Deepest Atlantic Molluscs: Hadal Limpets (Mollusca, Gastropoda, Cocculiniformia) from the Northern Boundary of the Caribbean Plate

José H. Leal; M. G. Harasewych

Invertebrate Biology, Vol. 118, No. 2. (Spring, 1999), pp. 116-136.

Stable URL:
http://links.jstor.org/sici?sici=1077-8306%28199921%29118%3A2%3C116%3ADAMHL%28%3E2.0.CO%3B2-B

Invertebrate Biology is currently published by American Microscopical Society.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/amicros.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org
Mon Feb 25 19:10:28 2008

Invertebrate Biology 118(2): 116–136.

Deepest Atlantic molluscs: hadal limpets (Mollusca, Gastropoda, Cocculiniformia) from the northern boundary of the Caribbean Plate

José H. Leal[1,a] and M. G. Harasewych[2]

[1] The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957 USA
[2] Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution,
Washington, D.C. 20560-0118 USA

Abstract. Descriptions and scanning electron micrographs of the shell, protoconch, radula, and gross external anatomy are provided for four species of cocculiniform limpets collected from hadal depths of the Cayman and Puerto Rico trenches. Of these, one represents a new genus and species, *Macleaniella moskalevi* (Cocculinidae), endemic to the Puerto Rico Trench. Another, *Amphiplica plutonica* (Pseudococculinidae), represents a new species from the Cayman Trench of a globally distributed abyssal genus. The original descriptions of the remaining two species, *Fedikovella caymanensis* (Cocculinidae) and *Caymanabyssia spina* (Pseudococculinidae), both from the Cayman Trench and type species of their respective genera, contained only poorly reproduced illustrations of portions of the shells, and line drawings of isolated rows of radular teeth. These four species, each apparently endemic to their respective trenches, represent the deepest records of molluscs collected in the Atlantic Ocean.

Additional key words: Deep-sea, Cocculinidae, Pseudococculinidae

Cocculiniform limpets have remained one of the most taxonomically perplexing and enigmatic groups of gastropods since their first discovery at bathyal depths along the western Atlantic over a century ago (Dall 1882). Since then, the accelerating pace of deep-sea sampling, especially through the use of research submersibles, has greatly increased the number of known cocculiniform taxa. This, in turn, has prompted growing interest in all aspects of the systematics and biology of these animals (e.g., Moskalev 1976; Hickman 1983; Marshall 1986; Haszprunar 1987, 1988a,b; McLean 1987, 1988, 1991, 1992; Dantart & Luque 1994; McLean & Harasewych 1995; Haszprunar & McLean 1996). Today, well over a hundred species are divided among two superfamilies and ten families, with each family restricted to one or a very few biogenic substrates that sink into the deep sea (see Haszprunar 1988a). Of these, the best known and most diverse are the Cocculinidae (superfamily Cocculinoidea) and the Pseudococculinidae (superfamily Lepetelloidea), by virtue of their association with sunken wood and plant material, which are more easily sampled than other substrates.

In a recent review of the cocculinid and pseudococculinid limpets of the western Atlantic, McLean & Harasewych (1995) provided morphological data on previously described and new bathyal and abyssal species, but were unable to examine representatives of the two known hadal taxa. Subsequently, we were able to study samples from 24 hadal bottom trawlings on the floors of the Cayman and Puerto Rico Trenches that were collected by the University of Miami research vessels *John Elliott Pillsbury* and *James M. Gilliss* during the late 1960s and 1970s. Collected as part of the National Geographic Society/National Science Foundation-funded project "Investigations of the Biology and Distribution of the Tropical Deep-sea Fauna" (Table 1; Voss 1973, 1976), the samples were deposited in the Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami (UMML). Similar explorations in the same two trenches were carried out during Cruise 14 of the Russian vessel *Akademik Kurchatov* in 1973 (Pasternak et al. 1975; Wolff 1979). Aside from brief references in articles on deep-sea ecology (e.g., George & Higgins 1979; Wolff 1979, 1980), the bulk of the UMML samples, which include hadal representatives of several invertebrate groups, remained essentially untouched. Four species of cocculiniform limpets were present in 10 of these 24 trawlings. The species referable to the family Cocculinidae are *Fedikovella caymanensis* Moskalev, 1976 and *Maclean-*

---

[a] Author for correspondence. E-mail: leal@water.net

Table 1. Hadal stations occupied by the University of Miami R/Vs *John Elliott Pillsbury* (P) and *James M. Gilliss* (GS) along the northern boundary of the Caribbean Plate. Locations are Puerto Rico Trench (PRT), north of Puerto Rico Trench (NPRT) and Cayman Trench (CT). Depths are corrected. Locations represented by stations P-1406 and GS-121 are also respectively known as Milwaukee Deep and Oriente Deep. Station P-1376 is not hadal, but provided specimens of *Macleaniella moskalevi*. Gear used was either 10′ Blake trawl (BT) or 41′ otter trawl (OT). Signs (+) indicate stations yielding benthic molluscs, and (++) stations yielding cocculiniform limpets.

Cruise	Station	Location	Coordinates	Depth (m)	Date	Gear	Molluscs
P-6902	P-811	PRT	19°26.5′–19°26′N 66°29.4′–66°22.5′W	7375–7567	25 Jan. 1969	BT	++
P-6902	P-812	PRT	19°37′–19°41.5′N 66°51′–66°49′W	7545–7649	25–26 Jan. 1969	BT	
P-6902	P-816	PRT	19°33.5′–19°41.5′N 66°29′–66°19′W	7850–7610	28 Jan. 1969	BT	
P-6902	P-818	PRT	19°38′–19°40′N 67°37′–67°43′W	7961–7961	29 Jan. 1969	BT	++
P-6907	P-993	PRT	19°22.5′–19°26.4′N 66°13.8′–66°08.5′W	7540–7320	25–26 Jul. 1969	BT	
P-7001	P-1164	PRT	19°23′–19°33′N 66°23′–66°19′W	7338–7338	19 Jan. 1970	BT	
P-7001	P-1166	PRT	19°47′–19°49′N 66°17.5′–66°17′W	7960–7960	20 Jan. 1970	BT	
P-7001	P-1168	PRT	19°42.5′–19°43′N 67°05′–67°05′W	7961–7970	21 Jan. 1970	OT	++
P-7106	P-1376	NPRT	20°45.4′–20°46.8′N 65°00.5′–64°58.3′W	5179–5184	03 Jul. 1971	OT	++
P-7106	P-1380	PRT	19°37.7′–19°39.8′N 65°04.0′–65°04.2′W	7380–7358	04 Jul. 1971	OT	+
P-7106	P-1382	PRT	19°16′–19°23.2′N 65°50.7′–65°50.0′W	7282–7363	05 Jul. 1971	OT	+
P-7106	P-1384	PRT	19°45′–19°49′N 65°00′–66°56.5′W	7956–7919	06 Jul. 1971	OT	+
P-7106	P-1406	PRT	19°31.8′–19°36.5′N 68°07.5′–68°08.5′W	7850–7910	16–17 Jul. 1971	OT	+
GS-7301	GS-59	PRT	19°22.9′–19°30.5′N 66°50.0′–66°49.6′W	7498—7461	18 Jan. 1973	OT	+
GS-7301	GS-60	PRT	19°39.5′–19°46.4′N 66°08.0′–66°06.0′W	7968–7955	19 Jan. 1973	OT	+
GS-7301	GS-61	PRT	20°05.9′–20°09.7′N 65°26.0′–65°27.3′W	6995–6584	20 Jan. 1973	OT	+
GS-7301	GS-62	PRT	19°44.3′–19°49.0′N 64°50.7′–64°57.5′W	6967–7452	21 Jan. 1973	OT	+
GS-7506	GS-108	PRT	19°38.1′–19°40.1′N 68°01.2′–67°59.1′W	8567–8567	11 Jul. 1975	OT	++
GS-7506	GS-109	PRT	19°40.6′–19°43.2′N 67°19.4′–67°19.9′W	8595–8595	12 Jul. 1975	OT	++
GS-7506	GS-111	PRT	19°15.6′–19°16.7′N 67°25.8′–67°27.5′W	7406–6755	13 Jul. 1975	OT	+
GS-7506	GS-113	PRT	19°26.0′–19°27.6′N 66°24.0′–66°27.3′W	7640–7650	14 Jul. 1975	OT	++
GS-7506	GS-114	PRT	19°51.0′–19°50.8′N 65°31.3′–65°33.7′W	7745–7600	15 Jul. 1975	OT	
GS-7506	GS-121	CT	19°38.0′–19°39.3′N 76°18.1′–76°15.5′W	6466–6600	21 Jul. 1975	OT	++
GS-7506	GS-127	CT	19°08.4′–19°07.5′N 79°53.7′–79°55.5′W	7247–7225	23 Jul. 1975	OT	++
GS-7506	GS-128	CT	19°04.6′–19°05.0′N 80°06.0′–80°10.0′W	6870–6910	24 Jul. 1975	OT	++

iella moskalevi new genus, new species, while those referable to Pseudococculinidae are *Caymanabyssia spina* MOSKALEV, 1976, and *Amphiplica plutonica* new species. *Macleaniella moskalevi* appears to be endemic to the Puerto Rico Trench, while the remaining three species occur sympatrically and are presently known only from the Cayman Trench. In this study we provide descriptions of these four species based on adult shell characters, protoconch, radula, and gross external morphology. Detailed anatomical studies of *Macleaniella moskalevi* are provided in an accompanying article by Strong & Harasewych (1999).

Geological and environmental setting

The Caribbean Plate is a separate and relatively small tectonic feature that, according to an interpretation of shallow earthquakes and faulting patterns at the plate boundaries (Sykes et al. 1982), has been moving in an ENE direction since at least the late Eocene (38 Ma). The Puerto Rico Trench, which includes the deepest point in the Atlantic Ocean (–8605 m) is the product of a combination of strike-slip faulting (on its western segment) and subduction of the North American Plate under the Caribbean Plate (on its eastern segment). The Cayman Trench resulted from a complex interaction between the strike-slip movement of the Caribbean Plate past the North American Plate and the production of new seafloor at the Mid-Cayman Spreading Center around 81.5°W (Malfait & Dinkelman 1972; Sykes et al. 1982; Bonini et al. 1984; U.S. Department of Defense 1992).

Methods

The bulk of the material examined in this study was collected between January 1969 and July 1975 as part of the project "Investigations of the Biology and Distribution of the Tropical Deep-sea Fauna", and deposited in the Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami. The collecting gear used was either a 10′ Blake trawl or a 41′ otter trawl (Voss 1973, 1976). Some specimens had been sorted immediately after the respective cruises. Other limpets were retrieved by the senior author from several one- or five-gallon jars containing trench-floor sediment samples, plant remains generally resembling the assortment described by Gunn & Dennis (1976) for station P-1168, and other debris. The shells of these specimens were mostly decalcified, in some cases completely dissolved, leaving only the periostracum; this was apparently due to prolonged exposure (20+ years) to the acidic ($pH=4.5 \pm 0.5$) alcohol in the "debris" jars. Low pH in these jars was most likely caused by leaching of humic and tannic acids from plant material into 70% ethanol. These "soft specimens" were accessioned under different numbers from those of pre-sorted and better-preserved samples from the same stations.

The junior author was able to examine the type series of *Fedikovella caymanensis* and *Caymanabyssia spina* housed in the Zoological Museum of Moscow State University (ZMMU). Drs. L. Moskalev and D.L. Ivanov generously made this material available for study and re-illustration, and provided paratypes of each of these species for the collections of the National Museum of Natural History, Smithsonian Institution (USNM).

Preserved soft parts of several specimens were further dehydrated through standard alcoholic series and critical-point dried with carbon dioxide as the transitional fluid, or chemically dried with hexamethyldisilizane (HMDS). Radular ribbons were macerated in 10% NaOH for 48 h at room temperature, thoroughly rinsed in deionized water, sonicated for 5–30 s, dehydrated in standard alcoholic series, and mounted on scanning electron microscope (SEM) stubs using double-sided carbon tape. Dried tissue, shells, and radulae were coated with palladium or carbon and gold, and examined under Hitachi S-570 or International Scientific Instruments ISI-130 Dual Stage SEMs.

Shells were measured using an optical micrometer on a Leica MZ-8 dissecting microscope, according to parameters specified in McLean & Harasewych (1995; fig. 1). Protoconch measurements are based on scanning electron micrographs.

