

Classification and
Systematic Relationships of the
Abyssochrysidae, a Relict Family
of Bathyal Snails
(Prosobranchia: Gastropoda)

RICHARD S. HOUBRICK

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ABSTRACT

Houbrick, Richard S. Classification and Systematic Relationships of the Abyssochrysidæ, a Relict Family of Bathyal Snails (Prosobranchia; Gastropoda). *Smithsonian Contributions of Zoology*, number 290, 21 pages, 11 figures, 1979.—The nomenclatural history of the Abyssochrysidæ and the uncertainty of their taxonomic placement and phylogenetic relationships are discussed. One genus and two species are recognized, *Abyssochrysos melanoides* Tomlin and *A. melvilli* (Schepman), both from the bathyal zone. Shells, radulae, and gross anatomy indicate that the Abyssochrysidæ are simple mesogastropods. The animals are blind, have deep mantle cavities, long monopectinate ctenidia, closed pallial gonoducts, and a large, right-dorsal mantle process that is interpreted as a copulatory organ. The rachidian tooth of the taenioglossate radula is unique among prosobranchs. Anatomical features do not fit the limits of any recent prosobranch superfamily. The shells are superficially like those of fresh-water melanians, but do not closely resemble those of any other living or Cenozoic group.

Descriptions of the two living species and their synonymies, bathymetric and geographic distributions are presented. The shell physiognomy of *Abyssochrysos* species is closest to that of members of the Palaeozoic-Mesozoic families Zygopleuridae Wenz and Pseudozygopleuridae Knight of the superfamily Loxonematacea Koken. The Abyssochrysidæ are provisionally assigned to the Loxonematacea and are considered to have close affinities to the superfamilies Viviparacea, Valvatacea, Rissoacea, and Cerithiacea.

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Classification and Systematic Relationships of the Abyssochrysidae, a Relict Family of Bathyal Snails (Prosobranchia: Gastropoda)

Richard S. Houbrick

Introduction

In 1927 Tomlin described a deep-water prosobranch dredged by the *Pieter Faure* from a depth of 1645–1828 meters off the Cape of Good Hope, South Africa. Although similar to fresh-water melaniids in shell form and sculpture, this new species could not be assigned to any known genus or family of Recent gastropods. The radula and head-foot portion of the animal were not studied by Tomlin personally, but drawings and observations of the animal and its radula made by Lt. Colonel Peile were incorporated into Tomlin's (1927) description. Although the drawings are superficial and sketchy, they show an animal with a penis, posterior and slightly dorsal to the right cephalic tentacle; a short, bilobed snout; two thick cephalic tentacles that lack eyes; and a unique, taenioglossate radula.

Tomlin (1927) named this species *Abyssochrysos melanoides* and proposed a new family, Abyssochrysidae, to accommodate it. He undoubtedly considered it a member of the Cerithiacea but did not specifically refer it to any superfamily. Later, Tomlin (1931:423) mentioned that it showed affinities

with the Littorinidae Gray and Thiaridae Troschel. Barnard (1963b:144) also recognized a second species, *Abyssochrysos melvilli* (Schepman).

On the basis of new data provided by shell characters of numerous specimens, gross anatomy, scanning electron micrographs of the radula, hydrographic records, and a thorough search of the fossil record, I suggest that *Abyssochrysos melanoides* and *A. melvilli* are not cerithids or members of any living superfamily heretofore recognized. I provisionally regard them as deep-water relicts of the Palaeozoic-Mesozoic superfamily, Loxonematacea Koken, with close affinities to the families Zygo-pleuridae Wenz, Paleozygopleuridae Horný, and Pseudozygopleuridae Knight. My reasons for these radical conclusions follow in the discussion portion of this paper. I herein present descriptions of *Abyssochrysos melanoides* and *A. melvilli*, and discussions of their geographic distributions and relationships to other prosobranch taxa.

ACKNOWLEDGMENTS.—I thank Dr. D. T. Barry, South African Museum, and Dr. Brian Kensley, formerly of the South African Museum, for the loan of type-material and specimens of *Abyssochrysos* species in their charge. I am also indebted to Dr. Henry Coomans, Zoologisch Museum, Amsterdam, for photographs of the holotype of *Argyropeza*

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melvilli. I thank Victor Krantz, Photographic Services, and Walter Brown, Scanning Electron Microscope Laboratory, National Museum of Natural History, Smithsonian Institution, for their assistance. I am indebted to Dr. Robert Linsley, Colgate University; Dr. Winston Ponder, Australian Museum, Sydney; Dr. David Schindel, Yale University; and Drs. Norman Sohl, John Pojeta, and Ellis Yochelson, United States Geological Survey, for reading drafts of this paper and for their comments and suggestions during its preparation. Dr. Joseph Rosewater, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, kindly read the final draft. Figure 4 was drawn by Miss Cynthia Mason, and the typing of the final manuscript was done by Mrs. Sherylitta Lee.

Taxonomic History

The short nomenclatural history of this taxon reflects the uncertainty of its relationships and taxonomic placement. Thiele (1931:202) referred the family Abysochrysidae to his "stirps" Cerithiacea and questioningly placed it between the families Melaniidae and Planaxidae. He remarked that the presence of a penis made the placement of this taxon in the Cerithiacea unlikely. Wenz (1939:720) included the family Abysochrysidae in the superfamily Cerithiacea between families Thiaridae and Planaxidae but indicated his uncertainty about its placement. Pchelintsev and Korobkov (1960) failed to include the Abysochrysidae in their classification. Taylor and Sohl (1962:10) followed Thiele (1931) and Wenz (1939) in their assignment of *Abysochrysos melanoides* to the Cerithiacea, where they placed it between the Pleuroceridae and Planaxidae, but again, with uncertainty. Franc (1968:279) noted that the systematic position of the family was uncertain and included it between the Thiaridae and Planaxidae. In the most recent review of higher prosobranch systematics, Golikov and Starabogatov (1975:211) excluded the family Abysochrysidae from the Cerithiacea because of the presence of a penis, and provisionally assigned it to the superfamily Rissoidae [sic] on the basis of shell characters. In their scheme of classification, the family Abysochrysidae follows the Rissoidae and the Merelinidae.

Barnard (1963a:439) noted that *Abysochrysos melanoides* had been found at depths as great as 2712 meters. He later (1963b:141) discussed the placement of the Abysochrysidae, referring it to the Cerithiacea, and described a second species taken off Durban, South Africa at 440 fathoms, which he named *Abysochrysos tomlini*. The ambiguity of Tomlin's (1927:78, fig. 2) sketchy figures of the animal of *Abysochrysos melanoides* was noted by Barnard (1963b:141) who said he had examined the anatomy of six specimens from the type-lot. Barnard regarded the structure Tomlin (1927) described as a penis to be a large oviduct that projected beyond the mantle edge. Furthermore, Barnard (1963b:141) noted that this structure was attached to the inside of the mantle and not to the head-foot region. He presented several new figures of shells, external anatomy, and radula of *A. melanoides* and transferred *Argyropeza melvilli* Schepman, 1909, to the Abysochrysidae. To my knowledge, no other worker has published anything further on this family.

Material and Methods

While studying the collection of deep-water mollusks made by the U.S. Fisheries Steamer *Albatross* in the western Pacific (1907-1910), I discovered eight lots of *Abysochrysos melvilli* that were dredged in the Philippines and Indonesia. One of the shells contained a dried animal that I was able to soften and dissect. I have examined all the specimens of *Abysochrysos* in the South African Museum. These include the type and five lots comprising 127 specimens of *A. melanoides* and the lectotype and paralectotype of *A. tomlini* [*A. melvilli*]. Eight specimens of *A. melanoides* had dried animals that were reconstituted for anatomical dissection. Although they are not in the best state of preservation, the head-foot, upper whorls, and mantle cavity with associated organs were studied and some internal organs reconstructed. I have also examined three specimens from the type-lot of *A. melanoides* at the British Museum (Natural History) that had the buccal masses and radulae preserved. An additional two paratypes deposited at the Academy of Natural Sciences of Philadelphia were also seen. These specimens, from different geographic sites, have added data about interspecific variation of shell sculpture in the two species.

Order CAENOGASTROPODA Cox, 1959

?Superfamily LOXONEMATACEA Koken, 1889

Family ABYSSOCHRYSIDAE Tomlin, 1927

ABYSSOCHRYSIDAE Tomlin, 1927:77-79; 1931:423.—Thiele, 1931:202.—Wenz, 1939:720.—Taylor and Sohl, 1962:10.—Barnard, 1963a:439; 1963b:141.—Franc, 1968:279.—Golikov and Starabogatov, 1975:211, 219.

This deep-water group is characterized by turreted shells sculptured with prominent axial ribs and covered with a brownish green periostracum. The animals are blind, have deep mantle cavities and closed pallial gonoducts with copulatory organs that arise from the mantle skirt. The family comprises a single genus and two species and, on the basis of shell characters, appears to have close affinities with the families Loxonematidae Koken, 1889, Pseudozygopleuridae Knight, 1930, Zygopleuridae Wenz, 1938, and Palaeozygopleuridae Horný, 1955.

Genus *Abyssochrysos* Tomlin, 1927

Abyssochrysos Tomlin, 1927:78 [type-species, by monotypy: *Abyssochrysos melanoides* Tomlin, 1927].—Thiele, 1931:202.—Wenz, 1939:720.—Barnard, 1963a:439; 1963b:141-144.

This genus comprises only two species that occur in the bathyal zones of the Indo-West-Pacific and South African marine provinces. Members of the genus are characterized by elongate, turreted shells sculptured with prominent, angular axial ribs that do not necessarily follow the growth lines. The suture is distinct and slightly overhung by the preceding whorl. The aperture is ovate and the outer lip sinuous. Shells are covered with a glossy, brownish yellow or brownish green periostracum. The operculum is thin, corneous, ovate, and paucispiral with a sub-central nucleus. The mantle cavity is deep and has a long, monopectinate ctenidium and osphradium, to the left. A right dorsal, penis-like organ arises from the inner mantle skirt and the pallial gonoducts are apparently closed. The head has a short snout and thick cephalic tentacles that lack eyes. A large esophageal gland is present. The radula is taenioglossate (2+1+1+1+2) with a unique, semilunar-shaped rachidian tooth and thick, sinuous, sharply cusped lateral teeth. Species in this genus closely resemble fossils of the Paleozoic genera *Paleostylus* Mansuy, 1914 and *Pseudozygopleura* (*Stephenozyga*) Knight, 1930.

