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Charles D. and Mary Vaux Walcott Research Fund

MORPHOLOGY AND SYSTEMATICS OF THE BRYOZOAN GENUS *METRARABDOTOS*

(WITH EIGHTEEN PLATES)

BY
ALAN H. CHEETHAM
U. S. NATIONAL MUSEUM
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ABSTRACT

THE CHEILOSTOME BRYOZOAN genus *Metrarabdotos* is represented in modern marine epifaunas by two partially sympatric species, distributed in the tropical Panamic, Caribbean, and West African biogeographic provinces. The morphology and taxonomy of these species provide a basis for interpreting the systematics of their fossil congeners, which include at least eleven species having allopatric distributions in areas bordering the Atlantic, the Gulf of Mexico, the Caribbean, and the Mediterranean in deposits as old as late Eocene.

Detailed collections from the American Tertiary, less detailed Recent and Eurafrican Tertiary material, and museum specimens have been studied to clarify external and internal morphologic features and their taxonomic distribution through the genus. Extensive overlap in single morphologic characters among species has necessitated use of biometric techniques, including variation, correlation, and principal components analyses, to evaluate quantitative characters and numerical and clustering procedures to compare samples. The five resulting phenetic groups, based on twenty-three characters expressed in weighted codes, were projected into a time-stratigraphic framework. Inferred phylogenetic relationships within and among groups provided a basis for taxonomic interpretation. The morphologic overlap among groups resulted from convergent and parallel trends in size, position, orientation, and differentiation of avicularia and in denticulation of the secondary orifice in the American and Eurafrican stocks which probably were isolated through most of their history.

The complex of fossil and Recent material studied includes four polytypic species, divided into twelve subspecies, and seven monotypic species here assigned to the following subgenera: *M.* (*Metrarabdotos*) Canu, upper Miocene-Pleistocene (type species: *Eschara monilifera* Milne Edwards); *M.* (*Porometra*), n. subgen., middle Miocene-Pliocene (type species: *Trigonopora helvetica* Roger and Buge); *M.* (*Rhabdotometra*), n. subgen., upper Eocene-lower Miocene (type species: *Escharella micropora* Gabb and Horn); *M.* (*Biavicularium*), n. subgen., lower Miocene-Recent (type species: *Smittia tenuis* Busk); *M.* (*Uniavicularium*), n. subgen., upper Miocene-Recent (type species: *Metrarabdotos unguiculatum* Canu and

Bassler). Another eight nominal species or subspecies, recognizable as *Metrarabdotos,* are insufficiently preserved to assign to subgenera on the basis of observed morphology and stratigraphic position.

Comparison with morphologically similar genera, e.g., *Schizostomella,* and with phylogenetically related genera, e.g., *Escharoides* and *Trigonopora,* required elevation of the subfamily Metrarabdotosinae Vigneaux to family rank, erection of the superfamily Umbonulacea Canu to receive Metrarabdotosidae, Umbonulidae, and Exochellidae, and removal of the Adeonidae from their conventional proximity to *Metrarabdotos* and its allies.

The following new species and subspecies are described here: *M.* (*R.*) *micropora floridanum,* n. subsp., Vicksburg of Florida and Georgia; *M.* (*R.*) *micropora butlerae,* n. subsp., Tampa of Florida; *M.* (*R.*) *vigneauxi,* n. sp., Stampian of France; *M.* (*B.*) *chipolanum,* n. sp., Alum Bluff of Florida; *M.* (*U.*) *kugleri,* n. sp., Miocene of Trinidad; *M.* (*U.*) *unguiculatum cookae,* n. subsp., Recent of Ghana; *M.* (*P.*) *helveticum canariense,* n. subsp., Miocene of the Canary Islands and Pliocene of Rhodes; *M.* (*P.*) *helveticum thomasi,* n. subsp., Miocene or Pliocene of Sierra Leone; and *M.* (*P.*) *maleckii,* Leithakalk of Austria, Czechoslovakia, and Poland.

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MORPHOLOGY AND SYSTEMATICS OF THE BRYOZOAN GENUS *METRARABDOTOS*

By ALAN H. CHEETHAM

U. S. National Museum
Smithsonian Institution

(With Eighteen Plates)

INTRODUCTION

Among fossils encountered most frequently in marine sediments of Tertiary age on both sides of the Atlantic are cheilostome Bryozoa belonging to the genus *Metrarabdotos* Canu, 1914. Where they occur, especially in such formations as the Red Bluff and Marianna (upper Eocene and Oligocene) of the southeastern United States, the Faluns (Miocene and Pliocene) of western France, and the Coralline Crag (Pliocene) of eastern England, fossil representatives of the genus are usually the dominant component of the epifauna. Their sturdy, erect, arborescent zoaria served as substrate for annelids, hydroids, barnacles, oysters, and other bryozoans in habitats where large detritus suitable for encrustation was at a premium. This complex of fossil species includes at least seven monotypic and three polytypic species here assigned to five subgenera.

In addition, *Metrarabdotos* is represented in modern seas by two species. *M.* (*Biavicularium*) *tenue* (Busk, 1884) is presently monotypic and restricted to the tropical west Atlantic from Puerto Rico to central Brazil. In zoarial architecture and many aspects of zooecial structure, it resembles its fossil congeners more than it does the other Recent species; presumably its ecologic requirements are more like those of fossil species also. The other surviving species *M.* (*Uniavicularium*) *unguiculatum* Canu and Bassler, 1928, is polytypic. The nominate subspecies is in part sympatric with *M.* (*B.*) *tenue,* and extends from the northeastern Gulf of Mexico to Brazil. *M.* (*U.*) *u. cookae,* n. subsp., occurs in the tropical east Atlantic from the Cape Verde Islands to the Gulf of Guinea. *M.* (*U.*) *u. pacificum* (Osburn, 1952) known from a single occurrence off Panama in the tropical east Pacific, is the only extra-Atlantic representative of the genus, living or fossil. *M.* (*U.*) *unguiculatum* differs from all other species of *Metrarabdotos* in substrate tolerance; its encrusting zoaria require a coarse-grained substrate at least for initial growth. This niche differentiation has made possible the overlap in geographic ranges of the two surviving species. Fossil species, as interpreted in this paper, all have allopatric distributions in keeping with their similar zoarial architecture and, presumably, their single ecologic niche. Buge and Galopim de Carvalho (1963; 1964) and Galopim de Carvalho (1966), using a somewhat different taxonomic approach, have listed occurrences, e.g., Miocene at Cléré-les-Pins, France, and Pliocene at Salir do Porto, Portugal, with as many as three sympatric nominal species each.

Metrarabdotos is a particularly tantalizing subject for systematic investigation because it is a close-knit group of species which, though separated from other genera by large, multidimensional gaps, are themselves intricately intertwined. The object of the present investigation is to fit the systematics of the genus to inferred phylogenetic relationships. This objective has required detailed study of morphology, both external and internal, to clarify the geometric and growth relationships of zooecial walls (especially that on the frontal side), of oral structures, of brooding individuals, and of avicularia. Many of the morphologic and taxonomic interpretations made here consequently differ appreciably from those made by previous workers, including Buge and Galopim de Carvalho (1963), who restudied many of the same species. Quantitative and other numerical methods were required to evaluate characters and their distribution in population samples of all species for which material was accessible. Sample groupings were then projected into a time-morphologic grid so their phylogenetic relationships could be determined.

American species of the genus have been less fully worked out than their European and African counterparts; therefore, the American species have been made the focal point of the present study. The nominal species *M. vicksburgicum* (Roger and Buge), *M. grande* Canu and Bassler, *M. colligatum* Canu and Bassler, *M. lacrymosum* Canu and Bassler, *M. auriculatum* Canu and Bassler, *M. tuberosum*

Canu and Bassler, *M. unguiculatum* Canu and Bassler, *M. pacificum* (Osburn) have been investigated here in detail. Some Eurafrican species, such as *M. helveticum* (Roger and Buge) and *M. canui* Buge and Galopim de Carvalho (in part), have received approximately the same attention here.

Five subgenera have been established through phylogenetic interpretation of numerical-morphologic (phenetic) groupings.

Comparison of this assemblage with similar genera, such as *Schizostomella* Canu and Bassler, and related genera, such as *Escharoides* Milne Edwards and *Trigonopora* Maplestone, has indicated the necessity for revisions at the generic and suprageneric levels. The subfamily Metrarabdotosinae Vigneaux is elevated here to familial rank and the superfamily Umbonulacea Canu is established for its reception.

The material on which this investigation was undertaken includes stratigraphic collections from the Gulf Coast and England; specimens studied at their repositories in the U. S. National Museum and the British Museum (Natural History); specimens studied on loan from the Allan Hancock Foundation, Los Angeles; the British Museum (Natural History); the Academy of Natural Sciences of Philadelphia; the Royal Institute of Natural Sciences, Brussels; the Florida Geological Survey, Tallahassee; the Seminario Conciliar, Barcelona; the University of Bordeaux; the Geologisches Staatsinstitut, Hamburg; and specimens obtained by exchange with Dr. H. V. Howe, Baton Rouge; Professor M. Vigneaux, Bordeaux; Professor J. Malecki, Krakow; Dr. H. D. Kugler, Basel; Dr. S. Schager, Stockholm; Dr. P. A. Sandberg, Urbana; and the late Dr. H. D. Thomas, London. Their help is gratefully acknowledged.

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I owe a special debt of gratitude to Dr. Anna B. Hastings and the late Dr. H. Dighton Thomas for valuable advice and suggestions about initiating this study; to Dr. John Imbrie, Brown University, to Dr. G. P. Larwood, University of Durham, and to Dr. R. S. Boardman and Dr. M. A. Buzas, Smithsonian Institution, for reading the manuscript and offering suggestions for its improvement; and to Dr. R. Lagaaij, Shell Exploration and Production Laboratory, Miss P. L. Cook, British Museum, and Dr. Sten Schager, University of Stockholm, for providing much helpful discussion of various aspects of the investigation.

Dr. Porter M. Kier, Smithsonian Institution, and Dr. Joseph E. Hazel, U. S. Geological Survey, made many useful suggestions concerning photographic techniques.

Computations were made at the Smithsonian Institution, the University of Kansas, and the University of Stockholm. The courtesy of Dr. R. R. Sokal, who permitted use of the NTSYS (Numerical Taxonomy System) programs at Kansas, the Swedish Board for Computing Machinery and Mrs. Nan Strååt of the Stockholm Center, who provided multivariate calculations, and W. R. Wheeler and Henry Feldman of the Smithsonian Information Systems Division, who developed CLUSTR (Clustering by correlations) and CLUSTD (Clustering by distances) programs in BASIC (Beginners All-purpose Symbolic Input Code), is gratefully acknowledged.

Thin sections were prepared by Lorenzo Ford. The figures were drawn by Mrs. Martha Deboo, Department of Geology, Louisiana State University, and L. B. Isham, Smithsonian Institution.

Financial support was provided by research grants from the Smithsonian Research Foundation, Louisiana State University, and the University of Stockholm.

MORPHOLOGY

ZOARIAL CHARACTERS

Form and mode of growth.—All species of *Metrarabdotos* possess robust zoaria; both unilaminate and bilaminate forms occur among Recent species; known fossil colonies are all bilaminate.

Unilaminate colonies are at least initially broad, pavement-like encrustations (pl. 10, fig. 1), but they usually rise distally in irregular, branching, hollow tubes. Tubular offshoots emanate from cumulate zooecia or develop from the coalescence of different growing edges of the colony (pl. 10, fig. 2).

Bilaminate zoaria originate in a small encrusting base and usually develop an erect, narrow, subcylindrical stem (pl. 15, fig. 2) which expands into narrow (pl. 2, fig. 3; pl. 9, fig. 1), broad (pl. 5, fig. 1), or foliaceous (pl. 15, fig. 1) fronds. The growing edge of the colony is at the distal tips of the branches; frontal budding has not been found in zoaria of this form. Where different growing edges come into contact, they do not coalesce; either growth ceases in one branch or the two branches grow away from each other producing a pseudoanastomosing pattern (pl. 15, fig. 1).

The pattern of development of zooecia in the proximal part of the zoarium of *Metrarabdotos* has not been described heretofore, at least in part because the erect form of most species does not expose the ancestrula and early formed zooecia. Encrusting zoaria of *M.* (*U.*) *unguiculatum,* however, are amenable to astogenetic observation, and a single specimen preserving this region (pl. 10, fig. 1) was available for this study.

The ancestrula, broken frontally on the specimen studied, has a distal oral shelf and, therefore, probably had oral and frontal structure similar to that of later formed zooecia. Development of zooecia from the ancestrula (Figure 1) follows the roughly bilaterally symmetrical pattern of multiserial growth characteristic of many encrusting Cheilostomata (Harmer, 1931, pp. 122-124; Cheetham, 1954, pp. 180-182; Medd, 1966). Three zooecia, displaying fully developed frontal and oral structure but lacking avicularia, budded distally and distolaterally from the ancestrula. This triadic grouping is evident as late as the fifth generation, but limited space and different growth rates in different areas of the zoarium imposed predominantly linear, bifurcating patterns in the more distal parts. Fragments of large, unilaminate zoaria are, therefore, more likely to display linear than quincuncial arrangements of zooecia.

Unlike most encrusting cheilostomes (Medd, 1966, p. 14) in which periancestrular budding usually results in encirclement of the ancestrula by the second to fourth generation, the specimen of *M.* (*U.*) *unguiculatum* grew hemiperipherally all the way through the six generations represented despite availability of seemingly suitable substrate. The strong vector of growth distal to the ancestrula in this species is related perhaps to the fact that it descended from erect ancestors with essentially unidirectional growth.

Avicularia appear on some zooecia as early as the second generation, and even on much later zooecia on other specimens they are not invariably present. The developmental stage at which gonoecia first appear cannot be determined from the material at hand; it cannot be assumed, just because gonoecia are absent from the specimen studied, to be invariably the seventh or a later generation.

Astogenetic groups of zooecia are more difficult to define in *M.*

(U.) unguiculatum than in the Cretaceous membranimorph cheilostomes analyzed by Medd (1966). Four groups can be determined from zooecial length and width and presence or absence of avicularia (Figure 2): (1) the *ancestrula* is both shorter and narrower than succeeding zooecia and lacks an avicularium; (2) *early zooecia* are distinctly longer but only slightly wider than the ancestrula and also lack avicularia; (3) *transitional zooecia* are generally slightly longer and wider than the early zooecia and commonly have avicularia; and (4) *late zooecia* are generally markedly longer and wider than the transitional zooecia and almost all have avicularia. Medd's (1966, pp. 14, 15) use of young and adult for zooecia of groups 2 and 4 is not followed here because of possible confusion with ontogenetic stages (discussed below).

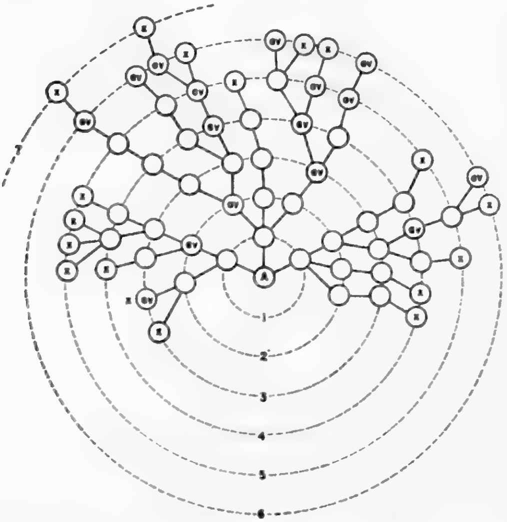

FIGURE 1.—Initial zoarial development of *Metrarabdotos (Uniavicularium) unguiculatum unguiculatum* (USNM (Z) 11940; illustrated on pl. 10, fig. 1). Terminology and representation follow Medd's (1966) method A with slight modification. Angles between lines of budding approximate those on zoarium; positions of zooecia are diagrammatic. *A,* ancestrula; *1-7,* zooecial generations; *X,* terminal zooecium; *av,* zooecium having avicularium.

Zooecial arrangement and intercommunication.—In later developmental stages, both types of zoarium display zooecia in regular longitudinal rows with those in adjacent rows alternating in position

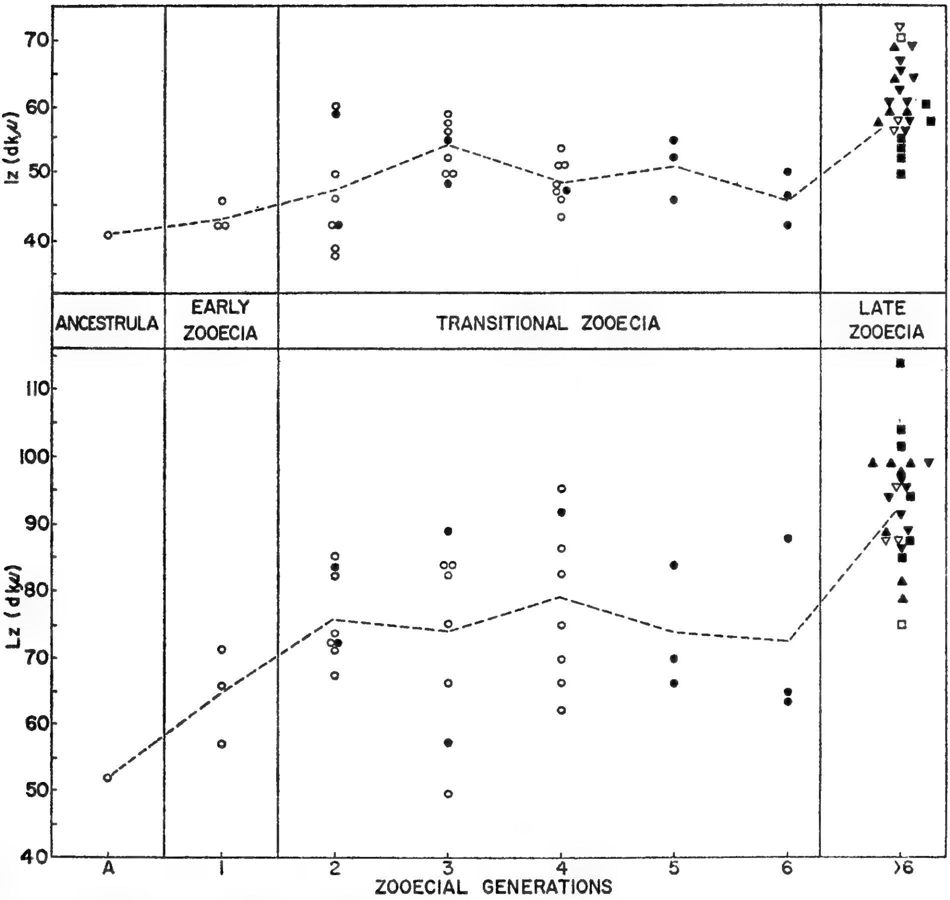

FIGURE 2.—Variation in zooecial length and width and occurrence of avicularia in early zoarial development of *Metrarabdotos* (*Uniavicularium*) *unguiculatum unguiculatum* (composite of four specimens). *Lz,* zooecial length; *lz,* zooecial width; *circles,* specimen USNM (Z) 11940; *squares,* specimen USNM (Z) 8571; *triangles,* specimen USNM (Z) 11941; *inverted triangles,* specimen USNM (Z) 7556; *open symbols,* avicularia lacking; *solid symbols,* avicularia present. Dashed lines connect mean values.

(e.g., pl. 11, figs. 1-4; pl. 2, figs. 2-4); there is also a tendency to alternation in the opposing laminae of erect colonies (pl. 17, fig. 7). Each zooecium thus shares its distal wall with the proximal portion of the next zooecium in the row. Full basal and lateral walls are present in each zooecium of both unilaminate and bilaminate colonies.

This regular pattern is interrupted in three situations: (1) around gonoecia where because of the very large ovisac the distal and distolateral zooecia are distorted (e.g., pl. 1, fig. 3); (2) at points of increase in the number of zooecial rows where the daughter zooecia are distorted and out of phase with those in adjacent rows (e.g., pl. 4, fig. 4); and (3) along the lateral margins of bilaminate zoaria where the marginal zooecia may be broadened (pl. 8, figs. 3-4) or otherwise modified (pl. 7, fig. 3).

Adjacent zooecia communicate through simple pores in a single line about midway between basal and frontal margins of the vertical walls; two or three occur in the distal wall and about ten are placed in each lateral wall (pl. 10, fig. 3; pl. 17, figs. 2, 7). Pores also occur in the vertical walls of the distal half of a gonoecium connecting it to the distally and distolaterally adjacent zooecia. In Recent specimens communication pores are occupied by uniporous chitinous rosette plates.

The statement by Canu and Bassler (1928a, p. 129) that the zooecia of *M.* (*U.*) *unguiculatum* communicate through parietal dietellae has not been substantiated by the present study. Buge (1966, p. 40) included parietal dietellae in his diagnosis of the genus.

Increase in the number of zooecial rows occurs where the mother zooecium gives rise to two daughters, a distal one continuing the old row and a distolateral one initiating a new row. Where the primoserial zooecium occupies a more distal position on the axillary zooecium (pl. 6, fig. 1), the new row appears to arise by bifurcation; where the primoserial zooecium is less distal on the axillary zooecium (pl. 12, fig. 3), the new row appears to arise by intercalation. The difference between the two patterns is only superficial, however.

ZOOECIAL CHARACTERS

Form and mode of growth.—The zooecia of *Metrarabdotos* are box-shaped, irregularly rectangular to claviform in frontal aspect, and uniformly thin walled except frontally (pl. 17, figs. 6-7).

Zooecial ontogeny was interpreted in this study from the growing edges of Recent colonies of *M.* (*U.*) *unguiculatum unguiculatum* (pl. 10, fig. 3) and *M.* (*B.*) *tenue tenue* (pl. 9, fig. 3) and from thin sections of fossil and Recent specimens (pls. 17-18).