Abbreviations of museum repositories are: ANSP, Academy of Natural Sciences, Philadelphia; BMSM, Bailey-Matthews Shell Museum, Sanibel, Florida; LACM, Los Angeles County Museum of Natural History; MNHN, Muséum national d'Histoire naturelle, Paris; UMML, Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; ZMMU, Zoological Museum, Moscow State University.

Taxonomic Account

Class Gastropoda CUVIER 1797
Order Cocculiniformia HASZPRUNAR 1987

Cocculiniformia was originally proposed as a suborder of Archaeogastropoda to include a morphologically diverse group of hermaphroditic, symmetrical limpets with a central or posterior apex, rhipidoglossan radula, ventral statocysts, horseshoe-shaped shell muscles divided into bundles, a shallow mantle cavity with a single, left gill, and internal fertilization, although

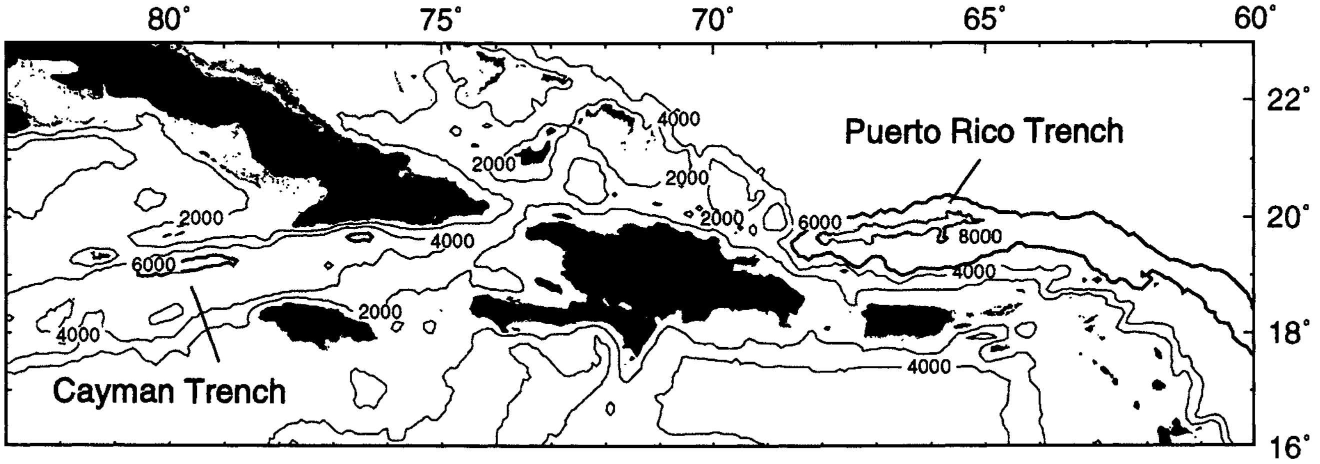


Fig. 1. Bathymetric chart showing the location of the trenches in the tropical western Atlantic Ocean.

several of these characters have been lost or modified in some lineages. All inhabit deep water, mostly at bathyal depths but extend into the abyssal and hadal zones, and colonize biogenic substrates, including sunken wood, shallow water plant debris, algal holdfasts, whale or fish bone, squid beaks, skate egg cases, crab carapaces, and polychaete tubes.

Cocculiniformia has been divided into two superfamilies, the Cocculinoidea Dall, 1882, containing two families, and the Lepetelloidea Dall, 1882, containing eight families. Limited ecological data suggest that each of these families is restricted to one or a few specific biogenic substrates (see Haszprunar 1988a: fig. 4; Hickman 1988).

While there is general agreement on the composition and monophyly of these two superfamilies, there has been recent debate regarding their relationship to each other. Most authors have treated Cocculiniformia as a monophyletic taxon (e.g., Hickman 1983, 1984; Marshall 1986; Haszprunar 1987, 1988b,c; McLean 1987, 1988, 1991, 1992; Dantart & Luque 1994; McLean & Harasewych 1995). In recent studies of gastropod phylogeny based on morphological characters (Ponder & Lindberg 1996, 1997), Cocculinoidea emerged as sister taxon to Neritopsina, and Lepetelloidea was placed within Vetigastropoda. While partial 18S rDNA sequences did not strongly support the monophyly of Cocculiniformia, they indicated that Cocculinoidea and Lepetelloidea are more closely related to each other and to patellogastropod limpets than to Neritopsina or Vetigastropoda (Harasewych et al. 1997).

A number of researchers have reviewed the systematics, biology, ecology, and evolutionary relationships of representatives of two of the more common cocculiniform families, the Cocculinidae (Cocculinoidea) and Pseudococculinidae (Lepetelloidea), which often co-occur on sunken wood and plant remains recovered from bathyal, abyssal, and hadal depths (Clarke 1962; Hickman 1983, 1984; Marshall 1986; Haszprunar 1987, 1988b,c; McLean 1987, 1988, 1991, 1992; Dantart & Luque 1994; McLean & Harasewych 1995; Haszprunar & McLean 1996).

Superfamily Cocculinoidea Dall 1882

This superfamily has been characterized by the presence of shell muscles divided into bundles, a pseudoplicatid gill, a single left kidney, a hermaphroditic gland with glandular gonoduct, a single pair of radular cartilages, a distinctive radula in which the rachidian teeth are weakly developed or absent, statocysts with a single statolith, and subpallial glands in some taxa (Haszprunar 1988a). Cocculinoidea is divided into two families, the Cocculinidae Dall, 1882, and the Bathysciadidae Dautzenberg & Fischer, 1900, both ranging from bathyal to hadal depths. The Cocculinidae occur on sunken wood, while the Bathysciadidae are found on cephalopod beaks. Several authors (Marshall 1986; Haszprunar 1988a; McLean & Harasewych 1995) have either noted the cocculinid affinities of *Teuthirostria* Moskalev, 1976, which occurs on squid beaks, or included the genus in Cocculinidae instead of Bathysciadidae.

Family Cocculinidae Dall 1882

Cocculinid limpets have thin, porcellaneous shells that may reach 12 mm in length. The distinctive protoconch, about 300 μm in length, is situated along the posterior midline of the shell, and has a short apical fold and reticulate sculpture over some or all of its surface. The radula is composed of a broad, often weakly defined rachidian tooth, three inner lateral teeth, a massive pluricuspid tooth, and numerous marginal teeth. Animals are simultaneous hermaphrodites, with a copulatory organ present on the right side of the body, either within the right cephalic tentacle, the right oral lappet, or emerging from the right side of the foot.

Genus *Fedikovella* Moskalev 1976

Synonymy—

Fedikovella Moskalev, 1976: 62; Marshall 1986: 506; Haszprunar 1987: 322; McLean & Harasewych 1995: 17.

Type species: *Fedikovella caymanensis* Moskalev, 1976, by original designation.

Diagnosis: Protoconch with concentric or reticulate sculpture on first ¾ whorl, smooth thereafter. Teleoconch tall, strongly convex dorsally. Apex along midline, below highest point of shell, overhanging concave posterior slope. Teleoconch sculpture clathrate, with concentric sculpture slightly more prominent than axial. Periostracum smooth. Cephalic tentacles equal in size, right tentacle serving as copulatory organ. Eyes absent. Single pair of epipodial tentacles. Radula with rachidian, first, and second lateral teeth all multicuspid. Pluricuspid tooth largest, with three broad denticles.

Remarks: Based on a detailed examination of the radula of *F. caymanensis,* Hickman (1983) did not feel that it differed sufficiently from that of *Cocculina* to warrant recognition of a separate genus. She questioned the utility of a tricuspid rachidian tooth as a defining character of the genus, especially as the number of cusps on the rachidian tooth of several species of cocculinids may vary not only intraspecifically, but also in the same individual (e.g., *F. caymanensis,* Fig. 3D; *F. beanii* (Dall, 1882) McLean & Harasewych 1995, fig. 56). Subsequent authors (Marshall 1986; Haszprunar 1987; McLean & Harasewych 1995) have recognized *Fedikovella* as a distinct genus, distinguishing it from *Cocculina* using features of the shell, protoconch, and copulatory organ.

In addition to the type species, Moskalev (1976) included the western Atlantic species, *Cocculina beanii* Dall, 1882, and the Indo-Pacific *C. capulus* Thiele, 1925, in *Fedikovella.* McLean & Harasewych (1995) concurred with Moskalev's (1976) allocation of *Cocculina beanii* to *Fedikovella* based on the presence of distinctive concentric protoconch sculpture in both species, and suggested that this feature may be diagnostic of the genus. These authors were reluctant to include *C. capulus* in *Fedikovella* based solely on the presence of a multicuspid rachidian tooth.

Fedikovella caymanensis Moskalev 1976
Figs. 2 A–D, 3 A–E

Synonymy—

Cocculinidae gen. sp. E Moskalev & Vilenkin (1975: 139).
Fedikovella caymanensis Moskalev, 1976: 62, fig. 1, pl. 2, figs. 1–2; Wolff 1979: 121,126; Hickman 1983: 82, fig. 23 (radula); McLean & Harasewych 1995: 17–18.

Description: Shell (Fig. 2A) small for family (length to 4.0 mm), strongly arched, elevated (height/length ~0.5). Protoconch (Fig. 2B,C) 320 μm in length, smooth with microscopic crystals forming a finely reticulated, net-like surface (Fig. 2C, D) along initial ¾ whorl, smooth, finely pitted thereafter. Teleoconch tall, recurved, with strongly convex anterior slope. Protoconch near posterior margin of shell, below mid-point of shell height, overhanging slightly concave posterior slope, which, measured from protoconch to posterior margin, comprises ~15% of shell length. Shell margin smooth, continuous. Teleoconch white, with clathrate sculpture of strong, concentric ribs crossed by low radial ridges, forming nearly equilateral rectangles. Periostracum light brown, thin, mostly worn in examined specimens. Aperture planar, oval, with lateral sides nearly parallel. Interior surface smooth, U-shaped muscle scar barely discernible. Animal (Fig. 3A,B) unpigmented, cephalic tentacles cylindrical, right tentacle (Fig. 3B: rct) serving as copulatory organ. Eyes absent. Oral lappets (Fig. 3B: ol) broad laterally, narrow along anterior margin of oral disk. Oral disk continuous and heavily ciliated anteriorly, interrupted posteriorly. Single pair of reduced epipodial tentacles. Radula (Fig. 3C) weakly asymmetrical, skewed right. Rachidian tooth (Fig. 3D,E: r) narrow, with outer edges weakly defined, distal third of tooth narrower, with prominent central cusp flanked by two to three smaller cusps on each side. Three inner lateral teeth (Fig. 3D: 1, 2, 3) with slender shafts and recurved cusps that are subdivided into denticles on first and second lateral teeth. Fourth lateral (pluricuspid Fig. 3D: pc) tooth massive, tricuspid, with central cusp largest. Marginal teeth similar in size, with elongated and flattened shafts, ending in strongly hooked, serrated cusps.

Type locality: Western part of Cayman Trench, 19°00.6′N, 80°29.5′W, 6800 m, on pieces of wood, R/V *Akademik Kurchatov,* cruise 14, station 1242-A, 2.5 m Sigsbee trawl, 20 March 1973.

Type material: Holotype, ZMMU Lc-22850; paratypes, ZMMU Lc-22851; 4 paratypes USNM 880300; all from type locality.

