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A remarkable new genus of carnivorous, sessile bivalves (Mollusca: Anomalodesmata: Poromyidae) with descriptions of two new species

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Abstract

Dilemma, a new genus of sessile septibranch bivalves is described. The new taxon encompasses at least three species, of which two are new: *D. frumarkernorum* new species, from off the Florida Keys, *D. spectralis* new species, from off Vanuatu, and *"Corculum" inexpectatum* Crozier, 1966, from off the Three Kings Islands, New Zealand, known only from its shell. The absence of ctenidia and presence of a septum, size and arrangement of siphons and siphonal tentacles, extensive fusion of the mantle margins allocate the new genus within the septibranch bivalves. A siphonal area with 15 tentacles, a large and eversible incurrent siphon, ostial apertures in the septum, and a hermaphroditic reproductive system suggest inclusion in the Poromyidae. The presence of three paired groups of septal ostia in the new genus is a feature shared with poromyids in the genus *Cetoconcha.* Unusual symmetry and form constitute the most striking features of the new genus. There is a strong anteroposterior compression and lateral expansion associated with ca. 30º rotation of the largest dimension (height) in relation to the anteroposterior axis. The shell hinge includes a single tooth and socket on each valve, and an external, but deeply sunken ligament. The two new species, mutually distinguishable by shell and anatomical characters, are known from live-collected specimens found adhering to rocks by means of robust byssus, which indicates attachment for life. The presence of ostracod remains in the digestive tract of one specimen of one of the new species and of a cirolanid isopod in the stomach of the holotype of the second new species are evidence of predation. Although predation by infaunal and free-living bivalves is known to occur throughout the Anomalodesmata, in particular within the septibranchs, discovery of the new genus reveals an unusual instance of predation by sessile, permanently attached mollusks.

Key words: Septibranchia, *Dilemma, Cetoconcha, Poromya,* deep-sea, bathyal

Introduction

This study was prompted by the discovery off of the Florida Keys in 2006 of five specimens of a new bivalve species. The most notable feature of that species is the strong compression and lateral expansion in relation to the symmetry and form of a "standard" bivalve. At first glance, the shell shape, outline, and placement of the umbones invited comparisons with the monotypic cardiid *Corculum* Röding, 1798 (e.g., Oliver, 1992; Schneider, 1998). However, more careful examination of shell morphology (e.g., lack of typically complicated heterodont hinge arrangement, sunken and external ligament) and gross anatomy (e.g., lack of ctenidia, siphonal morphology, presence of a septum with septal ostia, hermaphroditic reproductive system) pointed toward allocation of that new species within the septibranch bivalves.

A similar species was collected in the Tasman Sea at 805 m depth and described as *Corculum inexpectatum* by Crozier (1966). Despite some differences in size, shell sculpture, and the lack of soft parts of *C. inexpectatum* for study, general shell morphology and hinge dentition on the left valve suggested that this and the new species from Florida were closely related species.

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A single specimen, preserved in ethanol, of a third species is deposited at the Muséum national d'Histoire naturelle, in Paris. It was collected in 1994 off Vanuatu, at 950–961 m depth, during the cruise MUSORSTOM 8. The Vanuatu specimen shares general proportions, shape, and symmetry with the two species mentioned above. Additionally, hinge dentition and general gross anatomy are also very similar, as discussed below in this paper. However, details of shell sculpture and periostracum, number and arrangement of siphonal tentacles, arrangement of septal ostia, incurrent siphonal morphology, shape and position of the adductor and byssal retractor muscles, shape and size of the foot, among other characters, indicate that the Vanuatu specimen represents a third species of the same group, and a second new species.

These three unusual species clearly define a morphologically cohesive, aberrant clade within the septibranch bivalves. This clade is obviously distinctive enough to warrant the establishment of a new taxon, which deserves no less than generic rank.

The objectives of this report are (1) to describe this new genus of anomalodesmatan bivalves, (2) to provide the best approximation for its familial allocation, (3) to describe two new species in the new genus, and (4) in the process, to compare the new genus with the morphologically closest taxa, which, as I will try to demonstrate, could be members of the Poromyidae either in the genus *Poromya* Forbes, 1844, or *Cetoconcha*, Dall, 1886.

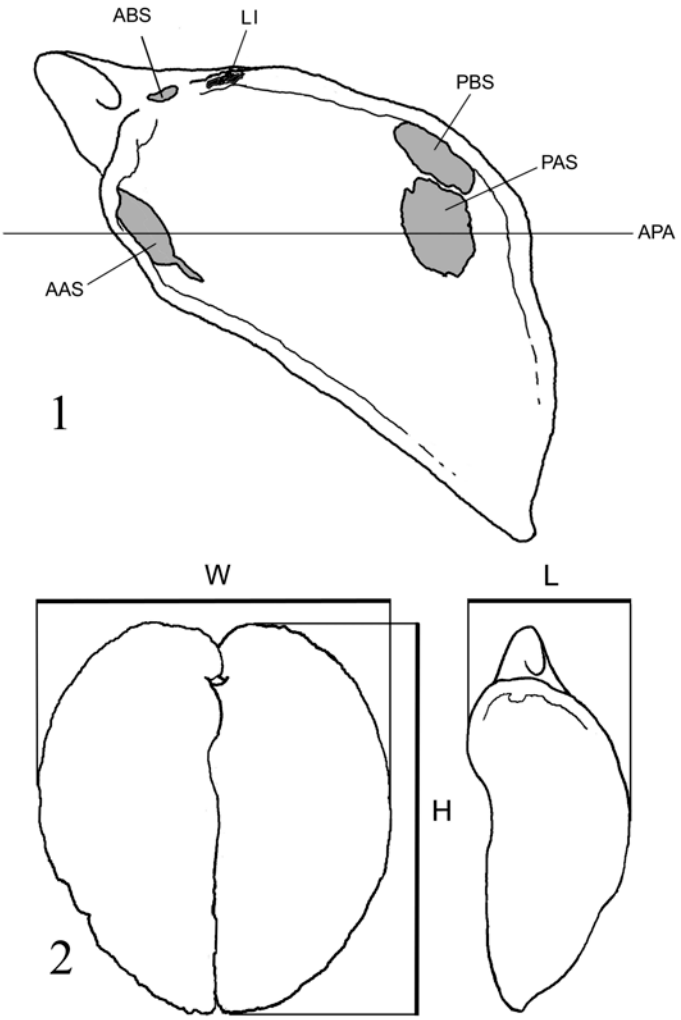
Materials and methods

All material of the two new species was live-collected at the respective type localities. Specimens in the type series of *Dilemma frumarkernorum* were found living attached to a metallic nodule, which in turn was collected from a globigerina-ooze substratum via a deep-sea dredge operating from a lobster boat.

Four specimens were deep-frozen immediately after collection. A fifth specimen was not preserved but its shell was retained in dry conditions. Frozen materials were thawed and (1) one specimen (Paratype 3) was transferred to 80% ETOH and (2) three specimens (Holotype and Paratypes 1–2) fixed in a solution of 4% glutaraldehyde in cacodylate buffer and preserved in 80% ETOH before dissections. None of the soft-part materials were properly fixed and preserved for histological study or microdissections. The types of *Dilemma frumarkernorum* were repeatedly frozen and thawed before final fixation and the holotype of *D. spectralis* was preserved, upon collection, in ethanol buffered with a large concentration of borax.

Dissections and photography of soft parts were accomplished with specimens submerged in the preserving fluid. Scanning electron micrographs (SEM) of uncoated valves were taken at the Scanning Electron Microscopy Laboratory at the National Museum of Natural History, Smithsonian Institution.

For descriptive purposes, the anteroposterior shell axis is a line defined by the median points of the anterior and posterior adductor scars when these latter are projected onto the sagittal plane as defined by Allen (1985) and explained in Figure 1. The anteroposterior plane contains the anteroposterior axis. Shells were measured with a digital caliper to the nearest tenth of a millimeter. All shell dimensions measured are mutually orthogonal. Dimensions length (L), height (H), and width (W) are explained in Figure 2. Institutional acronyms used are: BMSM, The Bailey-Matthews Shell Museum, Sanibel, Florida; MNHN, Muséum national d'Histoire naturelle, Paris; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; UF, Florida Museum of Natural History, Gainesville, Florida; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.



FIGURES 1–2. *Dilemma frumarkernorum*. **1.** Major muscle scars and anteroposterior shell axis. Axis defined by a line joining median points of the anterior and posterior adductors scars projected onto the sagittal shell plane (Allen, 1985). **2.** Dimensional orientations. Abbreviations: **AAS** = scar of anterior adductor muscle; **ABS** = Anterior byssal retractor muscle scar seen by transparency, situated in umbonal cavity; **APA** = anteroposterior axis; **H** = height; **L** = length; **LI** = ligament; **PAS** = scar of posterior adductor muscle; **PBS** = scar of posterior byssal retractor muscle; **W** = width.