Little is known of the ecology of *Abyssochrysos* species. The bathyal zone is aphotic and lies within the 11°C and 4°C isotherms. Hickman (1974) noted that mesogastropods are predominately carnivorous at bathyal depths in both Recent and Tertiary faunas. All specimens of *Abyssochrysos* have been found on muddy sediment. The length of the radular ribbons, the lack of eyes, and analysis of their fecal pellets suggest that they are deposit feeders and not carnivores. Several specimens of each species had drill holes in their shells indicating predation by naticid snails. All specimens had the upper whorls badly eroded. The greenish brown periostracum of the Abyssochrysidae is similar to that of fresh-water gastropods and is probably a protection against erosion by carbonic acid.

A possible third species of *Abyssochrysos* is *Cerithiopsis turbonilloides* Dautzenberg and Fischer, 1896, described from deep water off the Azores. Dautzenberg and Fischer (1927:108-109, pl. 1: fig. 25) were unsure about its assignment to *Cerithiopsis* because their specimens lacked protoconchs. It bears close resemblance to the general shell physiognomy of *Abyssochrysos*, and, although the specimen figured by Dautzenberg and Fischer is only 13 mm long, it may have been an immature one. I have not seen the types or examined any specimens of this species; consequently, its assignment to *Abyssochrysos* remains uncertain.

Locard described *Bittium eburneum*, a species that looks very much like *Abyssochrysos melanoides*. *Bittium eburneum* was dredged by the *Talisman* in 1193 meters off the coast of Spanish Sahara. Locard (1897:389), noting that his description of the species was based on two immature specimens, was unsure of his taxon's assignment to *Bittium* and suggested that it might constitute a new genus. I have not examined the types but suspect that *Bittium eburneum* is probably another *Abyssochrysos* species or possibly conspecific with *Abyssochrysos melanoides*. Should these specimens prove to be immature forms of *Abyssochrysos melanoides*, the name *eburneum* Locard, 1897 will have priority.

Abyssochrysos melanoides Tomlin

FIGURES 1-6

Abyssochrysos melanoides Tomlin, 1927:78-79, figs. 1-3 [holotype: South African Museum, A-5116; 13 paratypes;

type locality: Cape Point, 900–1000 fms, South Africa]; 1931:423.—Barnard, 1963a:439; 1963b:141–143, fig. 27a-c.

DESCRIPTION.—*Shell* (Figure 1): Shell elongate, turreted, thin in younger specimens, thicker in more mature ones. Mean length of shell, 39.9 mm, mean width, 10 mm; shell length-width ratio, 3.39. Shell has 13+ sinuous whorls that are slightly bulbous at their bases and almost overhang the suture. Apical angle 20–40 degrees. Protoconch one and one-half whorls and smooth. Apical whorls usually decollate or badly eroded. Juvenile whorls frequently with three strong spiral cords that cross 12 axial ribs creating a cancellate effect. Middle whorls sculptured with 12–14 prominent, oblique, pendant axial ribs, sinuous axial growth lines that cross axial ribs, thin, spiral cord at top of whorl, and 1–3 spiral cords at the base of each whorl. Upper spiral cord varies in intensity and forms weak nodules where it crosses axial ribs. Lower spiral cords cross bases of axial ribs and are adjacent to suture. Spiral sculpture variable, generally more prominent on upper whorls. On the last two whorls of mature specimens, axial ribs become weaker, but more numerous (18–20), and spiral sculpture is entirely lacking. Suture distinct, impressed; slight sutural ramp sometimes present on earlier whorls. Base of body whorl somewhat flattened and with 2–5 weak spiral lirae and numerous fine spiral striae and grooves that vary in number and intensity. Aperture subrhomboidal, angulate, one-fifth to one-sixth the length of the shell. Columella concave, outer lip thin, smooth, and very sinuous. Weak, pointed, shallow, anterior siphon present, no umbilicus. Periostracum thin, glossy, and golden yellow, sometimes brown color.

Animal (Figures 2–3): Animal with short, thick snout that is bilobed at tip and has slit-like mouth between lobes. Tentacles (Figures 2–3, *t*) thick, about one-half width of snout. No eyes. Foot moderately short and thick. Propodium (Figure 2, *pp*) with glandular-like lobes, each with one small epipodial tentacle at tip (Figure 2, *ept*). Ovate attachment scar from operculum at posterior dorsal surface of foot. Mantle edge smooth at center but with many small papillae (Figure 2, *mp*) laterally. No papillae on ventral portion of mantle edge. Mantle folded and forming respiratory cavity at right center. Mantle cavity deep, about two and one-half whorls. Thin osphradium, sinuous near mantle edge (Figure 3, *os*), and wide, long monopectinate cteni-

dium (Figure 3, *ct*) extend length of mantle cavity to left. Large hypobranchial gland present (Figures 2–3, *hg*). Pallial gonoducts thick, closed. Large penis-like organ (Figure 3, *p*) arises from under roof of left portion of mantle, is about 2.5 mm long, has small white tip, and overhangs mantle edge. Smaller papilla (Figure 3, *pp*) arises from mantle dorsal to “penis” and also overhangs mantle edge. Intestine long and thin, filled with small, ovoid fecal pellets composed of fine sand and detritus. Anal opening (Figure 3, *a*) behind and dorsal to penis. Large single-lobed kidney (Figure 2, *k*) present. Stomach not observed. Buccal mass relatively large and muscular. Long supraesophageal connective present. Two dark, loosely compacted salivary glands lie in lateral cavity of mid-esophagus just posterior to nerve ring. Larger, dark, compact esophageal gland (Figure 3, *esg*) of columnar structure surrounds entire mid-esophagus. Two chitinous, semi-lunar-shaped jaws present, brownish at their weakly serrated edges and composed of numerous plates commonly subrhomboidal but occasionally pentagonal. Jaws small in relation to buccal mass, about 0.35 mm long. Operculum (Figure 4) chitinous, thin, ovate, concave, and paucispiral with subcentral sunken nucleus. Edges of previous opercular whorls slightly laminate. Growth lines oblique, microscopic. Area of attachment scar ovate, about two-thirds the area of operculum. Color tan to light brown with darker thin, brown band at periphery of whorls.

Radula (Figure 5): Radula robust, taenioglossate (2+1+1+1+2), moderately long (three radulae range in length from 2–3.5 mm and have an average of 109 rows of teeth). Rachidian tooth trapezoidal, laterally elongate, almost straight at top with slight median concave dip. Lateral sides of rachidian each drawn out into long, ventral, sickle-shaped extension. Base of rachidian with slight median, convex bulge but main line of base concave, extending to each ventral lateral extension. Rachidian tooth has long, sharp, median cusp bordered on each side with two to four well-defined, sharp denticles that vary in number from tooth to tooth. Lateral tooth extremely robust, moderately thick and sinuously elongate; top of cusped portion concave. There are three large pointed cusps, the second of which is largest, and two to four smaller blunt denticles that become progressively smaller toward the end of the cutting edge of the tooth.