Literature records: 5 specimens, eastern end of Cayman Trench, 19°38.5′N, 76°37.8′W, 6740–6780 m, on assorted plant remains, R/V *Akademik Kurchatov,*

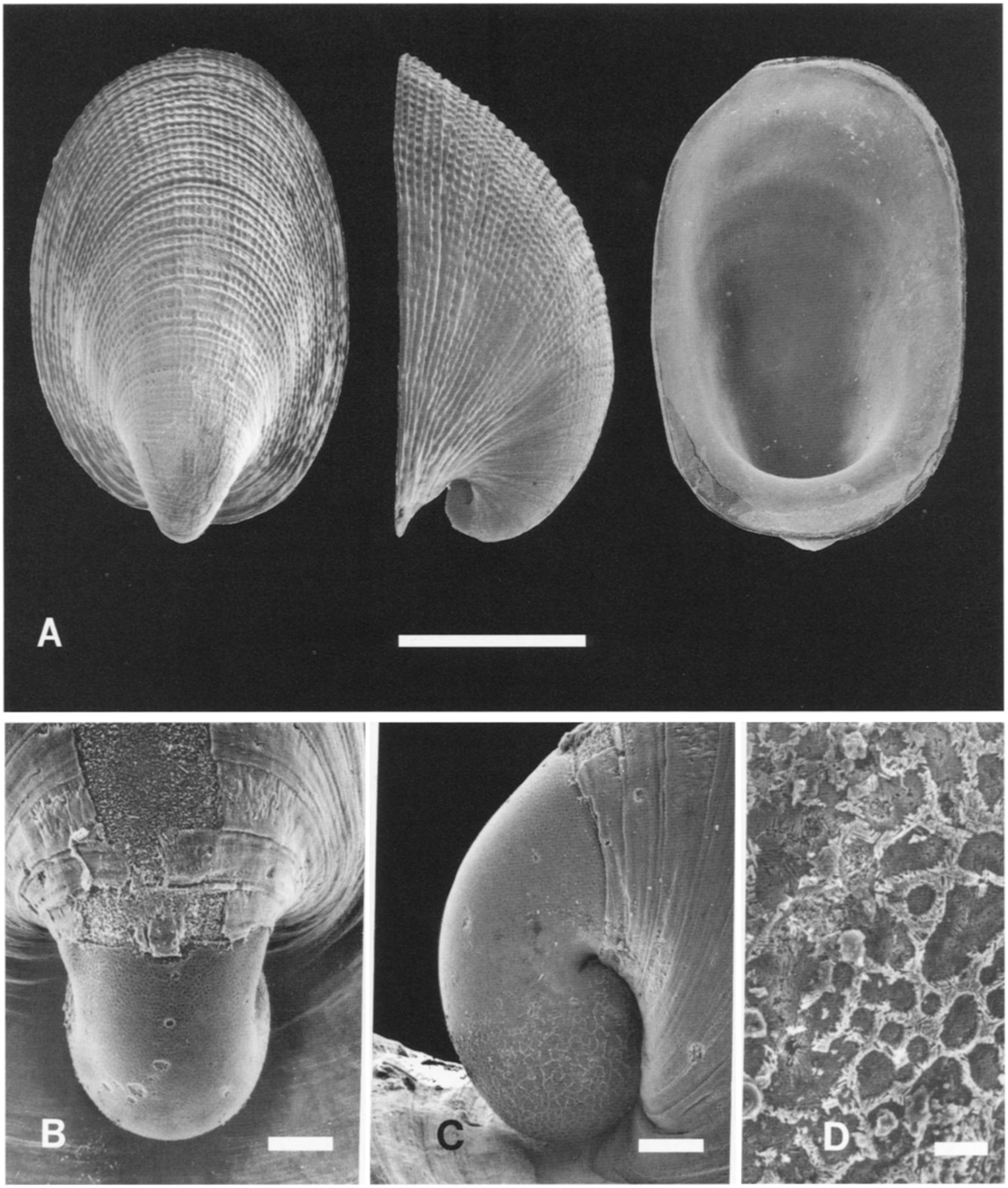


Fig. 2. *Fedikovella caymanensis* Moskalev, 1976. **A.** Dorsal, lateral, and ventral views of paratype (USNM 880300). Scale bar, 1.5 mm. **B.** Dorsal and **C.** lateral view of protoconch. Scale bar, 50 μm. **D.** Detail of protoconch sculpture. Scale bar, 10 μm.

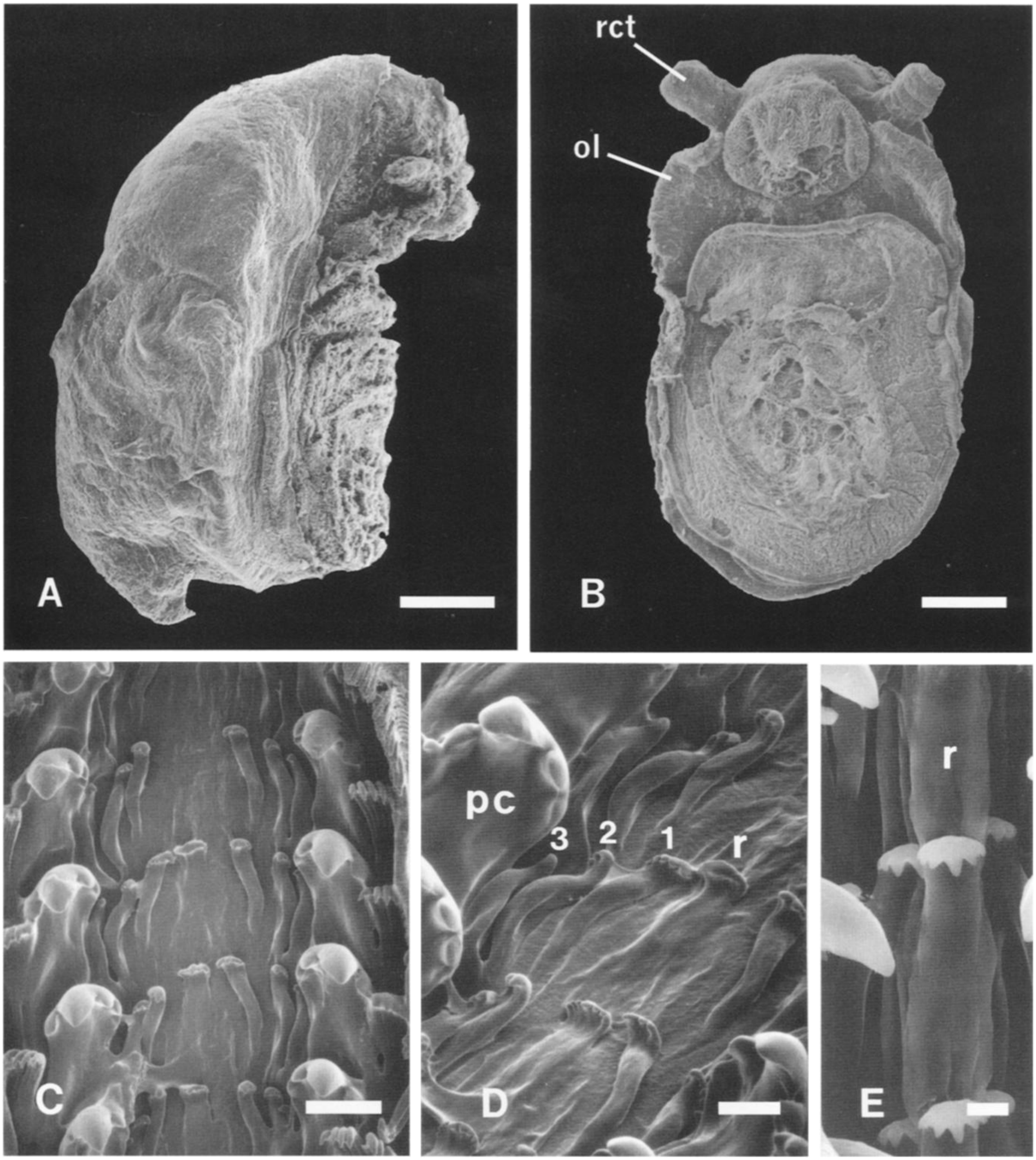


Fig. 3. *Fedikovella caymanensis* Moskalev, 1976. **A.** Left lateral and **B.** ventral views of critical point dried animal of paratype. Scale bar, 500 μm. **C.** Dorsal and **D.** postero-lateral view of central field of radular ribbon. Scale bar, 10 μm. **E.** Detail of rachidian tooth. Scale bar, 5 μm.—ol, oral lappet; pc, pluricuspid tooth; r, rachidian tooth; rct, right cephalic tentacle; 1, first lateral tooth; 2, second lateral tooth; 3, third lateral tooth.

cruise 14, station 1267, 2.5 m Sigsbee trawl, 24–25 March 1973 (Moskalev 1976: 62).

Other material examined: UMML 30.8425, 4 intact specimens; UMML 30.9177, 10 specimens with heavily decalcified shells due to prolonged preservation in acidic alcohol; all from the western part of the Cayman Trench, 19°08.4′–19°07.5′N, 79°53.7′–79°55.5′W, 7247–7225 m, R/V *James M. Gilliss,* cruise GS-7506, station GS-127, 41 ft. otter trawl, 23 July 1975.

Distribution: Known only from the hadal zone of Cayman Trench (6740–7247 m).

Remarks: *Fedikovella caymanensis,* a species apparently endemic to the Cayman Trench, is known to live and feed on sunken wood (Moskalev 1976; Wolff 1979). Hickman (1983) has illustrated the radula of this species, while a detailed discussion of its anatomy will be presented by Haszprunar (pers. comm.), in all cases based on samples collected during Cruise 14 of the R/V *Akademik Kurchatov.* The data presented here are based on four paratypes recently sent on exchange to the National Museum of Natural History, Smithsonian Institution, as well as 14 specimens collected by the R/V *James M. Gilliss.*

In addition to illustrating the entire shell and details of the protoconch for the first time, we are able to confirm several features of the external anatomy of this species. Moskalev (1976) described the cephalic tentacles as similar to each other. Our observations indicate that the unmodified right tentacle serves as a copulatory organ. McLean & Harasewych (1995) reported a personal communication from Marshall indicating that the copulatory organ of *Fedikovella beanii* was located behind the base of the right cephalic tentacle. This discrepancy suggests a reassessment of the relationships of *F. beanii* may be in order.

Genus *Macleaniella* new genus

Type species: *Macleaniella moskalevi* new species.

Diagnosis: Protoconch smooth, unsculptured. Teleoconch tall, strongly convex dorsally, recurved. Apex near the posterior margin of the shell, well below its highest point, overhanging concave posterior slope. Teleoconch sculpture primarily of fine, low, radial cords. Periostracum smooth, thicker along radial cords. Interior with large, sinuated, asymmetrical septum originating at the protoconch. Animal with right cephalic tentacle broadened to form copulatory organ that is distally bilobed. Eyes absent. Single pair of short, triangular, epipodial tentacles. Shell septum separates terminal portion of visceral mass containing gonad from remaining tissues. Radula with weakly denticulated rachidian and first and second lateral teeth. Pluricuspid tooth largest, with three broad denticles.

Etymology: This genus is named in honor of James H. McLean, of the Los Angeles County Museum of Natural History, in recognition for his contributions to the systematics of deep-sea limpets.

Remarks: *Macleaniella* has unique features and combinations of characters that preclude the inclusion of its type species in any of the presently named genera within the family Cocculinidae. The presence of a copulatory organ formed from the right cephalic tentacle is a feature that *Macleaniella* shares only with the genera *Coccocrater* HASZPRUNAR, 1987 and *Fedikovella,* which differ in having an unmodified right cephalic tentacle. In *Teuthirostria* MOSKALEV, 1976 and *Coccopigya* MARSHALL, 1986, the copulatory organ forms an appendage on the right cephalic tentacle; in *Cocculina* DALL, 1882, the copulatory organ is on the tip of the right oral lappet; while in *Paracocculina* HASZPRUNAR, 1987, the copulatory organ emerges from the side of the foot behind the cephalic tentacle. *Macleaniella* may be readily distinguished from *Coccocrater* on the basis of conchological characters, specifically in lacking the reticulate protoconch sculpture and pitted, radial teleoconch sculpture of *Coccocrater.* The shell of *Macleaniella* may be most easily identified by the presence of a large internal septum that is unique within Cocculinidae.

