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RHOMBOPSAMMIA, A NEW GENUS OF THE FAMILY MICRABACIIDAE (COELENTERATA: SCLERACTINIA)

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Abstract.—*Rhombopsammia,* a new genus of deep-water micrabaciid corals, and two new species, *R. squiresi* and *R. niphada,* are described and figured. *Rhombopsammia* bears a marked superficial resemblance to *Letepsammia,* but examination of the corallum structure, microstructure, and microarchitecture of the new genus through thin-section and light microscope study reveals that it differs from *Letepsammia* in having essentially imperforate septa, prominent vepreculae which alternate in position on either side of the septum, ridge-like tracings of trabeculae on septal flanks and dentate columella. Its known geographic distribution (China and Philippine seas) is more restricted than that of *Letepsammia,* but its bathymetric range (68–930 m) is only slightly less. Allusions by Squires (1967 and ca. 1967) to an undescribed species of micrabaciid coral from the Pliocene of Italy suggest that this species may belong to the new genus. If true, *Rhombopsammia* will conform with the evolutionary trend of the family towards increasing depth of occurrence with progressive geologic age.

The Micrabaciidae is a small family of solitary, ahermatypic corals known from the shallow waters of Cretaceous continental shelves and inland seas to the deep waters of today's Indo-Pacific. When Vaughan (1905) defined the family, he included in it *Micrabacia* Milne-Edwards and Haime, *Diafungia* Duncan, *Microsmilia* Koby, *Podoseris* Duncan, and *Antilloseris* Vaughan, largely on the basis of their solid septa and perforate walls. Later, Wells (1933) emended the family to emphasize the structural significance of an alternation of septa and costae. He thus excluded from it all but *Micrabacia* and *Diafungia,* and included in it *Stephanophyllia* Michelin and *Leptopenus* Moseley. In revising the Scleractinia, Vaughan and Wells (1943) determined that *Micrabacia* and *Diafungia* were synonymous, and defined the Micrabaciidae as consisting of three genera: *Micrabacia, Stephanophyllia,* and *Leptopenus.* Most current workers accept this definition of the family.

For many years most of the species of these genera were classified primarily on the basis of external characters observable in whole-mount study; consequently, many species were grouped together more or less according to superficial resemblances and broadly defined generic characteristics that sometimes masked structural and microstructural differences that are significant enough to warrant generic separation. This was particularly true of many of the species comprising *Stephanophyllia.* On re-examination of this genus, Yabe and Eguchi (1932) detected subtle but fundamental differences in morphology and component elements among the species which led them to erect four subgenera of *Stephanophyllia,* one of which was *Letepsammia,* a group of micrabaciid corals distinguishable by their highly perforated septa. Wells (1956) considered

Letepsammia to be synonymous with *Stephanophyllia,* but more recent workers, particularly Squires (1967 and ca. 1967) and Owens (1984), have deemed septal perforations to be a valid generic characteristic and have therefore referred to *Letepsammia* as a discrete genus of micrabaciid corals.

In examining the *Albatross* collection of deep-sea corals, Squires (ca. 1967) separated from those sorted by National Museum workers as *Stephanophyllia* a group which differed from that genus in having essentially imperforate septa. Although he obviously felt this group deserved further study, he left it undescribed. This group was later included in a study of the structure, microstructure, and microarchitecture of the Micrabaciidae (Owens 1984). As a result of this latter study of the family both in whole mount and in thin section, a new genus, *Rhombopsammia,* is designated in this paper.

Rhombopsammia consists at present of two species, *R. squiresi* and *R. niphada,* both Recent. Squires (1967 and ca. 1967) alluded to a fossil coral of the Pliocene of Italy that apparently belongs to this new taxon; however, his fossil species could not be found or verified for this study. This paper, therefore, describes only the two Recent species, but acknowledges the possible existence of a Pliocene member. In light of the evolutionary trend of the family (Steinmann 1908, Squires 1967, Owens 1984) towards increasing depth of occurrence with progressively younger geologic age, a Pliocene member of this genus with a depth range similar to the Recent species is highly probable.