Systematics

Poromyoidea Pelseneer, 1906

Poromyidae Dall, 1886

Dilemma new genus

Diagnosis. Shell apparently nacreous internally, strongly compressed in anteroposterior direction and laterally expanded; shell compression associated with ca. 30º rotation of the largest dimension (height) in relation to the anteroposterior axis; lateral outline cardioid; height larger than width; width larger than length. Byssus very well developed (indicating attachment for life); foot vestigial, never leaving infraseptal chamber; posterior byssal retractor muscles wider in cross-section than posterior adductor muscles; anterior labial palps very well developed, cup-shaped; posterior labial palps very reduced, consisting of short projections flush to surrounding surface.

Description. Shell apparently nacreous internally, thin, equivalve (except for slight anteroposterior overlap at umbo), inequilateral, strongly compressed in anteroposterior direction, lateral outline cardioid, anteroventral surface flat or slightly concave, height larger than width, width larger than length. Umbones projecting dorsally, anterior. Byssal gap anteroventral when present.

Hinge with sub-triangular, cardinal-like tooth in each valve; tooth in left valve with cleft distal extremity and more developed than that in right.

Ligament external, sunken; inner ligamental layer apparently calcified, white. Outer ligamental layer brown, splitting and diverging anteriorly, with each half curved as a result of tangential component of shell growth; periostracum fused externally with outer ligamental layer. Lithodesma absent.

Posterior byssal retractor scar larger than posterior adductor scar, elongate. Lunule absent; escutcheon smooth, well-defined.

Animal compressed in anteroventral to posterodorsal direction. Mantle lobes thin, except in siphonal area, with three apertures (see below).

Incurrent siphonal length and siphonal opening diameter larger than equivalent dimensions in excurrent siphon. Incurrent siphon eversible, resting inside infraseptal chamber. Incurrent siphonal opening separated from byssal gape by well-developed ventral portion of perisiphonal suture.

Base of incurrent siphon surrounded by up to 15 tentacles; tentacles simple, tapered, with one large unpaired tentacle along fused mantle margin dorsal to excurrent siphon; pair of tentacles present internally, in supraseptal chamber, between posterior margin of excurrent siphon and posterior adductor muscle.

Septum thin, perforated by byssal opening and by groups of ostia arranged to roughly define three pairs of line segments deployed in septum around byssal opening.

Adductor muscles almost parallel to attachment surfaces on valves. Anterior adductor short, flattened; posterior adductor longer, also flattened. Posterior byssal retractors very well developed, attaching to locations close to posterior margin of valves. Anterior byssal retractors thinner, attaching dorsally to internal surface of entrance to umbonal cavity. (I prefer to use *byssal retractor muscles* instead of *pedal retractor muscles*.)

Byssus well-developed, prominent, circular in cross section. Vestigial foot dorsal to byssus, narrow, or consisting only of an expansion around the middle region of byssus. Position and size of vestigial foot indicates that it can never exit infraseptal chamber.

Mouth indicated by beginning of pleats that continue inside esophagus. Posterior labial palps reduced to two small projections flush with surrounding surface and united along midline. Posterior palps not extending posteroventrally on either side of vestigial foot. Anterior labial palps strongly developed, large, folded in the shape of cups over mouth, free from anterior adductor muscle, potentially expandable in posteroventral direction (toward siphonal area).

Esophagus very short, with strong internal folds, penetrating stomach anterodorsally. Stomach of Type II, compact, strongly muscular, situated in dorsal orientation in relation to mouth, between two “horns” that house digestive diverticula and ovary. Midgut relatively short, connecting to stomach in anterodorsal position, ventral to esophagus. Testes situated in anteroventral position in relation to ovary, ovary overlying the testes. Kidneys situated posterodorsally between remaining of visceral mass and posterior byssal retractor muscle. Kidneys comprising two elongate structures, one on each side of midline of posterior region.

Type Species. *Dilemma frumarkernorum* new species, by original designation.

Etymology. The generic name is the Greek noun *dilemma,* a proposition consisting of questionable alternatives. It is used in this case to denote the impasses faced by the author in the course of this work.

Dilemma frumarkernorum **new species**

(Figures 1–33, 58)

Diagnosis. Shell with sculpture of coarse growth lines; escutcheon not well separated from remainder of shell; foot filiform; byssus relatively thick, robust; siphonal cowl of moderate size; siphonal tentacles arranged around entire incurrent siphonal opening; septal ostia arranged to define three pairs of line segments deployed around byssal opening, roughly delineating a hexagon; siphonal ostia distributed as follows: three anterior, four median, and four posterior.

Description. SHELL (Figures 1–29, 33): Apparently nacreous internally, thin, equivalve (except for slight anteroposterior overlap at umbo), inequilateral, strongly compressed in anteroposterior direction, cardioid in lateral outline. Large byssal gap present in anteroventral position, on central portion of anterior shell surface.

Shell sculpture consisting of coarse growth lines, with well-developed carina separating anterior from posterior shell regions. Carina sometimes set by a constriction that resembles a “pinched” line parallel to main shell outline.

Umbones (Figure 26, U) projecting dorsally, located in anterior position. Umbonal cavity, large, spacious.

Hinge with subtriangular, cardinal-like tooth (Figure 26, CT) in each valve, tooth in left valve with cleft distal extremity and more developed than that in right. Corresponding sockets (Figure 26, HS) present in each valve, that in right valve deeper than that in left valve. Posterior lateral tooth elongate, about 1/10 shell height, low, present on right valve only (Figures 25, 26, 27, LAT) interlocking with notched depression on left valve (Figure 27, LG).

Ligament (Figures 25, 26, 27, LI) external, sunken; inner ligamental layer (Figure 28, IL) in part white, hard, possibly calcified (Figure 28, CIL); outer ligamental layer (Figure 28, OL) brown, with dorsal periostracum adhering to outer layer.

Anterior adductor muscle scar (Figures 25, 26, 29, AAS) located on projection close to margin of valve, dorsal to byssal gap. Posterior adductor muscle scar (Figure 25, PAS) about same size as anterior adductor scar. Anterior byssal retractor scar (Figure 26, 29, ABS) small, relatively deep, situated on internal entrance to umbonal cavity. Posterior byssal retractor scar (Figure 25, PBS) larger than posterior adductor scar, elongate. Pallial line (Figures 25, 29, PAL) continuous, strong.

Lunule absent. Escutcheon relatively poorly defined, not separated by a prominent groove, but distinguishable from remainder of shell by slightly smoother texture and commarginal band of lighter color.

In specimens examined, shell color ranging from dull light-brown to olive-brown, sometimes suffused with peach-orange, usually on posteroventral part of valves. Periostracum light-brown, laid in coarse commarginal lamellae, mostly flaking in live-collected specimens.

Macroanatomy. MANTLE MARGIN AND SIPHONS: Mantle margins fused (Figure 31, FM) leaving two siphonal openings (Figures 30, 32, 33, ES, IS) and byssal gape (Figure 31, BGA). Byssal gape circular to elliptical. Siphonal apertures separate; siphonal area sometimes colorful in freshly preserved animals, siphons formed by fusion of inner mantle folds (“Type A” of Yonge, 1982).

Incurrent siphonal opening (Figures 30, 32, IS) located ventrally, much larger (at least twice as wide) than that of excurrent siphonal opening (Figures 30, 32, 33, ES); siphonal cowl (Figure 32, SC) inverted, resting inside infraseptal chamber, covering incurrent siphonal opening internally, probably eversible for prey capture, relatively short. Base of incurrent siphon surrounded by 15 tentacles (Figures 30–32, TN); tentacles simple, tapered. Large unpaired tentacle (Figures 30, 32, UT) present along fused mantle margin dorsal to excurrent siphonal opening; following six (3+3) tentacles deployed along membranous hem-like projection of middle mantle fold on each side of intersiphonal junction. Remaining eight tentacles arranged around incurrent siphonal opening.

Incurrent siphonal opening located almost ventrally, at least twice as wide as excurrent siphonal opening. Excurrent siphonal opening located posteriorly; angle formed by junction of margins of two valves in posterior direction subtending excurrent siphonal opening (Figures 30, 33).

MANTLE CAVITY: Septum (Figure 32, SE) located dorso-ventrally within mantle cavity; septum roughly parallel to anterior shell surface. Septum thin, strong, dividing the mantle cavity into two chambers, the supraseptal (posterior) (Figure 32, SSC) and infraseptal (anterior) (Figure 32, ISC) chambers. Septum attaching to dorsal region of shell posterior to anterior adductor muscles but attaching to ventral region of shell anterior to posterior adductor muscle.

Septum perforated by byssal opening (Figure 58 [left], BO) and by groups of ostia arranged to define three pairs of line segments deployed around byssal opening, roughly delineating a hexagon. Ostia distributed as follows: three anterior (Figure 58 [left], ASO), four median (Figure 58 [left], MSO), and four posterior (Figure 58 [left], PSO).