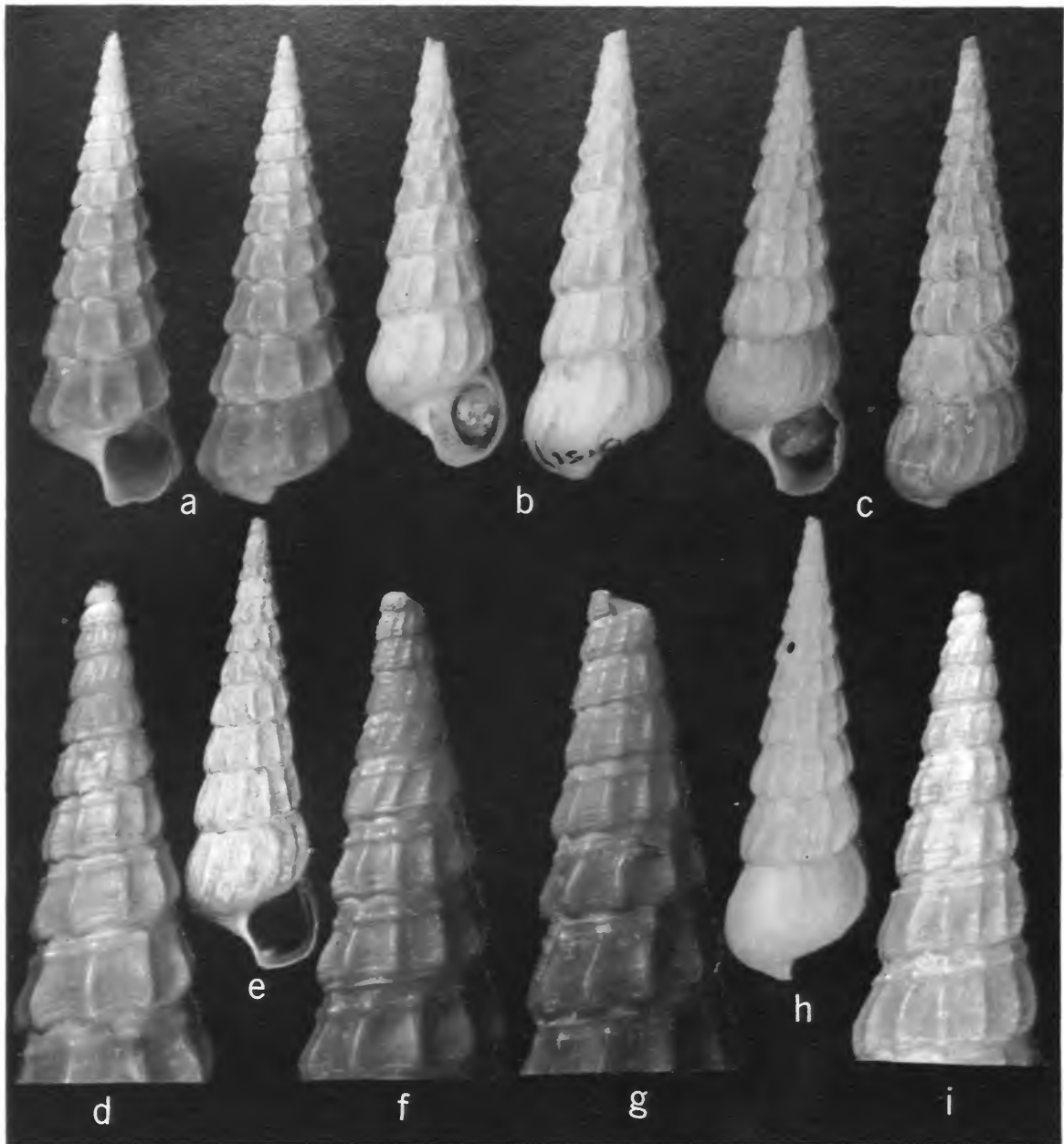


FIGURE 1.—*Alyssochrysos melanoides* Tomlin (all specimens collected in 1462–2724 meters' depth off Cape Point, South Africa): *a*, shell with pronounced pendant ribs (27.3 × 6.6 mm); *b*, specimen with unbroken outer lip and operculum in situ (29 × 8.8 mm); *c*, holotype, South African Museum A-5116 (41 × 12 mm); *d,f,g,i*, sculptural details of early whorls showing variation in spiral threads; *e,h*, large, thick-shelled specimen (48 × 13.5 mm).



FIGURE 2.—*Abyssochrysos melanoides* Tomlin, animal removed from shell to show major anatomical features (a = anus; acp = accessory copulatory process; ct = ctenidium; d = duct leading to pallial penis; ebw = end of first whorl; emc = end of mantle cavity; es = esophagus; esg = esophageal gland; exs = exhalant siphon; f = foot; fp = fecal pellet; g = gonad; hg = hypobranchial gland; int = intestine; is = incurrent siphon; k = kidney; m = mouth; me = mantle edge; op = operculum; os = osphradium; pap = pallial papillae; pg = pallial gonoduct; pp = pallial process (penis); prp = propodium; pt = propodial tentacle; sn = snout; t = tentacle).

Inner marginal tooth spatulate, broad, elongate, slightly curved, broad especially in the center, and strongly cusped with four sharp denticles positioned on the terminal, outer surface of teeth. Outer mar-

ginal tooth the same, but with only three cusps and a little shorter.

REMARKS.—Members of this species are easily distinguished from *A. melvilli* by their basic

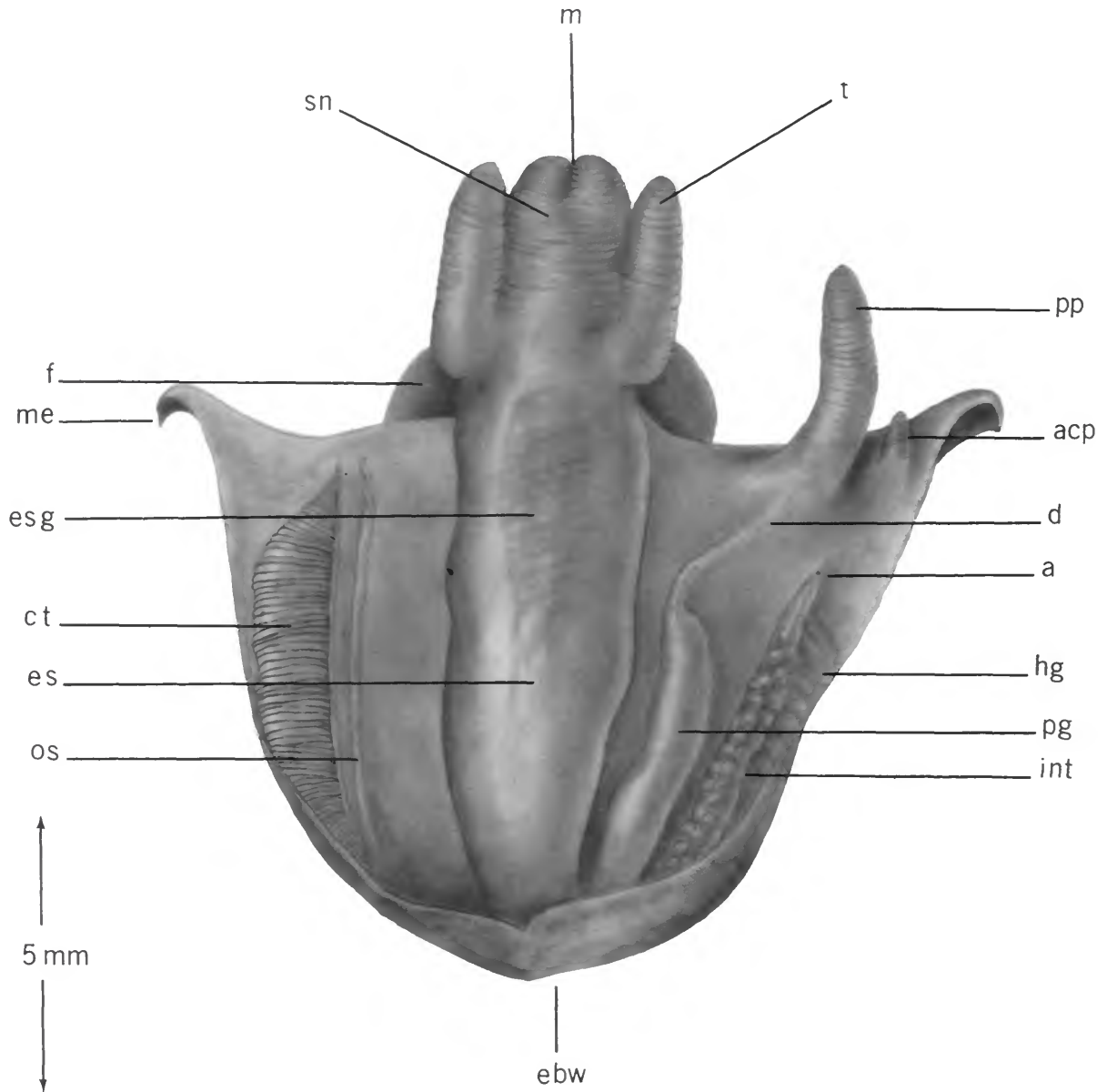


FIGURE 3.—*Abyssochrysos melanoides* Tomlin, dorsal view of head, foot and first body whorl (mantle cut mid-dorsally to end of first whorl and reflected back to show internal pallial organs; abbreviations same as in Figure 2).

shell physiognomy. The shell of *A. melanoides* has a wider apical angle, a lower aperture-length, shell-length ratio. A sample of 32 individuals varied in length from 20.8–49.3 mm and in width from 7.0–15.25 mm. The axial ribs are more pendant and less nodulose than the nodular, biangulate ribs of *A. melvilli*. Spiral sculpture is more prevalent and the earlier whorls are cancellate. The shell of *A. melanoides* is also far more variable in sculpture than that of *A. melvilli* (see Figure 1).

Abyssochrysos melanoides has been found only in the Atlantic Ocean at bathyal depths off of Cape Point, South Africa (Figure 6). It has been taken from six stations, all about 40 miles offshore, and in depths ranging from 1462 to 2724 meters, where it appears to be common and lives on bottom composed of green mud. A large sample of shells (114) ranged 20.8 mm to 49.3 mm in length and 7.0 mm to 15.75 mm in width.

I examined six dried animals that I was able to reconstitute for dissection. Although not in the best state of preservation, the mantle cavity and asso-

ciated organs were suitable for study and the anatomical features were reconstructed. The pallial gonoducts (Figure 3, *pg*) are thick, glandular, and quite large. They appear to be closed ducts: cross-sections reveal a thin, slit-like lumen that may have collapsed in the preserved animal due to poor preservation. There is no opening from the ducts into the mantle cavity. All of the animals I examined have a cylindrical, penis-like process (Figures 2–3, *p*) that protrudes from the upper right side of the mantle cavity. Above and to the left of this process there is a smaller papilla (Figures 2–3, *pp*) that likewise protrudes from the mantle. When the mantle is opened and reflected back, this structure and the associated papilla are seen to be attached to the inside of the mantle roof a short distance behind the mantle edge (Figure 3). The mantle process thus arises from the mantle roof and not from the head-foot portion of the animal. It is covered with fine spiral folds, has a small white tip, and is flatter and wider at the area of attachment. Here a narrow duct (Figure 3, *pd*) runs from it down

