar to *A. shep-*

maniana. When more material is available for comparison *A. verecunda* may prove to be either a subspecies or a phenotypic variation of *A. shepmaniana*. Although similar, *A. verecunda* is distinguished from *A. shepmaniana* by its small size and by four spiral cords on most of the whorls of the teleoconch. It also has fewer and less prominent varices and axial ribs that are most evenly spaced.

Melville and Standen (1903:300) originally referred this species to the genus *Cerithium* Bruguière and noted that some individuals in their sample were smaller and less ventricose. They did not, however, believe this difference was a specific one. Later, Melville (1904:161), pointing out a few minor morphological differences, named the smaller morphs *Cerithium pervicax*. I have examined the types and consider these slight sculptural

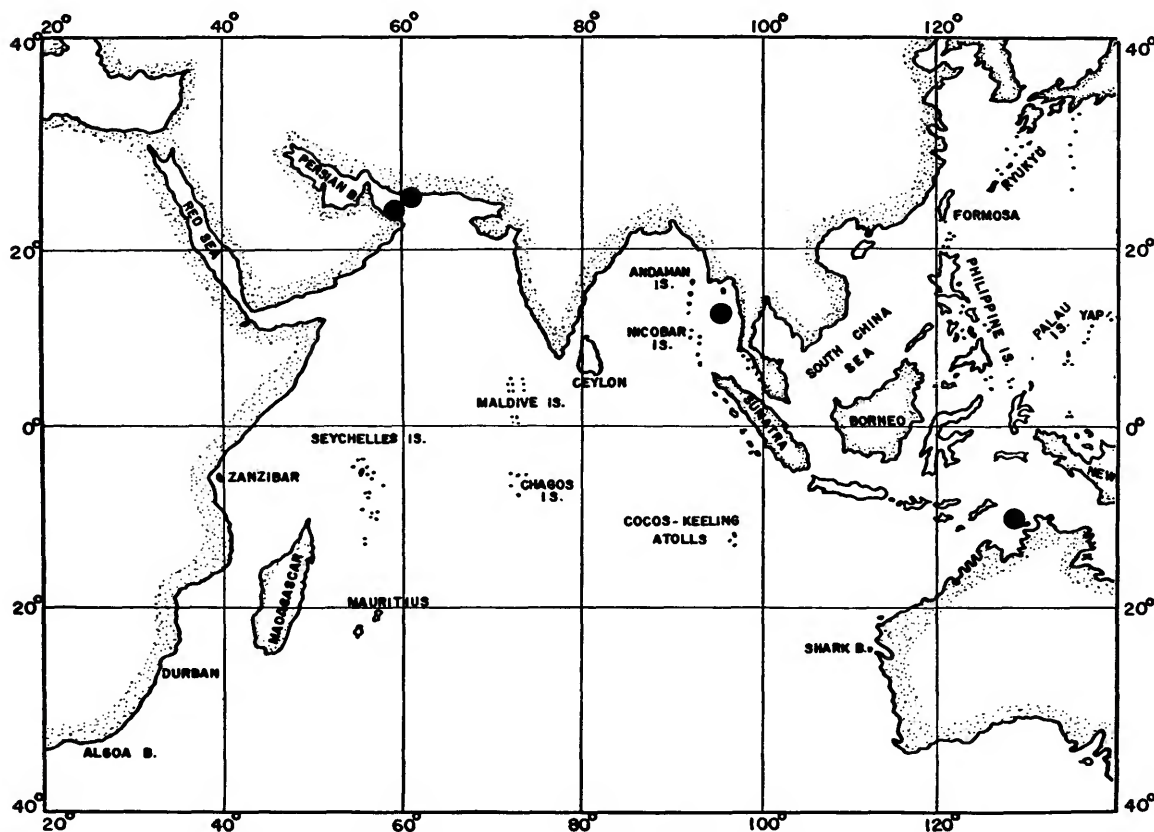


FIGURE 12.—Geographic distribution of *Argyropeza verecunda* Melville and Standen.

differences to be within the normal range of variation *A. verecunda*. Additional specimens from the Andaman Sea and the Philippines have confirmed this interpretation. I thus regard *A. pervicax* as a synonym of *A. verecunda*. *Obtortio elongella* Melvill, 1910 also appears similar to *A. verecunda*. I have not seen the types of the former, but the illustration in Melvill (1910, pl. 1, fig. 14) looks very much like *A. verecunda*. The figured syntype of this species (BM(NH) Reg. No. 1912.8.1b.96) looks like an immature specimen and does not show a distinct anterior siphonal canal. This may also be due to a damaged aperture. I have not examined any other material; consequently, I am hesitant to place it in the synonymy of *A. verecunda*.

ECOLOGY.—The few records that exist indicate that *A. verecunda* is a lower sublittoral-bathyal species that has a bathymetric range of 39–285 meters and a mean depth range of 162 meters. Melvill (1904:161) recorded it (cited as *Cerithium*

pervicax) to be abundant on a shell-sand bottom at 284 meters and specimens from the Andaman Sea were collected at 39 meters on a sand-shell substratum. It is the only species that is not found on muddy, fine grained substrata, but records are sparse and future collecting may reveal better ecological information.