MAJOR SHELL MUSCLES: Strong modification of shell shape associated with shape and positioning of adductor muscles: adductor muscles almost parallel to valve surfaces to which they are attached. Anterior adductor muscles (Figures 31, 32, AA) short, flattened; posterior adductor muscles (Figures 30, 32, PA) longer, also flattened. Posterior byssal retractor muscles (Figure 30, 32, PBR) Y-shaped, very well developed, attaching to locations close to posterior margin of valves. Anterior byssal retractor muscles much thinner, attaching dorsally to internal surface of entrance to umbonal cavity. Septal attachment muscles difficult to observe given poor preservation of specimens.

BYSSUS AND FOOT: Byssus (Figures 31, 32, BY) well-developed, prominent, circular in cross section, in preserved animals attached to grains of calcareous sediment, consisting of bundle of very fine, fused filaments, cylindrical in cross-section. Byssus originating from a thickened section of vestigial foot (Figure 31, F), which is narrow and filiform. Position and size of vestigial foot indicates that it might never exit infraseptal chamber.

MOUTH AND LABIAL PALPS: Mouth ridged internally along entire circumference; posterior labial palps reduced to two vestigial projections flush with surrounding surface. Anterior labial palps very well developed, broad, folded over mouth, potentially expandable in posterodorsal direction.

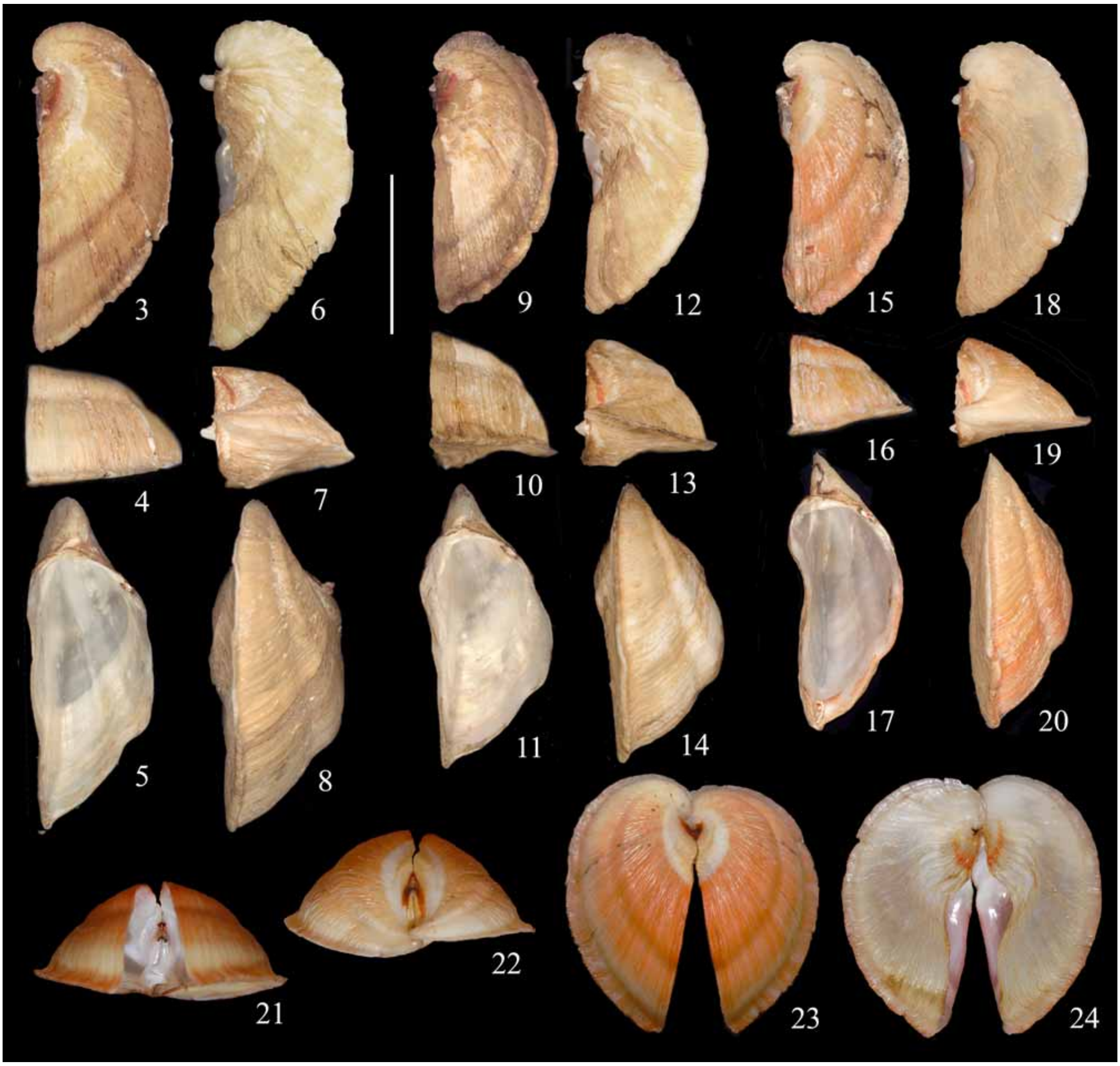
ALIMENTARY SYSTEM: Esophagus with strong folds, very short, opening anterodorsally into stomach. Stomach (Figure 30, ST) of Type II, compact, slightly elongate dorsoventrally, forming posteroventral projection, internally ridged, with ridges stronger in ventral surface. Crystalline style situated just ventral to esophagus opening, projecting slightly into stomach, surrounded by chitinous shield. Openings of digestive diverticula not observed because of poor fixation. Digestive diverticula located in dorsal “horns” (Figures 30, DD). Midgut short, connecting to stomach anteroventral position, ventral to esophagus, curving to more posterodorsal position, anus opening in supra-septal chamber near opening of excurrent siphon between posterior byssal retractor muscles.

STOMACH CONTENTS: Examination of stomach contents of four paratypes revealed, in one specimen, partially digested remains of unidentifiable ostracod species.

KIDNEYS: Kidneys situated posterodorsally between the remainder of visceral mass and posterior byssal retractor muscle. Kidneys comprising two elongate structures, one on each side of the midline of posterior region (Figure 30, K).

REPRODUCTIVE SYSTEM: Testes (Figure 31, TE) elongated situated in anteroventral position in relation to ovaries, ovary overlying the testes. Ovaries (Figures 30, OV) consisting of pair of elongated sacs symmetrically deployed on each side of midline. Ovaries and testis ventral to digestive diverticula.

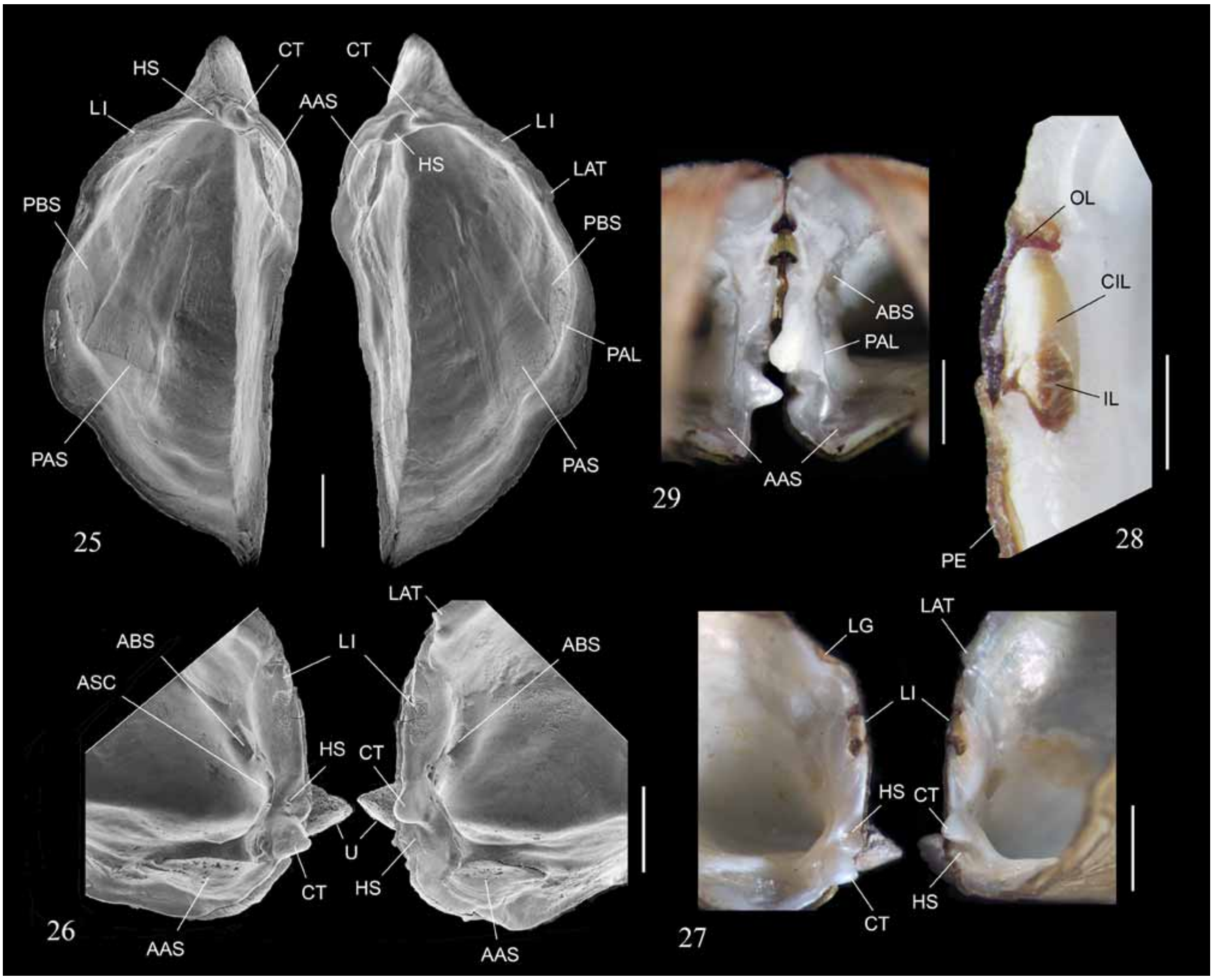
Type material. Holotype, BMSM 15029, (length×height×width [in mm] = 7.41×20.37×16.55) Paratype 1, USNM 1112670 (6.61×16.76×14.87).