New buds are wedge shaped. The basal wall calcifies first, in increments separated by transverse growth lines. Lateral walls follow the distally advancing basal wall in the form of distally pointing triangles like those of Cretaceous membranimorphs (Medd, 1966, p. 16). The lateral walls become rectangular when the distal wall is complete, so the zooecium at this stage has the form of a box with a membrane top, distinguishable from a simple anascan only at its proximal margin. There, a new membranous lobe advances distally along a concave front over the frontal membrane. The intervening space is the ascus (Figure 3). Calcification proceeds just beneath the epifrontal membrane to form the frontal wall, which consists initially of a thin, convex shield continuous with and indistinguishable in structure from the basal, lateral, and distal walls (pl. 10, fig. 3; pl. 17, fig. 5; pl. 18, fig. 2). This primary frontal wall (olocyst, in part, of Canu and Bassler, 1920, p. 47) extends from the proximal margin of the zooecium to the distal end, where it forms the proximal and lateral boundaries of the apparent orifice (discussed below). The primary wall is smooth and perforated only on its proximal and lateral margins where pores bearing uniporous rosette plates (pl. 10, fig. 3) are placed in areolae separated by buttresses and lined and covered with epifrontal membrane. The pores permit communication between the epifrontal membrane and endozooecial epithelium (Figure 3) that is similar to interzooecial connection. The epifrontal membrane is continuous across zooecial boundaries and open only at the orifices (pl. 10, fig. 4).

With completion of the primary frontal wall, a superficial layer (pleurocyst of Canu and Bassler, 1920, p. 50) begins to calcify beneath the epifrontal membrane on a concave, distally advancing front. This layer differs from the primary one in that it originates in clumps of granules in the areolae and on the intervening buttresses (pl. 10, fig. 3; pl. 18, figs. 1-2), spreads as a distally thinning lamella, and in species having bilaminate zoaria becomes multilamellar (pl. 17, figs. 2-3; Figure 3), each successive lamella overlapping earlier ones distally. As the superficial layer thickens, the lateral walls, which form prominent zooecial boundaries in frontal aspect (e.g., pl. 1, fig. 2; pl. 12, fig. 3), may be topped so the boundaries are erased (pl. 8, figs. 2-3), and new, false ones may develop (pl. 8, fig. 1; Marcus, 1955, pl. 7, fig. 77). In zooecia near the proximal ends of large, bilaminate zoaria, the superficial layer is enormously thick with outer lamellae sealing the areolae and even the orifice (pl. 17, figs. 2-3; pl. 15, fig. 1).

The two-layer character of the frontal wall is preserved in some fossils (pl. 17, figs. 2-3) and obliterated in others (pl. 17, figs. 1, 4).

It seems probable that the basal, lateral, and distal walls and the primary layer of the frontal wall are secreted by a distally moving wave of cells similar to those observed in *Bugula avicularia* (Linné)

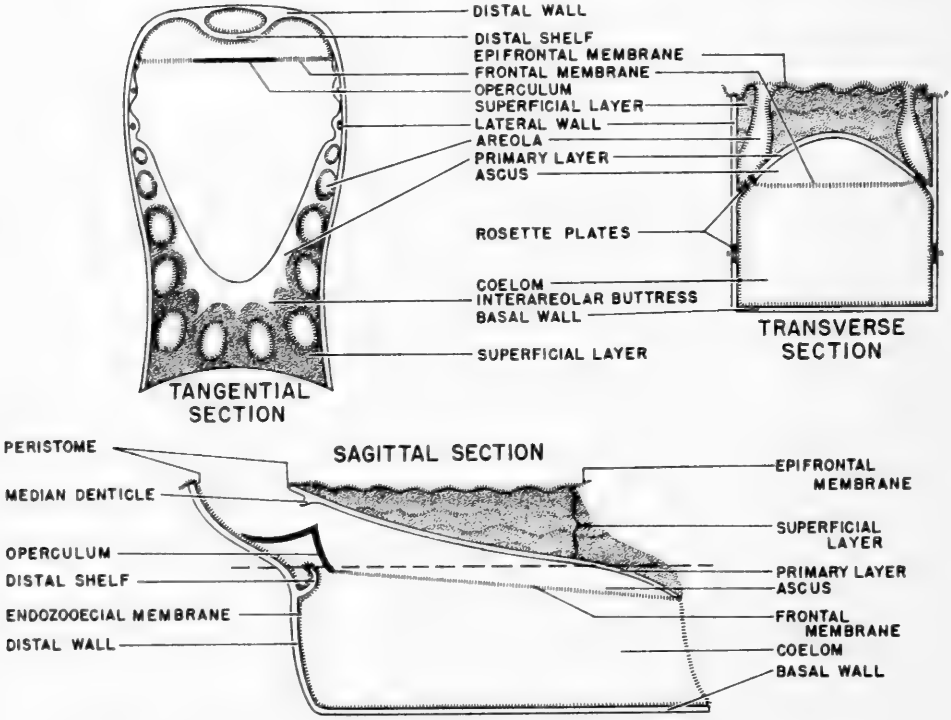

FIGURE 3.—Idealized sections through a fully developed zooecium, moderately thickened frontally, showing relationships of skeletal and epithelial tissues. The diagrams are based on thin sections of skeletal tissue and on dissections of dried specimens in which membranes, muscles, and polypides are preserved. Polypides and muscles have been omitted to emphasize skeleton-membrane relationships. Frontal and oral structures differ slightly from those shown by Marcus (1955, pl. 7, fig. 73), especially in the operculum and associated structures. Membrane is shown as broken lines; chitinous structures are in solid black; calcareous structures of primary layer are outlined, and the superficial calcareous layer of the frontal wall is stippled. Except for the coarse lamellae of the superficial layer of the frontal wall, skeletal microstructure is not indicated. The dashed line in the sagittal section is the plane of the tangential section.

by Schneider (1963, pp. 359-363), whereas the superficial layer of the frontal wall is produced by the general surface of the epifrontal membrane, which retains its secretory power throughout ontogeny. This method of growth, permitting late ontogenetic thickening of the outer wall accompanied by sealing of areolae and orifices, has functional importance in the proximal part of erect colonies in which the architecture of the zoarium itself must provide the support afforded by the substrate to an encrusting form. In the latter, however, mural thickening might require deleterious diversion of growth effort from the initial surge required to develop relatively larger zooecia having more covering power in the competition for space. Therefore, evolution of the encrusting form from the erect one in *Metrarabdotos* may have required a paedomorphic emphasis on formation of the primary walls at the expense of the superficial layer of the frontal wall.

The epifrontal membrane thus bears primary responsibility for the ontogenetic changes in the frontal aspect of the zooecium from anasciform to heavily shielded. Unfortunately, the microstructure of the membrane was not discernible in the dried material available for study. Because the changes come about through accretion of the frontal wall in a frontal direction, the membrane must enclose some structural complexity between its outer covering cuticle and its secretory epithelium. Mesodermal or perhaps even coelomic extensions may continue from the areolae over the calcified frontal wall. Continued calcification, even after the connections of the epifrontal membrane with the epithelium lining the zooecium beneath it have been severed by the sealing of areolae, suggests that in late ontogenetic stages these extensions are continuous with those of adjacent zooids. The membrane, which begins as a zooidal structure, becomes a continuous zoarial cover.

Oral structure.—The orifice in Cheilostomata, strictly speaking, is the opening filled with and, therefore, conforming in shape and size to the operculum or opercular valve. The operculum is derived from the original frontal membrane and remains connected to the homologue of that membrane even in those cheilostomes, such as *Metrarabdotos,* in which the frontal surface is calcified. The anasciform membrane of *Metrarabdotos* forms the floor of the ascus, and at its distal margin the weakly chitinized, quadripartite, poorly defined operculum (Marcus, 1955, p. 305, pl. 7, figs. 73, 76; Cook, 1967, p. 348) is attached to it. Therefore, the apparent orifice on the surface of the calcified frontal wall is not the primary orifice; the assumption that it is has led to confusing interpretations of the hinging apparatus for the operculum. Inasmuch as the operculum of *Metrarabdotos* is connected only to membrane proximally, there is no skeletal structure for its hingement.

Canu (1914, p. 472) ascribed a medially notched hinge line with a central tooth to the genus. Absence of the median tooth ("pseudolyrule") in fossil material has been attributed to poor preservation (Canu and Bassler, 1920, p. 536; Canu and Lecointre, 1928, p. 54).

Canu and Bassler (1928a, p. 129) described part of the operculum in one of their preparations (1928a, pl. 23, fig. 9) as "a kind of lyrule." Lagaaij (1952, p. 122), Buge (1957, p. 298; 1966, p. 40), and Brown (1958, p. 64) have concentrated on the median notch in their comparison of the oral structure of *Metrarabdotos* with that of *Schizoporella.* The primary orifice in all species of *Metrarabdotos* can best be regarded as the simple oval above which a variable number of denticles are developed in the proximal part of the peristomial vestibule.

The most characteristic oral structure in *Metrarabdotos,* not mentioned in previous descriptions, is here termed the distal oral shelf. This feature (Figure 3; pl. 17, figs. 6-7; pl. 18, figs. 1-2) projects from the distal wall just below opercular level. Its lateral margins serve as origin for the opercular occlusor muscles, which in the dried material available have pulled the operculum toward the convex proximal margin of the shelf. A similar, but less developed, feature in *Escharoides* Milne Edwards has been called a vestibular arch by Levinsen (1909, p. 317); Osburn (1952, p. 347) used this term in a different sense. The functional significance of the shelf and the quadripartite operculum is unknown.

The proximal peristomial denticles (Figure 4) vary in number and position, in some species even in the same zoarium. The simplest pattern is shallow unidenticulate in which a single, median, bluntly tapering tooth, in some zooecia partly overlapped by a frontal mucro (e.g., pl. 1, figs. 2-4), is placed at the lip of the secondary orifice. The species having this type of denticulation, *M.* (*R.*) *micropora* subspp., displays short, only slightly notched peristomes. In all other species longer peristomes enclose the denticles and hide them partly or wholly from frontal view.

The deep-unidenticulate pattern of *M.* (*R.*) *vigneauxi* and *M.* (*B.*) *chipolanum* is the result of peristomial elongation without multiplication of denticles. The tooth may be simple or bifid. A slightly more complex pattern is tridenticulate in which lateral denticles have been added without suppression of the median one. *M.* (*B.*) *tenue colligatum, M.* (*B.*) *lacrymosum,* and *M.* (*U.*) *kugleri* display this arrangement.

M. (*P.*) *helveticum* subspp. and *M.* (*P.*) *maleckii* have transitional structure; the same zoarium yields tridenticulate and bidenticulate orifices. Simple bidenticulate orifices, in which lateral denticles have been emphasized at the expense of the median one, characterize *M.* (*M.*) *nysti, M.* (*M.*) *moniliferum, M.* (*B.*) *tenue auriculatum, M.* (*B.*) *t. tenue,* and *M.* (*U.*) *unguiculatum pacificum.* More complex

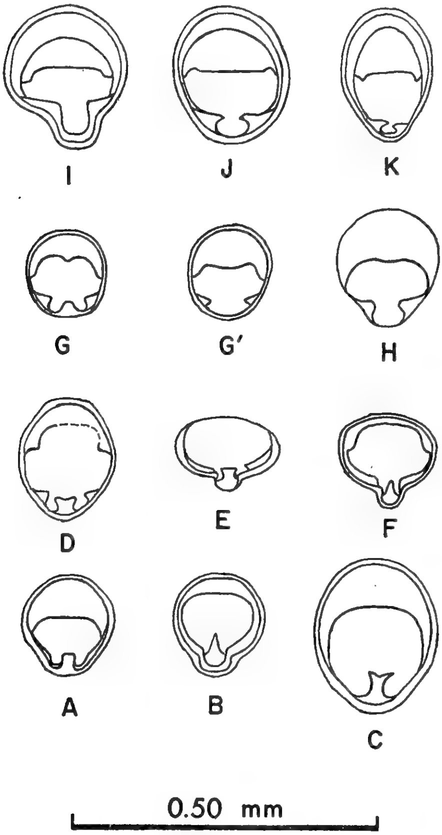

FIGURE 4.—Oral structure in *Metrarabdotos* from Eocene-Oligocene (**A**, **B**) through Miocene (**D-G′**) and Pliocene (**H**) to Recent (**I-K**). **A**, shallow-unidenticulate with simple distal shelf (*M.* (*R.*) *micropora micropora*, USNM 650789). **B**, deep-unidenticulate with simple tooth and simple distal shelf (*M.* (*R.*) *vigneauxi*, USNM 650834). **C**, deep-unidenticulate with bifid tooth and simple distal shelf (*M.* (*B.*) *chipolanum*, USNM 650837). **D**, tridenticulate with bifid median tooth and pouch-like distal shelf (*M.* (*B.*) *tenue colligatum*, USNM 650844); **E**, tridenticulate with flattened median tooth (*M.* (*B.*) *lacrymosum*, USNM 650871); **F**, tridenticulate with pointed median tooth and pouch-like distal shelf (*M.* (*U.*) *kugleri*, USNM 650873); **G**, **G′**, tridenticulate-bidenticulate transitional with pouch-like distal shelf (*M.* (*P.*) *helveticum thomasi*, USNM 650886); **H**, bidenticulate, simple, with blunt teeth and pouch-like distal shelf (*M.* (*M.*) *moniliferum*, BM(NH) D.35145); **I**, bidenticulate, lamellar, with pouch-like distal shelf (*M.* (*U.*) *unguiculatum unguiculatum*, USNM (Z) 11945); **J**, **K**, bidenticulate, simple, with teeth nearly meeting and pouch-like distal shelf (*M.* (*B.*) *tenue auriculatum*, USNM 650862; *M.* (*B.*) *tenue tenue*, USNM (Z) 9759).

derivatives of the bidenticulate pattern include the lamellar bidenticulate orifice of *M.* (*U.*) *u. unguiculatum,* in which the paired denticles continue as ridges up the elongate peristome, and the repeated bidenticulate pattern of *M.* (*U.*) *u. cookae,* in which a second pair of lateral denticles forms above the first pair in the elongate peristome.

The succession of changes in denticulation and its relation to peristomial elongation suggest that the denticles are so placed as to check the free margin of the weak operculum as it opens for eversion of the tentacle crown. They would thus act as a safety device to prevent the operculum from sealing the entrance to the ascus. In this role bidenticulate and tridenticulate patterns would offer more stable support, and the bidenticulate one does so without interposing so many obstacles to the flow of water to the ascus.

HETEROZOOECIAL CHARACTERS

Avicularian structure and distribution.—Avicularia are present in all species of *Metrarabdotos* studied. They may fail to develop, however, on some zooecia or even over a large area of a zoarium, or they may be overgrown during subsequent thickening of the frontal wall, or they may be difficult to observe because of poor preservation. Type specimens of the nominal species *M. grande* and *M. tarraconense,* both of which have been described as lacking avicularia, were found in the present study to possess them. The avicularia in all species are adventitious, developed from the most distal areola or group of areolae on one or both sides of the zooecium (pl. 10, fig. 3; pl. 18, fig. 1) as an extension and elaboration of the primary layer of the frontal wall. The avicularian chamber, which thus rests on the primary frontal wall and is immersed in the superficial layer of that wall, is usually elongate with its rostral end riding up on the peristome to a sharp or subspatulate tip near the secondary orifice. The frontal opening of the chamber is divided near its antirostral end by a transverse bar developed from coalescence of a pair of denticles (pl. 10, fig. 3). A cryptocyst-like lamina closes part or nearly all of the antirostral opening (pl. 8, figs. 3-4; pl. 10, fig. 3), and another forms a narrow rostral shelf.

The avicularium is covered entirely by epifrontal membrane (pl. 9, fig. 2; pl. 10, fig. 4). The mandible is attached to the membrane on the transverse bar; abductor muscles insert on it from the antirostral side and adductor muscles from the rostral side. The mandible closes on the membrane on the rostral side which thus forms a rostral palate conforming in size and shape to the mandible; abducted, it lies on the frontal surface of the distally or laterally adjacent zooecium. In Recent species the mandible is more heavily chitinized than the operculum, and it may be either single pointed (pl. 10, fig. 4) or bilobed (pl. 8, fig. 3; pl. 9, fig. 2). The outer lobe of the bilobed mandible occludes with the rostral palate and the inner lobe with the inside of the zooecial peristome. The axis of the mandible and of the rostrum is usually straight, rarely curved (Figure 5).

Avicularia are monomorphic in the subgenus *M.* (*Uniavicularium*) and dimorphic in all other subgenera of *Metrarabdotos*. Despite its widespread occurrence in the genus, avicularian dimorphism has been only rarely noted (Marcus, 1955, p. 305; Buge, 1957, p. 303; Buge and Galopim de Carvalho, 1963, pp. 151, 152, 166, 172; "hypertrophie avicularienne"). "Ordinary avicularia," as the term is used here, are those on zooecia (and commonly gonoecia) over the zoarium at large. They are present in all species and are the only avicularia present in monomorphic species. "Special avicularia," as the term is used here, are those which occur on zooecia at special locations in the zoarium and which have a distinctly greater length than the ordinary ones in the same zoarium. Thus, they are present only in dimorphic species.

Ordinary avicularia (Figure 5) may be large or small, single or paired, and in Recent species have a single-lobed mandible that occludes with a straight or curved, pointed rostrum. In addition to variation in size (discussed below), they display diversity in distribution, position, and orientation, on the basis of which the following types are recognizable.

1. Paired, laterally or slightly distally or proximally placed, proximally and usually inwardly directed: most *M.* (*R.*) *micropora micropora, M.* (*R.*) *micropora floridanum, M.* (*R.*) *vigneauxi, M.* (*B.*) *chipolanum, M.* (*P.*) *helveticum* subspp., *M.* (*P.*) *maleckii,* few *M.* (*B.*) *tenue auriculatum.*
2. Paired, laterally placed, transversely inwardly directed: *M.* (*R.*) *micropora butlerae.*
3. Paired, distally placed, proximally outwardly directed: few *M.* (*R.*) *micropora micropora,* most *M.* (*B.*) *tenue* subspp.
4. Paired, proximally placed, proximally inwardly directed: *M.* (*M.*) *moniliferum.*
5. Paired, proximally placed, distally directed: *M.* (*B.*) *lacrymosum, M.* (*M.*) *nysti.*
6. Usually single, laterally placed, proximally inwardly directed; *M.* (*U.*) *kugleri.*

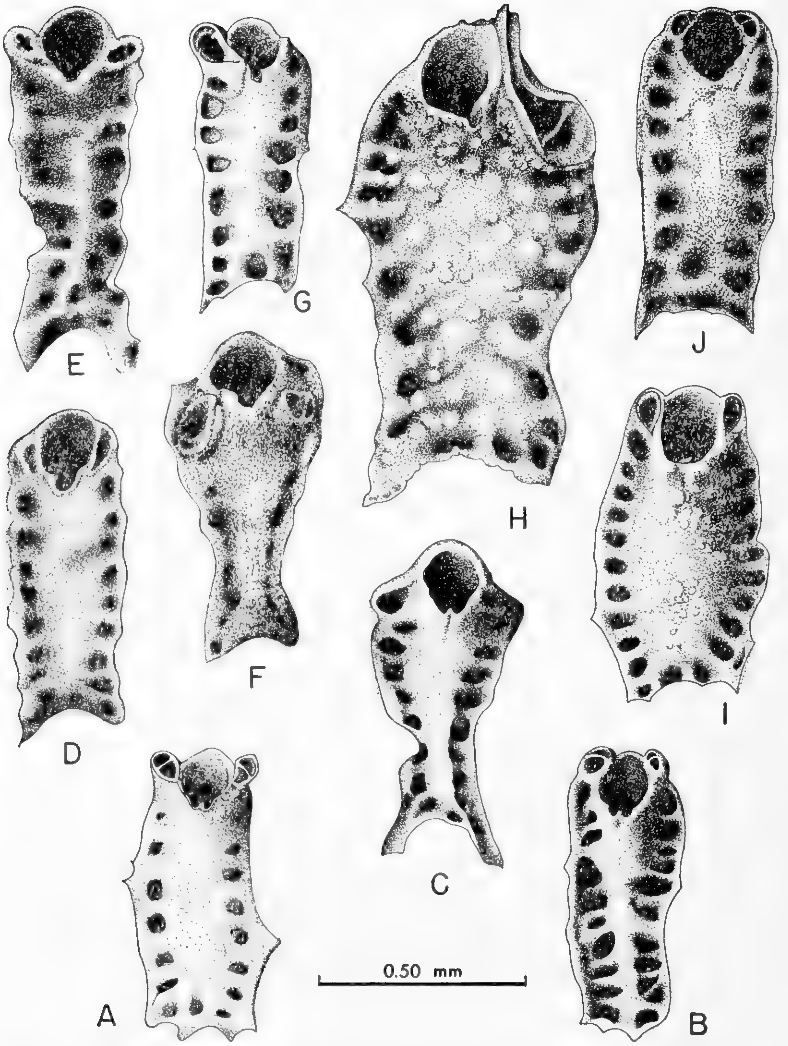

FIGURE 5.—Distribution, position, and orientation of ordinary avicularia in *Metrarabdotos* from Eocene-Oligocene (**A, B**) through Miocene (**C, D, G, I, J**) and Pliocene (**E, F**) to Recent (**H**). **A,** paired, distal, proximally inwardly directed (*M.* (*R.*) *micropora micropora,* USNM 650789); **B,** paired, distal, proximally outwardly directed (*M.* (*R.*) *micropora micropora,* USNM 650820); **C,** paired, lateral, inwardly directed (*M.* (*R.*) *micropora butlerae,* USNM 650822); **D,** paired, lateral, proximally directed (*M.* (*P.*) *helveticum canariense,* BM(NH) D.9292); **E,** paired, proximal, proximally inwardly directed (*M.* (*M.*) *moniliferum,* BM(NH) D. 35145); **F,** paired, proximal, distally directed (*M.* (*B.*) *lacrymosum,* USNM 650871); **G,** single, lateral, proximally inwardly directed (*M.* (*U.*) *kugleri,* USNM 650872); **H,** single, proximal, distally directed (*M.* (*U.*) *unguiculatum unguiculatum,* USNM (Z) 11945); **I,** paired, distal, proximally directed (*M.* (*B.*) *chipolanum,* USNM 650837); **J,** paired, distal, distally outwardly directed (*M.* (*B.*) *tenue colligatum,* USNM 650844).