Order Scleractinia Bourne, 1900
Suborder Fungiida Duncan, 1881
Superfamily Fungioidea
Vaughan and Wells, 1943
Family Micrabaciidae Vaughan, 1905
Rhombopsammia, new genus

Diagnosis.—Corallum large, loosely built, strongly convex orally and nearly flat to patellate aborally, with narrow to wide marginal shelf formed by non-elevated extensions of septa alternating with costae. Septa essentially imperforate, coarsely dentate, rising steeply proximally and distally, forming a crown above the basal wall. Tracings of trabeculae visible on septal flanks. Deltas broad, porous. Vepreculae numerous, alternating in position on either side of septa. Synapticulae scarce, mainly near base of septa. Calicular depression deep, elongate. Costae thin, finely serrate or complex with recumbent teeth, connected by closely spaced concentric rows of synapticulae. Intercostal loculi broader than costae. Wall perforate, moderately to strongly laterally flattened. Columella porous, deeply set, elongate, and dentate on exposed upper surface. Corallum completely invested in soft tissue of the polyp.

Occurrence.—(?)Pliocene, Italy; Recent, China and Philippine seas; 68–930 m.

Type species.—*Rhombopsammia squiresi,* new species.

Etymology.—The generic name refers to the convexo-patellate shape of *R. squiresi,* and is derived from the Greek *rhombos* = spinning top + *psammos* = sand. Gender: feminine.

Discussion.—Specimens of both *Rhombopsammia* and *Letepsammia* have generally been sorted by museum workers as *Stephanophyllia.* The three do bear a resemblance, though the former two are more alike than either is like the latter. The resemblances are greatly diminished, however, when specimens of *Rhombopsammia* are closely examined by use of a light microscope and thin sections, or when septal perforations are taken into account. *Rhombopsammia* differs from *Stephanophyllia* in its imperforate septa, convexo-patellate corallum, marginal shelf, spongy columella, and large, loosely built corallum; it differs from *Letepsammia* in its imperforate septa, prominent vepreculae which alternate in

position on either side of the septum, ridge-like tracings of trabeculae on septal flanks, and dentate upper margin of the columella. In thin section, the trabecular structure in *Rhombopsammia* is seen to be more widely spaced than in *Stephanophyllia,* less sinuous than in *Letepsammia.*

Only two species of *Rhombopsammia* are described below. A third species, a fossil form from the Pliocene of Italy, was reported by Squires (1967 and ca. 1967), but was not described and could not be located for this study.

Steinmann (1908), Squires (1967), and Owens (1984) have noted an evolutionary trend of the Micrabaciidae towards increasing depth of occurrence with progressively younger geologic age. *Rhombopsammia,* with its bathymetric range of 68–930 m and its probable age of Pliocene to Recent, fits well into this trend. However, its virtually imperforate septa present a departure from another apparent trend of the family towards increasing septal perforations with depth (Steinmann 1908, Owens 1984). *Stephanophyllia* is moderately perforated, whereas *Letepsammia* is highly perforated. Inasmuch as *Rhombopsammia* falls between *Stephanophyllia* and *Letepsammia* in both age and depth of occurrence, one would anticipate its also falling between the two in septal perforations.

In many respects, *Rhombopsammia* appears to be a transitional genus between *Stephanophyllia* and *Letepsammia,* for its species have characters found in each genus, and though its bathymetric range is close to that of *Letepsammia,* its maximum depth of occurrence nonetheless falls more than 50 m shorter. However, the evolutionary placement of *Rhombopsammia* between two genera with well-developed septal perforations is troublesome. The question arises as to whether *Rhombopsammia* is indeed part of a linear evolutionary progression toward adaptation to life at deeper and deeper depths and, possibly, also a transitional genus between *Stephanophyllia* and *Letepsammia,* or a divergent member of the family following a different but parallel evolutionary path. More study along the lines of alternative solutions to the problem of adapting to life in deep waters is needed before that question can be satisfactorily answered.