FIGURES 3–24. *Dilemma frumarkernorum*. Views of shells. **3–8.** Holotype, BMSM 15029. **3–5.** Right valve. **3.** Posterior. **4.** Ventral. **5.** Lateral (internal). **6–8.** Left valve. **6.** Anterior. **7.** Dorsal. **8.** Lateral. **9–14.** Paratype 2, UF 416419. **9–11.** Right valve. **9.** Posterior. **10.** Ventral. **11.** Lateral (internal). **12–14.** Left valve. **12.** Anterior. **13.** Dorsal. **14.** Lateral. **15–20.** Paratype 1, USNM 1112670. **15–17.** Right valve. **9.** Posterior. **10.** Ventral. **11.** Lateral (internal). **18–20.** Left valve. **18.** Anterior. **19.** Dorsal. **20.** Lateral. **21–24.** Paratype 4, Frank Frumar Collection, complete shell, partially open. **21.** Ventral. **22.** Dorsal. **23.** Posterior. **24.** Anterior. Scale bar (all images at same scale) = 10 mm.

Paratype 2, UF 416419 (7.85×17.34×14.90), Paratype 3, collection of Steve Kern unnumbered (6.79×17.24×14.52), Paratype 4, collection of Frank Frumar (6×16×14; not measured with same accuracy as other types), unnumbered. All from type locality, Steve Kern coll. May 2006, dredged, lobster boat.

Type locality. Southwest of Key West, Monroe County, Florida, USA, 229 m depth.

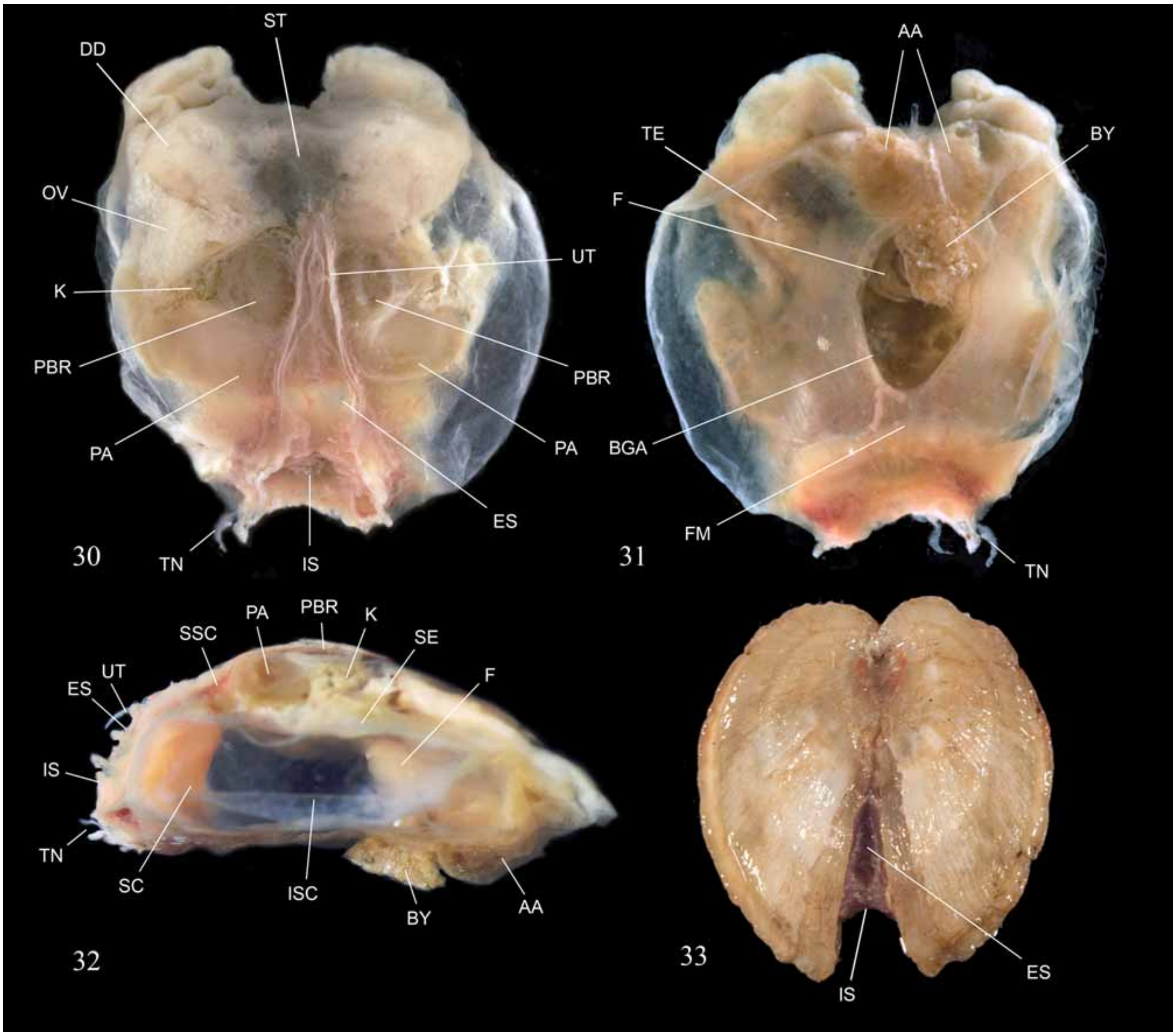


FIGURES 25–29. *Dilemma frumarkernorum.* Shell hinge and ligament. **25–28.** Paratype 2. **25.** Internal views of shell, SEM. Left valve on left side. **26.** Hinge in posteroventral view, SEM. **27.** Same view, optical photography. **28.** Detail of right valve showing ligament. **29.** Paratype 1. Attached valves in ventro-lateral view showing hinge with interlocking teeth and sockets. Scale bars: Figures 25–27, 29 = 2 mm; Figure 28 = 1 mm.
Abbreviations: **AAS** = scar of anterior adductor muscle; **ABS** = scar of anterior byssal retractor muscle; **ASC** = scar of anterior septal muscle; **CIL** = calcified part of inner ligament layer; **CT** = cardinal-like tooth; **HS** = hinge socket; **IL** = inner ligament layer; **LAT** = lateral tooth; **LG** = lateral groove; **LI** = ligament; **OL** = outer ligament layer; **PAL** = pallial line; **PAS** = scar of posterior adductor muscle; **PBS** = scar of posterior byssal retractor muscle; **PE** = periostracum; **OL** = outer ligament layer; **U** = umbo.

Etymology. The new species is named simultaneously after Frank Frumar and Steve Kern, for kindly making the material available for study.

Remarks on habitat and type locality. The depth given above for the type locality is as related by the collector. The two other congeners (below) were collected much deeper, between 805 and 961 m depth.

Remarks. See comparative remarks below, under *Dilemma spectralis* new species and *Dilemma inexpectatum* new combination.