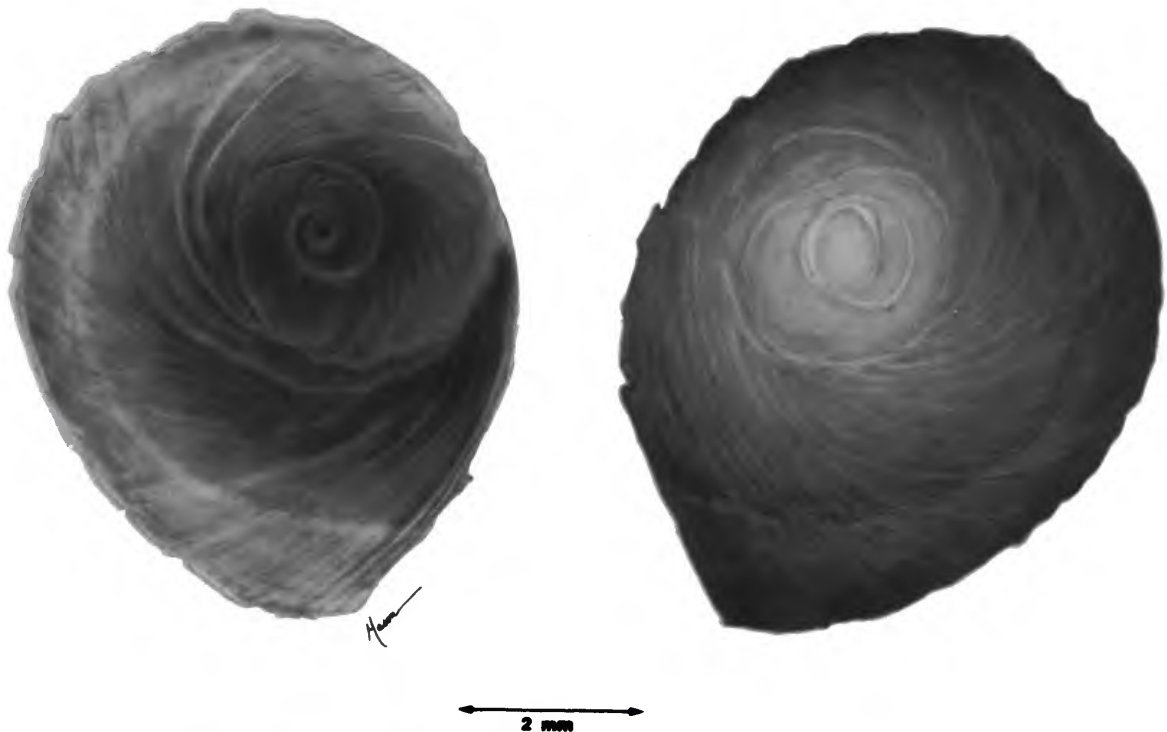


FIGURE 4.—Operculum of *Abyssochrysos melanoides* showing attached side (right) and free side (left).

the right side of the mantle and joins the closed gonoduct. Cross sections through the distal portion of this "penis" show that it is round at the tip and middle. There appears to be a lumen in the center

that is surrounded by lighter pigmented tissue. The lumen was collapsed and plugged due to the poor preservation. The tissue surrounding the lumen is columnar. The lumen becomes a lateral slit in the

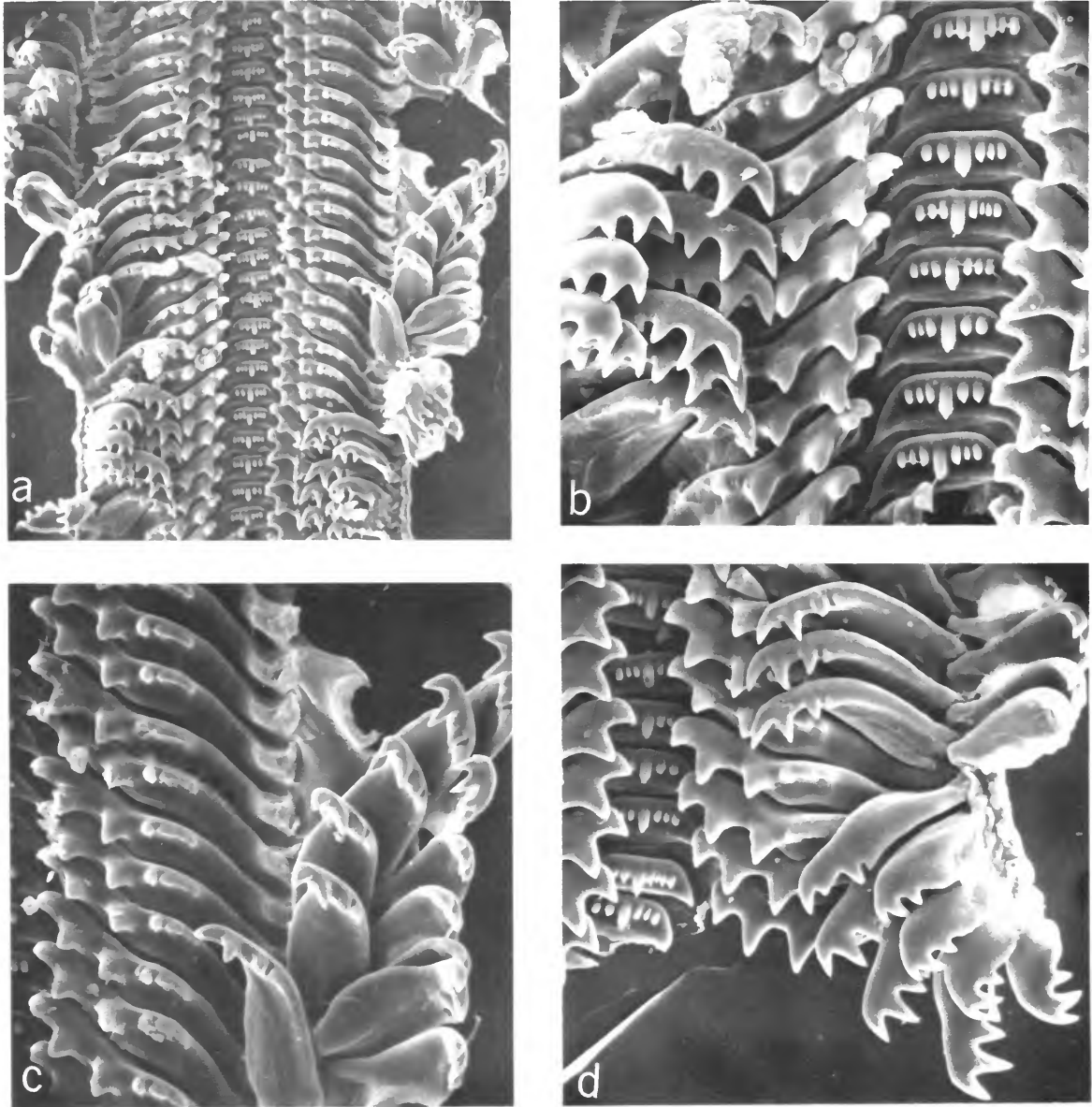


FIGURE 5.—Scanning electron micrographs of radula of *Abyssochrysos melanoides*: *a*, central portion of radular ribbon (190 \times); *b*, detail of rachidian, lateral and marginal teeth (500 \times ; note variation in number of denticles on rachidian tooth); *c*, detail of lateral and marginal teeth (400 \times); *d*, detail of marginal teeth showing hook-like cusps and attachment to basal membrane (400 \times).

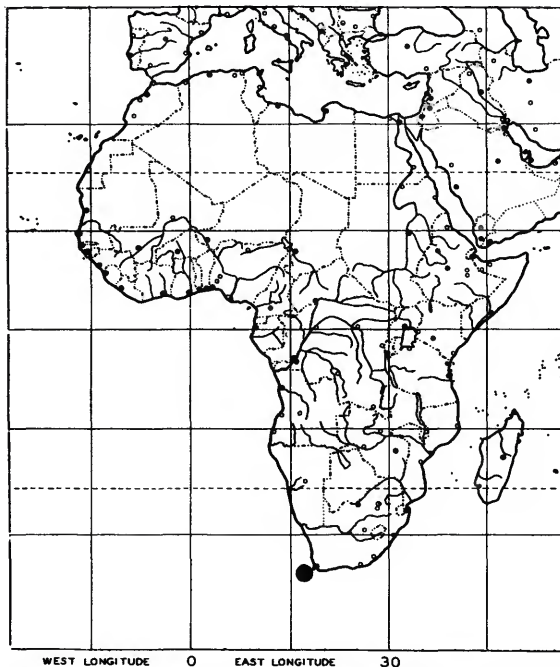


FIGURE 6.—Geographic distribution of *Abyssochrysis melanoides* (all collecting stations are relatively close together).

proximal portion of the process. Barnard (1963b: 141) believed that Tomlin (1927) was mistaken in assuming that this structure was a penis. He said that he had examined six preserved specimens and thought that two were female and that the process was a large oviduct that projected beyond the mantle edge. The other four specimens were without this process and he assumed that these were males. Barnard did not mention whether the gonoducts were closed or open. All of the preserved specimens I examined have the mantle process or "penis" and the associated papilla, although in one animal these structures were very small. I doubt that it is an extended oviduct because there are no precedents for this kind of anatomy among the prosobranchs. There are, however, mesogastropods in which a copulatory organ arises from the mantle of the male (e.g., the Pilidae and the Tiphobiinae); moreover, even females possess an atrophied penis in the Pilidae. I will discuss this further in this paper. Although the digestive gland and gonad (Figure 2, g) were intact in the specimens I examined, it is difficult to determine the sex of the

individuals on the basis of poorly preserved gonadal tissue; thus, I am uncertain of the sex of any of these specimens.

Although the stomachs were too poorly preserved for dissection, the intestines (Figures 2–3 *int*) were filled with many ovoid fecal pellets (Figures 2–3 *fp*) composed of fine sediment, and it is reasonable to assume that *A. melanoides* is a deposit feeder.

MATERIAL EXAMINED.—103 specimens (South African Museum A-5114, A-5115, A-5116, A-5117), dredged by R. S. Pieter Faure in 1638 m off Cape Point, South Africa; 1 specimen (South African Museum A-9718), dredged in 2675–2712 m by R. S. *Africana* II, 34°05'S, 16°58'E; 7 specimens (South African Museum A-9845), dredged in 2675–2712 m by R. S. *Africana* II, 34°05'S, 16°58'E; 3 specimens (British Museum (Natural History) Reg. No. 19601517), 1456–1638 m off Cape Point, South Africa.

Abyssochrysis melvilli (Schepman)

FIGURES 7–10

Argyropeza melvilli Schepman, 1909:170, pl. 12, fig. 1 [holotype: Zoologisches Museum, Amsterdam, 2915; type-locality: Sulu Sea, 535 m, Siboga Expedition, Sta 102].

Abyssochrysis melvilli (Schepman).—Barnard, 1963b:141–144.

Abyssochrysis tomlini Barnard, 1963b:143–144, fig. 27f [lectotype, herein designated: larger of two syntypes, South African Museum, A9101; type-locality: 24 mi off Cape Natal (Durban) at 801 m, South Africa].