Rhombopsammia squiresi, new species
Figs. 1, 2A

Description.—Corallum large, loosely built, and strongly convexo-patellate, with wide marginal shelf. Calicular depression deep and long, but narrow. Wall finely perforate. Deltas broad, porous, with proximal edges of secondaries distinct. Diameter of specimens 30.3–32.6 mm; height 13.3–13.7 mm; average H:D ratio 43:100. Ninety-six septa.

Costae thin, finely granulated axially, coarsening distally; costae and synapticulae adorned with irregular, recumbent teeth, beginning about midway between axis and periphery. Intercostal loculi as broad or broader than costae axially, but obscured distally. Costae begin as 6 (first cycle) at apex of wide cone forming basal wall and bifurcate immediately (second cycle); all new costae immediately bifurcate again (third cycle); outer costae bifurcate before inner at about one-tenth and one-seventh, respectively, distance from center to periphery (fourth cycle); final bifurcations (fifth cycle) begin at one-third distance to periphery with first and fourth costae of each quartuplet in each system bifurcating first.

Septa imperforate and thin, with interspaces as wide or wider than septa. Vepreculae radially aligned and alternate in position on either side of each septum, giving septal margins a fluted appearance. Dentation slightly lobulate, becoming slightly lacerate at inner margins of all but primaries. All but highest cycle septa tall and approximately same height; inner margins of primaries more rounded than those of the deltas. Primaries inserted straight and free