FIGURES 30–33. *Dilemma frumarkernorum.* **30–32.** Paratype 1. **30.** Posterior, **31.** anterior, and **32.** right lateral views of animal removed from shell and submerged in fixative. Mantle lobes are intact in all three views. **33.** Paratype 2. Animal in shell showing relaxed excurrent siphonal opening. Abbreviations: **AA** = anterior adductor muscle; **BGA** = byssal gape; **BY** = byssus; **DD** = digestive diverticula; **ES** = excurrent siphonal opening; **F** = foot; **FM** = fused mantle margin; **IS** = incurrent siphonal opening; **ISC** = infraseptal chamber; **K** = kidney; **PA** = posterior adductor muscle; **PBR** = posterior byssal retractor muscle; **OV** = ovary; **SE** = septum; **SC** = incurrent siphonal cowl; **SSC** = supraseptal chamber; **ST** = stomach; **TN** = tentacles (on siphonal area); **TE** = testis; **UT** = unpaired tentacle. Scale bar: Figures 30–32 = 5 mm.

Dilemma spectralis **new species**

(Figures 34–40, 46–58)

Diagnosis. Shell thin, with sculpture of shell pores on external shell layer (and corresponding periostracal spicules); foot digitiform (rather than filiform), large (relative to previous species); byssus narrow; siphonal cowl large, and siphonal tentacles more concentrated ventral to the incurrent siphonal opening; arrangement of siphonal ostia with middle and posterior groups of ostia not converging but forming lines roughly parallel with each other; siphonal ostia distributed as follows: five anterior, four median, and six posterior.

Description. SHELL (Figures 34–40): General shape and proportions as for genus (above). Shell with minute pores on external layer (Figure 39) arranged in lines oblique to shell margin (Figure 39, SM). Shell apparently nacreous internally, very thin, equivalve (except for slight anteroposterior overlap at umbo), inequilateral, strongly compressed in anteroposterior direction; lateral outline cardioid (Figures 34, 35). Moderate byssal gap (Figure 35, BG) in anteroventral position, on central portion of anterior shell surface. Well-developed carina separating anterior and posterior shell regions (Figures 36, 44).

Umbones, (Figure 37), umbonal cavity, hinge, cardinal-like teeth (Figure 40, CT), hinge sockets, and posterior lateral tooth (present in right valve only) as in previous species.

Ligament, inner ligamental layer (Figure 40, IL), outer ligamental layer (Figure 37, OL) as in previous species, with dorsal periostracum adhering to outer layer.

Anterior adductor muscle scar, posterior adductor muscle scar anterior byssal retractor scar, and posterior byssal retractor scar as in previous species. Pallial line continuous.

Lunule absent. Escutcheon smooth, relatively well-defined, not separated by prominent groove, but distinguishable from remainder of shell by smoother texture and commarginal band of lighter color.

Shell color dull-white. Periostracum yellowish-brown, with hollow spicules (Figures 38, 39) along lines oblique to the shell margin; spicules coinciding with minute pores on external shell layer.

Macroanatomy. MANTLE MARGIN AND SIPHONS: Mantle margins (Figures 47, 49, FM), and siphonal openings as in previous species. Byssal gape (Figures 35, 49, BGA) circular to elliptical. Siphons separate; siphonal area well-defined; siphons formed by fusion of inner mantle folds (“Type A” of Yonge, 1982).

Incurrent siphonal opening (Figures 46, 47, 57, IS) and excurrent siphonal opening (Figures 46, 51, 55, 57, ES) as in previous species; siphonal cowl (Figures 47–51, 54, SC) as in previous species but considerably larger. Base of the incurrent siphon surrounded by 15 simple, tapered tentacles (Figure 46, TN). Large unpaired tentacle (Figure 46, 57, UT) as in previous species; following four tentacles (2+2) (Figure 57, JTN) deployed along each side of intersiphonal junction. Remaining ten tentacles (5+5) (Figure 57, ITN) deployed below ventral half of incurrent siphonal opening. Incurrent siphonal opening located almost ventrally, at least twice as wide as excurrent siphonal opening. Relationship between excurrent siphonal opening and angle formed by junction of margins of two valves in posterior direction as in previous species.

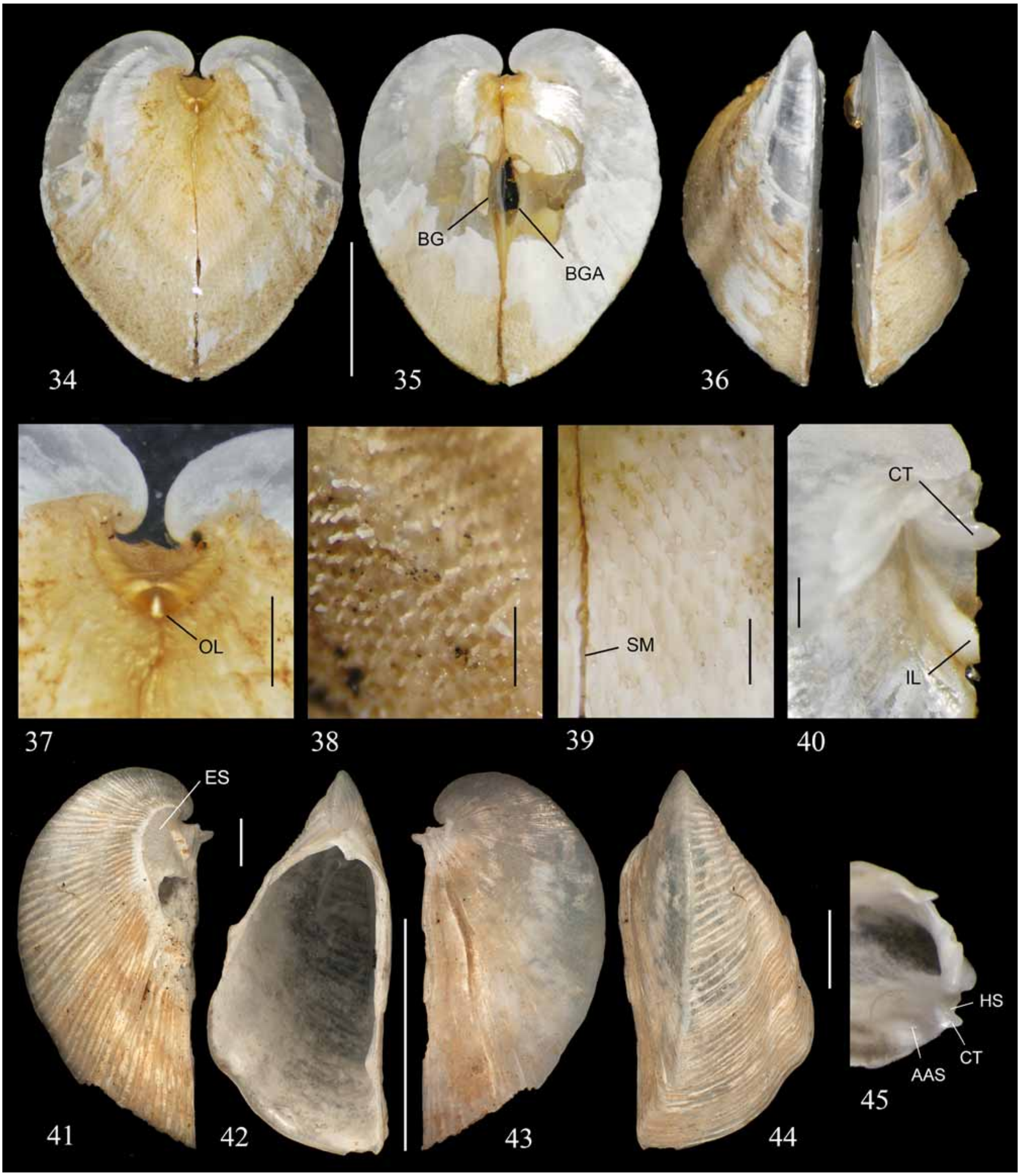
Pair of tentacles present internally (Figures 51, 55, IT), in supraseptal chamber, between posterior margin of excurrent siphon and posterior adductor muscle.

MANTLE CAVITY: Septum (Figures 50, 51, 54, SE), supraseptal (posterior) chamber (Figure 48, 55, SSC), and infraseptal (anterior) chamber (Figures 48, 54, ISC) as in previous species. Septum attachment to internal shell surface as in previous species.

Septum perforated by byssal opening (Figure 58 [right], BO) and by groups of ostia arranged to define three pairs of line segments deployed around byssal gape. Segments containing posterior (Figures 47, 49, 52, 58 [right], PSO) and middle (Figures 49, 52, 58 [right], MSO) groups of ostia roughly parallel to one another, each forming ca. 45º angle with sagittal plane; segment defined by anterior group of ostia (Figures 46, 52, 58 [right], ASO) forming ca. 135º angle with sagittal plane. Ostia distributed as follows: five anterior, four median, and six posterior.

MAJOR SHELL MUSCLES: Relationship between strongly modified shell shape and positioning of adductor muscles as in previous species. Anterior adductor muscles (Figures 47–50, 54, AA), posterior adductor muscles (Figures 46, 48, 50, 51, 54, 55, 57, PA), posterior byssal retractor muscles (Figures 46, 48, 50, 51, 54, 55, 57, PBR), anterior byssal retractor muscles as in previous species. Anterior and lateral septal muscle insertions difficult to observe due to poor specimen preservation. Posterior septal muscle insertions Figure 46, PSM) located adjacent to insertion of posterior adductor muscles.