Macleaniella moskalevi new species
Figs. 4A–E, 5A–G, Table 2

Description: Shell (Fig. 4A) small for family (length to 5.17 mm), thin, strongly arched, elevated (height/length 0.46–0.64), whitish, not eroded. Anterior slope strongly convex. Posterior slope ~25% of shell length, weakly concave, beneath strongly recurved early teleoconch. Protoconch situated just anterior of posterior shell margin (0.90 shell length from anterior margin), slightly above mid-height of shell. Shell margin generally smooth, continuous, may have one or two weak steps most notable in lateral view. Protoconch (Fig. 4B,C) length 395 μm, smooth, except for minute, irregularly distributed granules (Fig. 4E). Teleoconch sculpture of low radial cords ~20 μm apart with finer threads in interspaces. Concentric sculpture limited to fine growth lines. Periostracum light brown, thin, thicker along radial cords and threads (Fig. 4D). Aperture broadly ovate, nearly planar. Large, sinuate, asymmetrical septum strongly indented to right of mid-line, extends from protoconch, spans posterior quarter of shell interior. Muscle scars barely distinguishable. Animal (Fig. 5A,B) tall, unpigmented, with uppermost portion of visceral mass

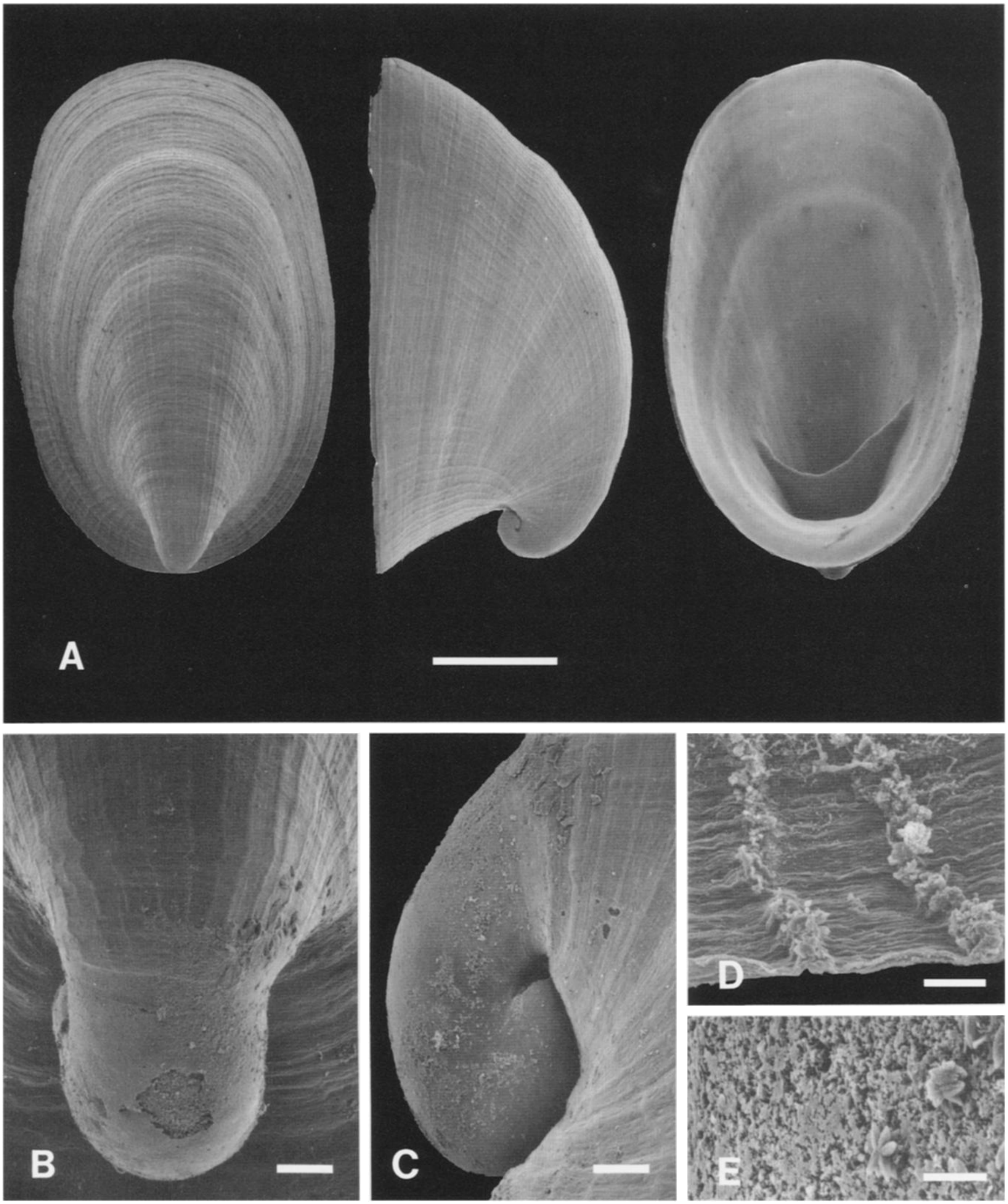


Fig. 4. *Macleaniella moskalevi,* new species. **A.** Dorsal, lateral, and ventral views of holotype (USNM 880301). Scale bar, 1.0 mm. **B.** Dorsal and **C.** lateral view of protoconch. Scale bar, 50 µm. **D.** Detail periostracum at shell edge. Scale bar, 50 µm. **E.** Detail of protoconch sculpture. Scale bar, 5 µm.

Table 2. *Macleaniella moskalevi* new species. Measurements of shell characters (Parameters measured as in McLean & Harasewych 1995:fig. 1). Linear measurements in mm (n = 17).

Character	Mean	σ	Range
Shell length (SL)	4.23	0.74	2.92–5.17
Shell width (SW)	2.83	0.50	2.00–3.63
Shell Height (SH)	2.32	0.62	1.50–3.25
SL/SW	1.49	0.05	1.41–1.58
SH/SL	0.54	0.06	0.46–0.64

separated by shell septum. Right cephalic tentacle twice as broad as left, flattened, bilobed (Fig. 5C,D: rct), forming copulatory organ. Oral lappets broad laterally, narrow along anterior surface of oral disk. Oral disk continuous, uninterrupted, heavily ciliated anteriorly. Epipodial tentacles (Fig. 5B: et) one per side, short, triangular. Radula weakly asymmetrical, skewed right (Fig. 5E). Rachidian tooth (Fig. 5G: r) broad basally, narrow distally, with a large central cusp and small, indistinct lateral cusps (2–3 per side). Three inner lateral teeth (Fig. 5G: 1, 2, 3) with slender, curved shafts and recurved distal ends subdivided into denticles. Pluricuspid tooth massive, tricuspid, central cusp largest (Fig. 5E). Marginal teeth with elongated, flattened shafts. First marginal tooth with single, terminal cusp, remaining marginal teeth with 3–6 serrate cusps adjacent to terminal cusp (Fig. 5F). A detailed anatomical investigation of this species is reported in an accompanying article by Strong & Harasewych (1999).

Etymology: This species honors Dr. Lev Moskalev, of the P. P. Shirsov Institute of Oceanology, Russian Academy of Sciences, for his discovery of and pioneering work on hadal cocculiniform limpets.

Type locality: Western part of Puerto Rico Trench, 19°40.6′–19°43.2′N, 67°19.4′–67°19.9′W, 8595–8595 m, R/V *James M. Gilliss,* cruise GS-7506, station GS-109, 41 ft. otter trawl, 12 July 1975.

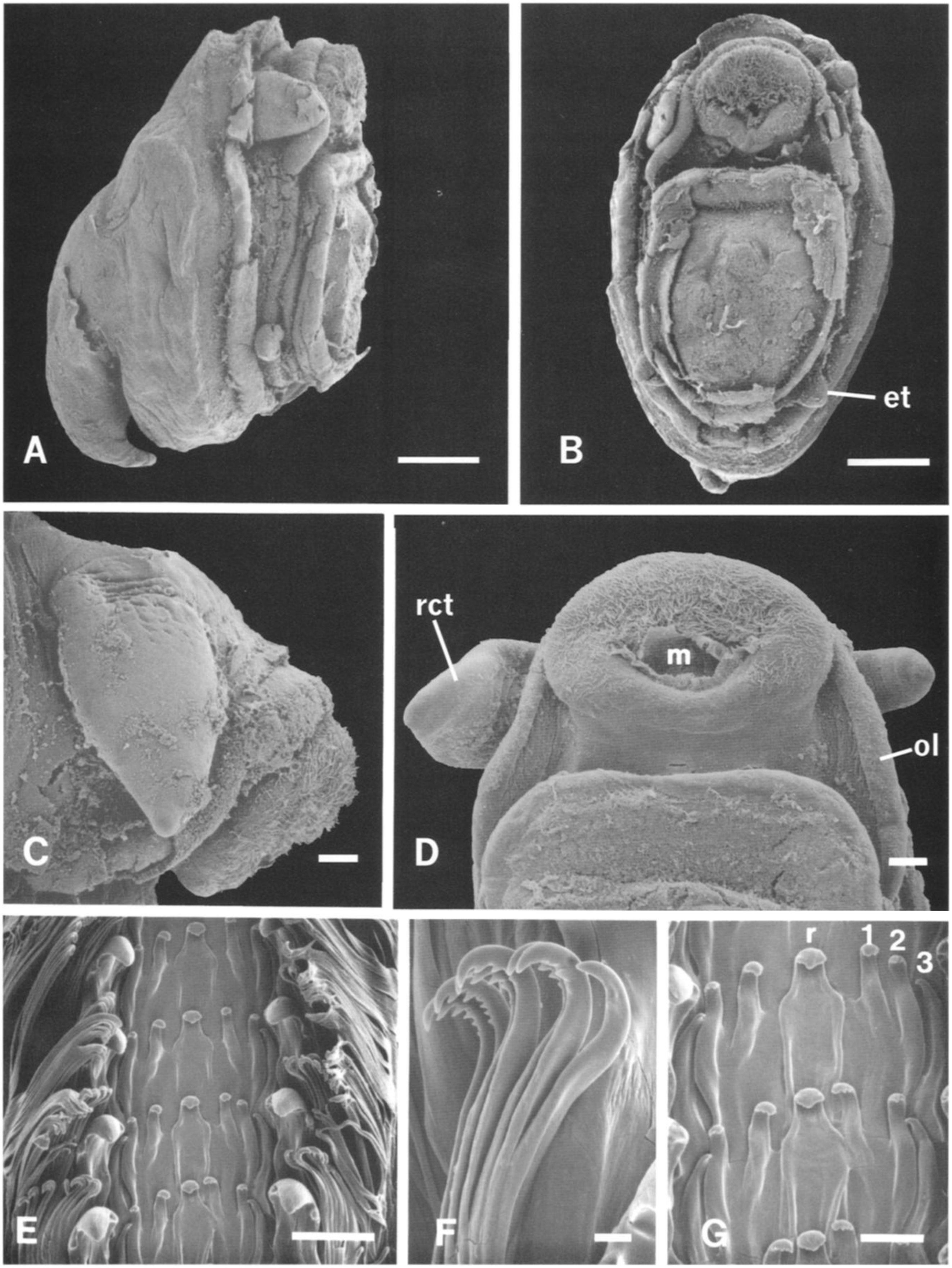
Type material: Holotype, USNM 880301 (ex-UMML 30.8385), from type locality. All paratypes in alcohol: BMSM 1000, 6 paratypes (ex-UMML 30.8385); UMML 30.8387, 14 paratypes (5 shells intact), heavily decalcified; all from type locality; UMML 30.8386, 15 paratypes (3 intact shells); USNM 880302, 8 paratypes; LACM, 3 paratypes; MNHN unnumbered, 2 paratypes; ANSP 399809, 3 paratypes; ZMMU Lc-22852, 3 paratypes; all from western part of Puerto Rico Trench, 19°42.5′–19°43.0′N, 67°05.0′–67°05.0′W, 7961–7970 m, R/V *John Elliott Pillsbury,* cruise P-7001, station P-1168, 41 ft. otter trawl, 21 January 1970; (ex-UMML 30.8386); USNM 880303, 6 paratypes (2 shells intact), western part of Puerto Rico Trench, 19°26.0′–19°27.6′N, 66°24.0′–66°27.3′W, 7640–7650 m, R/V *James M. Gilliss,* cruise GS-7506, station GS-113, 41 ft. otter trawl, 14 July 1975 (ex-UMML 30.8424, entire lot); UMML 30.8421, 5 paratypes (two shells intact), heavily decalcified, western part of Puerto Rico Trench, 19°38′–19°40′N, 67°37′–67°43′W, 7961–7961 m, R/V *John Elliott Pillsbury,* cruise P-6902, station P-818, 10 ft. Blake trawl, 29 January 1969.

Other material examined: UMML 30.8388, 3 specimens (one intact shell), western part of Puerto Rico Trench, 19°26.5′–19°26.0′N, 66°29.4′–66°22.5′W, 7375–7567 m, R/V *John Elliott Pillsbury,* cruise P-6902, station P-811, 10 ft. Blake trawl, 25 January 1969; UMML 30.8385, 7 specimens without shells; UMML 30.8422, 1 specimen, northeastern slope of Puerto Rico Trench, 20°45.4′–20°46.8′N, 65°00.5′–64°58.3′W, 5179–5184 m, R/V *John Elliott Pillsbury,* cruise P-7106, station P-1376, 41 ft. otter trawl, 3 July 1971; UMML 30.8423, 2 specimens, heavily decalcified, western end of Puerto Rico Trench, 19°38.1′–19°40.1′N, 68°01.2′–67°59.1′W, 8567–8567 m, R/V *James M. Gilliss,* cruise GS-7506, station GS-108, 41 ft. otter trawl, 11 July 1975.

Distribution: Known from the lower abyssal and hadal regions of the western portion of the Puerto Rico Trench (5179–8595 m).