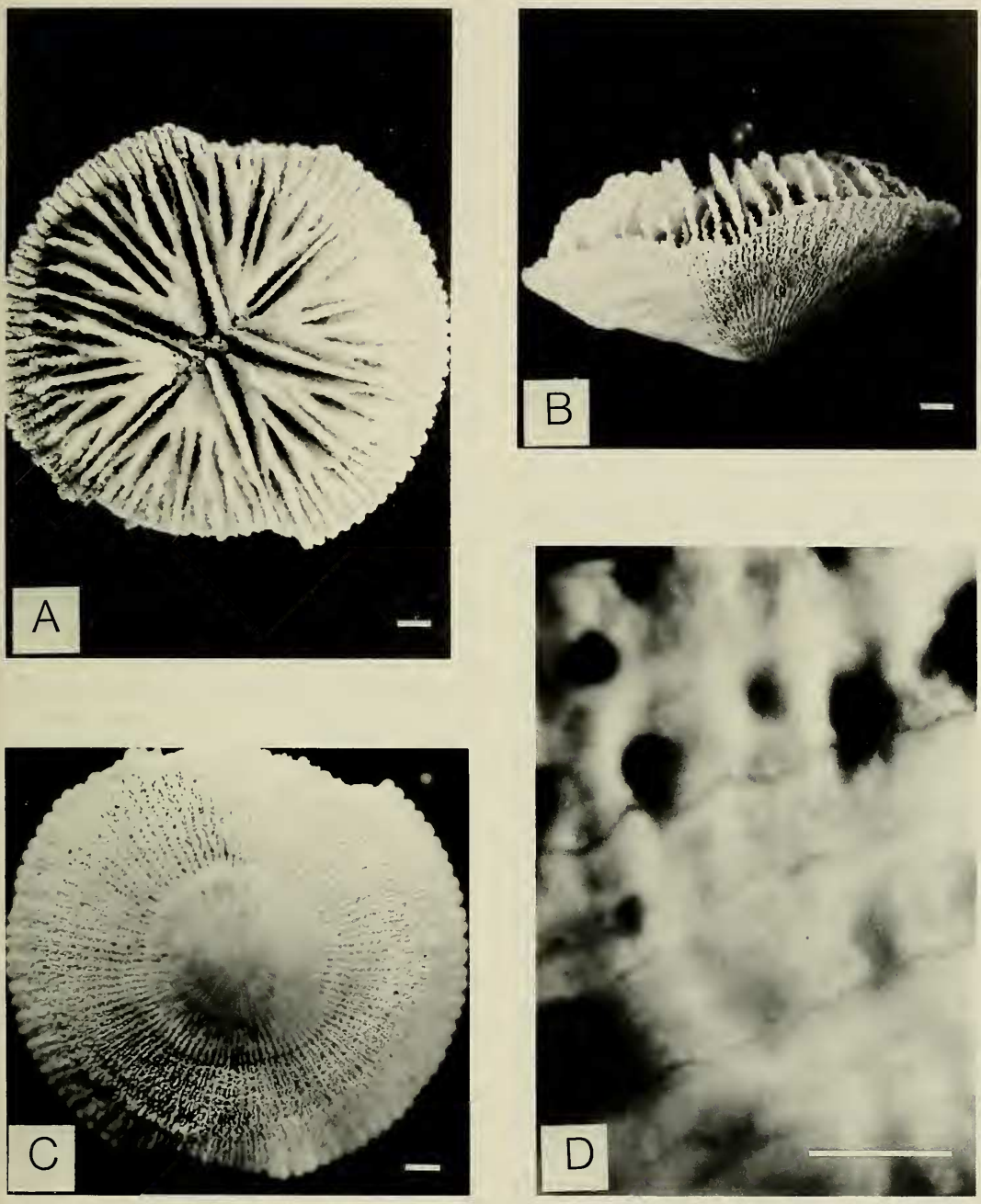

Fig. 1. *Rhombopsammia squiresi*: A, Oral view of holotype (USNM 72797), *Albatross* 5423: 9°38′30″N, 121°11′E, 930 m; B, Side view of holotype; C, Aboral view of holotype; D, Thin section of septum of a paratype (USNM 72798), under reflected light, showing thin, wavy trabeculae with growth laminae. Holes in septum were caused by mechanical grinding to make thin section. *Albatross* 5427: 9°11′30″N, 118°37′08″E, 68 m. Scale bars = 2 mm.

and extend to columella. Secondaries straight and free until joined with others in deltas. Tertiaries divide just beyond deltas, and these septa successively divide symmetrically, with final division occurring at inner edge of shelf. Slightly porous sheets mark points of division. Synapticulae scarce, mainly at base of septa, particularly distally.

Columella porous, spongy, terminating at upper surface in mass of lacerate-like teeth.

Trabeculae in slightly diffuse fan system, visible along septal flanks as faint tracings. Growth laminae prominent, expressed as undulating ridges along the sides of the septa.

Types.—Holotype: USNM 72797; *Albatross* Sta 5423 (9°38′30″N, 121°11′E; 930 m). Paratypes: USNM 72799, 72800, 72798; *Albatross* Sta 5513 (8°16′45″N, 124°02′48″E; 924 m), 5425 (9°37′45″N, 121°11′E; 906 m), and 5427 (9°11′30″N, 118°37′08″E; 68 m), respectively.

Occurrence.—Recent, China Sea, Philippine Sea; 68—930 m.

Remarks.—The pronounced convexo-patellate corallum, high crown of septa, wide marginal shelf, and recumbent costal and basal synapticular teeth make *R. squiresi* a very distinctive species, quite unlike any other micrabaciid coral save *R. niphada,* with which it bears a slight structural but stronger microstructural resemblance. That it is a micrabaciid coral is obvious from its alternation of septa and costae. Its pattern of septal insertions (Fig. 2A) is very similar to that seen in other micrabaciids which possess true deltas, and typically has the quinaries proximal to the primaries merging with the quaternaries closer to the center than the inner quinaries.

One or two random pores were observed in a few septa in each specimen, but as these pores lacked any regularity in frequency, position, or even cycle of septa in which they occurred, the septa are considered essentially imperforate.

In thin section, the arcuate manner in which the ends of the sclerodermites of neighboring trabeculae merge proved to contribute to the fluted appearance of the septa. The arcs described by the sclerodermites persist not only in the plane of the septum, but also swing laterally to form cusps along the flanks. This arcuate pattern between trabeculae is found also in *R. niphada* but to a lesser degree, and explains why the septa in the latter species are less wavy.

Etymology.—The species name is in honor of Donald F. Squires, whose recognition that this group of corals differed from the other species of *Stephanophyllia* inspired this study.