7. Usually single, proximally placed, distally directed: *M.* (*U.*) *unguiculatum* subspp.

Special avicularia (Figure 6) may be slightly, moderately, or strongly differentiated from the ordinary ones, single or paired with an ordinary one, and in Recent species have a bilobed mandible, the outer lobe of which occludes with a subspatulate rostrum. The rostrum has a straight axis, in fossil specimens may be subspatulate or pointed, and is directed proximally, proximally inward, or transversely inward. Extra areolae margin the outer part of the rostral chamber in most species (e.g., pl. 12, fig. 2). The antirostral end protrudes beyond the distal or distolateral margin of the zooecium, so the avicularium is nearly interzooecial; however, it never overlaps zooecia other than the one from which it develops as a modification of distal areolae (pl. 18, fig. 1) in the same manner as an ordinary avicularium. In addition to the degree to which they are differentiated from ordinary avicularia (discussed below), special avicularia display diversity in zoarial location, on the basis of which three types are recognizable.

1. Those on zooecia distolateral to gonoecia: *M.* (*R.*) *micropora* subspp., *M.* (*R.*) *vigneauxi, M.* (*B.*) *chipolanum, M.* (*B.*) *tenue colligatum, M.* (*B.*) *tenue auriculatum, M.* (*P.*) *helveticum* subspp., *M.* (*M.*) *nysti, M.* (*M.*) *moniliferum,* possibly *M.* (*P.*) *maleckii.*

2. Those on axillary zooecia: *M.* (*B.*) *chipolanum, M.* (*B.*) *tenue auriculatum, M.* (*B.*) *tenue tenue, M.* (*B.*) *lacrymosum, M.* (*M.*) *moniliferum.*

3. Those on zooecia along the zoarial margins: *M.* (*B.*) *chipolanum, M.* (*B.*) *tenue* subspp., *M.* (*P.*) *helveticum* subspp., *M.* (*M.*) *nysti, M.* (*M.*) *moniliferum.*

Seemingly random placement of special avicularia occurs in subspecies of *M.* (*R.*) *micropora* in which the special avicularia are weakly differentiated. Unlike the marginal vicarious avicularia in *Beisselina* Canu (Wiesemann, 1963, p. 57), the marginal special avicularia in *Metrarabdotos* occur on narrow as well as broad branches.

The constancy, prominence, shifts in position and orientation, and differentiation in size of avicularia in species of *Metrarabdotos* remove most of the grounds for denial (e.g., Jullien, 1888, p. 90) that avicularia have functional significance. The problem of whether they fulfill primarily a defensive (Harmer, 1909, pp. 719-720) or a rheogenic (Canu and Bassler, 1920, p. 64, in part; 1929, pp. 360, 361, in part) role cannot be resolved yet, though overgrowth of seemingly healthy mandibles by epibionts (pl. 10, fig. 4) suggests inefficiency

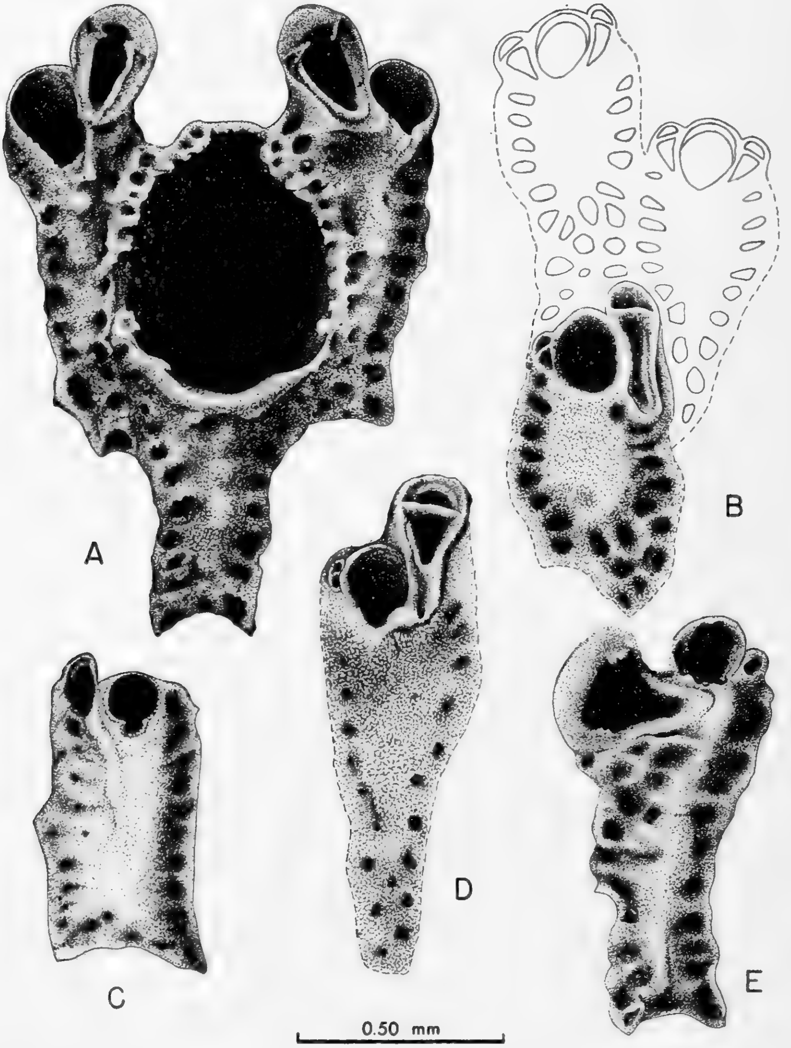

FIGURE 6.—Distribution, orientation, and structure of special avicularia in *Metrarabdotos*. **A,** single special avicularia on zooecia distolateral to gonoecium, distal cover of which is broken (*M.* (*M.*) *moniliferum,* BM (NH) D.35145); **B,** special avicularium, paired with ordinary one on axillary zooecium (*M.* (*B.*) *tenue auriculatum,* USNM 650862); **C,** special avicularium, paired with ordinary one, on outer side of broadened marginal zooecium (*M.* (*P.*) *helveticum thomasi,* USNM 650886); **D,** proximally directed special avicularium, with subspatulate rostrum, on axillary zooecium (*M.* (*B.*) *tenue tenue,* USNM (Z) 9759); **E,** transversely inwardly directed special avicularium, with pointed rostrum, on axillary zooecium (*M.* (*M.*) *moniliferum,* BM(NH) D.35145).

in the discharge of a defensive office. Current generated by avicularian activity has been assumed to be mainly affluent (i.e., "to distribute the zoarial capture"; Canu and Bassler, 1929, p. 360), but ciliary activity of the everted tentacles has been observed to attract suspended food more effectively than uncoordinated, back-and-forth motion of mandibles might. Moreover, mandibular movement does not cease when most or all of the tentacle crowns have been introverted, a time at which an effluent current would be effective in dispersing discharge faeces. Concomitant advantages might include discouragement from settlement of larvae of potential epibionts and assurance of broadcast of the colony's own larvae. A role in zoarial sanitation in *Metrarabdotos* is not out of harmony with the oral location of the avicularia and with their opportunistic enlargement wherever zoarial geometry permits.

Gonoecial structure.—Among the most striking features of *Metrarabdotos* are its individuals (gonoecia, Figure 7) specialized for brooding larvae in their distal halves, which are vastly different in construction from those of zooecia. The orifice, which falls at midlength rather than at the distal end, is crescent shaped, lacks proximal

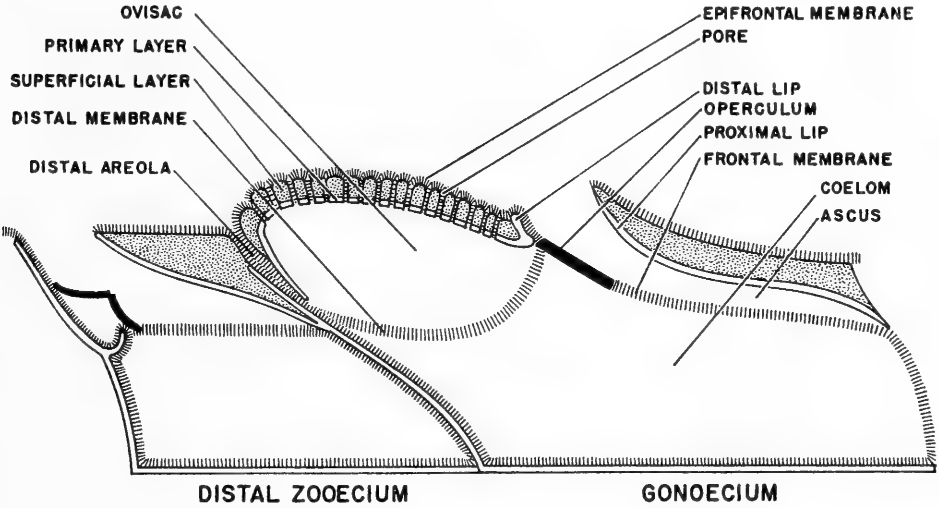

FIGURE 7.—Idealized sagittal section through a fully developed gonoecium and the zooecium distal to it, showing relationships of skeletal and epithelial tissues. The diagram is based on thin sections of skeletal tissue and on dissections of dried specimens in which membranes, muscles, and polypides are preserved. Polypides and muscles have been omitted to emphasize skeleton-membrane relationships. Symbols as in Figure 3.

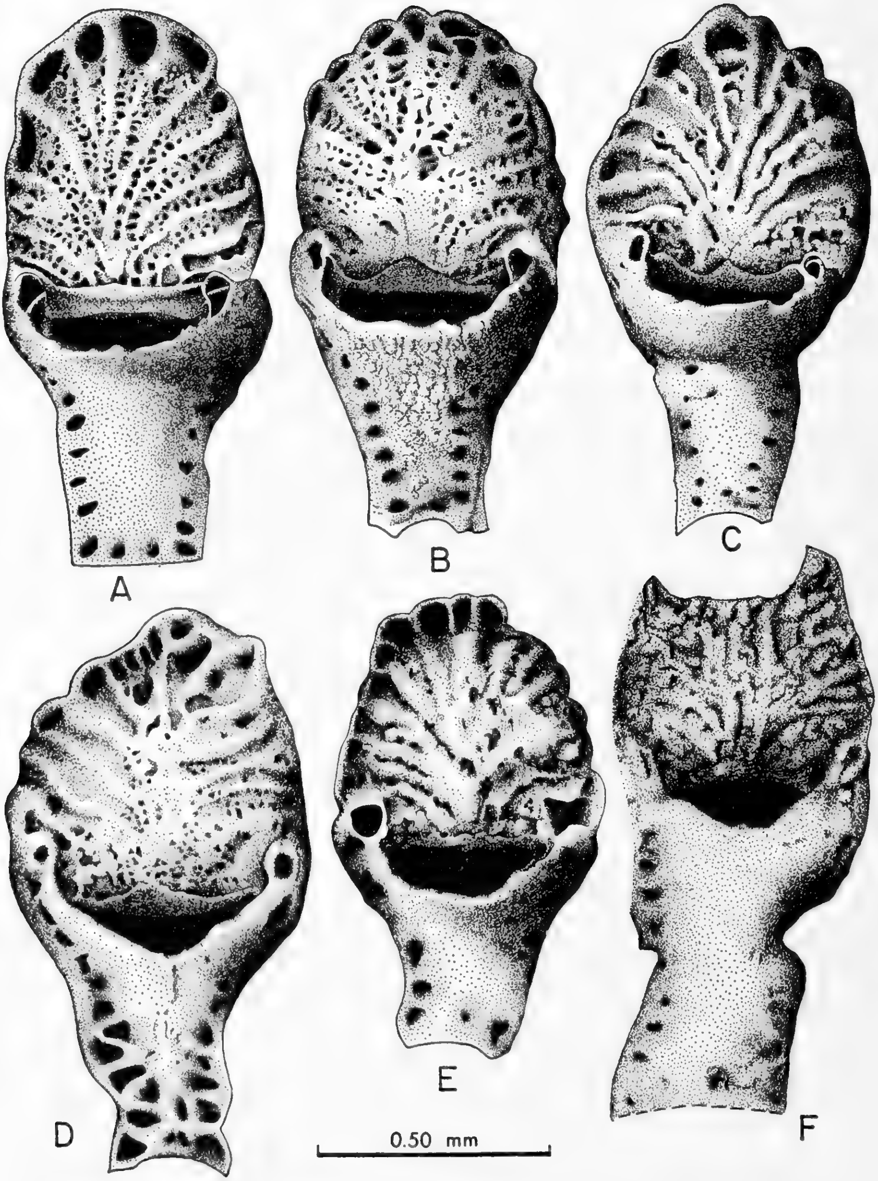

FIGURE 8.—Gonoecial structure in *Metrarabdotos* from Eocene (**A**) through Oligocene (**B, C, E, F**) to Miocene (**D**). **A-C, E,** gonoecia having avicularia, unhooded proximal lip, reflected distal lip, and strongly convex, variably costulate cover margined by graded areolae (*M.* (*R.*) *micropora micropora,* USNM 650791, USNM 650809, USNM 650808, USNM 650820); **D**, similar gonoecium having some of the distal areolae divided (*M.* (*R.*) *micropora butlerae,* USNM 650822); **F,** similar gonoecium having straight distal lip and less costulate distal cover (*M.* (*R.*) *vigneauxi,* USNM 650834).

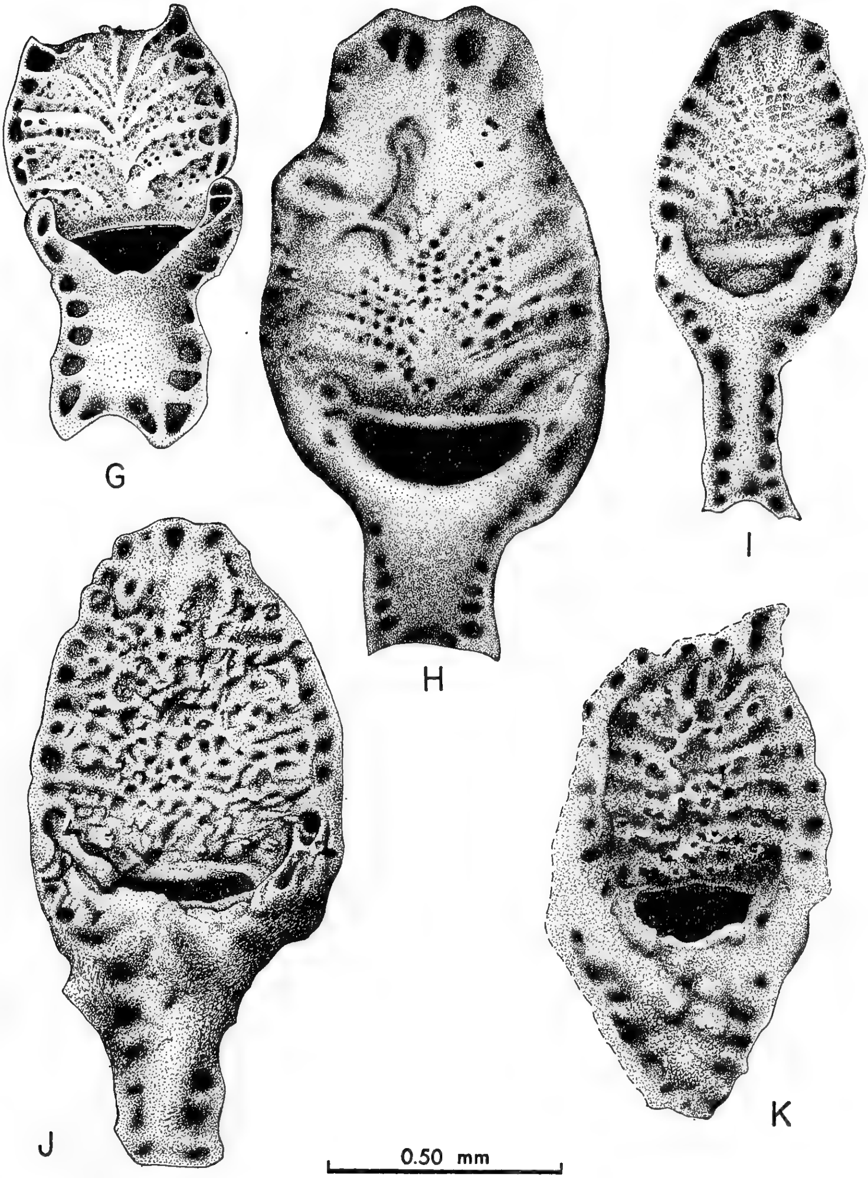

FIGURE 8 (*continued*).—Gonoecial structure in *Metrarabdotos* from Miocene (**G-I**) to Pliocene (**J**, **K**). **G**, gonoecium having avicularium, unhooded proximal lip, straight distal lip, and moderately convex, costulate distal cover margined by graded areolae (*M.* (*U.*) *kugleri*, USNM 650872); **H**, gonoecium having avicularia, unhooded proximal lip, unturned distal lip, and weakly convex, feebly costulate distal cover margined by subequal areolae (*M.*(*P.*) *helveticum canariense.* BM(NH) D.9294); **I**, similar gonoecium (*M.* (*P.*) *helveticum thomasi,* USNM 650886). **J**, gonoecium having avicularia, hooded proximal lip, straight distal lip, and flat, non-costulate distal cover margined by subequal areolae (*M.* (*M.*) *moniliferum,* USNM 650895); **K**, gonoecium lacking avicularia and having unhooded proximal lip, upturned distal lip, and flat, peripherally costulate distal cover margined by subequal areolae (*M.* (*B.*) *tenue auriculatum,* USNM 650862).

denticles and distal shelf, and closes with a one-piece, more heavily chitinized operculum. The gonoecial interior, divided by a membranous wall at the distal margin of the orifice into a proximal coelomic cavity and ascus and a distal ovisac, is continuous in fossils (pl. 6, fig. 4; pl. 17, fig. 4). The ovisac accommodates the large larva (0.48 mm. in *M.* (*B.*) *tenue tenue* according to Marcus, 1955, p. 305), and the wide orifice permits its egress. The proximal half of the gonoecium contains a polypide (Marcus, 1955, p. 305), though Canu and Bassler (1928a, p. 129) stated an opinion to the contrary.

Busk (1859, p. 69) recognized the structural difference between the brood chamber of *M.* (*M.*) *moniliferum* and the ovicells present in many other Cheilostomata; however, the gonoecia of *Metrarabdotos* have been described as entozooecially ovicelled (Canu, 1914, p. 472; Canu and Bassler, 1920, p. 533; 1923, p. 163; 1935, p. 53; Canu and Lecointre, 1928, p. 59; Lagaaij, 1952, p. 122; Buge, 1957, p. 306; 1966, p. 40; Brown 1958, p. 64; Cheetham, 1963, p. 70; Buge and Galopim de Carvalho, 1963) or hyperstomially ovicelled (Marcus, 1955, p. 305).

Variations in construction and sculpture of the gonoecium of *Metrarabdotos,* given maximal weighting as taxonomic characters by Roger and Buge (1947) and Buge and Galopim de Carvalho (1963), are complex (Figure 8). The present study indicates that no species of *Metrarabdotos* possesses an imperforate ovisac cover; therefore, two of the sculptural types, imperforate-costulate in the nominal species *M. vicksburgicum* and *M. grande* (Roger and Buge, 1947; Cheetham, 1963, p. 70; Buge and Galopim de Carvalho, 1963, pp. 144, 162) and imperforate-tuberculate in *M. unguiculatum* (Buge and Galopim de Carvalho, 1963, p. 184), have required revision. The suggestion made by Canu and Bassler (1920, p. 536) that gonoecial costulation varies significantly within some species is substantiated by the sculpture of specimens of *M.* (*R.*) *micropora micropora* (Figure 8, A-C; pl. 1, figs. 3-4; pl. 2, figs. 2-4; pl. 3, figs. 1, 3).

Seven types of gonoecium have been identified in the present study:

1. Distal cover strongly convex, vigorously costulate, margined by areolae increasing in size distally; orifice with distal lip reflected over the ovisac cover and proximal lip unhooded; paired avicularia present: *M.* (*R.*) *micropora* subspp.

2. Distal cover moderately convex and costulate, margined by areolae increasing in size distally; orifice with straight distal lip and unhooded proximal lip; paired or single avicularia present: *M.* (*R.*) *vigneauxi*, *M.* (*U.*) *kugleri.*

3. Distal cover moderately convex and costulate, margined by areolae of uniformly small size; orifice with upturned distal lip and unhooded proximal lip; paired avicularia present: *M.* (*B.*) *lacrymosum.*

4. Distal cover weakly convex, feebly costulate, margined by areolae of uniform size; orifice with upturned distal lip and unhooded proximal lip; paired avicularia present: *M.* (*P.*) *helveticum* subspp., probably *M.* (*P.*) *maleckii.*

5. Distal cover weakly convex, peripherally costulate, margined by areolae usually of uniform size; orifice with upturned distal lip and unhooded proximal lip; avicularia absent: *M.* (*B.*) *chipolanum, M.* (*B.*) *tenue* subspp., *M.* (*U.*) *unguiculatum* subspp.