Remarks: Specimens were found on sunken wood fragments and logs, where they cut long, sharp-sided grooves that were nearly semicircular in cross-section. The limpet illustrated as "Pseudococculinidae n.sp." by Wolff (1979: pl. 5, fig. F), based on a photograph by L. Moskalev, resembles this species. However, the locality indicated by Wolff is in the Cayman Trench, whereas verifiable records of *Macleaniella moskalevi* are confined to the Puerto Rico Trench. The type locality of *M. moskalevi* is at a depth of 8595 m on the trench floor, which represents the greatest depth sampled for benthic organisms in the Atlantic Ocean. While no other molluscs were found at this station, other animals included one species of the deep-sea anemone genus *Galatheanthemum,* one sponge, several polychaete worm tubes, one isopod, and four specimens of caridean shrimp.

Superficially, *M. moskalevi* appears most similar to *F. caymanensis.* Conchologically, *M. moskalevi* differs from *F. caymanensis* in having an internal septum as well as less prominent external shell sculpture consisting predominantly of radial elements. The sculpture of *F. caymanensis* is more strongly clathrate and dominated by concentric ridges. In contrast to *F. caymanensis,* the protoconch of *M. moskalevi* never projects beyond the posterior shell margin, and has a smooth surface, lacking the reticulate or concentric sculpture diagnostic of the genus *Fedikovella.*


A
B
et
C
rct
m
ol
D
r
1
2
3
E
F
G

Although the right cephalic tentacle serves as the copulatory organ in both *Fedikovella caymanensis* and *M. moskalevi,* this structure is unmodified in *F. caymanensis,* but enlarged, flattened, and distally bilobed in *M. moskalevi.* The oral disk is interrupted posteriorly in *F. caymanensis,* but not in *M. moskalevi.* Radular morphology of *M. moskalevi* is very similar to that of *Fedikovella caymanensis* and *F. beanii.* All of these taxa have rachidian teeth with narrow basal plates, long shafts, and multiple (>3) cusps, features uncommon among Cocculinidae. However, the innermost marginal tooth of *M. moskalevi* lacks the multiple cusps present on the second and subsequent marginal teeth (Fig. 5F) and on all marginal teeth in *Fedikovella caymanensis* and *F. beanii.*

Superfamily Lepetelloidea DALL 1882

Members of this superfamily can be distinguished by their undivided shell muscles (except Lepetellidae); secondary gill leaflets or reduced gills; lack of subpallial glands; paired kidneys (the right being larger); separate testes and ovary (Choristellidae are gonochoristic) with ciliated, non-glandular gonoducts; a radula with a well-developed, characteristic rachidian tooth; and statocysts with multiple statocones. Members of Lepetelloidea are divided into eight families that collectively range from sublittoral to hadal depths, and inhabit the range of biogenic substrates known to support cocculiniform limpets. The phylogenetic relationships of the lepetelloidean families have recently been examined by Haszprunar & McLean (1996).

Family Pseudococculinidae HICKMAN 1983

Pseudococculinid limpets have small (usually <6 mm), thin, often translucent shells. The protoconch is generally ~200 μm in length, has a long, narrow apical fold and sculpture ranging from smooth to encrusted with fine, cubic crystals, finely pustulose, subreticulate, or with anastomosing threads. The radula is strongly asymmetrical, consisting of a broad, uncusped rachidian tooth, four inner lateral teeth, a large pluricuspid tooth, and numerous marginal teeth. Animals are hermaphroditic. The right cephalic tentacle is generally enlarged or modified to serve as a copulatory organ.

Subfamily Caymanabyssiinae MARSHALL 1986

This subfamily was erected by Marshall (1986) to contain the genera *Caymanabyssia* and *Colotrachelus,* based on their having protoconch microsculpture consisting of prismatic crystals; extensively fused apical folds; distinctive radula with rachidian and lateral teeth lacking cutting surfaces; a ciliary band rather than a groove between the urogenital pore and the right cephalic tentacle. Haszprunar (1988c) added the genera *Yaquinabyssia, Copulabyssia,* and *Amphiplica,* and observed that, unlike Pseudococculiinae, Caymanabyssiinae had one or more gill leaflets on the left side of the body. McLean (1991: 46) suggested that dividing the Pseudococculinidae into the two subfamilies may be premature, as several characters do not segregate concordantly between the two groups.

Genus *Caymanabyssia* MOSKALEV 1976

Synonymy—

Caymanabyssia MOSKALEV, 1976: 65; Marshall 1986: 520, 538; Haszprunar 1988b: 177; McLean 1991: 39; McLean & Harasewych 1995: 28.

Type species: *Caymanabyssia spina* MOSKALEV, 1976 by original designation.

Diagnosis: Shell small (to 4 mm), white, translucent, low in profile. Protoconch with minute columnar prisms. Teleoconch sculpture of conical projections in diagonally reticulate pattern. Rachidian, lateral radular teeth degenerate, cusps lacking, rachidian tooth subquadrate. Single gill leaflet on left side, several on right side of body. Two epipodial tentacles on each side of body, outer tentacle blunt, cylindrical, inner tentacle long, filamentous.

Remarks: Following Moskalev's (1976) description of *Caymanabyssia* and its hadal type species, Marshall (1986) added two species from the upper bathyal zone of New Zealand, substantially expanding both the geographic and bathymetric range of this genus. McLean (1991) further added an abyssal species from the Gorda Ridge off northern California, as well

←

Fig. 5. *Macleaniella moskalevi,* new species. **A.** Left lateral and **B.** ventral views of critical point dried animal of holotype. Scale bar, 500 μm. **C.** Right lateral view of head, showing enlarged right cephalic tentacle, which serves as the copulatory organ. Scale bar, 50 μm. **D.** Ventral view of head. Scale bar, 50 μm. **E.** Dorsal view of radular ribbon. Scale bar, 20 μm. **F.** Detail of marginal teeth. Scale bar, 5 μm. **G.** Detail of central field of radular ribbon. Scale bar, 10 μm.—et, epipodial tentacle; m, mouth; ol, oral lappet; r, rachidian tooth; rct, right cephalic tentacle; 1, first lateral tooth; 2, second lateral tooth; 3, third lateral tooth.

as the subgenus *Dictyabyssia* to accommodate an additional abyssal species from the East Pacific Rise. All share the distinctive radular morphology of the genus, but the monotypic *Dictyabyssia* lacks the conical teleoconch sculpture present in all members of *Caymanabyssia sensu stricto.*

Caymanabyssia spina MOSKALEV 1976
Figs. 6A–E, 7A–F

Synonymy—

Caymanabyssia spina MOSKALEV, 1976: 65–66, fig. 1.4, pl. 2, figs. 7–8; Wolff 1979: 121, 126, pl. 5, fig. D; Hickman 1983: 85, fig. 26 (radula); McLean & Harasewych 1995: 28.

Description: Shell small for family (length to 3.0 mm), depressed (height/length 0.25–0.45). Protoconch (Fig. 6B,C,E) 240 μm in length, smooth, with regular, minute (3–4 μm diameter), circular/hexagonal features along initial ¼ whorl, smooth, pitted thereafter. Teleoconch low, nearly conical, with weakly convex anterior slope, straight posterior slope. Anterior, posterior ends rounded, lateral sides nearly straight, parallel. Apex posterior to midpoint of shell. Teleoconch white, slightly translucent. Sculpture of hollow or subsequently filled, elongate conical projections ~20 μm in diameter, most prominent at shell periphery (Fig. 6D), aligned along anastomosing network of curved, regularly spaced threads forming diagonally reticulate pattern. Periostracum thin, yellowish, mostly worn in examined specimens. Aperture oval-elliptical, broad, flat. Interior surface smooth, horseshoe-shaped muscle scar barely discernible. Animal (Fig. 7A) unpigmented, with small oral shield. Cephalic tentacles roughly equal in size. Eyes absent. Mantle edge with long, cylindrical papillae (Fig. 7B) that likely give rise to surface sculpture. Epipodial tentacles paired/bifid, with outer one shorter, blunt, cylindrical (Fig. 6A: oet), inner one longer, tapering (Fig. 6A: iet) on each side. Radula asymmetrical, skewed right, with rachidian, lateral, pluricuspid teeth cuspless, degenerate. Rachidian tooth (Fig. 7D: r) subquadrate, large, thin. Pluricuspid tooth (Fig. 7D: pc) somewhat thicker at distal end. Marginal teeth (Fig. 7F) multicuspid at distal edges, decreasing in size outwards.

Type locality: Eastern part of Cayman Trench, 19°38.5′N, 76°37.8′W, 6740–6780 m, R/V *Akademik Kurchatov,* cruise 14, station 1267, 2.5 m Sigsbee trawl, 24–25 March 1973.

Material examined: Holotype, ZMMU Lc-22854. Paratypes: ZMMU Lc-22855, USNM 880304, from type locality; UMML 30.8393, one specimen, western part of Cayman Trench, 19°08.4′–19°07.5′N, 79°53.7′–79°55.5′W, 7247–7225 m, R/V *James M. Gilliss,* station GS-127, 41 ft. otter trawl, 23 July 1975.

Additional records: 204 specimens on wood, seven on assorted plant debris, from type locality; two specimens on wood, western part of Cayman Trench, 19°00.6′N, 80°29.5′W, 6800 m, R/V *Akademik Kurchatov,* cruise 14, station 1242-A, 2.5 m Sigsbee trawl, 20 March 1973.

Distribution: Known only from the hadal zone of the Cayman Trench (6740–7247 m).

Remarks: The entire shell and details of the protoconch of *Caymanabyssia spina* are illustrated for the first time. This species is the only Atlantic member of the genus presently known, and the only species of the genus to inhabit hadal depths. Two New Zealand species, *C. sinespina* MARSHALL, 1986, and *C. rhina* MARSHALL, 1986, are both from bathyal depths (800–1200 m), while the eastern Pacific species *C. vandoverae* MCLEAN, 1991, and *C. fosteri* MCLEAN, 1991 occur at depths of 2700–3300 m. McLean (1991) erected *Dictyabyssia* as a subgenus of *Caymanabyssia* to contain *C. sinespina* and *C. fosteri,* distinguishing it from the nominotypical subgenus on the basis of its shell sculpture, which lacks conical granules.

The long, cylindrical mantle papillae of *C. spina* appear similar to those reported in *Kurilabyssia antipodensis* (Haszprunar 1988b, fig. 7F), while shorter mantle papillae have been illustrated for *Copulabyssia corrugata* (Dantart & Luque 1994: fig. 67) and the lepetellid *Lepetella barrajoni* (Dantart & Luque 1994: fig. 49).

The two epipodial tentacles on each side of the body of *Caymanabyssia spina* have not previously been reported for this genus, although they can be discerned in *C. vandoverae* (McLean 1991: fig. 20). Similarly differentiated, paired epipodial tentacles have been described and illustrated in *Copulabyssia corrugata* (Dantart & Luque 1994: figs. 65, 66) and several species of the genus *Notocrater* (McLean & Harasewych 1994: fig.70).

Genus *Amphiplica* HASZPRUNAR, 1988

Synonymy—

Amphiplica HASZPRUNAR, 1988b: 177; McLean 1988: 155; McLean 1991: 44; McLean & Harasewych 1995: 29.

Type species: *Amphiplica venezuelensis* MCLEAN, 1988, by original designation.