Argyropeza? suvaensis Ladd, 1977:15–16, pl. 1: fig. 3; pl. 21: fig. 8 [holotype: USNM 174966; paratype: USNM 175062; type-locality: Suva, Fiji, early Miocene].

DESCRIPTION.—*Shell* (Figure 7): Shell thin, elongate, turreted, and consisting of 13–16 whorls in adults. Adult mean shell length 36 mm, mean width 9 mm wide, length-width ratio of 4:1, and with apical angle of 15–19 degrees. Whorls weakly inflated, pedunculate at their bases, sculptured with 17–18 strong, sinuous, biangulate axial ribs and numerous, minute, sinuous, axial growth lines that cross over the ribs. Each axial rib with a blunt nodule at top and slightly larger one at bottom. Top row of modules connected by weak spiral cord. Base of each whorl with fine but distinct spiral cord adjacent to suture. Suture strongly impressed. Axial sculpture not strong and sometimes lacking on body whorl. Base of body whorl concave, with two spiral cords at periphery and 5–7 weaker spiral cords on concave portion. Protoconch smooth, one and one-half whorls, about one-seventh the length of the shell. Columella concave, smooth, and with

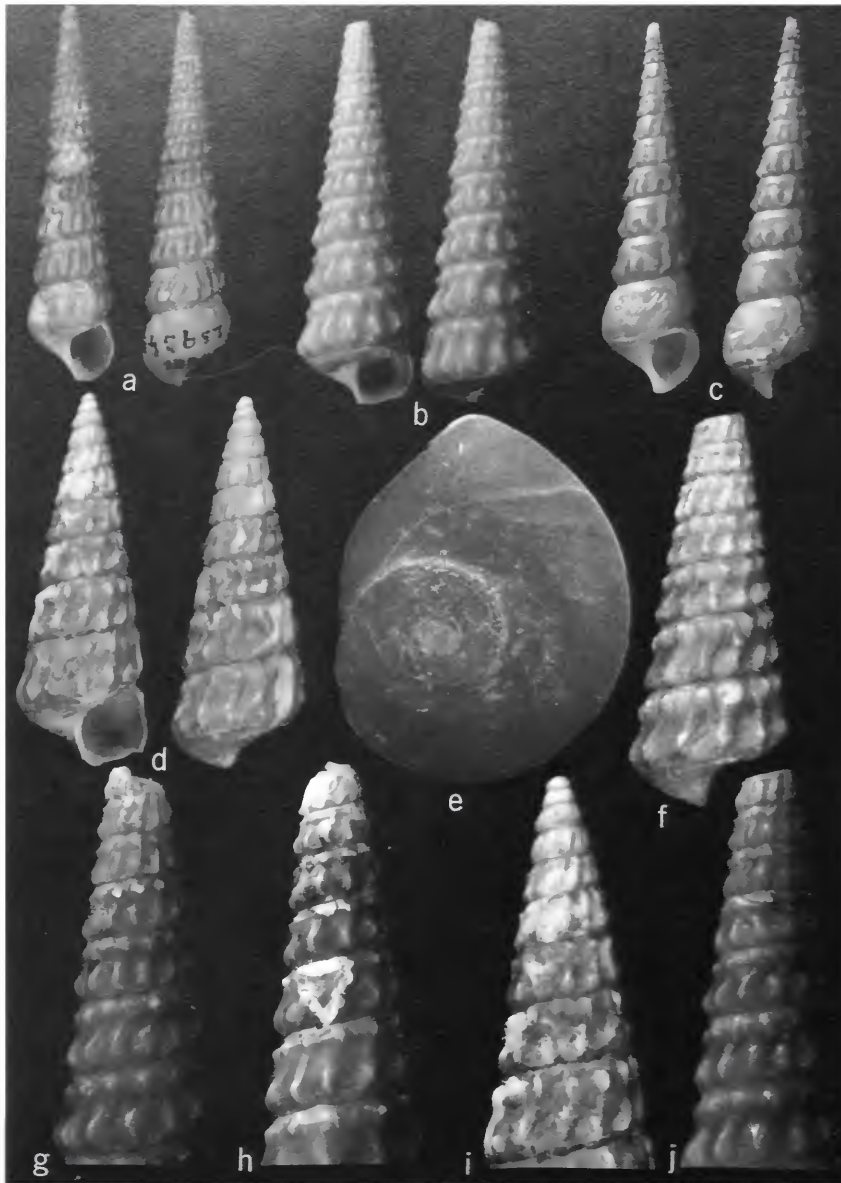


FIGURE 7.—*Abyssochrysos melvilli* (Schepman), showing variability in shell sculpture in specimens from different localities and outer surface of operculum: *a*, Buton Strait, Celebes, Indonesia, 949 m (USNM 239392, 47.3 × 10.6 mm); *b*, Buton Strait, Celebes, Indonesia, 1022 m (USNM 239417, 23.4 × 6.6 mm); *c*, Cabra Is., Lubang, Philippines, 527 m (USNM 237535, 45.6 × 11.3 mm); *d*, lectotype of *A. tomlini* Barnard, Cape Natal, South Africa, 535 m (South African Museum A-9101, 11.5 × 3.75 mm); *e*, SEM of outer surface of operculum on animal from Buton Strait, Celebes, Indonesia (21×); *f*, paratype of *A. tomlini* Barnard, Cape Natal, South Africa, 535 m (South African Museum A-9101, 11.6 × 3.9 mm); *g,h,i,j*, details of sculptural variation on early whorls of different shells; *i*, detail of protoconch of lectotype of *A. tomlini* Barnard.

thin callous. Outer lip very sinuous, thin. Weak, anterior siphonal shelf present, no umbilicus. Periostracum thin, glossy, and of brownish green to brownish yellow color.

Animal: Animal about 6–7 whorls, having prominent, thick snout that is bilobed at tip with slit-like mouth between lobes. Cephalic tentacles thick, about one-half width of snout. No eyes. Foot moderately short, with glandular lobes on propodium. Circular attachment scar for operculum at posterior dorsal surface of foot. Mantle skirt smooth, apparently lacking papillae at edge, and folded at right dorsal center, forming respiratory cavity. Mantle cavity deep, about two and one-half whorls and two-thirds the length of the animal. Thin osphradium and long, wide bipectinate ctenidium begin close behind mantle skirt and extend length of left portion of mantle cavity. No hypobranchial glands seen. Pallial gonoducts closed, thin, adjacent to right portion of columellar muscle. Large, dorsal, penis-like process arises from mantle under right edge of mantle skirt. Smaller papilla to the right of "penis" also arises from mantle skirt. "Penis" and associated papilla with numerous circular folds. Base of "penis" flattened where connected to mantle and with tubular connection to gonoduct. Intestine long and thin, filled with small ovoid fecal pellets that are composed of fine sediment. Anal opening behind and dorsal to "penis," about 2.5 mm from mantle edge. Buccal mass relatively large and muscular. Nerve ring and associated ganglia tightly concentrated. Two chitinous, semi-lunar-shaped jaws present in sides of anterior buccal cavity. Jaws tan, small in relation to buccal mass, about 0.35 mm long, and with weakly serrated edges; composed of numerous plates that are characteristically subrhomboidal but occasionally pentagonal. Operculum (Figure 7e) chitinous, thin, ovate, and paucispiral with a subcentral sunken nucleus. Edges of previous opercular whorls slightly laminate. Growth lines oblique, microscopic. Attachment scar of foot muscle almost round, occupying central portion of operculum. Color golden brown, but darker around circumference.

Radula (Figure 8): Radula robust, long (radular ribbon 3.25 mm in length, 0.50 mm wide and with 108 rows of teeth in animal 12 mm long). Radula identical to that of *A. melanoides* except rachidian tooth thinner at center.

REMARKS.—*Abyssochrysos melvilli* differs from *A.*

melanoides by having a more slender shell with a smaller apical angle and sculpture of blunt nodules on the tops and bottoms of the axial ribs (Figure 7g–j). Six specimens ranged in length from 22.1–47.3 mm and in width from 5.5–11.5 mm. Shell sculpture is more variable than in *A. melanoides* and presents an overall varicose effect. The ratios of shell length to shell width and of shell length to aperture length are higher than in *A. melanoides*. The rachidian tooth of the radula of *A. melvilli* (Figure 8c) differs by being thinner at its center. The operculum has an attachment scar that is more circular than in *A. melanoides*.

As Barnard (1963b:144) noted, Schepman (1909) was doubtful about the generic assignment of this species, but at Melville's suggestion, referred it to the genus *Argyropeza* Melville and Standen, 1901. Neither Barnard (1963b:144) nor Schepman (1909) had seen the soft parts or radula but Barnard (1963b:144), recognizing the affinity of this species to *Abyssochrysos melanoides*, transferred *Argyropeza melvilli* to *Abyssochrysos*.