Rhombopsammia niphada, new species
Figs. 2B, 3

Description.—Corallum large, delicate, loosely built, with narrow to wide prominent shelf; strongly convex orally and slightly patellate to nearly flat basally, but with pronounced basal apex. Calicular depression deep, long, and narrow. Deltas broad, porous, slightly spinose on inner margin. Diameter of specimens 21.5–36.0 mm; height 6.7–12.0 mm; H:D ratio 31:100. 144 septa.

Costae smooth, very thin, finely serrate on outer surface. Intercostal loculi broader than costae, but interrupted by closely spaced synapticulae connecting costae to bases of septa. Basal synapticulae smooth, lacking serration. Costae begin as 6 (first cycle) at apex of protuberant basal tip and bifurcate immediately (second cycle); each costa immediately bifurcates again (third cycle); outer pairs bifurcate fractionally before inner ones at about one-tenth distance from center to periphery (fourth cycle); bifurcations of fifth cycle begin about one-sixth distance from center with outermost costae of each system dividing first, followed closely by next outer and then innermost, other inner costae do not divide in this cycle; sixth cycle, also incomplete, begins again with outermost and next outer

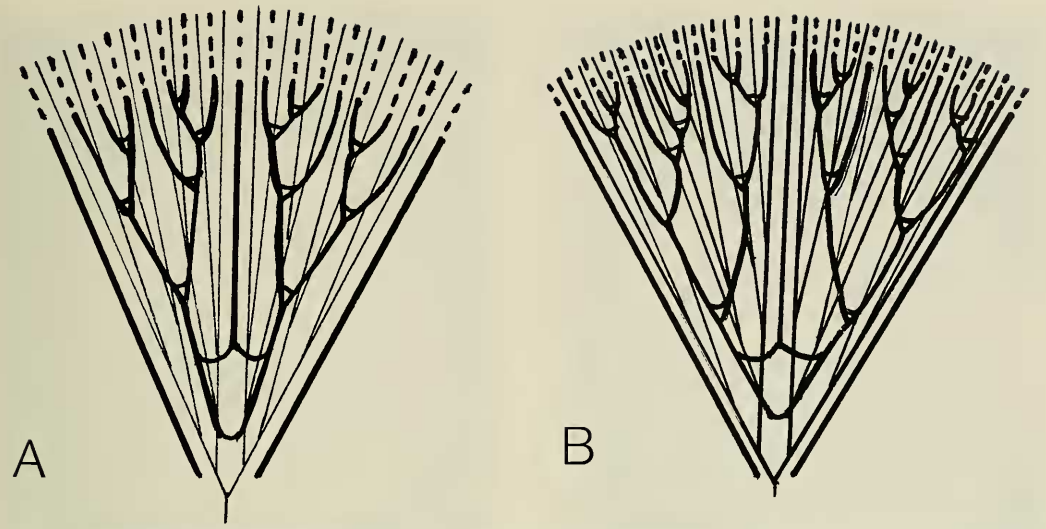

Fig. 2. Diagrammatic representations of one system: A, *Rhombopsammia squiresi*; B, *Rhombopsammia niphada*. Heavy lines represent septa; thin lines, costae; dotted lines, non-elevated extensions of septa.

dividing; followed symmetrically by 3 adjacent inner costae, those flanking each side not dividing. Final bifurcations occurring about one-third the distance to periphery.

Septa imperforate and thin, with interspaces wider than septa. Vepreculae radially aligned and alternate in position on either side of a septum, but produce only slight fluting effect. Dentation lobulate-like on upper and outer margins of septa, less so on inner margins of primaries. Synapticulae broad relative to width of septa and irregularly spaced deep in calice. Primaries straight, free, extending from shelf to columella. Secondaries straight and free to deltas. Tertiaries divide just beyond deltas, and quaternaries thus formed divide halfway between deltas and outer edge of calice, with outer quaternaries dividing slightly before inner ones. Quinaries proximal to the primaries and secondaries do not bifurcate until three-fourth distance from delta to shelf whereas of the two inner quinaries, the one closer to secondary does not bifurcate at all. At inner edge of shelf, beginning with no bifurcation of septa proximal to primaries, every other septum bifurcates for a final time, giving each system total of 24 septa. Coarsely porous sheets mark points of division.