6. Distal cover weakly convex, feebly costulate, margined by areolae of uniform size; orifice with hooded proximal lip; paired avicularia present: *M.* (*M.*) *nysti.*

7. Distal cover flat, not costulate, margined by areolae of uniform size; orifice with straight distal lip and hooded proximal lip; paired avicularia present: *M.* (*M.*) *moniliferum.*

QUANTITATIVE CHARACTERS

Introduction.—Standard variates (zooecial length, zooecial width, oral dimensions, brood chamber dimensions, size of avicularia or vibracula, and counts of spines, pores, or other meristic features) usually are recorded in the description of cheilostome Bryozoa (Cheetham, 1966, p. 16). In the present study eleven variates (Figure 9) were determined on selected, or in some cases on all available, zoarial fragments preserving the requisite morphologic features by rotating each one so that every zooecium or gonoecium observed had in turn its frontal surface perpendicular to the axis of the microscope. Measurements, including those of secondary orifice and avicularium, are thus of frontal projections.

The mode of growth described above for the frontal wall and associated structures in *Metrarabdotos* (pl. 9, fig. 3; pl. 10, fig. 3) precludes ontogenetic variation in the observed zooecial variates (Lz, lz, ho, lo, Lav, na) except within three zooecial generations of the growing edge of the zoarium. Moreover, astogenetic variation in zooecial variates (Figure 2) appears to be restricted to the first six generations from the ancestrula. Few specimens, all of them Recent, were found to preserve either of these regions. The computed sample statistics, therefore, can be used as estimates of the population parameters for late-formed, adult individuals.

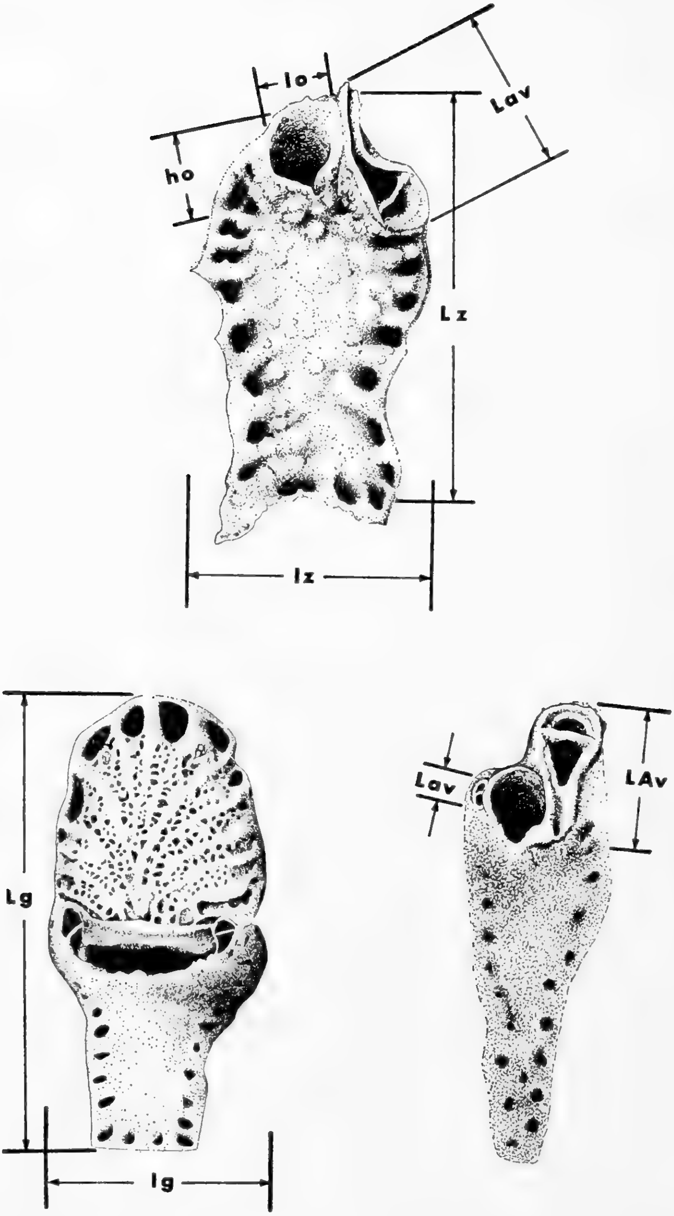

FIGURE 9.—Standard measurements made on frontal surfaces of zooecia and gonoecia of *Metrarabdotos* specimens. The ninth variate (na) was obtained by counting the number of whole areolae on each zooecium; divided areolae, such as the left distal one on the upper zooecium, were counted as one. The tenth and eleventh variates, length and width of gonoecial orifice, were obtained in the same way as the oral dimensions of zooecia.

Lz, length of zooecium; *lz,* width of zooecium; *ho,* length of secondary orifice; *lo,* width of secondary orifice; *Lav,* length of ordinary avicularium; *LAv,* length of special avicularium; *Lg,* length of gonoecium; *lg,* width of gonoecium.

The eleven variates were studied for taxonomic applicability in a series of biometric analyses. First, coefficients of variation were computed for all variates in each sampling unit and in the pool of samples to identify relatively variable and less variable characters (Cheetham, 1966, p. 20) and to compare within- and among-sample variation. Second, coefficients of correlation were calculated among the six zooecial variates for single and pooled sampling units to determine the degree of relationship among characters. Third, a principal components analysis was made on the six zooecial variates in the pool of samples to isolate and identify independent characters.

Sampling units.—A target of 25 observations of each variate in each sample was set to produce narrow confidence intervals for univariate statistics, and an attempt was made to deploy observations over at least five zoarial fragments in each sample to minimize clonal restrictions on within-sample variation (Tavener-Smith, 1966, p. 414). Limitations on availability of material and preservation of specimens reduced the size of some samples severely. Therefore, samples from similar stratigraphic positions at nearby localities were pooled to produce sampling units having nearer the target number of observations. For the six zooecial variates (Lz, lz, ho, lo, Lav, na), 42 percent of the sampling units thus formed consist of 25 or more individuals, 47 percent of 10 to 24, and 11 percent of fewer than 10. For gonoecial variates (Lg, lg, ho, lo) and special avicularian length (LAv), the number of observations is much smaller because of the comparative rarity of these features on most specimens. For calculation of bivariate and multivariate statistics, sample size is further reduced by data gaps for individuals lacking requisite morphologic features because of the state of their preservation or their intrazoarial variation.

The sampling units and the number of zoarial fragments included in each are listed in Table 1; the number of observations in each sampling unit for each variate is given in Tables 7-16.

Single characters.—Sampling unit means and standard deviations for each variate (Tables 7-16) were calculated from individual observations rather than from means over zoarial fragments (specimen means of Tavener-Smith, 1966, p. 421) so that the range of phenotypic variation could be depicted through computation of Pearson's coefficient of variation (V).

High within-sample variation in quantitative characters (Table 2) typifies *Metrarabdotos* as much as other cheilostomes previously

Table 1.—*Sampling units used in numerical analysis of* Metrarabdotos.

Unit symbol	
A 1-3.	***M. (R.) micropora floridanum***
1.	5 zoarial fragments; Bumpnose Ls.; Smith's quarry, Jackson Co., Florida (Puri and Vernon, 1964, p. 90, bed 4).
2.	3 zoarial fragments; Bumpnose Ls.; Marianna Lime Products Company quarry, Jackson Co., Florida (Cheetham, 1963, p. 85).
3.	3 zoarial fragments; Bumpnose Ls.; Avon Park Rifle Range well, Polk Co., Florida (Cheetham, 1963, p. 87, depth 320 ft.).
A 4.	***M. (R.) micropora floridanum*** 5 zoarial fragments; marl above Cooper Marl, Hawkinsville, Georgia (Herrick, Pickering, and Sachs, 1967).
B	***M. (R.) micropora micropora***
1.	1 zoarial fragment; Shubuta Clay, basal marly phase; old bridge at Shubuta, Mississippi (Deboo, 1965, p. 4).
2.	4 zoarial fragments; lower 4 ft. of Red Bluff Fm.; Little Stave Creek, Alabama (Cheetham, 1963, p. 81).
3.	4 zoarial fragments; lower 7 ft. of Red Bluff Fm.; St. Stephens quarry, Alabama (Cheetham and Deboo, 1963).
C	***M. (R.) micropora micropora***
1.	2 zoarial fragments; upper 4 ft. of Red Bluff Fm.; Little Stave Creek, Alabama.
2.	4 zoarial fragments; upper 5 ft. of Red Bluff Fm.; St. Stephens quarry, Alabama.
3.	1 zoarial fragment; *Corbula* bed, Red Bluff Fm.; Hiwannee, Mississippi (Deboo, 1965, p. 4).
D	***M. (R.) micropora micropora***
1.	2 zoarial fragments; upper 4 ft. of Mint Spring Marl; Mint Spring Bayou, Vicksburg, Mississippi (Cheetham and Glawe, 1964, p. 4).
2.	4 zoarial fragments; upper 2 ft. of Mint Spring Marl; Brandon quarry, Mississippi (Cheetham and Glawe, 1964, p. 7).
E	***M. (R.) micropora micropora***
1.	2 zoarial fragments; lower 5 ft. of Marianna Ls.; St. Stephens quarry, Alabama.
2.	2 zoarial fragments; lower 5 ft. of Marianna Ls.; Little Stave Creek, Alabama.
F	***M. (R.) micropora micropora***
1.	2 zoarial fragments; upper 5 ft. of exposed Marianna Ls.; Little Stave Creek, Alabama.
2.	6 zoarial fragments; Marianna Ls., Monroeville, Alabama (Canu
G	***M. (R.) micropora micropora***
1.	3 zoarial fragments; Glendon Ls.; 2.8 mi. south of Stafford Springs, Mississippi (Howe, 1942).
2.	2 zoarial fragments; 3 mi. southeast of Vosburg, Mississippi (Canu and Bassler, 1920, p. 16).

TABLE 1.—*Continued*

Unit symbol		
H		***M. (R.) micropora micropora***
		2 zoarial fragments; lower 2 ft. of Chickasawhay Fm.; St. Stephens quarry, Alabama (Glawe, 1968).
I		***M. (R.) vigneauxi***
		4 zoarial fragments; Stampian; borehole at Biganos (Gironde), France, depth 132.65-155.97 m. (M. Vigneaux, personal communication).
J		***M. (R.) micropora butlerae***
		7 zoarial fragments; lower 5 ft. of Tampa Fm.; Falling Waters Sink, Washington Co., Florida (Puri and Vernon, 1964, p. 114, bed 1).
K		***M. (B.) chipolanum***
		3 zoarial fragments; lower 5 ft. of Chipola Fm.; Tenmile Creek, Calhoun Co., Florida (Puri and Vernon, 1964, p. 126).
N		***M. (B.) tenue colligatum***
		7 zoarial fragments; Cercado Fm.; Cercado de Mao, Rio Mao, Dominican Republic (Sandberg, 1962).
L		***M. (B.) tenue auriculatum***
	1.	1 zoarial fragment; upper 4 ft. of Tamiami Fm.; Sunniland quarry, Collier Co., Florida (Puri and Vernon, 1964, p. 214).
	2.	1 zoarial fragment; Waccamaw Marl; Intracoastal Canal 15 mi. northeast of Myrtle Beach, South Carolina.
	3.	2 zoarial fragments; Caloosahatchee Marl; Shell Creek, De Soto Co., Florida (Puri and Vernon, 1964, p. 255).
	4.	3 zoarial fragments; Caloosahatchee Marl; Monroe Co., Florida (Canu and Bassler, 1923, p. 12).
L_1		***M. (B.) tenue tenue***
	1.	2 zoarial fragments; Recent; off Bahia, Brazil (Challenger), 10-20 fms. (Busk, 1884).
	2.	1 zoarial fragment; Recent; off northeast coast Puerto Rico (Caroline sta. 104), 80-120 fms. (Bartsch, 1933, p. 29).
	3.	2 zoarial fragments; Recent; off northeast coast Puerto Rico (Caroline sta. 68), 10 fms. (Bartsch, 1933, p. 19).
	4.	1 zoarial fragment; Recent; off Recife, Brazil (Albatross sta. 2758), 20 fms. (Albatross Sta. Records).
O		***M. (B.) lacrymosum***
		6 zoarial fragments; Bowden Marl; Bowden, Jamaica (Banner and Blow, 1965, p. 1166).
P		***M. (B.) kugleri***
		11 zoarial fragments; San José Calcareous Silt Member of Manzanilla Fm.; Manzanilla coast, Trinidad (van den Bold, 1963, p. 364, loc. 17).
Z		***M. (U.) unguiculatum pacificum***
		2 zoarial fragments; Recent; Secas Island, Panama (Hancock sta. 457-35), 10 fms. (Osburn, 1952, p. 443).

TABLE 1.—*Continued*

Unit symbol		
Y		***M. (U.) unguiculatum unguiculatum***
	1.	2 zoarial fragments; Recent; north of Yucatan (Albatross sta. 2363) 21 fms. (Canu and Bassler, 1928a, p. 128).
	2.	3 zoarial fragments; Recent; north of Yucatan (Albatross sta. 2362), 25 fms. (Canu and Bassler, 1928a, p. 128).
	3.	1 zoarial fragment; Recent; off Bahia, Brazil (Norseman sta. 348), 27 fms. (Canu and Bassler, 1928b, p. 92).
	4.	2 zoarial fragments; Recent; northeast Gulf of Mexico (Albatross sta. 2405), 30 fms. (Canu and Bassler, 1928a, p. 128).
Y_1		***M. (U.) unguiculatum cookae***
		5 zoarial fragments; Recent; off Accra, Ghana, 25 fms. (P. L. Cook, personal communication).
T_1		***M. (P.) helveticum helveticum***
	1.	6 zoarial fragments; Helvetian; Point-Levoy (Loir-et-Cher), France (Buge, 1957, p. 24).
	2.	3 zoarial fragments; Helvetian; Le Hagineau (Maine-et-Loire), France (Buge, 1957, p. 18).
	3.	4 zoarial fragments; Helvetian; La Placette, Ferrière-l'Arcon (Indre-et-Loire), France (Buge, 1957, p. 23).
R_1		***M. (P.) helveticum canariense***
		3 zoarial fragments; Miocene; Monte San Roque, Grand Canary Island (Dartevelle, 1937, p. 105).
S		***M. (P.) helveticum canariense***
		4 zoarial fragments; Pliocene; Rodhos, Island of Rhodes (Pergens, 1887a, p. 27).
R		***M. (P.) helveticum thomasi***
		7 zoarial fragments; Miocene or Pliocene; borehole (depth 85-100 ft.), Benguema, Sierra Leone (H. D. Thomas, personal communication).
T		***M. (P.) maleckii***
	1.	3 zoarial fragments; Leithakalk; Eisenstadt, Austria (Canu and Bassler, 1924, p. 682).
	2.	6 zoarial fragments; Leithakalk; Grzybóm, Poland (Malecki, 1952, p. 197).
	3.	6 zoarial fragments; Leithakalk; Zidlochovice, Czechoslovakia.
W		***M. (M.) nysti***
		2 zoarial fragments; lower Diestian; Antwerp and Bercham-lez-Anvers, Belgium (Lagaaij, 1952, p. 122).
U		***M. (M.) moniliferum***
	1.	2 zoarial fragments; Coralline Crag; Sudbourne Hall, Sudbourne, Suffolk (Chatwin, 1961, p. 44).
	2.	4 zoarial fragments; Coralline Crag; Crag Pit Farm, Aldeburgh, Suffolk (Chatwin, 1961, p. 44).
V		***M. (M) moniliferum***
		3 zoarial fragments; Red Crag; Walton-on-the-Naze, Essex (Chatwin, 1961, p. 45).

TABLE 2.—*Pearson coefficients of variation for 11 variates in 31 sampling units of* Metrarabdotos.

[Character symbols as in Figure 9; unit symbols as in Table 1.]

Species or subspecies	Unit symbol	Lz	lz	ho	lo	Lav	na	Lg	lg	ho	lo	LAv
M. (R.) m. floridanum	**A1-3**	11.16	12.99	13.79	12.33	18.34	10.14	9.62	8.85	45.66	13.92	22.79
	A4	11.58	10.54	9.76	11.27	28.48	10.65					
M. (R.) m. micropora	**B**	11.64	19.76	9.62	9.80	17.86	14.88	5.81	6.94	34.72	8.26	11.60
	C	12.84	15.36	11.49	12.48	22.12	16.89	10.53	5.40	41.32	8.06	
	D	11.14	9.35	15.53	9.43	20.62	10.09	6.29	8.20	18.25	6.99	
	E	10.87	18.35	11.64	13.02	21.46	10.88	4.46	7.35	19.92	12.25	
	F	7.25	13.00	15.15	13.11	23.75	8.06	5.24	2.82	21.05	11.83	
	G	9.62	6.55	17.79	13.65	11.86	17.35	7.16	5.93	10.82	2.34	
	H	18.56	6.03	12.18	9.84	16.83	14.61					
M. (R.) m. butlerae	**J**	8.26	7.09	8.42	12.15	30.96	8.06					
M. (R.) vigneauxi	**I**	10.29	6.37	12.02	14.00	9.90	7.63					
M. (B.) chipolanum	**K**	9.17	6.80	11.19	22.68	16.64	8.70	4.08	2.67			
M. (B.) t. colligatum	**N**	10.24	10.17	10.13	15.65	21.32	10.74	9.09	4.18	39.68	12.44	31.77
M. (B.) t. auriculatum	**L**	5.95	7.69	9.90	10.52	16.58	11.14	6.49	8.06	15.80	5.10	18.40
M. (B.) t. tenue	**L**$_1$	10.00	10.68	11.49	11.88	26.96	11.29	5.21	9.62	62.11	5.52	20.28
M. (B.) lacrymosum	**O**	12.42	11.42	6.85	8.40	28.57	13.87	10.50	7.45	28.69	9.76	
M. (U.) kugleri	**P**	8.40	7.87	9.80	8.13	22.37	3.56	12.69	10.18		5.59	
M. (U.) u. pacificum	**Z**	8.40	8.93	8.13	8.33	14.22	5.88	0.901	1.49	35.34	2.57	
M. (U.) u. unguiculatum	**Y**	15.72	13.76	16.98	14.04	17.27	14.47	9.52	4.26	49.50	8.33	
M. (U.) u. cookae	**Y**$_1$	11.53	9.80	12.90	7.41	18.90	8.93	2.54	12.41		7.63	
M. (P.) h. helveticum	**T**$_1$**1**	11.83	6.76	9.71	10.86	16.34	11.53	4.20	3.61		4.85	19.64
	T$_1$**2**	13.26	4.31	9.90	9.09	15.24	12.21					19.59
	T$_1$**3**	11.10	5.43	6.49	7.25	11.74	11.68					
M. (P.) h. canariense	**R**$_1$	7.75	12.24	14.29	11.29	15.65	7.63					37.40
	S	9.43	12.94	10.40	14.66	23.15	10.24					15.12
M. (P.) h. thomasi	**R**	4.78	7.69	9.80	9.62	20.41	5.88	4.52	7.52		7.63	21.25
M. (P.) maleckii	**T1**	8.85	10.62	11.15	5.43	20.20	10.00					
	T2	8.20	9.62	12.67	7.35	21.60	12.38	11.25	6.67		3.22	
	T3	11.88	4.29	11.31	7.52	9.26	11.02					
M. (M.) moniliferum	**U**	8.13	11.16	17.24	11.86	23.20	10.01	4.37	4.04		1.36	18.45
	V	15.43	10.16	8.33	11.35	22.27	8.26	10.76	2.53			

analyzed (Cheetham, 1966, pp. 17-21). Moreover, length of avicularium (both Lav and LAv) displays more variation in sampling units of *Metrarabdotos* than most other variates do, also in accordance with previous results; both the maximum coefficient of variation and the number of sampling units having coefficients greater than ten are appreciably higher for avicularian length (Table 3). The total variation in avicularian length among pooled samples of *Metrarabdotos,* however, not only is much higher than that in other characters but also exceeds the maximum within-sample variation. The conclusion, therefore, that avicularian length is a potentially less useful taxonomic character (Cheetham, 1966, p. 21) does not hold for *Metrarabdotos.* Gonoecial length (Lg), width (lg), and oral width (lo) show less variation than the corresponding zooecial dimensions (Tables 2 and 3), but gonoecial oral length is highly variable probably because of breakage of the vulnerable proximal lip.

Character pairs.—Pearson product-moment correlation coefficients were calculated for each zooecial character pair in each sampling unit and for the 31 units pooled. Significance (at the .05 level) of within-sample correlations and .95 confidence limits for pooled correlations (Table 4) were determined from David (1954). Correlations, both within and among units, are weak. Consistent positive correlations within units, accompanied by a relatively high value for pooled samples, are shown by only one character pair, Lz:na. Most other dimensions are positively correlated among, but not within, units. Number of areolae is not significantly correlated with zooecial width or with oral dimensions. Significant negative correlation of number of areolae and avicularian length among, but not within, sampling units results from the development of large ordinary avicularia from multiple rather than single-areolae sources in species of *Metrarabdotos* (*Uniavicularium*).

Principal components.—The correlation coefficient matrix calculated for the pooled data was analyzed for independence of characters by computing principal components. The meristic variate, na, was included in the analyses, despite the difference in units it introduces (Seal, 1964, p. 119), to test its seeming association with zooecial length. The magnitude of this variate approximates those of the dimensional variates expressed in dekamicrons. The principal component analysis (Table 5) provided a simple solution with highly identifiable components which are here interpreted in the manner suggested by Reyment and Naidin (1962). The first three (uncorrelated) components, identifiable with zooecial size, zooecial shape, and oral-

TABLE 3.—*Variation in 11 variates in 31 sampling units of* Metrarabdotos *compared with pooled variation.*

	Lz	lz	ho	lo	Lav	na	Lg	lg	ho	lo	LAv
Number of sampling units $V < 10$..	13	16	12	14	2	10	16	19	0	15	0
Number of sampling units $V \geqslant 10$..	18	15	19	17	29	21	5	2	13	4	11
Maximum V within sampling unit...	18.56	19.76	17.79	22.68	30.96	17.35	12.69	12.41	62.11	13.97	37.39
Total V pooled sampling units......	12.5	18.7	15.6	11.6	39.6	15.2	DATA INSUFFICIENT				

TABLE 4.—*Intercorrelations of 6 zooecial variates among and within 30 sampling units of* Metrarabdotos.