Schepman (1909) described *A. melvilli* from one immature specimen that was taken in the Sulu Sea (Figure 9). His description and excellent depiction of this species (1909:170, pl. 12: fig. 1a, b) agree perfectly with the material I have examined from the Philippines and Indonesia. I have also examined photographs of the holotype (Figure 9). It lacks the periostracum but is unequivocally the same as *A. tomlini*. The addition of new material from the Philippines and Indonesia convinces me that *A. tomlini* Barnard (1963b) is conspecific with *A. melvilli* Schepman. Barnard (1963b:144), noting the close resemblance between his shells from Cape Natal and Schepman's Sulu Sea species, questioned whether they were specifically distinct but decided to separate the two on the basis of several small sculptural differences. The additional material I have seen demonstrates that *A. melvilli* is quite variable in sculptural details (see figure 7a–j) and that these differences do not justify the recognition of *Abyssochrysos tomlini* as a separate species. Barnard (1963b:143–144) described *A. tomlini* from two immature shells taken on a muddy bottom in 801 meters off Cape Natal, South Africa. There are two syntypes, the larger of which is herein designated as the lectotype (Figure 7d). It has a protoconch consisting of two and one-half whorls (Figure 7i). The types undoubtedly are shells of immature ani-

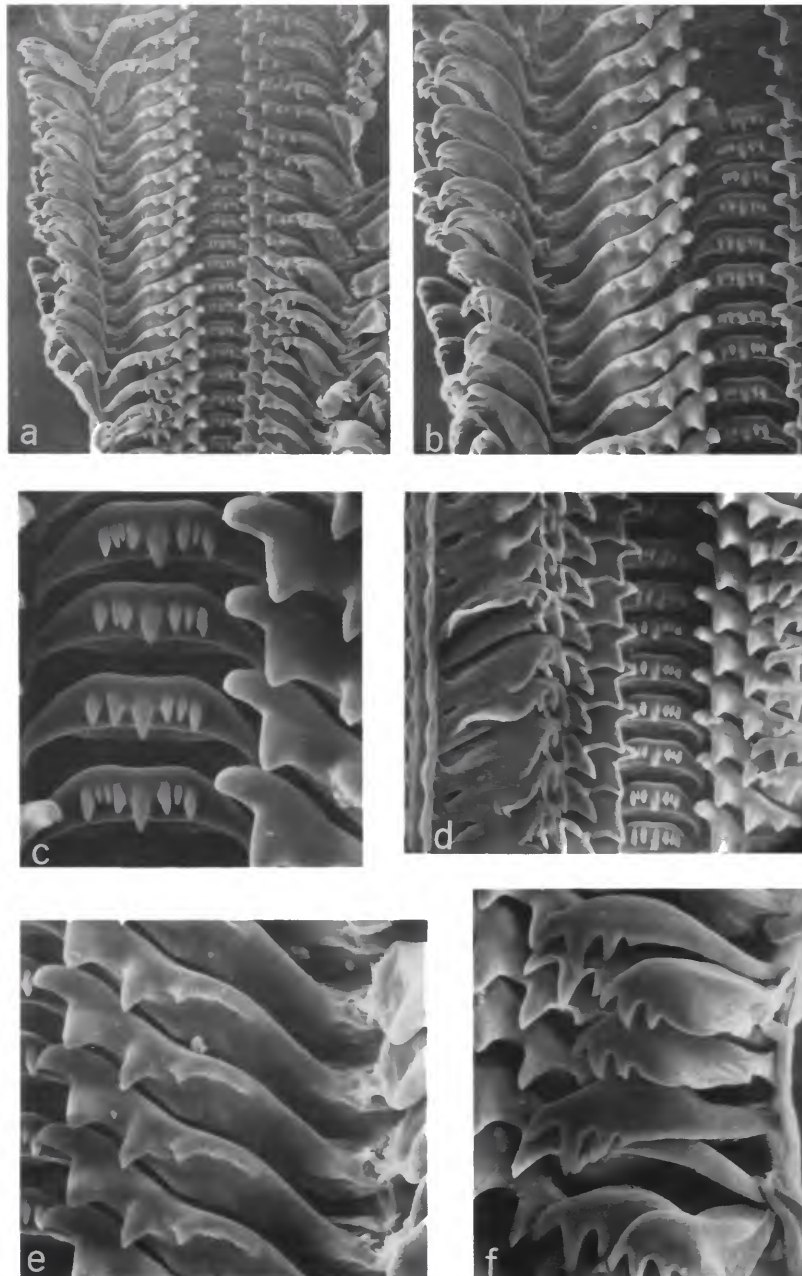


FIGURE 8.—Scanning electron micrograph of radula of *Abyssochrysis melvilli* from Gulf of Boni, Celebes, Indonesia (note similarity to radula of *A. melanoides*): *a*, central portion of radular ribbon (140 \times); *b*, detail of lateral and marginal teeth (marginals folded back to show attachment to subradular membrane, 20 \times); *c*, detail of rachidian teeth (note variation in number of denticles, 610 \times); *d*, detail of marginal teeth in unfolded state, resting on laterals (300 \times); *e*, detail of lateral teeth (525 \times); *f*, detail of marginal teeth showing hook-like cusps (500 \times).

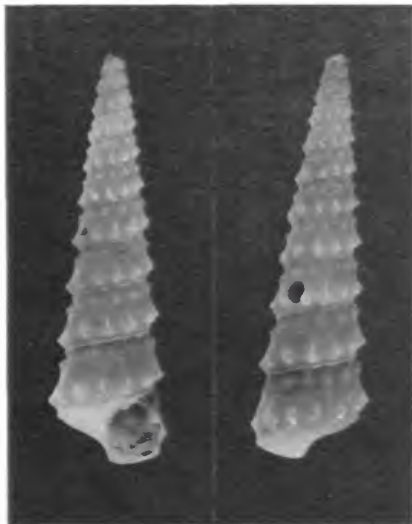


FIGURE 9.—Holotype of *Argyropeza melvilli* Schepman from Sulu Sea, 535 m (Zoologisches Museum, Amsterdam, 10.5×3.25 mm).

mals, as the Philippine and Indonesian specimens are considerably larger. All of the specimens of *A. melvilli* I have seen have damaged outer lips and three have drill holes.

Examination of the types of *Argyropeza suvaensis* Ladd, 1977 convinces me that these fossils are conspecific with *A. melvilli*. Ladd (1977:15) noted a close relationship between the two but was uncertain about their generic relationship.

Museum records indicate that this species lives on muddy or fine, sandy bottoms in the bathyal zone. The three Philippine specimens were found at depths of 491–960 meters. Schepman's (1909) Sulu Sea specimen is from 535 meters; those from Indonesia were taken at 870–1479 meters depth. Barnard's specimens were from 804 meters. The disjoint geographic distribution (Figure 10) reflects both the rarity of this species and the paucity of deep sea material from the Indian Ocean. *Abyssochrysos melvilli* probably occurs at bathyal depths throughout the western Indo-Pacific Province.

MATERIAL EXAMINED.—2 specimens, lectotype and paralectotype (South African Museum A-9101), dredged in 801 m by R. S. Pieter Faure off Cape Natal, South Africa; 1 specimen (USNM 237535), dredged by 956 m off Cabra Is., Lubang, Philippines; 1 specimen (USNM 244970), 490 m off Malavatuan Is., W. Luzon, Philippines; 1 specimen (USNM 239417), 1074 m, off North Is., Buton Strait, Celebes, Indo-

nesia; 1 specimen (USNM 239426), 983 m off Tg Lamulu, Gulf of Boni, Celebes, Indonesia; 1 specimen (USNM 258507), 866 m off Sipadan Is., Sibuko Bay, Borneo, Indonesia; 1 specimen (USNM 239341), 1472 m off Doworra Is., Moluccas, Indonesia; 1 specimen (USNM 239392), 945 m off North Is., Buton Strait, Celebes, Indonesia; 1 specimen (USNM 239343), 1472 m off Doworra Is., Moluccas, Indonesia.

Discussion

Before considering the inclusion of the Abyssochrysidae in the Loxonematacea, a word should be said about the state of the material upon which some of the evidence is based. The animals of *Abyssochrysos melanoides* and *A. melvilli* had been dried in their shells for many years and were poorly preserved. Many organs, such as the stomach, were too compressed to examine even after reconstitution. None of the material was suitable for histological study. Although I was able to study the mantle cavity and its associated organs, I could not ascertain unequivocally the presence of a duct or lumen through the pallial gonoducts. This structure had been compressed and the internal ducts were in a collapsed state. Nevertheless, I believe my observations relative to the closed state of the pallial gonoducts and their connection to the mantle process or "penis" are correct, as explained below.

ANATOMY.—There are a number of objections that may be raised about the transfer of the family Abyssochrysidae to the superfamily Loxonematacea, a group thought to be extinct since the Upper Jurassic (Knight et al, 1960:1315). The most obvious one is the fact that we have no way of knowing what the soft parts of the animals in this extinct group were like, and must rely solely on shell characters for speculation about their phylogenetic relationships. Although the shells of the two *Abyssochrysos* species are very similar to those of the Paleozoic loxonemataceans (see Figure 11), there is the possibility that this is due to convergence and does not indicate relationship. For example, the shells and periostracum of *Abyssochrysos* species are similar to those of species in the genera *Melanoides* A. Adams, *Stenomelania* Fischer and *Namratua* Abbott of the large fresh-water family Thiariidae Troschel (= Melaniidae Latreille). Indeed, Tomlin (1927) named *Abyssochrysos melanoides* in reference to this resemblance. There is a striking likeness of sculpture between *Melanoides admirabilis* E. A. Smith, 1880, and *A. melanoides*, although the aper-

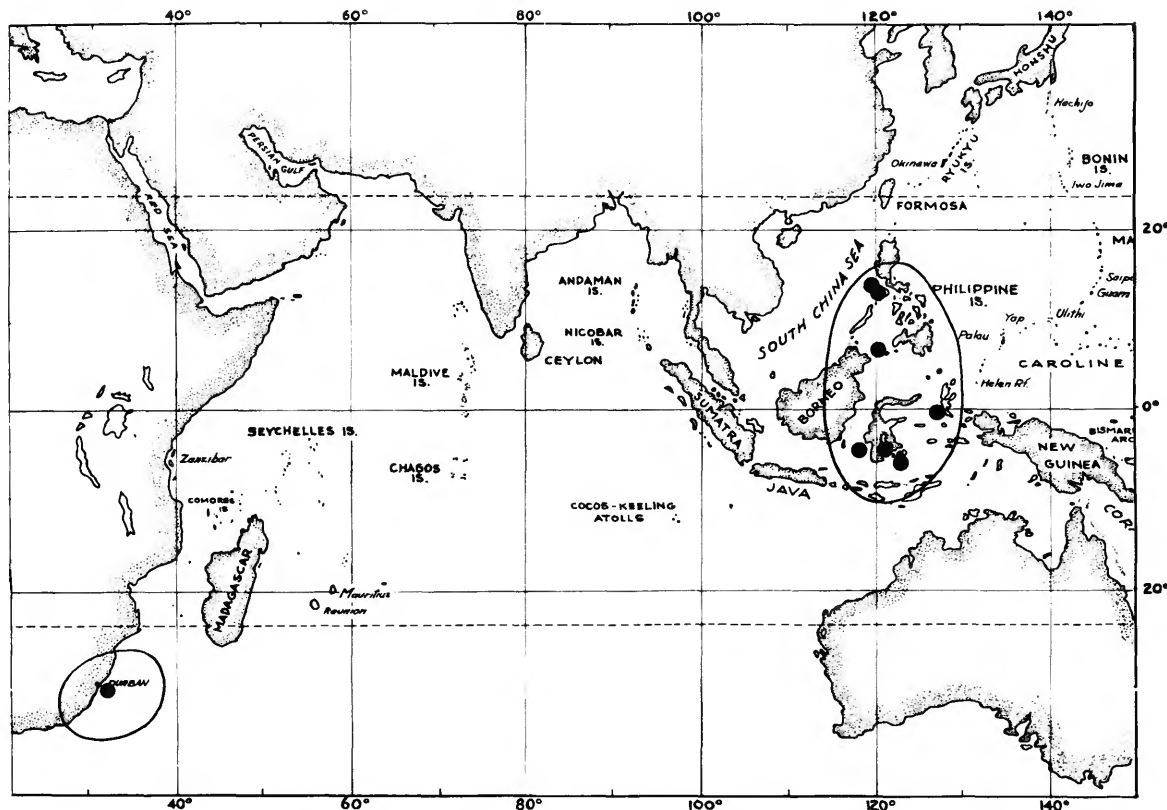


FIGURE 10.—Geographic distribution of *Abyssochrysis melvilli* (Schepman) (disjunct distribution may be sampling artifact: this species probably occurs throughout Indo-West Pacific).