Diagnosis: Largest known pseudococculinid. Shell reaching 15 mm in length, low to moderately high in profile. Apex central, highest point on shell. Protoconch sculpture known only for the subgenus *Gordabyssia* MCLEAN, 1991, consists of dense net pattern

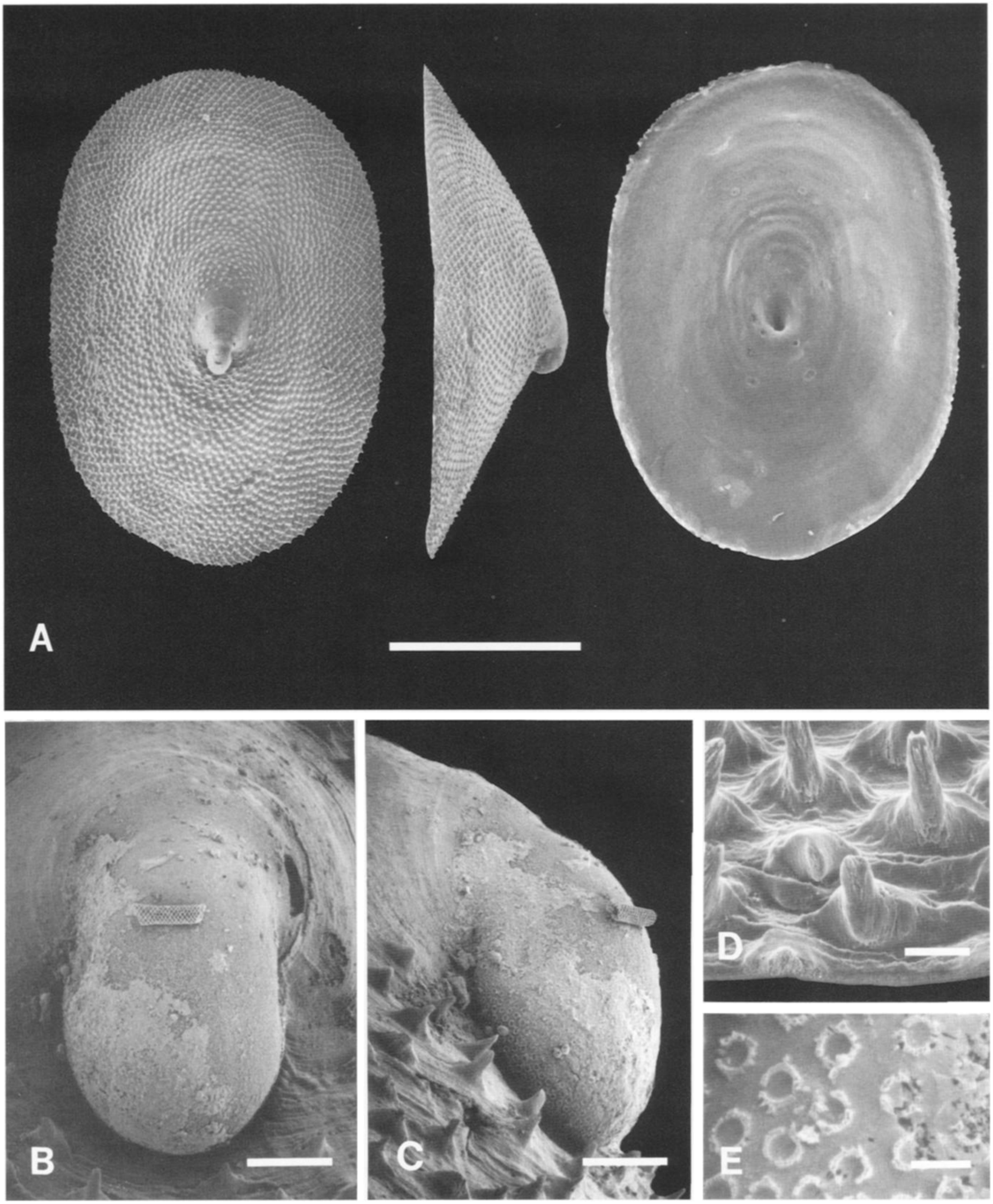


Fig. 6. *Caymanabyssia spina* Moskalev, 1976. **A.** Dorsal, lateral, and ventral views of paratype (USNM 880304). Scale bar, 1.0 mm. **B.** Dorsal and **C.** lateral view of protoconch. Scale bar, 50 µm. **D.** Detail of sculpture at shell edge. Scale bar, 20 µm. **E.** Detail of protoconch sculpture. Scale bar, 5 µm.

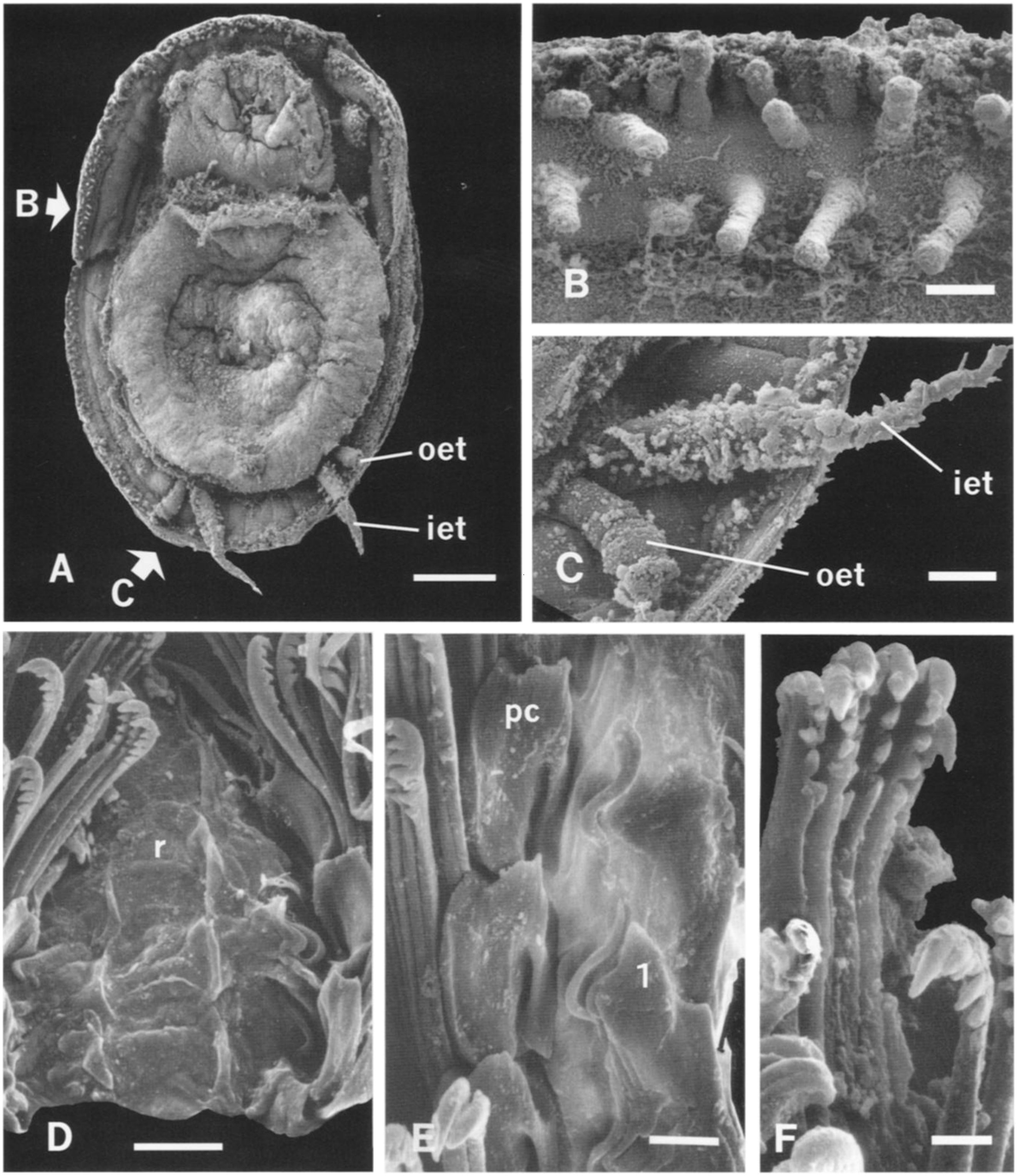


Fig. 7. *Caymanabyssia spina* Moskalev, 1976. **A.** ventral view of critical point dried animal of paratype. Scale bar, 200 μm. **B.** Detail of mantle edge (arrow B in A). Scale bar, 10 μm. **C.** Detail of right epipodial tentacles (arrow C in 7A). Scale bar, 50 μm. **D.** Detail of central field of radular ribbon. Scale bar, 10 μm. **E.** Detail of lateral and pluricuspid teeth. Scale bar, 5 μm. **F.** Detail of marginal teeth. Scale bar, 2 μm.—iet, inner epipodial tentacle; oet, outer epipodial tentacle; p, pluricuspid tooth; r, rachidian tooth; 1, first lateral tooth.

(McLean 1991: figs. 29, 30). Animal with multiple secondary gill leaflets along right and left sides of subpallial cavity. Right and left cephalic tentacles equal in size. Right cephalic tentacle acts as copulatory organ, with open, glandular, ciliated sperm groove extending to distal extremity of tentacle. Rachidian tooth broad, with horseshoe-shaped basal portion, single, blunt beak-like cusp. Pluricuspid tooth massive, with 4–5 minute subterminal cusps. Marginal teeth not fused at basal region. Inner marginal teeth with single, curved cusp.

Remarks: Other Atlantic species in the genus *Amphiplica* are *A. venezuelensis* McLean, 1988 from the abyssal zone (3476–5057 m) in the Venezuelan Basin of the southern Caribbean, and *A. concentrica* (Thiele, 1909), collected on a cable raised from an unspecified depth off the Azores. The genus is represented in the eastern Pacific Ocean by *A. gordensis* McLean, 1991 from abyssal (3305 m) sulfide crusts on the Escanaba Trough, Gorda Ridge, and in the western Pacific by *A. knudseni* McLean, 1988 from abyssal depths (3610 m) in the Tasman Basin, west of New Zealand. The radula of "Pseudococculinidae sp. c" from the Kermadec Trench (*Galathea* station 664, 4540 m) illustrated by Hickman (1983, figs. 27, 28, 40b) may belong to a species in the genus *Amphiplica,* but, due to the small degree of interspecific variation, it is impossible to tell from the radula illustrations alone whether it represents *A. knudseni* or yet another, unnamed species.

Amphiplica plutonica new species

Figs. 8A–C, 9A–G, Table 3

Description: Shell size average to large for family (length to 10.8 mm), thick, heavily eroded (Fig. 8B), opaque white. Shell elevated, (height/length 0.39–0.52), weakly arched, with apex pointing posteriorly. Anterior slope ~65% of shell length, convex. Posterior slope straight to strongly concave. Protoconch eroded in all available material. Teleoconch sculpture of collabral ridges at ~50 μm intervals, crossed by much smaller, fine, irregular, frequently divaricate, radial striae (Fig. 8C). Aperture elliptical, roughly planar, shell margin smooth. Muscle scars strong, horseshoe-shaped, elevated anteriorly, myostracum visible from exterior of shell in eroded specimens (Fig. 8B: ms). Animal unpigmented. Eyes absent. Cephalic tentacles of equal size. Right cephalic tentacle with open, ciliated sperm groove (Fig. 9C). Gill leaflets (6–10) present along both sides of subpallial cavity (Fig. 9B). Epipodial tentacles single, long (Fig. 9A: et). Radula asymmetrical, rachidian tooth rhomboid, broader at mid-section, with rounded, blunt, flat cusp with smooth cutting area. First lateral tooth triangular, large, with an outer basal projection that fits into a depression on second lateral tooth, and a straight, pointed, single cusp. Second, third, and fourth lateral teeth strongly curved, with simple, hook-like cusps. Pluricuspid tooth broad, club-like, with 4–5 subterminal denticle-like cusps. Latero-marginal plate present. Inner (first to ninth) marginal teeth unicuspid, with thick shafts, decreasing in size outwards. Second marginal tooth largest. Outer marginal teeth with complex serrations.

Type locality: Eastern part of Cayman Trench, 19°08.4′–19°07.5′N, 79°53.7′–79°55.5′W, 7247–7225 m, R/V *James M. Gilliss,* cruise GS-7506, station GS-127, 41 ft. otter trawl, 23 July 1975.

Type material: Holotype, USNM 880305 (ex-UMML 30.9178), from type locality. All paratypes in alcohol: UMML 30.8392, 8 paratypes; USNM 880306, 4 paratypes (ex-UMML 30.8392); ZMMU Lc-22853, 2 paratypes; ANSP 399810; MNHN, 3 paratypes in alcohol; LACM 2808, 5 paratypes; BMSM 1001, 5 paratypes; all from the type locality; UMML 30.8389, 2 paratypes (shells), eastern part of Cayman Trench, 19°38.0′–19°39.3′N, 76°18.1′–76°15.5′W, 6466–6600 m, R/V *James M. Gilliss,* cruise GS-7506, station GS-121, 41 ft. otter trawl, 21 July 1975; UMML 30.8408, 13 paratypes, eastern part of Cayman Trench, 19°04.6′–19°05.0′N, 80°06.0′–80°10.0′W, 6870–6910 m, R/V *James M. Gilliss,* cruise GS-7506, Station GS-128, 41 ft. otter trawl, 24 July 1975.

Other material examined: UMML 30.8390, 14 specimens + 2 shells; UMML 30.9177, several specimens without shells; UMML 30.9178, 13 specimens, heavily decalcified, all from type locality; UMML 30.8391, 1 specimen + 1 shell, eastern part of Cayman Trench, 19°38.0′–19°39.3′N, 76°18.1′–76°15.5′W, 6466–6600 m, R/V *James M. Gilliss,* cruise GS-7506, station GS-121, 41 ft. otter trawl, 21 July 1975.