BYSSUS AND FOOT: Byssus (Figures 47–50, 54, BY) well developed, elliptical in cross section; byssus of holotype attached to sliver of dense, apparently volcanic, rock. Byssus consisting of consisting of bundle of very fine, fused filaments, originating from collar-like expansion of vestigial foot (Figures 47, 49, 50, 53, F), the latter narrow, digitiform. As in previous species, position and size of vestigial foot indicates that it might never exit infraseptal chamber.



FIGURES 34–45. *Dilemma* species. **34–40.** *Dilemma spectralis.* Holotype, MNHN 20818, whole specimen and shell views. **34–35.** Whole specimen. **34.** Posterior. **35.** Anterior. Left valve is broken adjacent to byssal gape. **36.** Right and left valves, lateral. **37.** Ligament in posterodorsal view. **38.** Detail of posteroventral shell surface showing periostracum with spicules. **39.** Detail of anteroventral shell surface showing periostracum with worn spicules. **40.** Right valve, ventral view of internal surface showing hinge. Scale bars: Figures 34–36 = 5 mm; Figures 37–40 = 1 mm. **41–45.** *Dilemma inexpectatum* (Crozier, 1966). Holotype, NMNZ M.018488, left valve. **41–44.** Valve views, from left to right: posterior, internal lateral, anterior, external lateral. **45.** Detail showing cardinal-like tooth. Scale bars: Figures 41–44 = 5 mm; Figure 45 = 1 mm. Abbreviations: **AAS** = scar of anterior adductor muscle; **BG** = byssal gap; **BGA** = byssal gape (in mantle of broken shell); **CT** = cardinal-like tooth; **ES** = escutcheon; **HS** = hinge socket; **IL** = inner ligament layer; **OL** = outer ligament layer; **SM** = shell margin. Figures 41?44 courtesy Bruce Marshall, copyright Museum of New Zealand Te Papa Tongarewa.

MOUTH AND LABIAL PALPS: Mouth (Figures 53, 54, 56, MO) as in previous species; posterior labial palps (Figure 53, 56, PLP) reduced to two vestigial projections flush with surrounding surface. Anterior labial palps (Figure 47, 48, 53, 54, 56, ALP) very well developed, strongly ridged, pointed distally, potentially expandable in posterodorsal direction.

ALIMENTARY SYSTEM: Esophagus (Figure 54, OE) and stomach (Figures 46, 54, ST) generally as in previous species, but stomach more globose. Openings of digestive diverticula situated anteriorly, between esophagus and midgut opening in stomach. Digestive diverticula located in dorsal "horns" (Figures 46, 48, 54, DD.) Midgut (Figure 54, MG) and anus as in previous species.

STOMACH CONTENTS: Examination of stomach contents of holotype revealed single specimen, still relatively intact, of possibly unnamed cirolanid isopod (Marilyn Schotte, pers. comm., November 1, 2007); the stomach was greatly distended (Figure 57). Ms. Schotte could not find any evidence of eyes, ommatidia, or pigment, which indicates that the prey item was an eyeless isopod.

KIDNEYS: Kidneys situated posterodorsally between the remainder of visceral mass and posterior byssal retractor muscle. Kidneys comprising two elongate structures, one on each side of midline of posterior region. Proximal regions of kidney elongate, with distal regions broader, club-shaped (Figures 46–48, 54, 57, K).

REPRODUCTIVE SYSTEM: Testes (Figures 46, 48, TE) elongated situated in anteroventral position in relation to ovaries, ovary overlying the testes. Ovaries (Figures 46, 48, 54, OV) consisting of pair of elongated sacs symmetrically deployed on each side of midline. Ovaries and testes ventral to digestive diverticula.

Type Material. Holotype, MNHN 20818 (length×height×width [in mm] = 5.20×13.50×11.77), N/O ALIS, Campagne MUSORSTOM 8, station CP-1112 (beam trawl), P. Bouchet and B. Richer de Forges coll., 08 Oct. 1994, from type locality.

Type Locality. Off Republic of Vanuatu, 14°53' S, 167°12' E, 950–961 m, bottom with boulders.

Etymology. From the Latin *spectrum*, meaning apparition or an evanescent, supernatural image.

Remarks. *Dilemma spectralis* differs from *D. frumarkernorum* in having a thinner shell, shell pores (and corresponding periostracal spicules), a filiform (rather than digitiform) foot, a different arrangement of septal ostia, a larger siphonal cowl, and siphonal tentacles more concentrated ventral to the incurrent siphonal opening.

Dilemma inexpectatum **(Crozier, 1966) new combination**

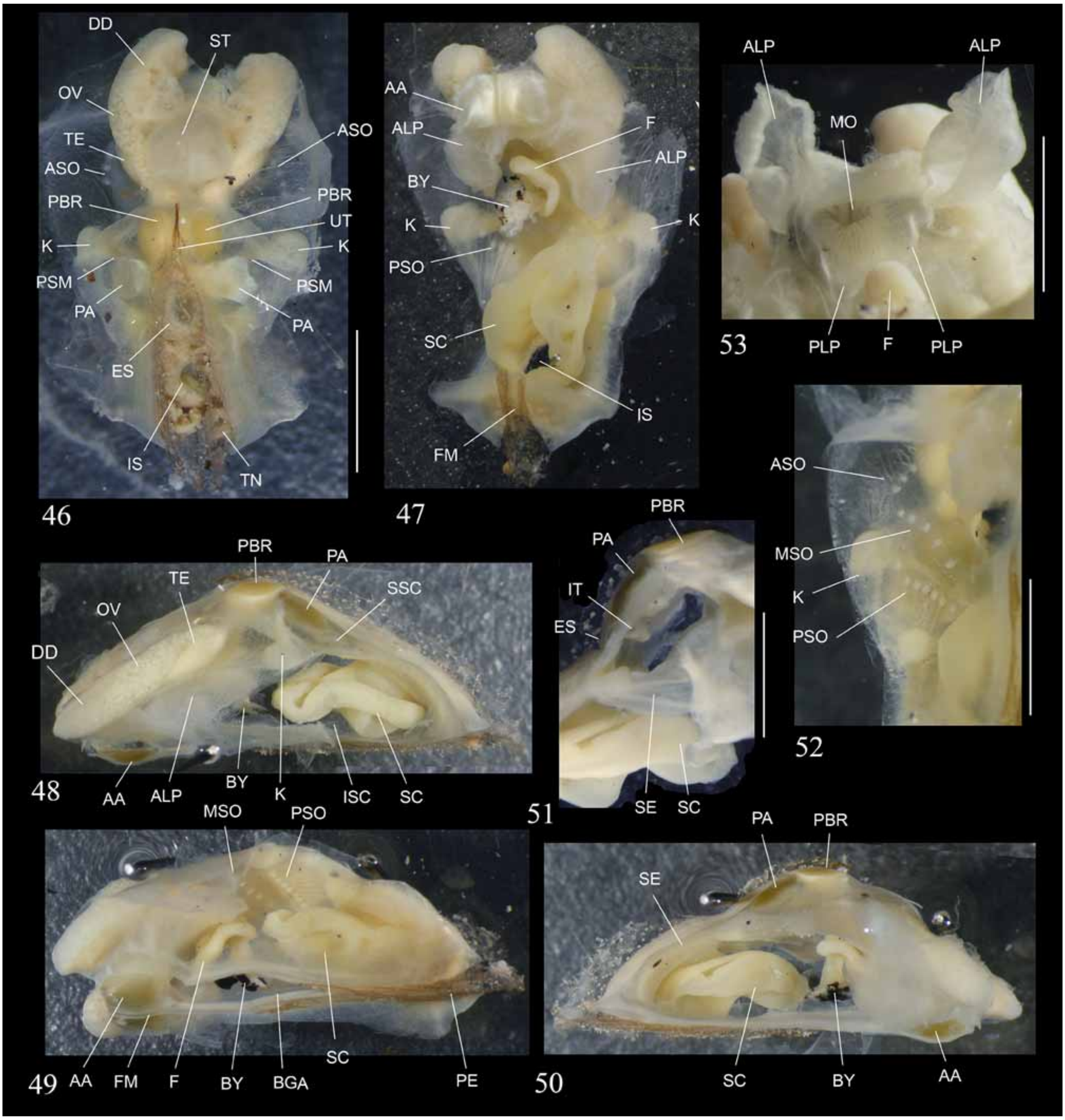
(Figures 41–45)

Corculum inexpectatum Crozier, 1966, p. 42, figs. 10–12; Powell, 1979, p. 413, fig. 109; ter Porter, 2005, p. 6.

Diagnosis. Shell with sculpture of strong, regular commarginal grooves on posterior surface, with interspaces twice as wide. Byssal gap absent. Escutcheon relatively large, smooth, well-defined, separated by prominent groove from remainder of posterior shell surface.