[Significance at .05 level within units: +, significant positive; —, significant negative; O, not significant, X, data insufficient.]

Character pair	$r_{.95}$ pooled sampling units	A	B	C	D	E	F	H	J	I	K	N	L1	L2-4	L_1	O	P	Z	Y	Y_1	$T_1$1	$T_1$2	$T_1$3	R_1	S	R	T1	T2	T3	U	V
Lz:lz	+0.28 to +0.41	+	—	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	+	O	—	O	O	O	O	O	O	O	O	O	O
Lz:ho	+0.19 to +0.33	O	O	O	+	O	O	O	O	O	O	O	O	O	O	O	O	O	+	O	O	O	O	O	O	O	O	O	O	—	O
Lz:lo	+0.24 to +0.36	O	+	O	O	+	O	O	—	—	O	O	O	O	O	O	O	O	+	O	O	O	O	O	O	O	O	O	O	O	O
Lz:Lav	+0.24 to +0.36	O	O	O	O	O	O	O	O	O	O	O	—	O	O	O	+	+	O	O	O	—	O	+	—	O	O	O	O	O	—
Lz:na	+0.35 to +0.47	+	+	+	+	+	+	+	O	O	O	+	O	O	+	+	O	X	+	O	+	+	O	O	O	+	+	O	+	+	O
lz:ho	+0.48 to +0.57	O	+	O	O	O	O	O	O	O	O	—	O	O	O	O	O	O	+	O	+	O	O	O	O	+	+	O	O	O	O
lz:lo	+0.55 to +0.65	+	+	+	O	+	+	O	+	O	O	O	O	O	O	O	O	O	+	O	+	O	+	O	+	O	O	O	O	+	O
lz:Lav	+0.74 to +0.81	O	+	+	O	O	O	O	O	O	O	O	O	O	O	O	O	O	+	O	+	O	O	—	O	O	O	O	O	+	O
lz:na	—0.04 to +0.10	O	O	O	O	+	O	O	O	O	O	O	O	O	O	O	O	X	+	O	O	O	O	O	—	O	+	O	O	—	O
ho:lo	+0.51 to +0.62	O	O	O	+	+	O	O	O	O	+	O	O	O	O	O	O	O	+	O	O	O	O	O	O	O	O	O	O	+	O
ho:Lav	+0.35 to +0.47	O	O	+	O	+	+	O	O	O	O	+	O	O	O	O	O	+	O	O	+	O	+	O	O	O	O	O	O	+	O
ho:na	—0.01 to +0.13	O	O	O	O	O	O	O	O	+	O	O	O	O	O	O	O	X	+	O	O	+	O	O	O	O	O	O	O	O	O
lo:Lav	+0.35 to +0.47	O	O	O	O	O	—	O	O	O	O	O	O	O	O	—	O	O	O	O	O	—	O	O	O	O	O	O	O	+	O
lo:na	—0.02 to +0.11	O	O	O	O	+	O	O	O	O	O	O	O	O	O	O	O	X	+	O	O	O	O	O	O	O	O	O	O	—	O
Lav:na	—0.21 to —0.08	—	O	—	O	O	O	O	O	O	O	O	O	O	O	O	O	X	+	—	+	O	O	O	—	O	O	O	—	—	O

TABLE 5.—*Principal components analysis of 6 zooecial variates in 31 sampling units of* Metrarabdotos. *Based on correlation-coefficient matrix calculated from 888 zooecia.*

Component	Variance (eigenvalue)	Percent total variance	Eigenvector ("loadings")						Nature of variation
			Lz	lz	ho	lo	Lav	na	
C_1	2.8839	48.06	+0.56	+0.89	+0.74	+0.78	+0.78	+0.12	Zooecial size measured by five dimensional variates.
C_2	1.3126	21.88	−0.61	+0.14	+0.04	+0.07	+0.31	−0.91	Zooecial shape measured by negative of Lz and na.
C_3	0.7335	12.22	−0.33	−0.17	+0.49	+0.39	−0.44	+0.10	Oral avicularian "ratio" measured by ho, lo:Lav, Lz in opposition.
C_4	0.4608	7.68	+0.45	−0.27	+0.10	+0.08	−0.14	−0.38	Complex shape component; not significant.
C_5	0.4352	7.25	−0.01	−0.05	+0.45	−0.47	+0.11	+0.01	Oral shape; not significant.
C_6	0.1740	2.90	−0.05	−0.30	0.00	+0.10	+0.26	+0.08	Width-avicularian "ratio"; not significant.

avicularian "ratio" (i.e., avicularian length relative to oral dimensions) in order of decreasing contributions, account for more than 82 percent of the total variance. Components C_4 and C_5 contribute about 7.5 percent each to the variance, and C_6 contributes less than 3 percent. Thus oral shape and areolar number, as suggested by the correlation study above, appear to be redundant for the description of the variation shown by the 31 sampling units.

Principal component analysis of a part of the variance-covariance matrix provided a similar solution consisting of three significant transformed characters: general size, zooecial shape, and avicularian size, in order of decreasing contribution. These three characters account for 91 percent of the variance. Though this approach to simple structure is in keeping with Seal's (1964, p. 120) statement that the variance-covariance matrix produces a simpler summarization than the correlation matrix, it may be in large measure the result of domination of the total variation by the largest variate, zooecial length. Therefore, the relatively less simple solution based on the correlation matrix, where the variates are more nearly equally weighted, has been used in the taxonomic analysis below.

In brief, the information in the six variates for which sufficient data were available can be expressed in large measure by three uncorrelated characters, zooecial size (measured by simultaneous variation in the first five variates), zooecial shape (measured by correlated negative variation in zooecial length and number of areolae), and size of avicularia (relative to oral dimensions). Of these, the last shows consistently greater variability among sampling units than within them. Three variates are redundant. Areolae, evenly spaced on the lateral margins of the zooecium, vary in number with zooecial length, both among and within sampling units and in opposition to avicularian length. Oral length and width are correlated with most other variates.

TAXONOMY

INTRODUCTION

Extensive overlap between sampling units for any combination of morphologic characters precludes monothetic approaches to the taxonomy of *Metrarabdotos*. Buge and Galopim de Carvalho (1963, p. 141, 142), for example, found it necessary to construct a key in part on stratigraphic and geographic separations as well as morphologic ones. The taxonomic procedure adopted for this study has consisted of: (1) grouping sampling units on significant morphologic resemblance, (2) projecting the similarity groups so obtained into a stratigraphic framework to infer their probable phylogenetic relationships, and (3) recognizing taxonomic clusters in the phylogenetic pattern. The taxa established on this basis are polythetic and, as far as interpretation of the data permits, monophyletic.

PHENETIC COMPARISON

Morphologic comparisons were made by expressing both qualitative and quantitative characters in numerical code, computing similarity and difference coefficients between every pair of sampling units and clustering units on the basis of the coefficients, all by standard numerical taxonomic operations (Sokal and Sneath, 1963).

Slightly more than half the characters were susceptible of expression in two-state code; the others required codes running to as many as five states (Table 6). Three methods of character weighting were employed.

1. Those quantitative characters which the multivariate analysis suggested to be redundant were omitted. Thus the mean values of the first three principal components, zooecial size and shape and avicularian-oral "ratio," were used in place of the six original variates.

2. Characters were decomposed if heterogeneity was indicated in the stratigraphic sequence of their states. For example, the trial character "number of oral denticles" has three states: 1, 2, and 3. Because their stratigraphic sequence is 1-3-2, a one-for-one scoring would result in spuriously high resemblance between sampling units having one denticle and those having two. Therefore, "number of oral denticles" was divided into two characters, "median denticle" and "lateral denticles," whose states are independent except for the nonoccurrence of the 0-0 combination.

3. The sequence of states was assigned stratigraphically but with the magnitude of morphologic difference reflected by the arithmetic difference between sequential states. In "orientation of ordinary avicularia," for example, the state "distally directed" is morphologically farther from the other three states than they are from each other. It should be noted that, because the data matrix was standardized by rows before calculation of similarity and difference coefficients, the sequence of and differences between states are significant, but whether states increase or decrease numerically with stratigraphic position is not.

TABLE 6.—*Character code used in analysis of 29 sampling units of* Metrarabdotos.

Character	States
1. Zoarial form	—1, encrusting; O, bilaminate, delicate; +1, bilaminate, foliaceous.
2. Zooecial size	O, small; 1, large.
3. Zooecial shape	—1, elongate; O, normal; +1, broad.
4. Areolae distribution	O, single row; 1, additional pores present.
5. Peristome length	O, terminal at zooecial margin; 1, extended beyond margin.
6. Oral denticles	O, simple; 1 lamellar; 2, repeated.
7. Median oral denticle	O, absent; 1, deep, present on fewer than half zooecia; 2, deep, present on more than half but not all zooecia; 3, deep, present on all zooecia; 4, shallow, present on all zooecia.
8. Lateral oral denticles	O, absent; 1, present.
9. Oral shelf	O, simple; 1, pouch-like.
10. Oral-avicularian "ratio"	O, avicularium small; 1, avicularium large.
11. Ordinary avicularia—distribution	O, usually single; 1, usually paired.
12. Ordinary avicularia—position	—1, usually distal; O, usually lateral; +1, usually proximal.
13. Ordinary avicularia—orientation	— 1, directed proximally and outward; O, directed proximally and inward; +1, directed transversely inward; +3, directed distally.
14. Special avicularia—differentiation	O, none or weak; 1, moderate; 2, strong.
15. Special avicularia—gonoecial	O, absent; 1, present.
16. Special avicularia—axillary	O, absent; 1, present.
17. Special avicularia—marginal	O, absent; 1, rarely present; 2, usually present.
18. Gonoecial avicularia	O, absent; 1, present.
19. Gonoecial size	O, small; 1, medium size 2, large.
20. Gonoecial distal cover	O, flat, noncostulate; 1, weakly convex, costulate; 2, strongly convex, costulate.
21. Gonoecial distal areolae	O, subequal; 1, graded.
22. Gonoecial proximal lip	O, unhooded; 1, hooded.
23. Gonoecial distal lip	O, straight; 1, upturned; 2, reflected.

Quantitative characters, including zooecial size, zooecial shape, ordinary avicularian length (relative to orifice size), special avicularian differentiation, and gonoecial size, were coded by grouping graphically 29 sampling units on the basis of mean values (Figures 10-13). Mean values of the first three characters were obtained by post-multiplying the inverse of the matrix of eigenvectors of the principal components by the matrix of mean vectors of the sampling units for the six standard variates.

Similarity (Pearson product-moment correlation) and difference (Sokal taxonomic distance) coefficients were computed from the Q-mode standardized matrix of character scores. Two dendrograms (Figures 14, 15) were constructed from each matrix by clustering sampling units by both the unweighted (UPGM) and the weighted (WPGM) pair-group methods using arithmetic means to recalculate matrices at the end of each clustering cycle (Sokal and Sneath, 1963,

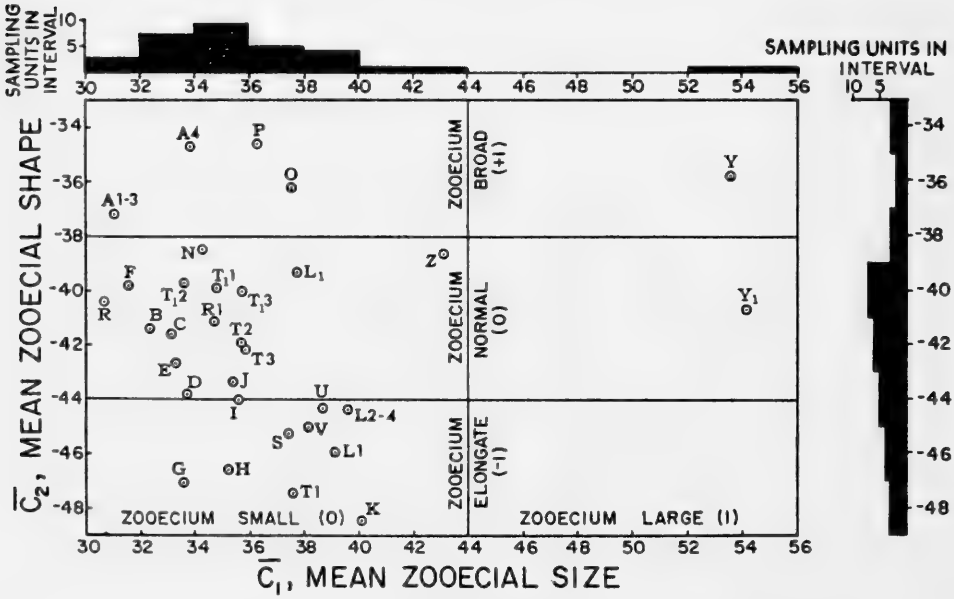

FIGURE 10.—Means of the first two principal components (zooecial size and shape) in 29 sampling units of *Metrarabdotos*. Coding for numerical analysis based on two apparent size groups and three shape groups. Unit symbols listed in Table 1.

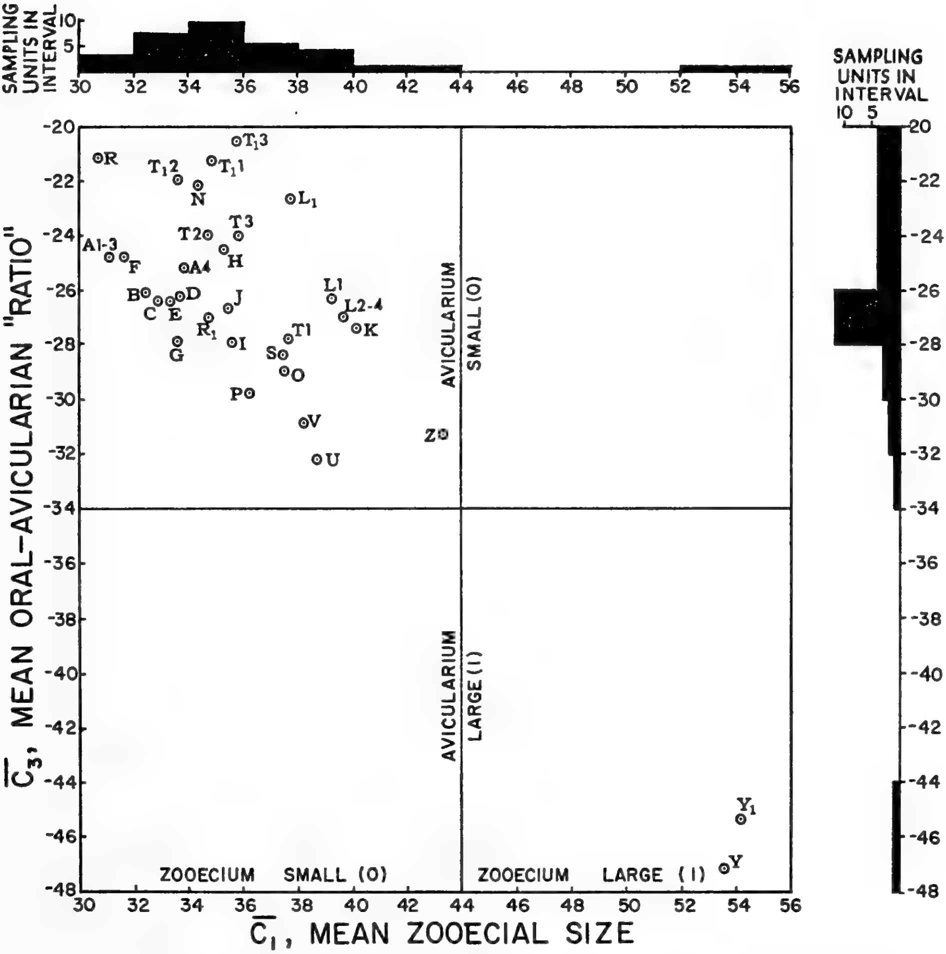

FIGURE 11.—Means of the second (zooecial shape) and third (oral-avicularian "ratio") principal components in 29 sampling units of *Metrarabdotos*. Coding for numerical analysis based on two apparent size groups (as in Figure 10) and two relative avicularian size groups. Unit symbols listed in Table 1.

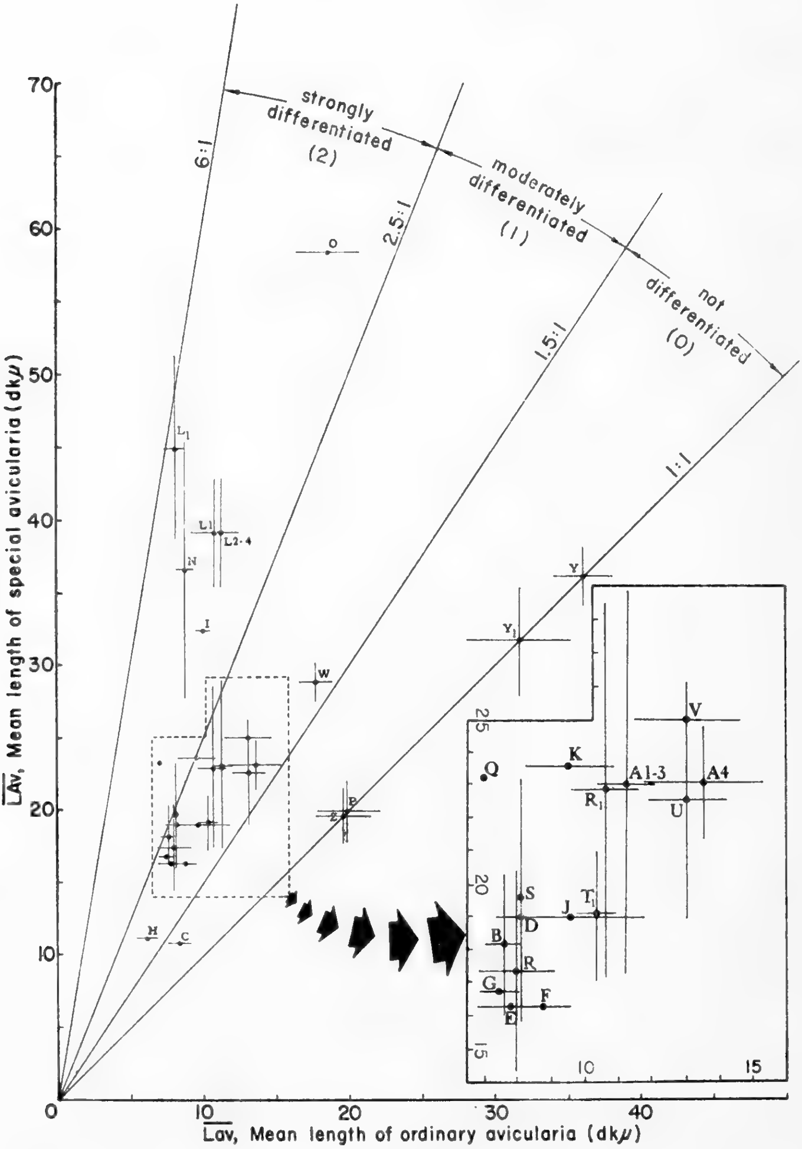

FIGURE 12.—Means and (where data are sufficient) their 95 percent confidence limits in 29 sampling units of *Metrarabdotos* of length of ordinary and special avicularia. Coding for numerical analysis based on three apparent LAv:Lav ratio groups. Unit symbols listed in Table 1. Confidence intervals shown as axes of 95 percent ellipses.

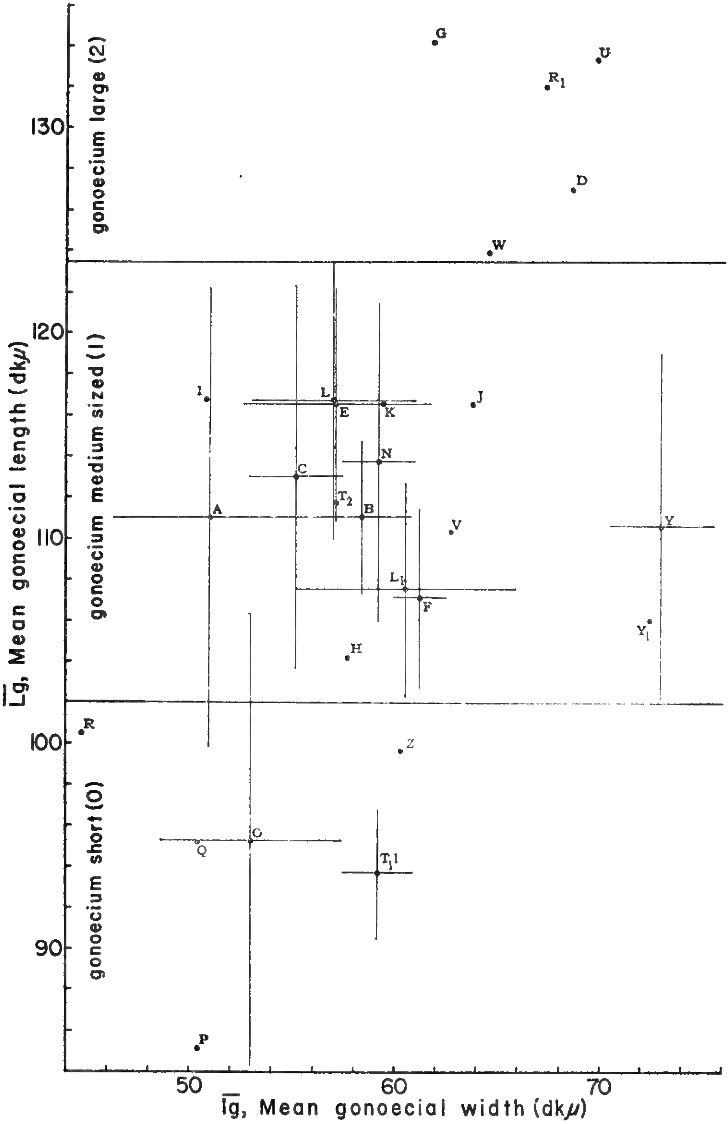

FIGURE 13.—Means and (where data are sufficient) their 95 percent confidence intervals in 27 sampling units of *Metrarabdotos* of gonoecial length and width. Coding for numerical analysis based on three apparent gonoecial size groups. Unit symbols listed in Table 1. Confidence intervals shown as axes of 95 percent ellipses.