Distribution: Known only from the hadal zone of Cayman Trench (6466–7247 m).

Remarks: Although this new species has the general shell shape and anastomosing, irregular radial striae prevalent in the genus *Copulabyssia,* we assign it to the genus *Amphiplica* on the basis of its multiple (6–10) gill leaflets along both sides of the body, a character diagnostic of *Amphiplica,* and its lack of a greatly enlarged right cephalic tentacle (copulatory organ) from which *Copulabyssia* derives its name.

Conchologically, *Amphiplica plutonica* differs from both *A. venezuelensis* and *A. concentrica* in having a proportionally taller shell with a strongly concave posterior slope and an apex that is situated at the posterior third of its shell length rather than near or slightly anterior to the midline.

Radulae of these species are similar, but the first lateral tooth in *A. plutonica* has a sharp, pointed, single

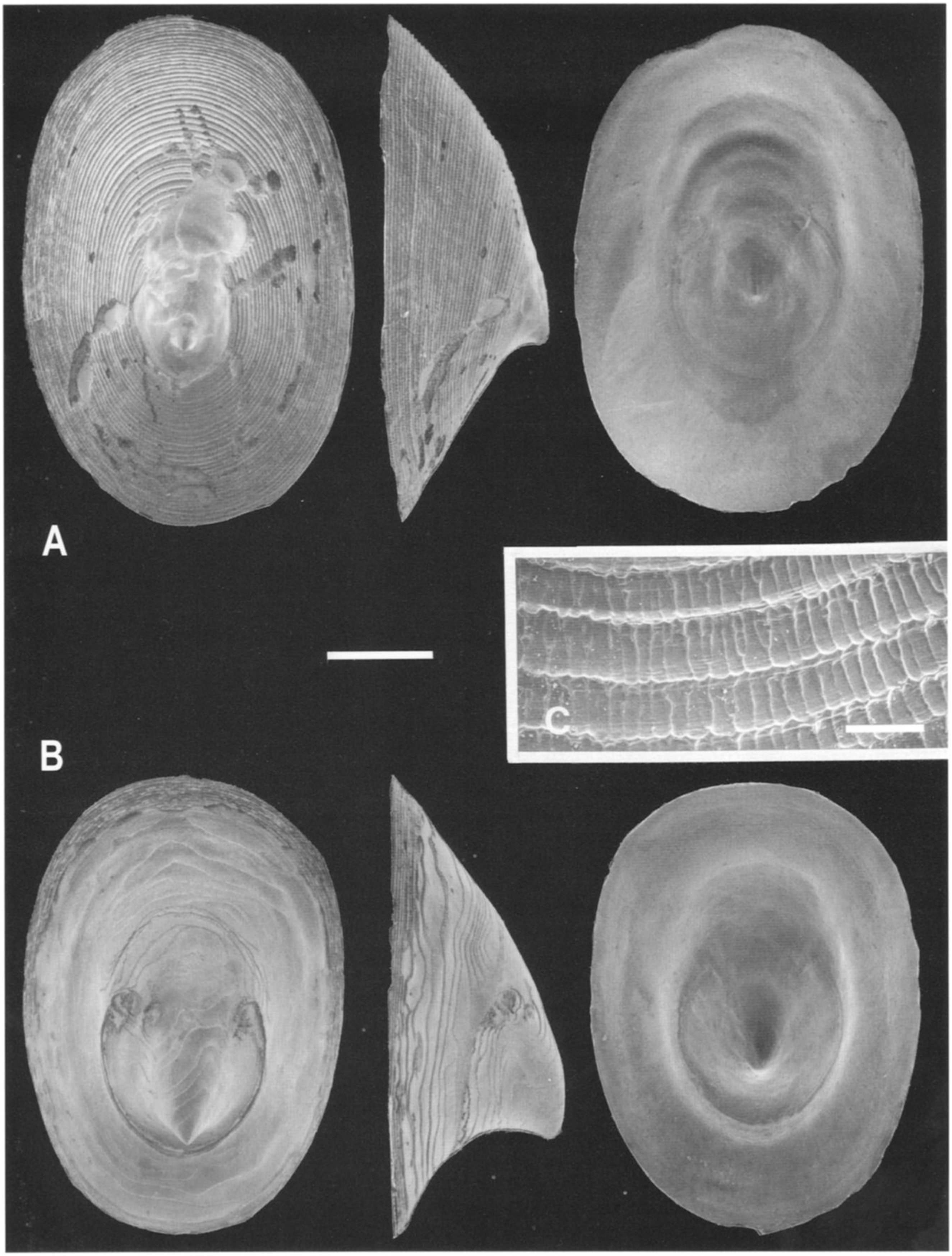

A
B
C

Table 3. *Amphiplica plutonica* new species. Measurements of shell characters (Parameters measured as in McLean & Harasewych 1995:fig. 1). Linear measurements in mm (n = 18).

Character	Mean	σ	Range
Shell length (SL)	6.50	1.41	5.00–10.83
Shell width (SW)	4.84	1.22	3.33–8.33
Shell Height (SH)	2.81	0.46	2.08–3.67
SL/SW	1.35	0.09	1.20–1.50
SH/SL	0.44	0.04	0.39–0.52

cusp, whereas this cusp is strongly curved and blunt in *A. venezuelensis* and *A. concentrica.* The fifth lateral tooth is relatively broader and more massive in *A. venezuelensis,* about twice the width of the rachidian tooth, but more delicate and smaller in *A. plutonica,* about the same width as the rachidian tooth. The latter two species apparently also differ in their feeding habits: *A. venezuelensis* feeds on wood, while *A. plutonica* was consistently found to occur on blades of turtle grass (*Thalassia testudinum*) preserved in the UMML "trench debris" museum jars. The report of *A. concentrica* from a submarine cable suggests that this species is capable of feeding on bacterial films or on organic coatings, possibly of plant origin, used to coat submarine cables in the late 1800s.

Discussion

The families Cocculinidae and Pseudococculinidae both have extremely broad bathymetric ranges, extending from sublittoral to hadal depths. The rapid increase in the numbers of described families, genera, and species over the past few decades correlates with increased sampling efforts in the deep-sea, and indicates that the diversity and distribution of these families is still significantly undersampled. Any patterns surmised from data presently available should therefore be considered tentative.

The four species treated in this paper each appear to be endemic to the trenches from which they are reported. Only *Macleaniella moskalevi* was present in limited, adjacent, abyssal samples. *Fedikovella caymanensis, Caymanabyssia spina,* and *Amphiplica plutonica* all are restricted to the Cayman Trench. *Fedikovella caymanensis,* and *Caymanabyssia spina* (bathymetric range 6740–7247 m) occur sympatrically at all three stations from which they have been reported. *Amphiplica plutonica* has a similar bathymetric range (6466–7247 m), and has been collected with *F. caymanensis* and *C. spina* at one station (R/V *James M. Gilliss,* Cruise GS-7506, station GS-127). These taxa seem to be substrate-specific, with *Fedikovella caymanensis* and *Caymanabyssia spina* inhabiting the same piece of wood, while *Amphiplica plutonica* is found on turtle grass blades, but not wood.

Macleaniella moskalevi was the only limpet to be collected in the Puerto Rico Trench and the adjacent abyssal plain to the north, despite sampling that was more extensive than that for the Cayman Trench. These two trenches are separated by a shallower sill (1500–2000 m) in the region of the Windward Passage between eastern Cuba and western Hispaniola.

The unique character of the fauna living within the hadal zone has been discussed, among others, by Zenkevitch (1954), Zenkevitch et al. (1954), Bruun (1956, 1957, 1958), Wolff (1960, 1970), Knudsen (1964); Belyaev (1966), Menzies et al. (1973), George & Higgins (1979), and Tietjen (1992). Belyaev (1966) and Wolff (1970) proposed that the marked change in faunal composition and high degree of endemism found in the hadal zone, when compared to the abyss, could be a combined result of increased hydrostatic pressure and enhanced food availability on trench floors in the form of organic debris that fall from shallower areas. Moore (1963) first identified one the major components of plant remains present on the floor of the Puerto Rico Trench to be blades of the turtle grass, *Thalassia testudinum* KÖNIG. Gunn & Dennis (1976) have identified and illustrated seeds and disseminules of the different plants trawled by the R/V *John Elliott Pillsbury* on the floor of the Puerto Rico Trench (station P-1168, see Table 1). This catch included propagules of the red mangrove (*Rhizophora mangle* LINNAEUS), seeds of the country almond (*Terminalia catappa* LINNAEUS), antidote vine (*Fevillea cordifolia* LINNAEUS), hogplum (*Spondias mombin* LINNAEUS), and assorted legumen pods. More recently, Wolff (1976, 1979, 1980) discussed the importance of these plant remains to the hadal ecosystem and provided many examples of associations between hadal invertebrates and assorted macroscopic remains of terrestrial or shallow-water plants that reach hadal depths via turbidity flows. Wolff (1979) examined specifically associations of invertebrates and plant remains in the

←

Fig. 8. *Amphiplica plutonica,* new species. **A.** Dorsal, lateral, and ventral views of holotype (USNM 880305). Scale bar, 1.0 mm. **B.** Dorsal, lateral, and ventral views of paratype (USNM 880306). Scale bar, 1.0 mm. **C.** Detail of sculpture of holotype. Scale bar, 100 μm.

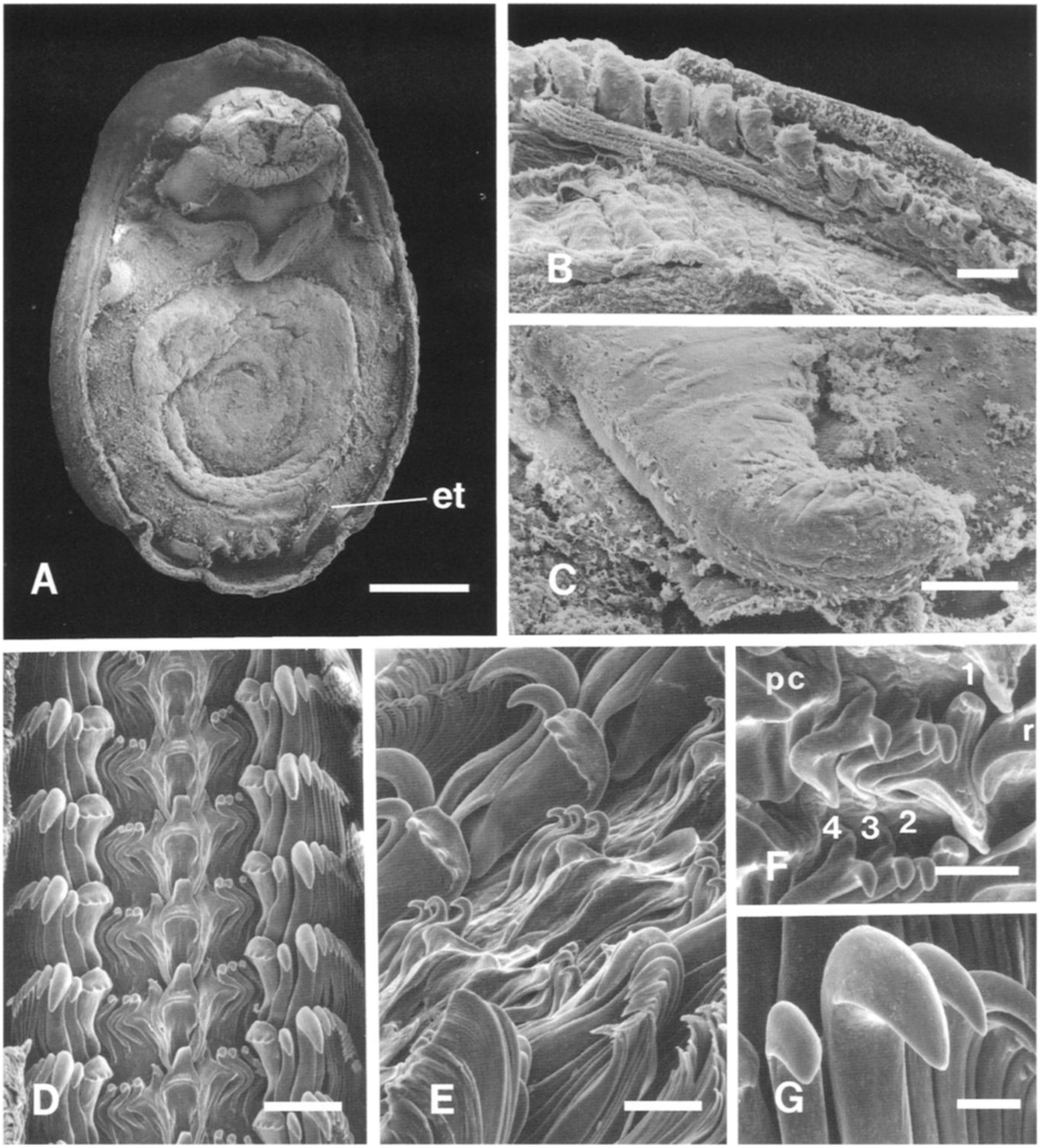


Fig. 9. *Amphiplica plutonica,* new species. **A.** Ventral view of critical point dried animal of paratype. Scale bar, 500 μm. **B.** Gill leaflets along left side of the body. Scale bar, 100 μm. **C.** Right cephalic tentacle, which serves as the copulatory organ. Scale bar, 50 μm. **D.** Dorsal view of radular ribbon. Scale bar, 50 μm. **E.** Lateral view of radular ribbon. Scale bar, 25 μm. **F.** Detail of lateral teeth. Scale bar, 20 μm. **G.** Detail of distal ends of inner marginal teeth. Scale bar, 10 μm.—et, epipodial tentacle; pc, pluricuspid tooth; r, rachidian tooth; 1, first lateral tooth; 2, second lateral tooth; 3, third lateral tooth; 4, fourth lateral tooth.