ture of the former is more attenuate. One can find other examples of sculptural resemblance among the thiarids, but similarity between the *Abyssochrysidae* and *Thiaridae* is clearly attributable to sculptural convergence. The apertures of the latter group are more elongate and fusiform; moreover, the thiarids are anatomically cerithiaceans.

The presence of closed pallial gonoducts and large penis-like organs in the species of *Abyssochrysis* excludes them from the superfamily *Cerithiacea* because the distinguishing anatomical characters of members of the superfamily are open pallial gonoducts and the aphyllid condition of males; there are a few minor exceptions to this among the *Pleuroceridae*, which will be discussed below. One might argue that the *Caecidae* Gray, which traditionally has been placed in the *Cerithiacea* Fleming (Thiele, 1931; Wenz, 1939) is an exception to this,

but modern workers no longer consider the *Caecidae* to be among the cerithiaceans. Fretter and Graham (1962:625) noted that the anatomical features of *Caecum* were highly unusual for a cerithiacean and suggested that the caecids were accidentally assigned to the superfamily merely on the basis of shell structure. Moore (1962:699) has shown that the anatomy of the *Caecidae* places them in the superfamily *Rissoaceae* Gray.

Other cerithiacean families with species that resemble the general shell physiognomy of the *Abyssochrysidae* are the *Cerithiidae* Fleming, *Syrnolopsidae* Bourguignat, *Turritelidae* Woodward, and *Potamididae* H. and A. Adams. All members of these large families are characterized by their open pallial gonoducts. The *Cerithiidae* and *Potamididae* have shells with distinct anterior canals. Johansson (1953:17) considered the open pallial gonoducts of

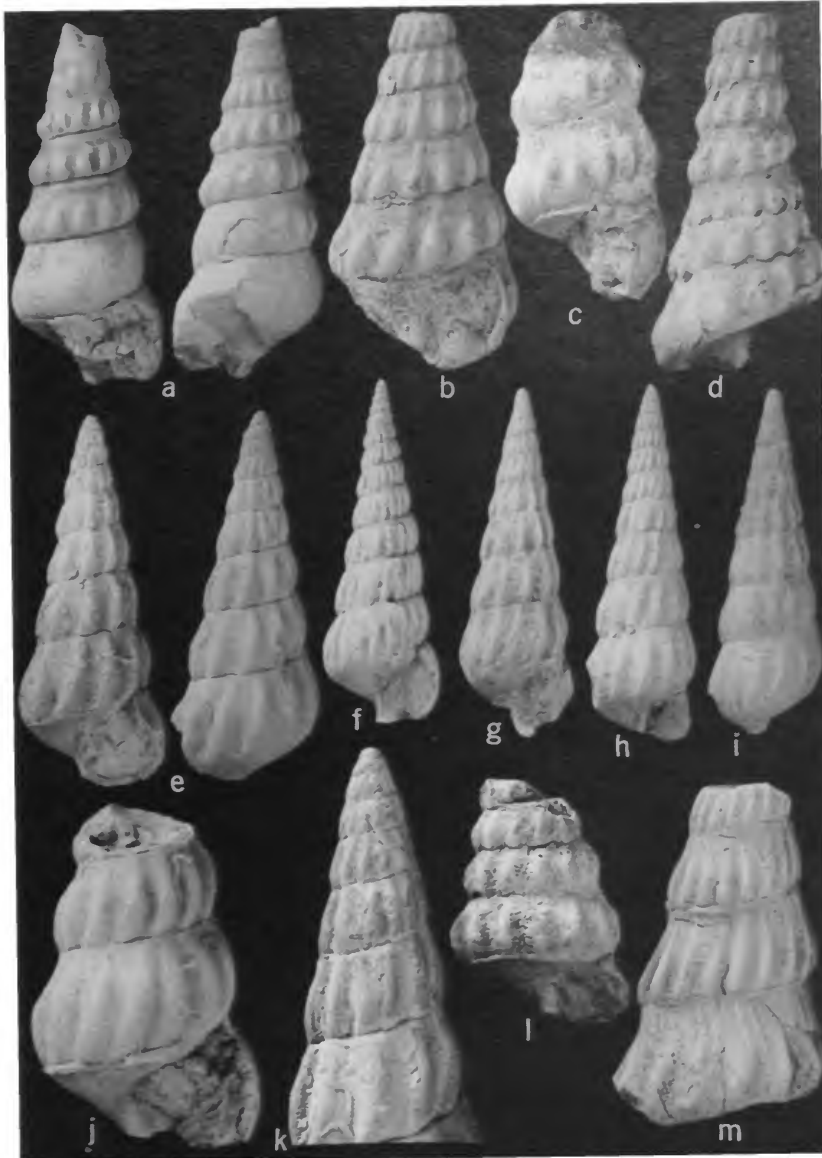


FIGURE 11.—Fossil loxonematid snails demonstrating similarity of shell physiognomy to living *Abyssochrysis* species: *a,c,d*, *Pseudozygopleura* sp. from Riley Ranch, Jacksboro, Texas, Permian (29.5×11.3 mm, 10.2×6.4 mm, 12.4×11.7 mm, respectively); *b,j*, *Pseudozygopleura* sp., Union Hill School, 6 mi NW of Mineral Wells, Texas, Permian (13.9×6.9 mm, 24×14.5 mm, respectively); *e*, *Pseudozygopleura* (*Stephanozyga*) *subnodosus*, Permian, of Texas (21×7.5 mm); *f-i*, *Pseudozygopleura* sp., Gonzales, roadside 3.9 mi NW of Finis, Young Co., Texas, Permian (21.2×6.6 mm, 16.3×4.9 mm, 26×8.5 mm, 29.8×4.9 mm, respectively); *k*, detail of early whorls of shell in Figure 12f; *l*, *Pseudozygopleura* (*Stephanozyga*) *lugosa*, Coyote Creek, near Black Lakes and Taos, New Mexico, Permian (15.4×10.1 mm); *m*, *Pseudozygopleura* (*Stephanozyga*) *simplex*, Baselo, Timor, Permian (20.3×11.9).

Cerithiacea to be a primitive trait. He also noted (1956:386) that the closed pallial gonoducts of the Rissoidae appear to be derived from open slits. Fretter (1951:583) and Fretter and Graham (1962:359) did not agree that the open ducts in the Cerithiacea were primitive characters and suggested that the open condition is correlated with a long, narrow mantle cavity and is thus a secondary and advantageous trait. If the *Abyssochrysidae* are indeed primitive, the presence of closed pallial gonoducts in this group would tend to support the latter point of view.

Another large group of mesogastropods to which the *Abyssochrysidae* may be related in the Rissoacea Gray. As I remarked earlier, Golikov and Starobogatov (1975:219) provisionally assigned the family to the Rissoacea on the basis of shell characters. There is sculptural similarity to some freshwater rissaceans, such as *Oncomelania* Gredler, 1881, and also to some marine rissaceans like *Truncatella* Risso, 1826, and *Rissoina* Orbigny, 1847. This similarity is superficial; most marine rissoids are tiny animals and their shells lack an anterior siphonal canal. No described rissacean radula resembles those of the *Abyssochrysos* species. Although little is known of the anatomy of many groups assigned to the superfamily Rissoacea, those that have been studied have females with closed pallial oviducts and males with cephalic penis and closed gonoducts. Exceptions are to be found in the subfamily Rissoidinae Stoliczka, in which the condition of the male pallial gonoduct may be open or closed (Ponder, 1967:209), and in the Bythiniidae, in which the penis of *Bithynia tentaculata* is of pallial origin (Fretter and Graham, 1962:350). In some rissoids the presence of a penis in females, as well as in males, has been noted by Thiriou-Quievreux (1977:781), who considered the condition due to successive hermaphroditism. Thus, although there are a few anatomical similarities between members of the Rissoacea and *Abyssochrysidae*, there is not enough evidence to consider the latter group as rissaceans.

The only other marine families that approach the general shell shape of the *Abyssochrysidae* are the Terebridae Mörch and Pyramidellidae Gray. The former are advanced toxoglossans and have a narrow aperture and a distinct twisted columella with a lower plait, while the latter are opistho-

branches, easily distinguished by their heterostrophic nuclear whorls and detorted anatomy.

Abyssochrysos shells are sculptured like those of extinct loxonemataceans in the family Pseudozygopleuridae. An interesting feature in *Abyssochrysos* is that the axial sculpture does not necessarily follow the growth lines of the shell and is thus not colabral sculpture. This is not the pattern in cerithid shells but is true for some loxonemataceans (Robert Linsley, pers. comm.). Fossil loxonemataceans have consistently thicker shells and straighter columellas than the *abyssochrysid*s. The labial sinus noted by Knight et al. (1960) in the shells of some fossil loxonematids has traditionally been interpreted as an anal sinus and, if in a central position, as an indication of a zygobranchous organization. Although a labial sinus does not occur in *Abyssochrysos* species, the presence of a pallial penis could account for the sinus in extinct forms of loxonemataceans. Thus, a labial sinus in fossils does not necessarily indicate the presence of an exhalant siphon and associated anus.