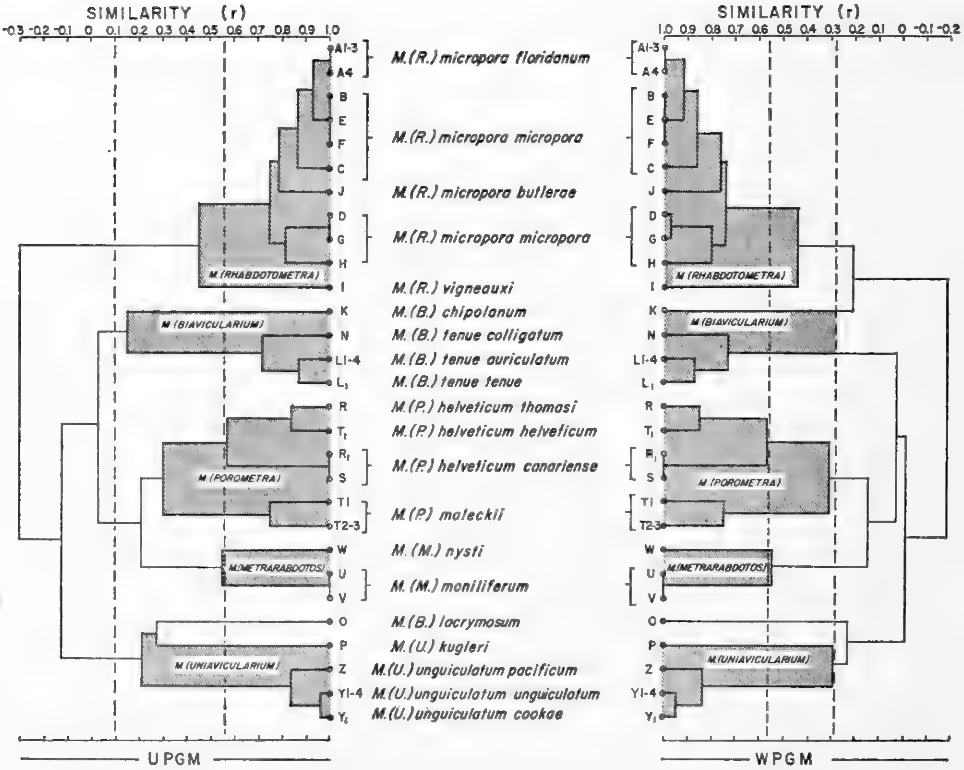

FIGURE 14.—Dendrogram obtained by WPGM and UPGM clustering of correlation coefficient matrix of 29 sampling units of *Metrarabdotos*. Five phenetic groups, including units clustered at the +0.28 level or higher, are consistent with stratigraphic sequence, and are interpreted as subgenera as indicated. Units K and O have phenetic positions different from their inferred phylogeny.

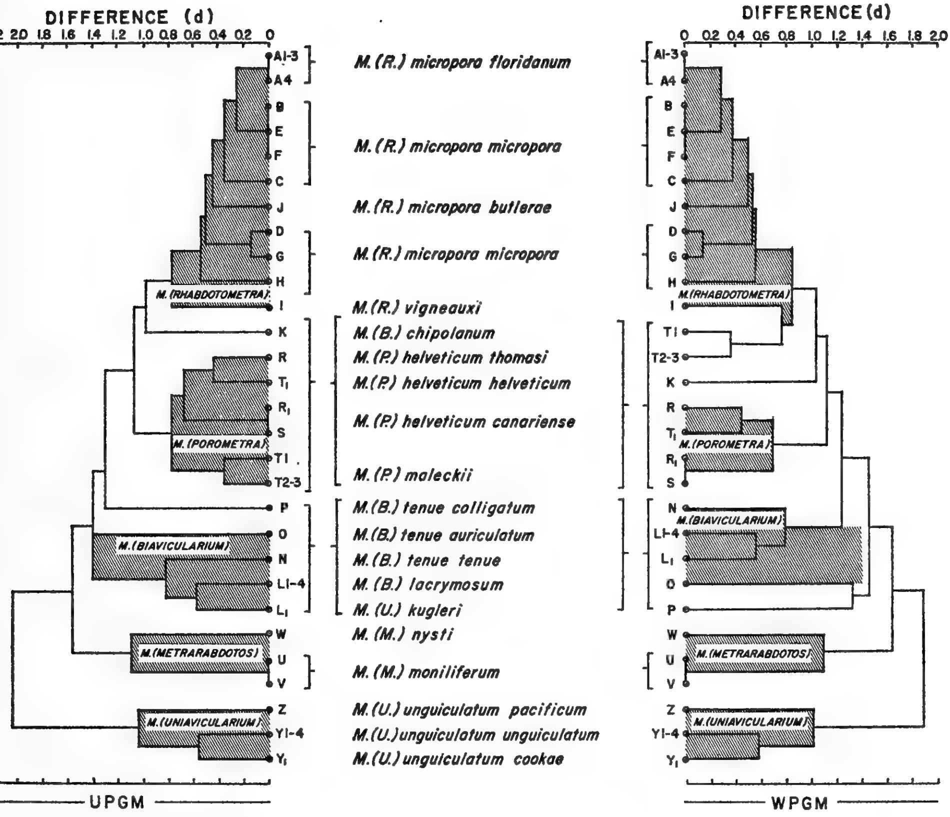

FIGURE 15.—Dendrogram obtained by WPGM and UPGM clustering of taxonomic distance matrix of 29 sampling units of *Metrarabdotos*. Phenetic groups are different from those based on correlation matrix (Figure 14), especially for K, P, and T.

p. 194). Despite recent criticism of the correlation coefficient for use in Q-mode studies (e.g., Eades, 1965), the dendrograms based on correlation are more nearly consistent with stratigraphic sequence than those based on distance. The five major phenetic groups comprising units A-J, K-O, R-T, U-W, and P, Y, Z obtained at the 0.28 level of resemblance by clustering on r were therefore used as the basis for taxonomic interpretation.

PHYLOGENETIC INTERPRETATION OF PHENETIC CLUSTERS

Phylogenetic representations cannot be made directly from dendrograms. Cladograms (Camin and Sokal, 1965) resemble dendrograms in placing all units at the tips of the branches rather than in stratigraphic position. An alternative graphic method of representing similarity groups in a phylogenetic context is based on the diagram presented by Sneath (1961). Phenetic relationships (distances or similarities) are shown on a horizontal morphologic field so that the third dimension can be used for stratigraphic position. Sampling units have been plotted on the two-dimensional fields (Figures 16-18) at distances proportional to their dissimilarity (1–r). This mode of representation, like the dendrogram, distorts phenetic relationships by forcing them into two dimensions. The greater the dissimilarity, i.e., the greater the number of dimensions of difference, the greater the distortion.

The morphologic field (Figure 16) including the phenetic group A–J was constructed by plotting at distances proportional to their dissimilarity, the positions of A, B, and D–J relative to central sample C. Points were located in order of decreasing distance from the central sampling unit, and the amount of distortion introduced was small as indicated by the size of the polygons of "error." In contrast, a more distant unit which belongs to a different phenetic group yields a large polygon of "error" because of the large amount of distortion in representing the multi-dimensional differences on a two-dimensional field. Projection of units A–J into stratigraphic position permits interpretation of their phylogenetic relationships. Relationships of K–O, R–T, U–W, and P–Y–Z were similarly interpreted (Figures 17, 18).

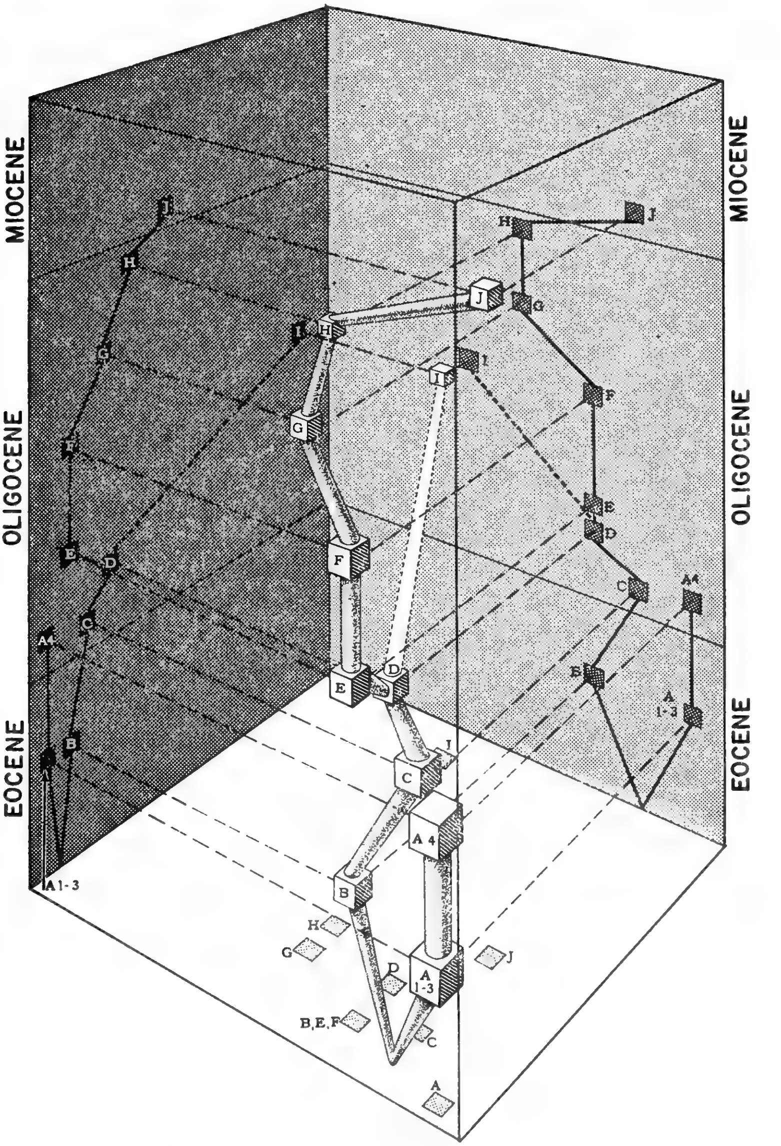

FIGURE 16.—Phylogenetic relationships of sampling units A–J, constituting the subgenus *M.* (*Rhabdotometra*), inferred from morphologic similarity (horizontal field) and stratigraphic position (vertical axis). Projected "shadows" emphasize chronocline B–J (left) and cladogenetic relationships with A and I (right). A1–3, A4, *M.* (*R.*) *micropora floridanum;* B–H, *M.* (*R.*) *micropora micropora;* J, *M.* (*R.*) *micropora butlerae;* I, *M.* (*R.*) *vigneauxi.*

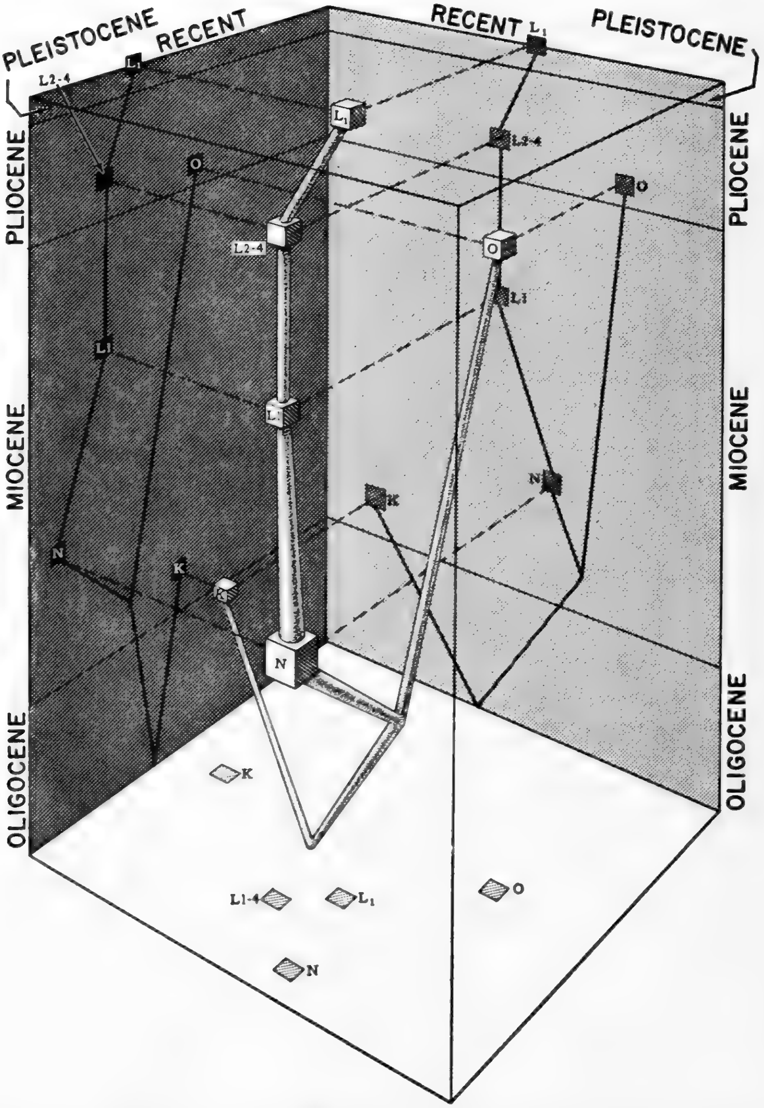

FIGURE 17.—Phylogenetic relationships of sampling units K–O, constituting the subgenus *M.* (*Biavicularium*), inferred in same way that Figure 16 was produced. Chronocline N–L_1 contrasts with cladogenetic relationships among K, N, and O. K, *M.* (*B.*) *chipolanum;* N, *M.*(*B.*) *tenue colligatum;* L1, L2-4, *M.* (*B.*) *tenue auriculatum;* L_1, *M.* (*B.*) *tenue tenue;* O, *M.* (*B.*) *lacrymosum.*

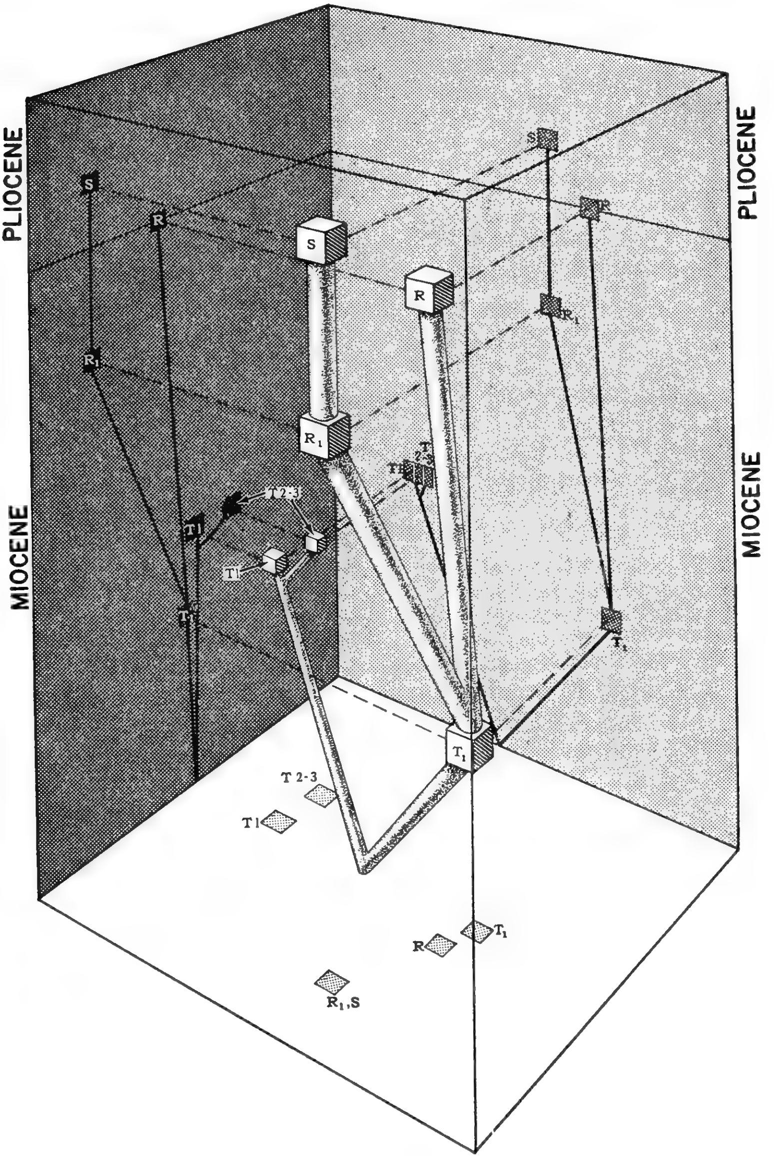

Figure 18.—Phylogenetic relationships of sampling units R–T, constituting the subgenus *M.* (*Porometra*), inferred in same way that Figure 16 was produced. Chronocline T_1–R_1–S contrasts with cladogenetic relationships among T_1, R, and T. T_1, *M.* (*P.*) *helveticum helveticum;* R, *M.* (*P.*) *helveticum thomasi;* R_1, S, *M.* (*P.*) *helveticum canariense;* T1, T2-3, *M.* (*P.*) *maleckii.*

TAXONOMIC INTERPRETATION OF PHENETIC CLUSTERS

To transform the phenetic relationships among all five major similarity groups and the sampling units composing them into a taxonomic hierarchy, a two-dimensional plot of their common morphologic field was constructed as follows (Figure 19). First, the relative positions

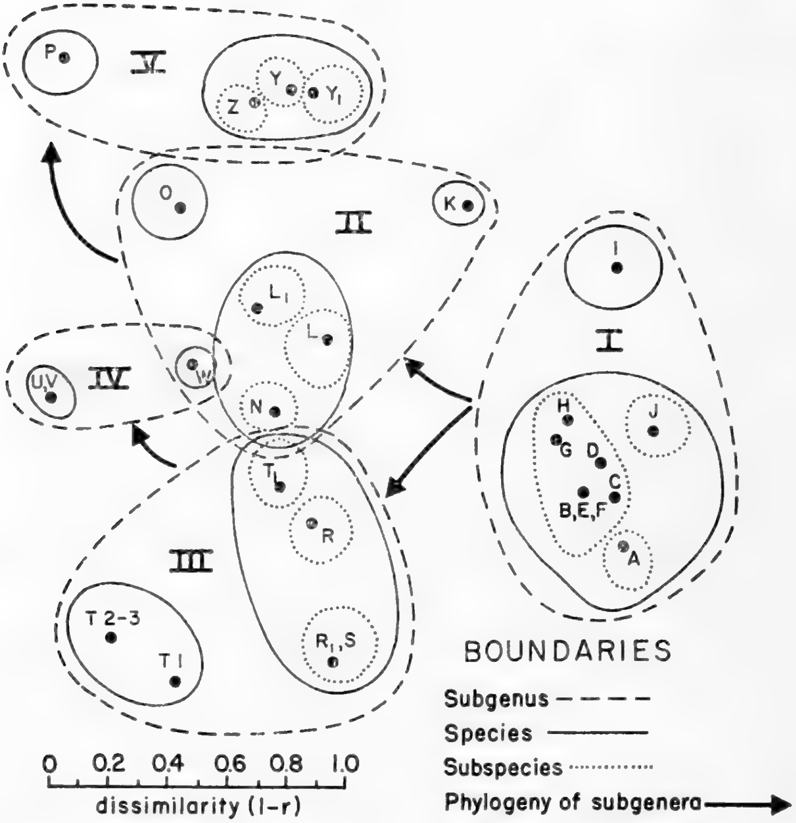

FIGURE 19.—Taxonomic interpretation of morphologic field of the five subgenera of *Metrarabdotos*. Apparent overlap of taxonomic boundaries results from distortion of 2-dimensional representation of 23-dimensional differences. Distances between sampling units within subgeneric boundaries, therefore, are less distorted. Arrows indicate inferred phylogenetic relationships; time parallels the morphologic shift from right to left. Evolutionary pattern is discussed in the text. I, *M.* (*Rhabdotometra*), upper Eocene-lower Miocene; II, *M.* (*Biavicularium*), middle Miocene–Recent; III, *M.* (*Porometra*), middle Miocene-Pliocene; IV, *M.* (*Metrarabdotos*), upper Miocene-Pleistocene; V, *M.* (*Uniavicularium*), upper Miocene-Recent. Unit symbols as in Table 1.

of the oldest representative units of each major group (B, K, P, T, and W) were located at the intersections of their dissimilarity radii in the same way in which the morphologic fields of the individual groups (Figures 16-18) were constructed. Then, the individual morphologic fields were rotated on these units as centers until a position was reached which was judged subjectively to approximate the distances among sampling units in different groups. Finally, taxonomic boundaries were drawn by choosing levels of morphologic resemblance which could be applied without violating the inferred phylogenetic relationships; these levels are correlation coefficients (Figure 14) of +0.55 for minor groups (species) and +0.28 for major groups (subgenera). The boundaries between subgroups (subspecies) were drawn at varying levels of resemblance adjusted to fit the inferred phylogeny. For example, the chronocline B–J (Figure 16) was divided into chronologic subspecies *M.* (*R.*) *micropora micropora* and *M.* (*R.*) *micropora butlerae* between H and J where the inferred rate of morphologic change is greatest. Also, units A and B and units Y, Y_1, and Z are here regarded as geographic subspecies, despite their high level of resemblance, because they show constant morphological differences correlated with geographic occurrence.