Cayman and Puerto Rico trenches, regions of the deep sea that are near high-productivity coastal areas and therefore prone to high accumulation rates of sinking debris. This allochtonous source of plant substrate and food led George & Higgins (1979) to consider the benthic community of the Puerto Rico Trench as part of a truly eutrophic system.

The cocculinid genera containing trench species appear to be far more restricted geographically and bathymetrically than are the pseudococculinid genera. *Macleaniella* is presently a monotypic genus, endemic to the Puerto Rico Trench. The inclusion of *Fedikovella beanii* in *Fedikovella* is provisional, indicating that this genus is restricted either to the Cayman Trench or to the bathyal to hadal depths of the western Atlantic. By contrast, both pseudococculinid genera represented in the Cayman Trench are broadly distributed, with representatives in the bathyal and abyssal zones of the western and eastern Pacific Ocean. This suggests that cocculinids either disperse more slowly or differentiate more rapidly than do pseudococculinids.

Acknowledgments. This paper is based on deep-sea material originally obtained by the University of Miami project "Investigations of the Biology and Distribution of the Tropical Atlantic Deep-sea Fauna" directed by the late Gilbert L. Voss and Frederick M. Bayer, and funded by the National Geographic Society/National Science Foundation. We thank Nancy A. Voss (RSMAS, University of Miami) for allowing unrestricted access to the UMML collection and for reading an early draft of this article. The junior author is extremely grateful to Dimitri L. Ivanov (ZMMU) and L. Moskalev (P.P. Shirsov Institute of Oceanology, Russian Academy of Sciences) for their hospitality and helpful discussions. We are also indebted to the following scientists for sharing comparative material or information on deep-sea limpets: James H. McLean (Los Angeles County Museum of Natural History), Bruce A. Marshall (National Museum of New Zealand), Tom Schiøtte (Zoological Museum, Copenhagen), the late Donald R. Moore (RSMAS, University of Miami), Lev Moskalev (Institute of Oceanology, Academy of Sciences of Russia, Moscow), Philippe Bouchet (Muséum National d'Histoire Naturelle, Paris, France), Gerhard Haszprunar (Zoologische Staatssammlung München). We thank Susanne R. Braden (National Museum of Natural History) for assistance with scanning electron microscopy. Afonso Paiva (RSMAS/University of Miami) helped with the GMT software and produced the chart in Fig. 1. Helen Albertson at the RSMAS Library helped with literature. This study was partly funded by a Conchologists of America Grant Award to the senior author.

References

Belyaev GM 1966. Hadal bottom fauna of the world ocean. Zenkevitch LA, ed. Institute of Oceanology, Academy of Sciences USSR, Moscow. [original in Russian; English translation by the Israel Program for Scientific Translation, Jerusalem, 1972] 199 pp.

Bonini WE, Hargraves RB, & Spagam R, eds. 1984. The Caribbean-South America plate boundary and regional tectonics. Memoir 162. The Geological Society of America. 421 pp.

Bruun A 1956. The abyssal fauna: its ecology, distribution and origin. Nature 177: 1105–1108.

——— 1957. Deep sea and abyssal depths. In: Treatise on Marine Ecology and Paleoecology. Hedgpeth JW, ed., pp. 641–672. Memoir 67. The Geological Society of America.

——— 1958. General introduction to the reports and list of deep-sea stations. Galathea Rep. 1: 7–48.

Clarke AH Jr. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. Bull. Natn. Mus. Can. 181, Biological Series 67: 1–114.

Dall WH 1882. On certain limpets and chitons from the deep waters off the eastern coast of the United States. Proc. U.S. Natl. Mus. 4: 400–414.

Dantart L & Luque A 1994. Cocculiniformia and Lepetidae (Gastropoda: Archaeogastropoda) from Iberian waters. J. Moll. Stud. 60: 277–313.

Dautzenberg P & Fischer H 1900. Description d'un mollusque nouveau. Bull. de la Soc. Zool. de France. 24: 207–209.

George RY & Higgins RP 1979. Eutrophic hadal benthic community in the Puerto Rico Trench. Ambio Special Report 6: 51–58.

Gunn CR & Dennis JV 1976. World guide to tropical drift seeds and fruits. Quadrangle/The New York Times Book Co. New York. 240 pp.

Harasewych MG, Adamkewicz SL, Blake JA, Saudek D, Spriggs T, & Bult CJ 1997. Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18S rDNA and cytochrome *c* oxidase I sequences. Mol. Mar. Biol. Biotech. 6(1): 1–20.

Haszprunar G 1987. Anatomy and affinities of cocculinid limpets (Mollusca, Archaeogastropoda). Zool. Scripta 16(4): 305–324.

——— 1988a. Comparative anatomy of cocculiniform gastropods and its bearing on gastropod systematics. Malac. Rev. (Suppl.) 4: 64–84.

——— 1988b. Anatomy and affinities of pseudococculinid limpets (Mollusca, Archaeogastropoda). Zool. Scripta 17: 161–179.

——— 1988c. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. J. Moll. Stud. 54: 367–411.

Haszprunar G & McLean JH 1996. Anatomy and systematics of bathyphytophilid limpets (Mollusca, Archeogastropoda) from the northeastern Pacific. Zool. Scripta 25: 35–49.

Hickman CS 1983. Radular patterns, systematics, diversity, and ecology of deep-sea limpets. The Veliger 26: 73–92.

——— 1984. Implications of radular tooth-row functional integration for archaeogastropod systematics. Malacologia 25: 143–160.

——— 1988. Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. Malac. Rev. (Suppl.) 4: 17–34.

Knudsen J 1964. Scaphopoda and Gastropoda from depths exceeding 6000 m. Galathea Rep. 7: 1–12.

Malfait BT & Dinkelman MG 1972. Circum-Caribbean tectonics and igneous activity and the evolution of the Caribbean plate. Bull. Geol. Soc. Am. 83: 251–272.

Marshall BA 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. N.Z. J. Zool. 12: 505–546.

McLean JH 1987. Taxonomic descriptions of cocculinid limpets (Mollusca, Archaeogastropoda): two new limpets and three rediscovered species. Zool. Scripta 16: 325–333.

——— 1988. Three new limpets of the family Pseudococculinidae from abyssal depths (Mollusca, Archaeogastropoda). Zool. Scripta 17: 155–160.

——— 1991. Four new pseudococculinid limpets collected by the deep-submersible Alvin in the eastern Pacific. The Veliger 34: 38–47.

——— 1992. Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. J. Moll. Stud. 58: 401–414.

McLean JH & Harasewych MG 1995. Review of western Atlantic species of cocculinid and pseudococculinid limpets, with descriptions of new species (Gastropoda: Cocculiniformia). Contributions in Science, Natural History Museum of Los Angeles County 453: 1–33.

Menzies RJ, George RY, & Rowe GT 1973. Abyssal environment and ecology of the world oceans. John Wiley and Sons, New York. 488 pp.

Moore DR 1963. Turtle grass in the deep sea. Science 139: 1234–1235.

Moskalev LI 1976. Concerning the generic diagnosis of the Cocculinidae (Gastropoda, Prosobranchia). Trudy P.P. Shirsov Inst. Okeanol. 99: 59–70, pl. 2. [In Russian]

Moskalev LI & Vilenkin BYa 1975. An exceptional case of allometry among the Cocculinidae (Gastropoda, Prosobranchia) and its significance for the taxonomy of this group. In: The Fifth Conference on the Investigation of Mollusks. Likharev IM, ed., pp. 138–139. Nauka, Leningrad. [In Russian]

Pasternak FA, Moskalev LI, & Fedikov NF 1975. Some characteristics of the distribution patterns of the deep-sea benthic fauna of the Caribbean Sea and Gulf of Mexico. Trudy P.P. Shirsov Inst. Okeanol. 101: 52–64. [In Russian]

Ponder WF & Lindberg DR 1996. Gastropod phylogeny—challenges for the 90s. In: Origin and Evolutionary Radiation of the Mollusca. Taylor JD, ed., pp. 135–154. Oxford University Press, Oxford.

——— 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zool. J. Linn. Soc. London 119: 83–265.

Strong EE & Harasewych MG 1999. Anatomy of the hadal limpet *Macleaniella moskalevi* (Gastropoda, Cocculinoidea). Invertebr. Biol. 118(2): 137–148.

Sykes LR, McCann WR, & Kafka AL 1982. Motion of the Caribbean Plate during the last 7 million years. J. Geophys. Res. 87 (B13): 10656–10676.

Tietjen JH 1992. Abundance and biomass of metazoan meiobenthos in the deep sea. In: Deep-Sea Food Chains and the Global Carbon Cycle. Rowe GT & Parenti V, eds., pp. 45–62. Kluwer Academic Press, Boston.

U.S. Department of Defense 1992. Puerto Rico and Virgin Islands (West Indies). Chart 25640. Washington: Defense Mapping Agency, Hydrographic and Topographic Center.

Voss GL 1973. Investigations of the biology and distribution of the deep-sea fauna, 1964–1966. National Geographic Society Research Reports [for] 1966: 271–281.

——— 1976. Investigations of the biology and distribution of the tropical Atlantic deep-sea fauna, 1967–1968. National Geographic Research Reports [for] 1968: 445–452.

Wolff T 1960. The hadal community, an introduction. Deep-Sea Res. 6: 95–124.

——— 1970. The concept of the hadal or ultra-abyssal fauna. Deep-Sea Res. 17: 983–1003.

——— 1976. Utilization of seagrass in the deep sea. Aquat. Bot. 2: 161–174.

——— 1979. Macrofaunal utilization of plant remains in the deep sea. Sarsia 64: 117–136, 5 pls.

——— 1980. Animals associated with seagrass in the deep sea. In: Handbook of Seagrass Biology: An Ecosystem Perspective. Philips RC & McRoy CP, eds., pp. 199–224. Garland STPM Press, New York.

Zenkevitch LA 1954. Erforshungen der Tiefsee fauna im nordwestlichen Teil des stillen Ozeans. International Zoology Congress, Copenhagen, Union Internat. Sci. Biol. (ser. B) 16: 72–85.

Zenkevitch LA, Birstein YA, & Belyaev GM 1954. Studies on the fauna of the Kurile Kamchatka Trench. Priroda 2: 61–74. [In Russian]

LINKED CITATIONS

- Page 1 of 1 -

You have printed the following article:

Deepest Atlantic Molluscs: Hadal Limpets (Mollusca, Gastropoda, Cocculiniformia) from the Northern Boundary of the Caribbean Plate

José H. Leal; M. G. Harasewych

Invertebrate Biology, Vol. 118, No. 2. (Spring, 1999), pp. 116-136.

Stable URL:

http://links.jstor.org/sici?sici=1077-8306%28199921%29118%3A2%3C116%3ADAMHL%28%3E2.0.CO%3B2-B

References

Turtle Grass in the Deep Sea

Donald R. Moore

Science, New Series, Vol. 139, No. 3560. (Mar. 22, 1963), pp. 1234-1235.

Stable URL:

http://links.jstor.org/sici?sici=0036-8075%2819630322%293%3A139%3A3560%3C1234%3ATGITDS%3E2.0.CO%3B2-7