Columella porous, spongy, elongate, but broader than in *R. squiresi*; ornamented at center with cluster of small, slightly spinose teeth.

Trabeculae, often ramified near distal margins, in moderately well-spaced fan system, and clearly visible as tracings along septal flanks. Ends of sclerodermites either joining together in arcuate pattern between trabeculae or diverging normally from axis to form vepreculae.

Types.—Holotype: USNM 72802; *Albatross* Sta 4911 (31°38′30″N, 129°19′E; 716 m). Paratypes: USNM 72801, 72804, 72803, 72805; *Albatross* Sta 4911 (same as holotype), 5283 (13°48′30″N, 120°28′40″E; 512 m), 5348 (10°57′45″N, 118°38′15″E; 686 m), and ND (no data), respectively.

Occurrence.—Recent, China Sea and Philippine Sea; 512–716 m.

Remarks.—*Rhombopsammia niphada* bears a close resemblance to species of *Letepsammia,* in that it shares with them a delicate, lacy corallum with a generally narrow marginal shelf, narrow columella, and highly perforated wall. However, close ex-

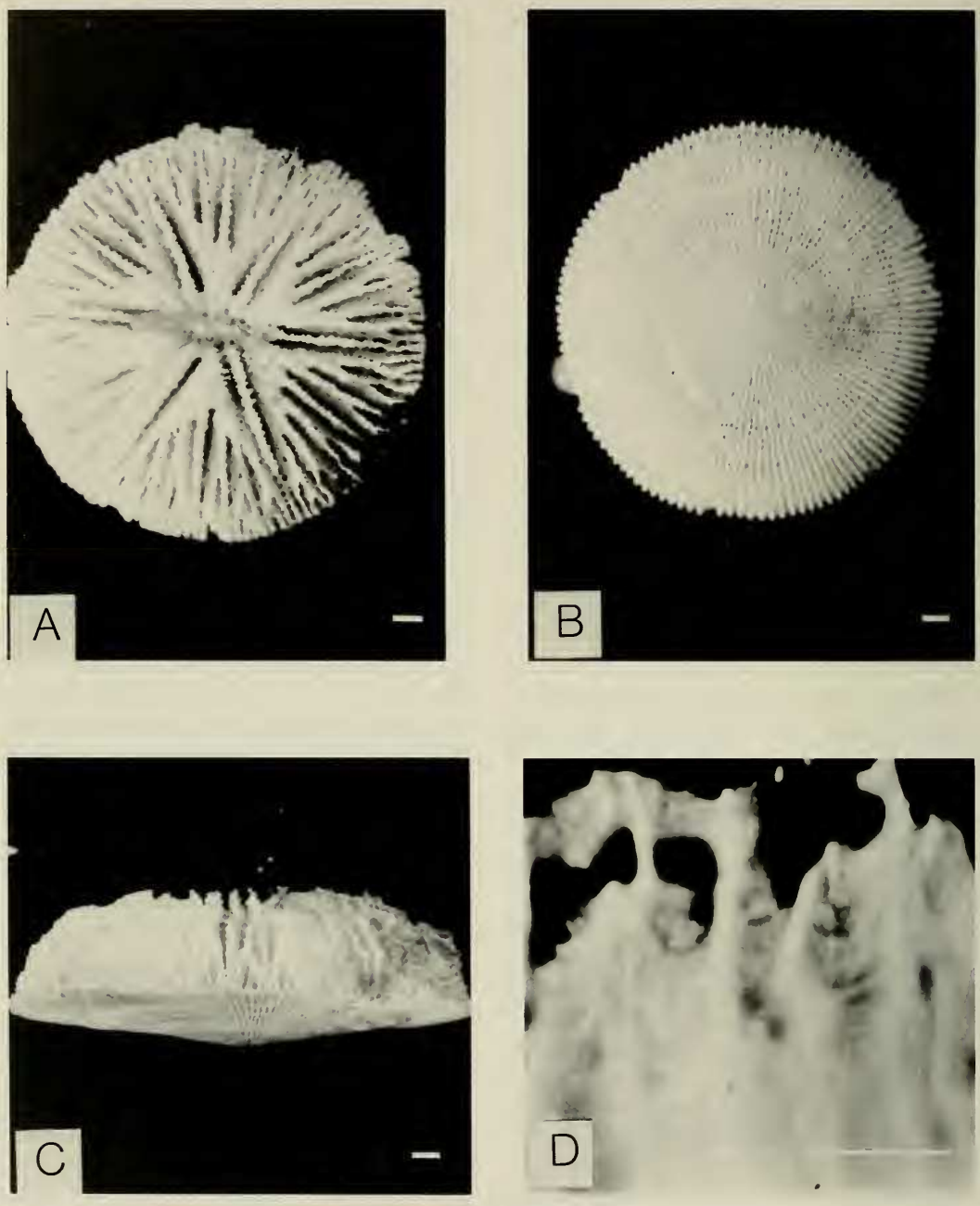

Fig. 3. *Rhombopsammia niphada*: A, Oral view of holotype (USNM 72802), *Albatross* 4911: 31°38′30″N, 129°19′E, 716 m; B, Aboral view of holotype; C, Side view of holotype; D, Thin section of septum of a paratype (USNM 72804), under reflected light, showing thin, wavy trabeculae with ends of sclerodermites merging in an arcuate pattern in the interarea. Note ramified trabecula at distal margin of septum in upper left. *Albatross* 5283: 13°48′30″N, 120°28′40″E, 512 m. Scale bars = 2 mm.

amination of the structure, microstructure, and microarchitecture of *R. niphada* distinctly separates it from *Letepsammia* and reveals its closer relationship with *R. squiresi.*

Both *R. niphada* and *R. squiresi* have essentially imperforate septa, numerous well-developed vepreculae, and strong fan-like trabeculae that impart ridge-like tracings on the sides of the septa and project along the outer margins as lobulate-like teeth. Also, in both the vepreculae alternate in position on either flank, giving the septa a fluted appearance. Both have a very protuberant basal apex, and their costal-intercostal spacings are similar.