Because this type of plot represents multicharacter relationships in two dimensions, the taxonomic diagram (Figure 19) like the dendrogram seriously distorts phenetic distances. Even three-dimensional representations, such as the taxonomic models of Reyment and Naidin (1962), cannot avoid this distortion. As a result of this distortion, four of the five major similarity groups (II-V on Figure 19) appear to overlap morphologically. In the combination of all 23 characters, however, all five are actually separate and distinct groups. The proximity on the two-dimensional morphologic field of units belonging to different major groups results in part from parallel and convergent evolution in single characters as discussed in the next section, but it has been greatly exaggerated by the two-dimensional representation.

By comparison with species in related genera, such as *Escharoides* Milne Edwards, the minor groups, delineated by similarity level of +0.55, are here regarded as species. This interpretation accords in large measure with species concepts established in *Metrarabdotos* by other approaches. The five major groups, delineated by similarity level of +0.28, are here regarded as subgenera. They show more internal variation than species in related genera do, but, on the other hand, they do not have the distinctiveness usually considered appropriate to generic rank. The least homogeneous of the subgenera is *M.* (*Biavicularium*), which lacks a unique character state displayed by every one of its component sampling units. The best definition that can be framed for it is a list of ten character states of which the included species possess as few as six and as many as nine, but of which no species of another subgenus shows more than three. *M.* (*Biavicularium*) is therefore a highly polythetic taxon, consisting of species that have mutually the greatest number of shared traits, no one of which is essential to membership in the subgenus. The polythetic character of *M.* (*Biavicularium*) and the other subgenera of *Metrarabdotos,* which possess it to a lesser degree, is a consequence of evolution and occurs in taxa at even higher categorical levels (Simpson, 1959, p. 407; 1961, p. 95).

The subgenera of *Metrarabdotos* proposed here, as well as their constituent taxa, are inferred evolutionary units based upon phylogenetic interpretation of morphology and occurrence. Membership of a species in a subgenus is thus determined by position in evolutionary pattern, what Simpson (1961, p. 153) has called a unitary evolutionary role, rather than by possession of particular morphologic features. The combination of morphologic features derived from the included species, and ultimately from the populations which compose them, is essential not only in determining evolutionary position but also in forming a diagnosis. The word statements of characters given below in the Systematic Descriptions have been derived in this manner as a basis for identification of material without the necessity of numerical analysis.

ORIGIN AND EVOLUTION

EVOLUTIONARY TRENDS

The phylogenetic relationships of the five subgenera of *Metrarabdotos* are summarized diagrammatically in Figures 19 and 20. Evolutionary trends in three structures—avicularia (Figures 21, 22), gonoecia (Figure 23), and orifice (Figure 24)—were plotted on the phylogenetic base. Because of convergence and parallelism, no one of the evolving characters gives a pattern fully congruent with another or with the phylogenetic scheme.

The complicated series of changes in avicularia seems to be related to an underlying theme of size increase (Figure 12) which was accomplished in at least two ways. In one group, represented only by the relatively recently evolved, but geographically widespread, subgenus *M.* (*Uniavicularium*), emphasis was on the ordinary avicularia to the immediate exclusion of the special avicularia. Enlargement in this group was accompanied by a shift of either the rostral or the antirostral end of the avicularium to a more proximal position, by a broadening of the zooecium, and finally by abandonment of the erect habitus for encrusting. In the other group, including *M.* (*Biavicularium*), *M.* (*Porometra*), and *Metrarabdotos* s. s., the primitive avicularian dimorphism of *M.* (*Rhabdotometra*) was at least retained, but usually accentuated; the special avicularia enlarged, and the ordinary avicularia either remained about the same size (in the first two subgenera) or enlarged too (in *Metrarabdotos* s. s. and *M.* (*B.*) *lacrymosum*). Accompanying the enlargement of special avicularia

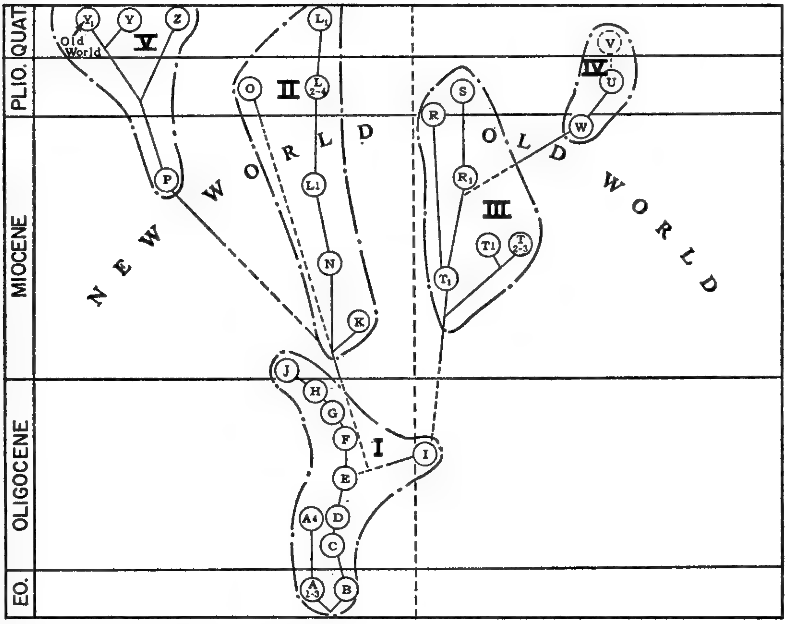

FIGURE 20.—Phylogenetic relationships of the five subgenera of *Metrarabdotos* based upon the morphologic representation of Figure 19 and the stratigraphic distribution of samples. The horizontal axis is dimensionless and suggests the amount of divergence only for samples in close proximity; convergence between subgenera II and IV, shown on Figure 19, for example, is not indicated here. The separate evolutionary histories of New World and Old World species, except in Oligocene and Quaternary time, are indicated by dashed vertical line.

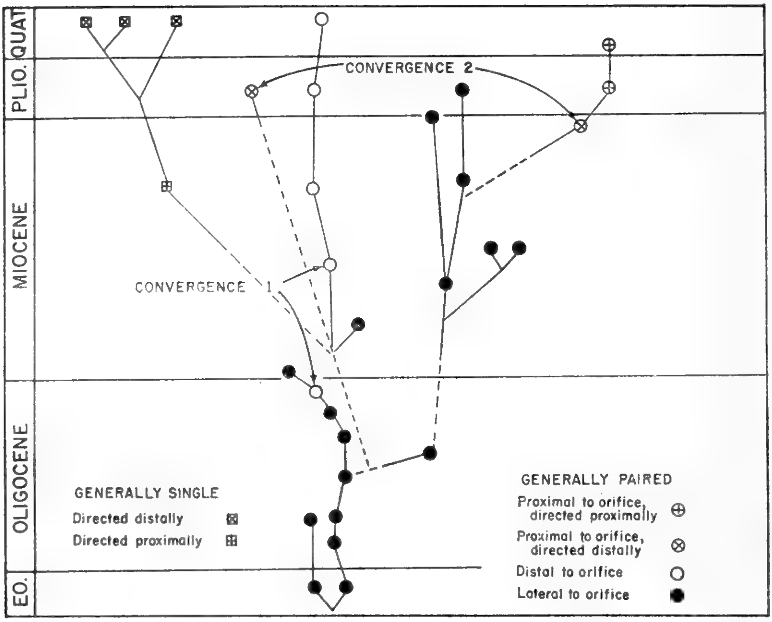

FIGURE 21.—Evolutionary trends in ordinary avicularia. Phylogenetic base as in Figure 20.

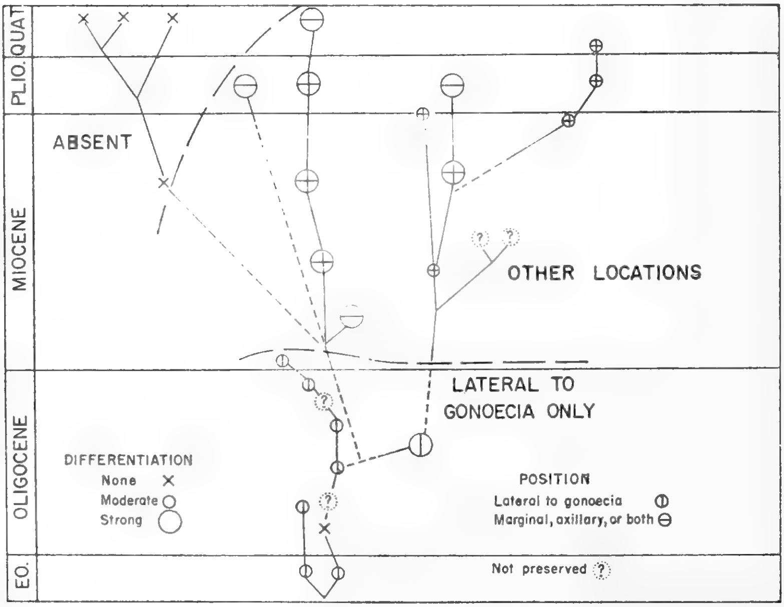

FIGURE 22.—Evolutionary trends in special avicularia. Phylogenetic base as in Figure 20.

were parallel trends in development of special avicularia at zoarial locations other than the primitive one distolateral to gonoecia. In the New World forms, i.e., *M.* (*Biavicularium*), there is a tendency for abandonment of the primitive location, whereas in the Old World forms, i.e., *M.* (*Porometra*) and *Metrarabdotos,* there is not. (The preservation of *M.* (*P.*) *maleckii* makes interpretation of dimorphism in that species doubtful.) Concentration of size on the special avicularia seems to have permitted greater variation in position and orientation in the ordinary ones. In this respect, the New World forms changed more rapidly than Old World forms. In the latter the primitive condition characteristic of *M.* (*Rhabdotometra*) persisted into the Pliocene, whereas in the former it was abandoned in early Miocene. In general, the ordinary avicularia shifted distally in New World forms and proximally in Old World forms, but convergent evolution (Figure 21) complicates the picture.

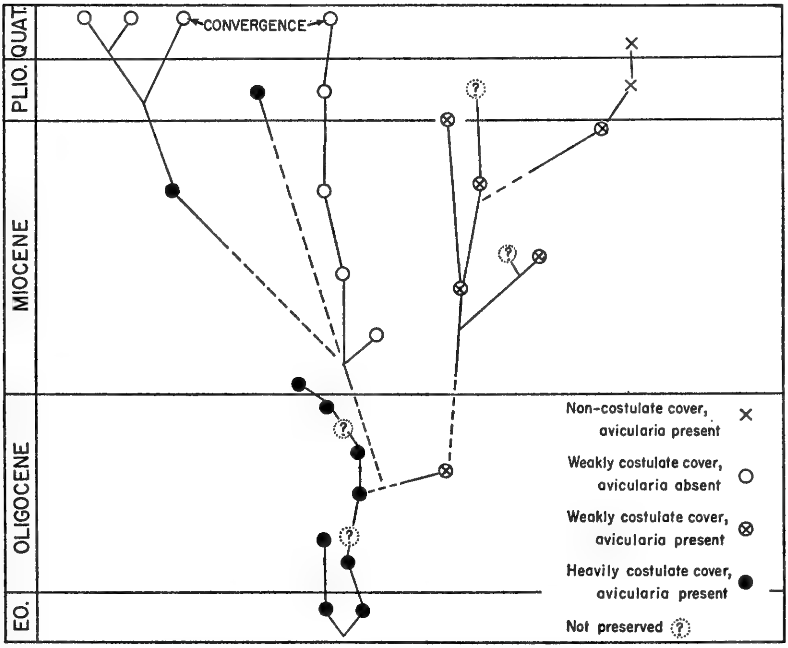

FIGURE 23.—Evolutionary trends in gonoecia.
Phylogenetic base as in Figure 20.

Lagaaij (1952, p. 126) pointed out that the gonoecia of *Metrarabdotos* follow complicated trends, with the Recent species *M.* (*U.*)

unguiculatum having a gonoecium of "Miocene" character. As shown in Figure 23, there has been a basic divergence between Old World and New World forms going back to mid-Oligocene representatives of *M.* (*Rhabdotometra*). The former show rapid reduction, and finally loss, of gonoecial costulation coupled with retention of gonoecial avicularia. Reduction in the costulation of the latter, on the other hand, was more gradual and never carried to completion. In two New World species, *M.* (*U.*) *kugleri* and *M.* (*B.*) *lacrymosum,* heavy costulation persisted very late. All of the New World forms, except the two last-named forms, lost their avicularia at an early stage. Parallelism or convergence produced weakly costulate gonoecia without avicularia in the two New World subgenera, *M.* (*Biavicularium*) and *M.* (*Uniavicularium*).

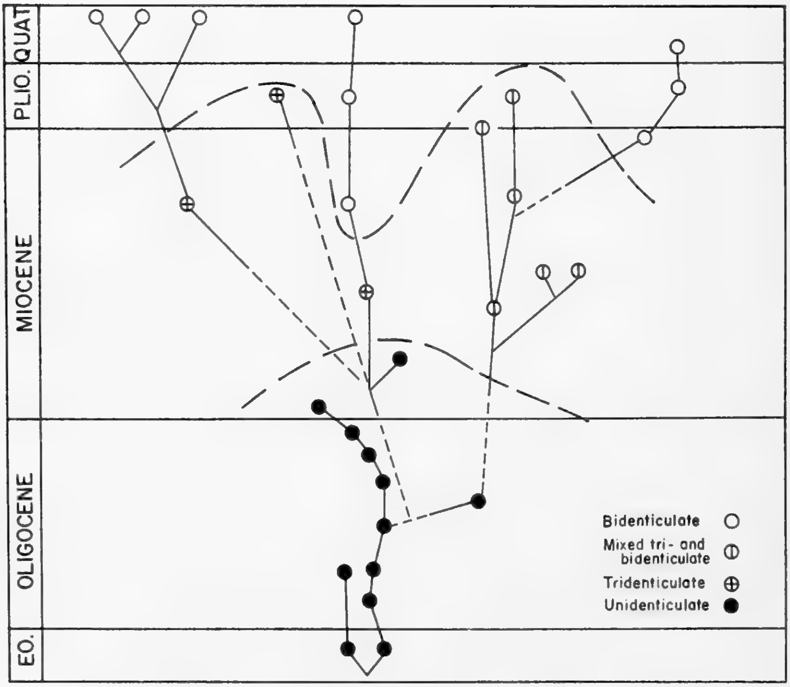

FIGURE 24.—Parallel evolution in oral denticulation. Phylogenetic base as in Figure 20.

The most obvious and deceptively simple evolutionary trend in *Metrarabdotos* is the change in oral denticulation (Figure 24) from unidenticulate in Eocene-early Miocene populations through tridenticulate in middle Miocene-Pliocene populations to bidenticulate in late Miocene-Recent populations. The separate evolutionary histories of coeval stocks displaying this trend were established on the basis of total morphologic change. The simple sequence, therefore, must be interpreted as parallel development.

ORIGIN

The origin of *Metrarabdotos* is a puzzle of long standing which has produced disagreement on the systematic placement of the genus (Buge and Galopim de Carvalho, 1963, pp. 139-141). Previous discussions have centered about morphologic comparisons without emphasizing their stratigraphic and geographic context. Moreover, as Harmer (1957) has shown, morphologic comparisons of Ascophora are meaningful only if account is taken of the development pattern of the frontal wall and its relation to the underlying ascus and to the orifice.

On this basis *Hippopodina* Levinsen, regarded by Canu (1914) and Canu and Bassler (1920, p. 524) as a close relative of *Metrarabdotos,* cannot be considered for an ancestral role because its evenly perforate frontal wall develops in nonumbonuloid fashion and its orifice is provided with condyles for hingement of the strongly chitinized operculum. This exclusion must be made even though species of *Hippopodina* occur in stratigraphic and geographic positions, in the upper Eocene of the North American Coastal Plain (Canu and Bassler, 1920, p. 532; Cheetham, 1962, p. 327), appropriate to the ancestry of *Metrarabdotos,* and they show oral dimorphism associated with larval brooding.

Likewise, *Trigonopora* Maplestone, identified with *Metrarabdotos* by Canu and Bassler (1935, p. 53) and many subsequent authors, cannot be given serious consideration because it is not known from pre-Oligocene rocks and occurs only in Australia. Morphologically, it resembles *Metrarabdotos* in having an umbonuloid frontal wall (cf., Brown, 1958, p. 64), shallow-unidenticulate secondary orifice, and lateral-oral avicularia with crossbars, and the two genera are related at the superfamily level.

The family Adeonidae Hincks includes a number of genera which have been compared morphologically with *Metrarabdotos.* Waters (1912, p. 497) called attention to the similarity of gonoecia of some adeonids and those of *M.* (*M.*) *moniliferum,* and Canu and Lecointre (1928, p. 59), followed by most subsequent authors, referred *Metrarabdotos* to that family. The genus with which it has been compared most frequently, either directly or by implication (Lagaaij, 1952, pp. 120-122; Buge, 1957, p. 291; and Canu, 1914, who referred *S. heteromorpha* to *Metrarabdotos*), is *Schizostomella* Canu and Bassler. Externally, some species of *Schizostomella* bear a striking resemblance to *Metrarabdotos* (pl. 16, fig. 1; Cheetham, 1966, figs. 67-69). Moreover, some of them, e.g., *S. crassa* (Canu) and *S. curryi* Cheetham, occur in middle and upper Eocene rocks. Unfortunately, *Schizostomella* became extinct in the Pliocene, so the relationship of its frontal wall to the secretory epithelium cannot be observed. In extant adeonids, however, such as *Adeonellopsis* MacGillivray, the wall develops in the nonumbonuloid mode (Harmer, 1957, pp. 645, 805), and in many genera it retains a separate opening (ascopore) to the sacciform ascus. Thin sections of Recent and fossil specimens of *Adeonellopsis* and of Eocene species of *Schizostomella* (pl. 18, figs. 4-5) reveal that the frontal wall, though it may be thick, is single layered and margined by a complete circumzooecial crown of areolae which originate low on the vertical walls ("parietal areolae" of Canu and Bassler, 1929, p. 376, and others). These structural relationships and the presence of ascopores on the gonoecia (pl. 16, fig. 1; Cheetham, 1966, p. 92) suggest that *Schizostomella* developed in nonumbonuloid fashion. Moreover, the distal part of the gonoecium of *Schizostomella* has an imperforate cover and is not recumbent on the distal zooecium (pl. 16, fig. 1; pl. 18, fig. 3). In this respect it is nearly identical to those of some species of *Adeonellopsis* (e.g., Cheetham, 1966, p. 97, fig. 75). The similarity of oral structure in *Metrarabdotos* and *Schizostomella* is more apparent than real; the tooth-like margins of the proximal sinus of the latter are part of the primary oral apparatus for hinging the operculum and, as such, are not homologous with the lateral oral denticles of some species of *Metrarabdotos*. Furthermore, the resemblance is with phylogenetically advanced, not primitive, species of *Metrarabdotos*. These arguments, and the fact that *Schizostomella* is an exclusively Old World genus, appear to remove it from an ancestral role. Other adeonid genera are morphologically even less like *Metrarabdotos* and need not be considered here.

The key to the origin of *Metrarabdotos*, aside from its umbonuloid frontal wall, is the distal shelf lying below its operculum, a feature which is lacking in all of the genera discussed above. *Escharoides* Milne Edwards, a widespread umbonuloid ranging from middle Eocene to Recent (Canu and Bassler, 1920, pp. 408-409; Brown, 1952, pp. 296-304; Levinsen, 1909, pp. 317-319; Cheetham, 1966, pp. 65-

68), possesses this feature in a less-developed state (pl. 16, fig. 3; Levinsen, 1909, p. 317; Cheetham, 1966, p. 65). *Escharoides* resembles species of *Metrarabdotos* in having a median proximal denticle in the secondary orifice; its paired lateral-oral avicularia develop at the distal end of the frontal wall (pl. 16, fig. 2); and its umbonuloid frontal wall (Harmer, 1902, p. 332) is margined with areolae only laterally and proximally.

Three major differences between *Escharoides* and *Metrarabdotos* provide an obstacle to casting the former in an ancestral role.

1. The brooding zooecia of *Escharoides* are ovicelled, and in most species, including the type species, the ovicells are imperforate (pl. 16, fig. 4). In at least two Eocene species, *E. aliferus* (pl. 16, fig. 2) and *E. laticella* (pl. 16, fig. 3), however, the ovicells are perforate and in the former are ornamented with costules and margined with graded areolae much like the distal cover of the gonoecium of primitive species of *Metrarabdotos*. The partial recumbency of the gonoecium of *Metrarabdotos* on the distal zooecium (pl. 17, fig. 4; Figure 7) suggests that its distal part may have been derived from a hyperstomial ovicell like that of *Escharoides*.

2. The zooecia of *Escharoides* communicate through pore chambers (dietellae) rather than simple pores (Levinsen, 1909, p. 317). The pore chambers are smaller in Eocene species (Cheetham, 1966, p. 66) than in later ones, and their presence is not constant even in some Recent species (Levinsen, 1909, pp. 318-319). The possibility of loss of pore chambers in the early evolution of *Metrarabdotos* cannot be discounted.