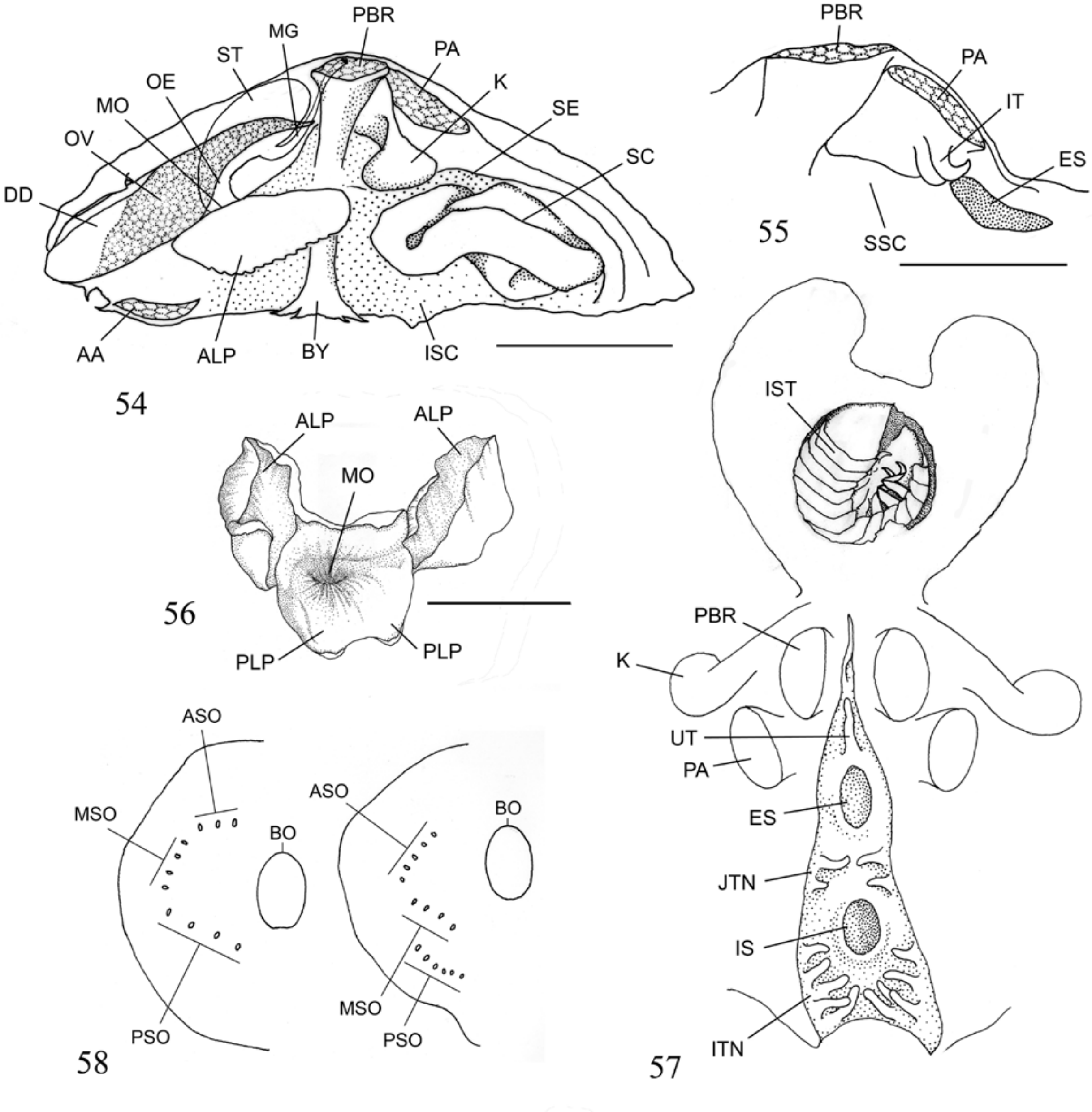
Description (based on holotype, a left shell valve). SHELL (Figures 41–45): Sculpture of strong, regular commarginal grooves on posterior surface, with interspaces at least twice as wide. Anterior shell surface smoother, with worn aspect and commarginal growth lines that often coincide with grooves on posterior surface. Shell apparently nacreous internally, relatively thick, compressed in anteroposterior direction, cardioid in lateral outline (assuming that right valve is symmetrical with left). Byssal gap absent. Well-developed carina separating anterior from posterior shell surfaces. Umbones and umbonal cavity as in previous species.

Umbones, umbonal cavity, hinge, cardinal-like teeth (Figures 40, 45, CT), hinge sockets (Figure 45, HS), as in previous species. Posterior lateral tooth (present in right valve only) not seen. Ligament lacking in examined holotype.



FIGURES 46–53. *Dilemma spectralis.* Holotype, gross anatomy, major organs and anatomical structures. **46.** Posterior view. **47.** Anterior view with anterior mantle wall removed. **48–49.** Left lateral views. **48.** With part of mantle wall removed. **49.** Tilted 30º to allow viewing of fused mantle margins and some septal ostia. **50.** Right lateral view with part of mantle wall removed. **51.** Detail of right side of supraseptal chamber showing internal tentacles anterior to excurrent siphons. **52.** Detail of right side of septum around byssal opening showing three groups of septal ostia. **53.** Detail of mouth area showing labial palps. Note small posterior labial palps and position of foot extremity in relation to mouth. Scale bars: Figure 46 = 3 mm; Figures 51, 52 = 2 mm; Figure 53 = 1 mm. Abbreviations: **AA** = anterior adductor muscle; **ALP** = anterior labial palps; **ASO** = anterior group of septal ostia; **BGA** = byssal gape; **BY** = byssus; **DD** = digestive diverticula; **ES** = excurrent siphonal opening; **F** = foot; **FM** = fused mantle margin; **IS** = incurrent siphonal opening; **ISC** = infraseptal chamber; **IT** = internal tentacles; **K** = kidney; **MO** = mouth; **MSO** = median group of septal ostia; **PA** = posterior adductor muscle; **PBR** = posterior byssal retractor muscle; **PE** = periostracum; **PLP** = posterior labial palps; **PSM** = posterior septal muscle; **PSO** = posterior group of septal ostia; **OV** = ovary; **SE** = septum; **SC** = incurrent siphonal cowl; **SSC** = supraseptal chamber; **ST** = stomach (engorged by content, see Figure 57); **UT** = unpaired tentacle; **TE** = testis; **TN** = tentacles (on siphonal area).

Anterior adductor muscle scars (Figure 45, AAS), posterior adductor muscle scars as in previous species. Anterior and posterior byssal retractor scars difficult to examine due to worn nature of holotype. Pallial line continuous.



FIGURES 54–58. *Dilemma* species, reconstructed macroanatomy. **54–57.** *Dilemma spectralis*. **54.** Left lateral view with part of mantle wall removed. **55.** Detail of mantle cavity in left lateral view showing pair of internal tentacles along posterior edge of excurrent siphon. **56.** Detail of mouth region showing labial palps. **57.** Posterior region showing siphonal opening, tentacles, and stomach with prey item (a cirolanid isopod.). **58.** Comparison of septal ostia in *D. frumarkernorum* (left) and *D. spectralis* (right). Posterior view, only left half of septum shown, with dorsal at top and not to scale. Scale bars: Figure 54 = 3 mm, Figure 55 = 2 mm, Figure 56 = 1 mm. Abbreviations: **AA** = anterior adductor muscle; **ALP** = anterior labial palps; **ASO** = anterior group of septal ostia; **BO** = byssal opening; **BY** = byssus; **DD** = digestive diverticula; **ES** = excurrent siphon; **IS** = incurrent siphonal opening; **ISC** = infraseptal chamber; **IST** = prey item in stomach (a cirolanid isopod); **IT** = internal tentacles; **ITN** = tentacles deployed ventrally to incurrent siphon; **JTN**= tentacles deployed alongside intersiphonal junction; **K** = kidney; **MG** = midgut; **MO** = mouth; **MSO** = median group of septal ostia; **OE** = esophagus; **PA** = posterior adductor muscle; **PBR** = posterior byssal retractor muscle; **PLP** = posterior labial palps; **PSO** = posterior group of septal ostia; **OV** = ovary; **SE** = septum; **SC** = incurrent siphonal cowl; **SSC** = supraseptal chamber; **ST** = stomach; **UT** = unpaired tentacle.

Lunule absent. Escutcheon (Figure 41, ES) relatively large, smooth, well-defined, separated by prominent groove from remainder of posterior shell surface.

Periostracum lacking in holotype. Shell color dirty-white with some staining evocative of iron oxide.