GEOGRAPHIC DISTRIBUTION (Figure 12).—*Argyropeza verecunda* is an uncommon species. Most records are from the northern latitudes of the Indian Ocean. A record from Northern Australia indicates that this species probably has a wider distribution. There are no fossil records.

SPECIMENS EXAMINED.—INDIAN OCEAN: 24°58'N, 56°54'E, Gulf of Oman, 385 m (BM(NH)); ANSP 164787; NM Victoria F8547; Gulf of Oman (USNM 424893); (AMS 6 specimens); Mekran Coast, off Charbar, Pakistan (BMNH); 57 mi (91.2 km) NW of Tavoy Id, Andaman Sea, 39 m (ANSP 293078, *Anton Bruun* Sta 37A). AUSTRALIA: 150 km NW of Melville Id, Northern Territory, 9°53'S, 130°2'E, 205 m (AMS).

Appendix

The following list of 14 species includes taxa that are easily confused with or erroneously assigned to the genus *Argyropeza*. They are listed in alphabetical order by species but are cited under the generic names given by original authors.

- Cerithium bicanaliferum* Brazier, 1877:317. (= *Cerithium trigonostomum* Melvill, 1910; = *Argyropeza involuta* Thiele, 1918.) This species, frequently collected with some *Argyropeza* species, may easily be distinguished from them by a large, swollen body whorl, marked anal canal, and smooth protoconch of 2.5 whorls.
- Bittium diplax* Watson, 1886:555–556, pl. 28: fig. 4. This species has an overall angulate appearance and may be confused with some *Argyropeza* species; however, the shell is nonvitreous and the protoconch consists of only 2.5 whorls and lacks the sinuigera sinus so typical of *Argyropeza* species.
- Argyropeza doriae* Hornung and Mermod, 1926: 208–209, figure. Neither the protoconch, shell sculpture, nor the aperture of this species are indicative of an assignment to *Argyropeza*.
- Obortio elongella* Melvill, 1910:9, pl. 1: fig. 14. The figured syntype of this species (BM(NH) Reg. No. 1912.8.16.96) may be an immature specimen and appears to lack an anterior canal. It is probably a true *Fenella*. I have not seen any other specimens. Should this species truly have an anterior canal it would be very close to *Argyropeza verecunda*.
- Bittium fuscocapitulum* Hedley and Petterd, 1906: 217–218, pl. 38: figs 10–11. The protoconch of this species is identical to those of other *Argyropeza* taxa but the sculpture and shape of the shell is so different that I am hesitant to assign this species to *Argyropeza*. Only dead shells were collected and I have not seen any other specimens. The radula and operculum are unknown.
- Argyropeza involuta* Thiele, 1918:120, pl. 9: figs. 20, 20a. This nominal species is conspecific with *Cerithium bicanaliferum* Brazier, 1877 and is not an *Argyropeza* species.
- Obortio liratus* Ludbrook, 1941:9–10, pl. 4: fig. 24. I have seen only the figure of this species and although it looks as if it may be assigned to *Argyropeza*, examination of more specimens is necessary before a decision may be made.
- Argyropeza melvilli* Schepman, 1909:170, pl. 12: fig. 1. This is an *Abyssochrysos* species.
- Bittium perparvulum* Watson, 1887:554–555, pl. 38: fig. 3. Although the sculpture and shape of the holotype look very much like those of *Argyropeza* species, the shell is non-vitreous and the smooth protoconch of 2.5 whorls is unlike those of any *Argyropeza* taxa. The status of *B. perparvulum* remains uncertain.
- Argyropeza suvaensis* Ladd, 1977:15–16, pl. 1: fig. 3; pl. 21: fig. 8. This early Miocene fossil is a synonym of *Abyssochrysos melvilli* (Schepman, 1909) and is not in the *Argyropeza* group (Houbbrick, 1979:14).
- Argyropeza tomlini* Barnard, 1963:143–144, fig. 27f. I have recently shown that this species is a synonym of *Abyssochrysos melvilli* (Schepman 1909) and not an *Argyropeza* species (Houbbrick, 1979:11–12).
- Cerithium trigonostomum* Melvill, 1910:10, pl. 1: fig. 5. This is a synonym of *C. bicanaliferum* Brazier (see remarks under this taxon and under *Argyropeza involuta* Thiele).
- Obortio vulnerata* Hedley, 1909:439, pl. 14: fig. 52. Examination of the holotype (AMS) convinces me that this taxon is not within the *Argyropeza* group. It does not have an anterior canal.
- Fenella xanthacme* Melvill, 1904:56, pl. 5: fig. 16. I

have examined the figured syntype of this species (BM(NH) Reg. No. 1904.7.29. 17–19) from the Gulf of Oman and believe that it is an epitoniid of the subfamily Nystiellinae rather than a *Fenella* or *Argyropeza* species. What ap-

pears to be an anterior canal is merely a break in the outer lip; moreover, the elongate protoconch with pronounced axially costate whorls is very different from those of other *Argyropeza* taxa.

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