As in all micrabaciid corals, *R. niphada* has an alternation of septa and costae. Its pattern of septal insertions (Fig. 3) is similar to that of other micrabaciids with true deltas, and is virtually identical with that seen in *R. squiresi* for an equal number of cycles and septa.

Rhombopsammia niphada differs most conspicuously from *R. squiresi* in its total number of septa (144) and its very slightly patellate to nearly flat base. It also lacks the recumbent basal teeth found in *R. squiresi.* Although the marginal shelf in *R. niphada* varies from narrow to wide, the shelf, even when as wide as in *R. squiresi,* is not as prominent due to the less steeply sloping distal edges of the septa.

Etymology.—The species name is derived from the Greek *niphados* = snowflake, and refers to the intricate design of the oral surface of the corallum. Gender: feminine.

Discussion.—*Rhombopsammia niphada* is distinguished by its 144 septa, which poses the most perplexing problem in its generic identity with *R. squiresi,* which has 96. In all other micrabaciid corals studied or described in the literature, the number of septa, except in an occasional deviant individual, has been so consistent within a genus as to suggest that it is a valid generic characteristic. But in *Rhombopsammia* a sufficient number of specimens in each species was examined to indicate that the difference in number of septa between the two species is not due to random deviation. *Within* each species the number of septa is consistent. The structural and microstructural similarities between *R. niphada* and *R. squiresi* argue convincingly for their generic identity in spite of the difference in septal number. Perhaps too much emphasis should not be placed on that character as a generic characteristic.

Interestingly, 144 septa are also found in the lectotype of *Letepsammia formosissima,* though all other specimens of that species studied had 120. Even if the lectotype of *L. formosissima* should prove to be a deviant individual, the occurrence of this unusual number of septa in both it and all specimens of *R. niphada* may be more than coincidental. When the similarities of *R. niphada* with *R. squiresi* and with species of *Letepsammia* are thoroughly considered, the strong suggestion arises that *R. niphada* may be an intermediate between *Rhombopsammia* and *Letepsammia.*

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