Type Material. Holotype, NMNZ M.018488, 3.94 mm (length) × 8.19 mm (height) × 8.16 mm (width; width was calculated by multiplying width of single left valve by two, assuming the shell to be perfectly equivalve), RNZFA TUI, 15 July 1962 (Images available online at Museum of New Zealand Te Papa Tongarewa, 2007.) Paratype, one right valve NMNZ M18491 (not seen; both assumed from type locality).

Type Locality. North of Three Kings Islands, 34º00' S, 171º55' E, 805 m depth, bryozoan and shell bottom.

Remarks. This species is also known only from its type locality. It was originally described as a *Corculum* (Cardiidae) from the holotype, a left valve (above), and one paratype, a right valve (not examined). The original description gave dimensions as “2.7 mm (length) × 8.0 mm (height).”

Notwithstanding the lack of known soft parts, *Dilemma inexpectatum* is easily separated from the two new species described above by its sculpture of strong grooves on its posterior surface that contrasts with a relatively large and very well-defined escutcheon devoid of sculpture, a relatively thicker shell, and the lack of a byssal gap on the anterior shell surface.

Discussion

The absence of ctenidia and presence of a septum, size and arrangement of siphons and siphonal tentacles, extensive fusion of the mantle margins allocate the new genus within the septibranch bivalves (which include the Cuspidariidae, Verticordiidae, and Poromyidae). A siphonal area with 15 tentacles, a large and eversible incurrent siphon, ostial apertures in the septum, and a hermaphroditic reproductive system, deeply sunken ligament with an outer ligamental layer covered by dorsal periostracum, and the absence of a lithodesma are characteristic of the Poromyidae (Allen & Morgan, 1981; Bernard, 1974; Krylova, 1997; Morton, 1981a; Poutiers & Bernard, 1995; Yonge & Morton, 1980). Yonge & Morton discussed the anteriorly divergent outer ligamental layer in *Poromya tornata* (Jeffreys, 1876), with each half curled around as a result of tangential growth in that species. This condition is also present, and exacerbated, in *Dilemma*. The inner ligamental layer differs, however, in *Dilemma*, by being hard and whitish, apparently in part calcified. Analyses of the ontogeny in species of *Dilemma* could elucidate whether this calcification represents the remnant of a lithodesma.

The main morphological departure exhibited by the new genus when compared to other poromyids (e.g., *Poromya*, *Cetoconcha;* see characterization of shell shape in the family, for instance, by Prezant, 1998) involves the shape of these bivalves. It is here suggested that there is allometric change including relative reduction in length associated with an increase in width (Figures 1, 2; see Allen, 1985, and Stasek, 1963, for more complete discussions on orientation of axes and form in bivalves). Compression along the anteroposterior axis results in a thin shell outline. Superficial similarities of form through convergence with the monotypic cardiid genus *Corculum* (compare with *C. cardissa* as presented in Oliver, 1982, and Schneider, 1998) are readily apparent. Even the shape and position of the anterior adductor muscle is very similar in that phylogenetically distant genus. In contrast to *Corculum*, however, there is a component of “shear” along the anteroposterior axis, pushing the dorsal region in an anterior direction and the ventral region in a posterior direction.

One of the macroanatomical changes resulting from the allometric change described above is that the relative distance between the foot and the visceral mass is greatly reduced when compared to other septibranchs. Likewise, the total length of the alimentary tract is relatively very short, with the path mouth-esophagus-stomach-midgut-anus short C-shaped structure in left lateral view.

From the macroanatomical standpoint, *Dilemma* exhibits (if one factors out the aberrant symmetry and the sessile mode of life) many characters in common with species in the poromyid genus *Poromya* and *Cetocon-*

cha (see Bernard, 1974; Allen & Morgan, 1981; Poutiers & Bernard, 1995). These include, but are not limited to, the presence of 15 simple, tapered tentacles on the siphonal area, and an internal pair of tentacles between the posterior edge of the excurrent siphon and the posterior adductor muscle (Allen & Morgan [1981: 513] suggested that the pair of internal tentacles "may help cleanse the suprabranchial [supraseptal] cavity of faecal material". *Dilemma* shares with *Cetoconcha* alone the presence of ostial apertures deployed in three paired groups forming a line segment.

As in *Dilemma*, well-developed anterior labial palps in association with reduced posterior labial palps occur in *Poromya granulata* (Nyst & Westendorp, 1839) (see Morton, 1981b) *Poromya tornata*, *Cetoconcha braziliensis* Allen & Morgan, 1981, and *C. angolensis* Allen & Morgan, 1981 (see Allen & Morgan, 1981). However, the degree of reduction of the posterior labial palps in the two species of the new genus *Dilemma* is extreme, with the palps represented by a pair of small flap-like projections in these two species.

The gross morphology of the alimentary system and particularly of the stomach in the two new species is very similar to that of *Poromya granulata* and *Cuspidaria cuspidata* (Olivi, 1792), with a very short esophagus that penetrates the stomach anterodorsally, and openings of the digestive diverticula in the anterior position of the stomach, between esophagus and mid-gut opening (Purchon, 1956; Yonge, 1928). The stomach is of the Type II of Purchon (1956).

Authors in the past have suggested that the simplified hinge teeth in the Anomalodesmata (e.g., *Poromya*, *Cuspidaria*) are secondarily derived (Yonge & Morton, 1980), not homologous to cardinal and lateral teeth in the "classic" heterodont arrangement. The assumption underlying the purported appearance of secondary hinge teeth is in the Anomalodesmata is that these teeth evolved *de novo* from a straight-hinged, edentulous anomalodesmatan ancestor (Yonge & Morton, 1980). The molecular phylogenetic hypotheses proposed by Dreyer *et al. (*2003), Harper *et al.* (2006), and Taylor *et al.* (2007) show Anomalodesmata as a well-supported clade nested within the Heterodonta. If that is the case, then future analyses could show that the hinge teeth of poromyids and other carnivorous anomalodesmatans could well be homologous to those of heterodonts. [Although this is not a point of discussion in the present article, overviews of the diverse family-level classifications of the "septibranchs" were given by Dreyer *et al.* (2003) and Harper *et al*. (2006). These authors could not find support nor reject the monophyly of Septibranchia as defined previously by other workers.]

Features of the new genus such as shells with critically modified symmetry (heart-shaped shells strongly compressed in the anteroposterior direction), a flat anterior shell surface, presence of a robust, wide byssus and byssal gap in the shell of at least two out of three species, and reduction of the foot to a vestigial appendage, are obviously associated with sessile, permanently attached mode of life.

Predation is suggested indirectly by macroanatomical features such as a potentially eversible incurrent siphon, very large anterior labial palps, and stomach of Type II, and directly by the presence of ostracod remains in the stomach contents of one paratype of *Dilemma frumarkernorum* and presence of an intact specimen of an unknown cirolanid isopod in the stomach of *D. spectralis*. The latter is a large prey item (about 4 mm carapace length) in relation to the size of the bivalve. Although predation by infaunal, free-living bivalves occurs in most of the Anomalodesmata (Bernard, 1974; Harper *et al.*, 2006; Morton, 1981a, 1987; Poutiers & Bernard, 1995; Prezant, 1998) and in particular within the septibranchs (Allen & Turner, 1974; Allen & Morgan, 1981; Morton, 1981b; Krylova, 1997; Yonge, 1928), discovery of the new genus reveals an unusual instance of predation by sessile, permanently attached mollusks. Furthermore, given that chance encounters alone with motile prey might not provide sufficient nourishment for a sessile predator, it is possible (although supporting data are currently lacking) that representatives of the new taxa could use physical or chemical attractants to increase number of encounters and facilitate the entrapment of prey.

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Frank Frumar and Steve Kern made available the material that constitutes the type series of *Dilemma frumarkernorum*. Harry G. Lee, Jacksonville, Florida, brought the type series of *D. frumarkernorum* to my attention. Bruce Marshall at the Te Papa Museum, Wellington, New Zealand, helped with the loan of the holotype of *Corculum inexpectatum,* provided Figures 41–44, and directed me to the single specimen (holotype) of *Dilemma spectralis*. Philippe Bouchet and Virginie Héros at MNHN helped with the loan of this latter specimen. Paula Mikkelsen, Rüdiger Bieler, and James Scatterday helped with literature. Yolanda Villacampa and M. G. Harasewych, National Museum of Natural History, Smithsonian Institution, prepared the SEM images. Kimberly Nealon did the line drawings of macroanatomy. Marilyn Schotte, National Museum of Natural History, Smithsonian Institution, helped identify the isopod specimen. James Scatterday and Paula Mikkelsen made suggestions that enhanced the quality of a pre-submission draft. Robert Prezant and an anonymous reviewer offered valuable criticisms and helped enhance the clarity of the manuscript. Access to online library resources was made possible through an adjunct professorship appointment with the Rosenstiel School of Marine and Atmospheric Science, University of Miami. This work was supported in part by Florida Department of State's Division of Cultural Affairs and the Sanibel-Captiva Shell Club. I dedicate this article to the memory of my colleague Osmar Domaneschi.

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