Perhaps the most unusual feature of the *abyssochrysid* snails is the presence of the large pallial process and its associated papilla. Although I interpret this structure as a penis, it may also be considered to have a number of other functions. It may be a right pallial tentacle such as exists in some rissaceans like *Cingula* Fleming, 1828 (Fretter and Graham, 1962:112) or in *Valvata* Müller 1774 of the family Valvatidae Thompson (Fretter and Graham, 1962:621). In these groups the pallial tentacle functions as a ciliated extension of the exhalant siphon. In *Abyssochrysos* the pallial process is very wide, thick, and not at all tentaculate in appearance. Moreover, there is an apparent axial lumen present and the proximal part of the process is attached to the inner surface of the mantle, a short distance behind the mantle edge. There is also an internal connection to the pallial gonoduct; accordingly, it is doubtful that the process is homologous to the papillae or tentacles of the mantle skirt.

Barnard (1963b:141) regarded the pallial process of *Abyssochrysos* as an extension of the oviduct. Only two of the animals he examined had this structure and he considered them to be females. The other four lacked the process and were regarded as males. I find Barnard's interpretation unlikely because I know of no other prosobranchs in

which the oviduct overhangs the mantle skirt. It is difficult to explain the functional significance of such a condition. I think it is simpler to consider this structure a penis and to regard the four animals lacking it as females. All of the animals of *A. melanoides* I examined had the process, although in a few it was much reduced. The one animal of *A. melvilli* that I studied also had the structure. Because I am not certain that the mantle process is a penis, I cannot unequivocally identify the sex of the animals I studied. There are two possibilities: (1) all the animals I saw were males; (2) males as well as females have the pallial process. The fact that the process is reduced in some animals indicates that it may be a senescent feature or that the Abyssochrysidae could be successive hermaphrodites. Barnard (1963b:141) thought that the papilla next to the penis was an anal papilla, but the anus is located far behind the papilla and has no apparent association with it. I believe it best to regard this structure as an accessory copulatory papilla.

Another possible interpretation of the pallial process is that it is an ovipositor. This is also doubtful because all other known ovipositors in mesogastropods are pedal structures and, from a functional view point, the position of an ovipositor above the head seems unlikely.

In my view, the interpretation of this structure as a penis is most acceptable. The penis is of pedal origin in most mesogastropods, but a penis of pallial origin, although unusual, is not unprecedented. Several examples occur in the superfamily Viviparacea among members of the Pilidae Connolly and Viviparidae Gray. In *Viviparus* the right cephalic tentacle is modified to function as a penis (Fretter and Graham, 1962:350). It is in the freshwater Pilidae that one finds structures analogous, though probably not homologous, to the condition observed in the Abyssochrysidae. Andrews (1964: 123-124) has shown that in the Pilidae the penis arises from right portion of the mantle and that it occurs in both males and females. The penis in this group differs from that of the Abyssochrysidae by having an elaborate penis sheath associated with it. Andrews (1966:134) suggested that the penis in the Pilidae may have originated from a pallial tentacle such as that of *Valvata*.

Other mesogastropods having a penis of mantle origin are in the family Pleuroceridae Fischer, superfamily Cerithiacea. Moore (1898:191, pl. 14:

figs. 45-46) described and figured a penis-like organ arising from the mantle and connected by a duct to the middle of the male pallial gonoduct in *Typhobia horei*, a member of the subfamily Typhobiinae Moore, endemic to lake Tanganyika. Moore (1898:191) considered this organ to be an eversible penis but did not think it was homologous with the penis of the Pilidae (cited as Ampullariae). Morrison (1954:373) later commented that the Typhobiinae were the only "Melanian" snails that possess any intromittent organ structure whatsoever. In *Typhobia*, the gonoduct is open only at its lower extremity. Thus the Typhobiinae differ markedly from most other cerithiaceans, a group characterized by aphyallic males and open pallial gonoducts.

Members of the genera *Cleopatra* Troschel and *Paludomus* Swainson, in the subfamily Paludominae also differ from "standard" pleurocerid reproductive anatomy. In *Cleopatra* the female pallial gonoduct is closed, according to Starmuhlner (1969: 181), but his drawing of this organ (fig. 259) is equivocal enough to render his interpretation of a "closed" gonoduct questionable. In *Paludomus*, as in *Typhobia*, the female pallial gonoduct is open only at its lower extremity (Seshaiya, 1934:207). The male pallial gonoduct is unusual in being swollen and closed except at the terminal portion where it becomes an open ciliated slit. A nonmuscular flagellar penis runs forward in the connective tissue of the mantle and lies on the rectal side of the terminal portion of the gonoduct (Seshaiya, 1934:203-204). This situation is similar to that observed in *Abyssochrysos*. Morrison (1954:369), however, discounted Seshaiya's interpretation, and noted that the penis was non-muscular and could not function as an intromittent organ. It is thus clear that the reproductive anatomy of the Paludominae, although still not clearly understood, is exceptional and does not resemble that of other cerithiaceans.

Fretter and Graham (1962:350) noted that in the Bithyniidae Troschel, superfamily Rissoacea, *Bithynia tentaculata* has a penis of pallial origin, although it appears superficially to emerge from the head.

Radula: The radulae of the two *Abyssochrysos* species (Figures 5,8) are nearly identical and although definitely taenioglossate, are much different from all other taenioglossate radulae. The distinctive rachidian and lateral teeth are not similar to

those of any other mesogastropods. A survey of numerous prosobranch radulae in Troschel (1856–1863), Sars (1878), Schepman (1909), and in a number of papers by Ponder (1965, 1966, 1967) and Ponder and Yoo (1976) illustrating radulae of unusual rissoaceans revealed none similar to *Abyssochrysos*.

SYSTEMATIC PLACEMENT.—The characters derived from the shell physiognomy, anatomy, and radulae of the two *Abyssochrysos* species do not fit the taxonomic limits of any Recent prosobranch superfamily. The bathyal habitat of these snails is also unusual. Similarly, there are no Cenozoic prosobranch groups to which the *Abyssochrysidae* may be assigned. One is thus confronted with the prospect of proposing a new superfamily. On the other hand, members of several families in the Paleozoic superfamily Loxonematacea Koken, 1889 have shell physiognomies that are strikingly like those of the *Abyssochrysidae* (Figure 11). The Paleozoic loxonemataceans were abundant in the Permian (Knight, 1930) and occur as fossils as late as the Upper Jurassic. There are three families in this group that closely resemble the *Abyssochrysidae*: the Paleozygopleuridae Horný, 1955, the Pseudozygopleuridae Knight, 1930, and the Zygopleuridae Wenz, 1938. They are characterized by species with turreted shells that are frequently ribbed and have smooth protoconchs of one and one-half whorls. Inner shell layers are not nacreous. Early members of the Loxonematacea have a slight sinus that tends to move toward the suture and become shallower in genera from later periods, but this feature is not present in all genera. According to Knight et al. (1960), the Pseudozygopleuridae arose in the Mississippian Period and comprised many genera and species. The Zygopleuridae were most common in the Triassic and Upper Jurassic. The loxonemataceans were common components of Paleozoic shallow-water faunas of inland seas. Numerous fossils of this group occur in shales (Knight, 1930:23) and some pseudozygopleurids are thought to have lived on muddy bottoms (David Schindel, pers. comm.). Although the loxonemataceans are thought to have disappeared after the Jurassic, it is interesting to note that early Miocene fossils of *Abyssochrysos melvilli* have been found in Fiji (Ladd, 1977).

ECOLOGY.—There are only two known living species of *Abyssochrysos*, both of which are uncommon and confined to bathyal zones of continental shelves.

Although the deep sea is no longer regarded as a refugium for an ancient fauna, (Clarke, 1962: Knudsen, 1970) both the abyssal and bathyal zones of the deep sea have provided habitats for other unusual mollusks that had their origins in the Paleozoic such as pleurotomaracean snails, monoplacophorans, and many archaic bivalves and scaphopods. Other invertebrate groups as well as some vertebrates of ancient lineage survive only in the deep sea. Parker (1962:286) suggested that many of the shelf-bottom faunas migrated down the slope during the Paleozoic and early Mesozoic times in response to competition. Menzies, George, and Rowe (1973:359) stated that most deep-sea endemic genera and families are derived from warm-water ancestors of the Mesozoic and Tertiary. They also pointed out that deep-sea animals have most likely been derived from shallow-water communities living on fine sediments. Most archaic types are found today on shelf or archibenthal depths rather than in the abyssal depths. Fossil loxonematids have thicker, heavier shells than *Abyssochrysos* species and lived in shallow seas. The thinner shells of the *Abyssochrysidae* are indicative of their bathyal habitat and are, in this respect, typical of deep-sea snails. Thus, it is not unreasonable to suggest that a few members of the Loxonematacea have persisted in this habitat. To date there are no records of *Abyssochrysos* from the abyssal zone.

Conclusions

The superfamily Loxonematacea is considered to be ancestral to the Cerithiacea (Fretter and Graham, 1962); both have been assigned to the order Caenogastropoda (=Mesogastropoda + Neogastropoda Wenz) by Knight et al (1960). The gross anatomy and taenioglossate radulae of the *Abyssochrysidae* are indicative of simple mesogastropods related to the superfamilies Viviparacea, Valvatacea, Rissoacea, and Cerithiacea. Rather than create a new superfamily to accommodate them and violate the principle of parsimony, I am provisionally recognizing the *Abyssochrysidae* as a relict family of loxonematid snails probably most closely related to the families Zygopleuridae and Pseudozygopleuridae. The collection of more specimens with well-preserved soft parts is necessary for any further speculation about their exact relationships within the Prosobranchia.

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