3. *Escharoides* is characterized by distal oral spines (pl. 16, figs. 3, 4), features wholly lacking in *Metrarabdotos;* spines are evanescent, however (Cheetham, 1966, figs. 40-41), or lacking (Lagaaij, 1952, p. 89) in some species.

On the whole, there are fewer serious objections to *Escharoides* than to any other genus as the ancestor of *Metrarabdotos*. An undiscovered species combining the frontal, oral, and avicularian features of *E. laticella* from the late Eocene of the Gulf and Atlantic Coastal Plain with the ovicell structure of *E. aliferus* from the late Eocene of Europe is the best possibility.

If *Escharoides* is the ancestor of *Metrarabdotos,* six modifications are required in the transition between the two: (1) loss of pore chambers; (2) loss of distal oral spines; (3) loss of calcified wall between ovicell and zooecial cavity; (4) development of oral dimorphism; (5) rotation of avicularian rostra onto peristome; and

(6) development of avicularian dimorphism. Once these changes were accomplished, only the last was reversed; loss of avicularian dimorphism within the genus *Metrarabdotos* is one aspect of the trend toward larger avicularia and occurred only in the subgenus *M.* (*Uniavicularium*).

RATES OF EVOLUTION

The phylogenetic pattern in *Metrarabdotos* (Figures 19, 20; time-scale after Funnell, 1964) suggests that rates of evolution either throughout the genus, or in subgeneric stocks, have not been constant. Stasigenetic interludes (e.g., B–H, N–L) followed bursts of cladogenetic activity (e.g., A–B, K–N–O) which took place soon after the inception of a subgenus. Only *M.* (*Metrarabdotos*) fails to show this speciation phase clearly; nevertheless, the incompletely known Pliocene Eurafrican species *M. elegans* Buge and Galopim de Carvalho, *M. lecointrei* Buge and Galopim de Carvalho, and *M. teixeirai* Buge and Galopim de Carvalho may be assignable to this subgenus and thus fill the gap in diversity. *M.* (*Uniavicularium*) has diversified only to the subspecies level and is probably some time away from its stasigenetic phase.

The phylogenetic pattern of the genus is nearly symmetrical on either side of the Atlantic Ocean. New World ranges, however, are slightly greater than those in the Old World. The diversification phase at the generic level took place in the Miocene. *M.* (*Uniavicularium*) is an incipient genus in that slight further divergence will result in a significant cumulative difference from the other subgenera.

REPOSITORIES

AHF: Allan Hancock Foundation, University of Southern California, Los Angeles.

ANSP: Academy of Natural Sciences of Philadelphia, Department of Geology.

BM (NH): British Museum (Natural History), London, Department of Palaeontology.

DCUB: Duvergier Collection, l'Université de Bordeaux.

FGS: Florida Geological Survey, Tallahassee.

IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels.

MNHN: Muséum National d'Histoire Naturelle, Paris.

RCSC: Reguant Collection, Seminario Conciliar, Barcelona.

USNM: U. S. National Museum, Department of Paleobiology.

USNM (Z): U. S. National Museum, Department of Invertebrate Zoology.

SYSTEMATIC DESCRIPTIONS

Order CHEILOSTOMATA Busk, 1852

Suborder ASCOPHORA Levinsen, 1909

Superfamily UMBONULACEA Canu, 1904, nom. transl.

Diagnosis.—Ascophora having frontal wall secreted by epifrontal membrane which develops from underlying anasciform membrane through proximal and lateral areolae; ascus not sacciform, floored by membrane, roofed directly by frontal wall; orifice usually with proximal or proximolateral denticles; brood chambers usually present; avicularia, where present, adventitious, with pointed or spatulate rostrum and pivotal bar.

Taxa included.—Families Umbonulidae Canu, 1904, Exochellidae Bassler, 1935, and Metrarabdotosidae Vigneaux, 1949.

Remarks.—The systematic significance of umbonuloid development of frontal walls in some ascophorans was first recognized by Harmer (1902, pp. 331, 332) and has been discussed subsequently by Hastings (1949, p. 527), Harmer (1957, pp. 644-646, 651), and Brown (1958, p. 64). Statements by Harmer and Hastings of suprafamilial implications of frontal wall patterns are, in part, the basis for establishing this taxon. Not all known umbonuloids (Ascophora Imperfecta Harmer, 1957) are included here, however. The families Exechonellidae Harmer, Chlidoniopsidae Harmer, Arachnopodiidae Jullien, Celleporariidae Harmer, Petraliidae Levinsen, and Petraliellidae Harmer, though having umbonuloid development of the frontal wall (Harmer, 1957, p. 646), are otherwise morphologically and probably phylogenetically different from Umbonulacea as here constituted.

Vigneaux (1949, pp. 14-20) proposed for ascophoran cheilostomes five nominal superfamilies, Schizoporellacea Jullien, 1903, Lepraliellacea Vigneaux, 1949, Smittinacea Levinsen, 1909, Reteporacea Smitt, 1867, and Galeopsacea Jullien, 1904. Two of them include genera placed by Harmer (1957) in the division Ascophora Imperfecta; the genus *Umbonula* Hincks was referred by Vigneaux to the superfamily Lepraliellacea, and other umbonulacean genera

(*Metrarabdotos* Canu, *Exochella* Jullien, *Escharoides* Milne Edwards, *Hippopleurifera* Canu and Bassler) were included by him in the superfamily Smittinacea. Unfortunately the type genera of both superfamilies are Ascophora Vera according to Harmer's (1957) assignments; thus neither name is available for the Umbonulacea as here conceived.

Family UMBONULIDAE Canu, 1904

Umbonulidae Canu, 1904, p. 18.

Diagnosis.—Umbonulacea having orifice without distal shelf and with or without a pair of proximolateral condyles hinging operculum; oral spines commonly present; avicularia, where present, lateral-suboral, rarely median-suboral; brood chambers either internal ovisacs or separated as entozooecial or hyperstomial ovicells, the brooding zooecia not otherwise different in form from autozooecia; interzooecial communication directly through uniporous or multiporous rosette plates set in large pores in distal and lateral walls.

Taxa included.—*Umbonula* Hincks, 1880, *Hippopleurifera* Canu and Bassler, 1924, *Hippomenella* Canu and Bassler, 1917, *Trigonopora* Maplestone, 1902, *Posterula* Jullien, 1903.

Remarks.—Hastings (1949, pp. 526, 527) referred *Hippopleurifera* to this family. Harmer (1902, p. 332) pointed out the resemblance between *Umbonula* and the type species of *Posterula.* The frontal wall of *Trigonopora* (pl. 16, figs. 5-6) and *Hippomenella* (both referred to the family Hippoporinidae Bassler by Brown, 1958) appears to be umbonuloid (cf. Brown, 1958, p. 64); therefore, they are here assigned to the family Umbonulidae.

Genus TRIGONOPORA Maplestone, 1902

TRIGONOPORA VERMICULARIS Maplestone, 1902

Plate 16, figures 5-6

Trigonopora vermicularis Maplestone; Brown, 1958, p. 64 (with synonymy).

Occurrence.—Oligocene (Janjukian), Victoria, Australia.

Material examined.—Two specimens USNM 650780–650781, Anticline Creek, Dartmoor, Victoria.

Remarks.—A row of areolae separates the ovicell from the frontal wall of the distal zooecium (pl. 16, fig. 5); therefore, the ovicell is hyperstomial rather than entozooecial (cf. Brown, 1958, p. 64). It differs further from the distal cover of the gonoecium of *Metra-*

rabdotos in having a single pair of fenestrae rather than intercostular perforations (pl. 16, fig. 6). The frontal wall and orifice of *T. vermicularis* are similar to those of *Metrarabdotos* at least superficially. A primary layer appears at the surface around the orifice, at the proximal denticle, on the lateral margins, and on the proximal margin of the ovicell. The superficial layer displays the typical vermiculate granulation of the frontal and ovicell surfaces.

Family EXOCHELLIDAE Bassler, 1935, nom. transl., Brown, 1952

Exochellinae Bassler, 1935, p. 33.
Exochellidae Bassler; Brown, 1952, p. 288.

Diagnosis.—Umbonulacea having orifice with feebly developed or no distal shelf below operculum and well-developed proximal denticles above it; oral spines; avicularia usually developed bilaterally; brood chambers separated as hyperstomial ovicells, the ovicelled zooecia not otherwise different in form from nonovicelled ones; interzooecial communication through pore-chambers.

Taxa included.—*Exochella* Jullien, 1888, *Escharoides* Milne Edwards, 1836.

Remarks.—Harmer (1902, p. 332) recognized the umbonuloid nature of the type species of *Escharoides*. Levinsen (1909, p. 84) called attention to the similarity in oral structure of *Escharoides* and *Exochella,* and Brown (1952, pp. 288, 289) considered them both to be umbonuloid.

Genus ESCHAROIDES Milne Edwards, 1836

ESCHAROIDES ALIFERUS (Reuss, 1869)

Plate 16, figure 2

Escharoides aliferus (Reuss); Cheetham, 1966, p. 66, figures 40-41 (with synonymy).

Occurrence.—Eocene (Lutetian-Ludian), France, England, Italy, Hungary, Poland, Rumania.

Material examined.—Specimen USNM 65765, Lutetian, Parnes, France.

Remarks.—This species has been restudied recently on the basis of material from the Auversian of Sussex, England (Cheetham, 1966, p. 66). The French Lutetian specimen illustrated here shows the stages of development of avicularian chambers, ringed with areolae, upon the frontal wall.

ESCHAROIDES LATICELLA (Canu and Bassler, 1920)

Plate 16, figure 3

Peristomella laticella Canu and Bassler, 1920, p. 413, pl. 54, figs. 5-7.

Occurrence.—Eocene (Jackson), Mississippi to North Carolina.

Material examined.—Lectotype (here designated) USNM 64107 (Canu and Bassler, 1920, pl. 54, fig. 7) and 2 paralectotypes USNM 650782–650783, Wilmington, North Carolina (1920, pl. 54, figs. 5-6); specimen USNM 650784 Jackson, Rankin Co., Mississippi.

Remarks.—The similarity of this species to *E. aliferus* is not as close as indicated by Canu and Bassler (1920, p. 413). The evenly perforate, globular ovicell, the smaller avicularian chambers, and the more prominent oral spines, in addition to the encrusting zoarial form and the smaller zooecia characterize *E. laticella.*

Among the occurrences of *E. laticella* given by Canu and Bassler (1920, p. 413), those in Alabama and Georgia could not be verified.

ESCHAROIDES COCCINEUS (Abildgaard, 1806)

Plate 16, figure 4

Cellepora coccinea Abildgaard, 1806, p. 30, pl. 146, figs. 1, 2.

Occurrence.—Recent, western France and British Isles to Shetland and Norway.

Material examined.—Specimen USNM (Z) 9462, Shetland.

Remarks.—The vermiculate tuberculation of the frontal wall and ovicell are developed in the superficial layer as in *Trigonopora vermicularis.*

Dissection of one zooecium of the Shetland specimen disclosed a distal oral shelf similar to but less developed than that of *Metrarabdotos.*

Family METRARABDOTOSIDAE Vigneaux, 1949, nom. transl.

Metrarabdotosinae Vigneaux, 1949, p. 90.

Diagnosis.—Umbonulacea having zooecial orifice with distal shelf below and proximal denticles above operculum; no oral spines; avicularia monomorphic or dimorphic, developed unilaterally or bilaterally from most distal group of frontal areolae, typically present on zooecia, present or absent on gonoecia; brood chambers not separated from zooecial cavity, the two forming a gonoecium with perforate and generally costulate distal cover and short, wide orifice lacking denticulation and distal shelf; interzooecial communication directly through uniporous rosette plates set in large pores in lateral and distal walls.

Taxa included.—Monotypic for *Metrarabdotos* Canu, 1914.

Remarks.—Vigneaux (1949, p. 90) proposed Metrarabdotosinae as a monotypic subfamily of Smittistomatidae Vigneaux, 1949, the other two genera of which, *Smittistoma* Canu, 1908, and *Bracebridgia* MacGillivray, 1886, belong to the family Adeonidae Hincks, 1884. The name Smittistomatidae (nom. correct. pro Smittistomidae Vigneaux) is thus a junior synonym of Adeonidae. *Metrarabdotos* is not an adeonid as defined below, and therefore the subfamily Metrarabdotosinae is here elevated to familial rank to receive that genus.

Genus METRARABDOTOS Canu, 1914

Metrarabdotos Canu, 1914, p. 472.

Diagnosis.—As for family.

Range.—Total range, uppermost Eocene to Recent. In the Gulf of Mexico-Caribbean region, it occurs virtually continuously throughout this interval; in the Mediterranean-Central European-North Sea region, it ranges from middle Oligocene to Pleistocene; in West Africa and off-shore islands, it ranges from Miocene to Recent; and in the Panamic Province, it is known only from Recent.

Type species.—*Eschara monilifera* Milne Edwards, 1836, by original designation.

Taxa included.—Eleven species, four of which are divided into twelve subspecies, are here assigned to five subgenera: *M.* (*Rhabdotometra*), *M.* (*Biavicularium*), *M.* (*Uniavicularium*), and *M.* (*Porometra*), all new; and *M.* (*Metrarabdotos*) Milne Edwards, 1836.

In addition, the following eight nominal taxa, though not assignable to subgenera on the basis of observable morphology, belong to *Metrarabdotos:*

M. canui Buge and Galopim de Carvalho, 1963, p. 170, pl. 2, fig. 3 (part—not pl. 2, figs. 1, 2); 1964, p. 655, pl. 1, figs. 2, 3; Galopim de Carvalho, 1964, p. 208, 209. Miocene, Portugal, Rhone Basin, Majorca, Morocco. [Probably related to *M.* (*Porometra*) *maleckii*, n. sp.]

Trigonopora colligata var. *catahoulana* McGuirt, 1941, p. 90, pl. 3, figs. 9, 12; pl. 4, figs. 1, 2. Miocene, Louisiana. [Probably related to *M.* (*Biavicularium*) *chipolanum*, n. sp.; types missing.]

M. elegans Buge and Galopim de Carvalho, 1963, p. 162, pl. 1, figs. 3-4; Galopim de Carvalho, 1966, p. 102; Buge, 1966, p. 42, pl. C, fig. 5. Pliocene, Portugal, Morocco. [Ordinary avicularia similar to those of *M.* (*Metrarabdotos*) *nysti* (Lagaaij).]

M. girondicum Duvergier, 1924, p. 40, pl. 5, figs. 1-7; Vigneaux, 1949, p. 90, pl. 8, figs. 11-12; Buge and Galopim de Carvalho, 1963, p. 160, fig. 12 [= *M. girondicum* var. *crispum* Duvergier, 1924, p. 41, pl. 5, fig. 8. = *Trigonopora girondica* (Duvergier); Roger and Buge, 1947, p. 227; Buge, 1964, p. 165. = *T. monilifera* (Milne Edwards); David and Demarq, 1964, p. 155]. Miocene, Aquitaine Basin, France. [The peculiar tuberculation of the syntypes of this species, well shown in the illustrations of Duvergier (1924), may be due to intergrowth with encrusting hydroids. Whatever its cause, the intense calcification of the frontal surface and the general absence of zoarial margins make difficult the interpretation of these specimens. The ordinary avicularia and the gonoecial special avicularia are like those of *M.* (*Porometra*) *helveticum* (Roger and Buge) but only one fourth of the zooecial orifices are tridenticulate and the gonoecium seems to lack avicularia.]

M. lecointrei Buge and Galopim de Carvalho, 1963, p. 174, pl. 2, fig. 4; 1964, p. 654, pl. 1, fig. 1; Galopim de Carvalho, 1966, p. 102, pl. 1, fig. 4, pl. 2, fig. 4; Buge, 1966, p. 44, pl. C, fig. 2. Pliocene, Portugal, Morocco. [Probably related to *M.* (*Metrarabdotos*) *moniliferum* (Milne Edwards).]

Trigonopora girondica tarraconensis Reguant, 1960, p. 128, fig. 2; 1961, p. 237. [= *M. tarraconense* (Reguant); Buge and Galopim de Carvalho, 1963, p. 178, fig. 22 (with synonymy).] Miocene, Spain. [The holotype and paratypes are very poorly preserved; the presence of ordinary and marginal special avicularia indicates probable relationship to *M.* (*Porometra*) *helveticum* (Roger and Buge).]

M. teixeirai Buge and Galopim de Carvalho, 1963, p. 157, pl. 1, figs. 1-2; 1964, p. 655; Galopim de Carvalho, 1966, p. 102; Buge, 1966, p. 41, pl. C, fig. 1. Pliocene, Portugal, Morocco; Neogene Cape Verde Islands. [Probably related to *M.* (*Metrarabdotos*) *moniliferum* (Milne Edwards).]

M. vinassai Panzera, 1932, p. 295, pl. 9, fig. 13; Buge and Galopim de Carvalho, 1963, p. 176 (with synonymy); Buge, 1964, p. 167. Miocene, Libya. [Topotypes in Voigt Collection, Hamburg, lack gonoecia; marginal special avicularia and tridenticulate orifices suggest affinity with *M.* (*Porometra*) *helveticum* (Roger and Buge).]

The following citations refer to *Metrarabdotos* but cannot be placed subgenerically or specifically on the basis of available evidence:

Eschara monilifera Milne Edwards; Seguenza, 1879, pp. 131, 208, 296, 371 (Miocene and Pliocene, Italy); Fuchs, 1883, p. 52, pl. 18, fig. 8 (Miocene, Egypt).

Mucronella monilifera (Milne Edwards); Namias, 1891, p. 497 (Pliocene, Italy).

Escharoides moniliferus (Milne Edwards); Neviani, 1891, p. 125 (Pliocene and Pleistocene, Italy); 1894, p. 667 (Pliocene, Italy); Almera, 1897, p. 379 (Miocene, Spain); de Angelis, 1898, p. 24 (Miocene, Spain); 1899, p. 40, pl. B, fig. 13 (Miocene, Spain).

Schizoporella monilifera (Milne Edwards); Neviani, 1895, p. 238 (Pliocene, Italy); 1896, p. 122 (Pleistocene, Italy); 1897, p. 587 (Miocene, Sardinia); 1898, pp. 101, 107 (Pliocene and Pleistocene, Italy); 1900a, p. 238 (Miocene, Italy); 1900b, p. 61 (Pliocene, Italy); 1900c, p. 366 (Pliocene, Italy); Canu, 1912, p. 209 (Miocene, Egypt); 1913, p. 127 (Miocene, France).

Metrarabdotos moniliferum var. *helveticum* (Roger and Buge); Buge, 1947, p. 347 (Pliocene, Tunisia).

Trigonopora monilifera (Milne Edwards); Reguant, 1961, p. 237 (Miocene, Spain; Pliocene, Majorca); Annoscia, 1963, p. 233, pl. 15, figs. 1a, b; pl. 16, figs. 1, 2; pl. 17, figs. 1-3 (Pleistocene, Italy).

Metrarabdotos moniliferum (Milne Edwards); Buge and Galopim de Carvalho, 1964, p. 654, pl. 1, fig. 4 (Pliocene, Portugal; Neogene, Cape Verde Islands); Galopim de Carvalho, 1966, p. 101 (Pliocene, Portugal); Buge 1966, p. 43, fig. 5 (Neogene, Spanish Morocco).

The following citations are here excluded from *Metrarabdotos:*

Eschara monilifera Milne Edwards; Stoliczka, 1862, p. 88 (Oligocene, Germany); Reuss, 1864, p. 35 (Oligocene, Germany); Gottardi, 1886, p. 305 (Eocene, Italy); Pergens, 1887b, p. 37 (Eocene, Rumania); 1889, p. 70 (Eocene, Poland).

Lepralia monilifera var. *armata* Waters, 1881, p. 335, pl. 15, fig. 24 (Miocene, Australia).

Lepralia monilifera (Milne Edwards); MacGillivray, 1895, p. 76, pl. 14, fig. 28 (Miocene, Australia).

Metrarabdotos heteromorphum (Reuss); Canu, 1914, p. 472, pl. 14, figs. 1-4 (Oligocene, France); 1918, p. 359 (Oligocene, France).

Trigonopora monilifera (Milne Edwards); Ghiurca, 1962, table 1 (Eocene, Rumania); Malecki, 1963, p. 130, pl. 14, fig. 1 (Eocene, Poland).

Remarks.—The name of the genus is not only unwieldy but, as it is presumably derived from *μητρα* and *ρ̆αβδωτος*, the terminal element is adjectival rather than substantive. The gender is thus indeterminate etymologically and is, therefore, that implied by its author (Canu, 1914, p. 472), who considered it neuter, not masculine (cf., Duvergier, 1924, p. 40; Buge and Galopim de Carvalho, 1963). The genitive stem of the name, equally undiscernible etymologically, is that attributed to it by the first author of a family-group name (Metrarabdotosinae Vigneaux, 1949) based on *Metrarabdotos.*

The earliest described species referable to *Metrarabdotos* as here conceived is *Eschara monilifera* Milne Edwards, 1836, the type chosen by Canu (1914). None of the five species originally included in *Eschara* Linné, 1758, is congeneric with *E. monilifera.*

D'Orbigny (1852, p. 448) referred *E. monilifera* to *Escharellina* d'Orbigny (1852, p. 206) which was erected for nine species, three living and six from the Miocene of the Vienna Basin. All of the latter had been described and figured by Reuss (1848) and include adeonids, umbonulids, and other forms. The one nominal species referable to *Metrarabdotos,* figured by Reuss (1848, pl. 8, figs. 25a, b) as *Eschara punctata* Philippi, was not placed by d'Orbigny (1852) in *Escharellina.* Therefore, whatever the fate of *Escharellina* (cf. Bassler, 1953, p. 235), it has no nomenclatural connection with the species here placed in *Metrarabdotos.*

Gabb and Horn (1862, p. 136) described a species here referred to *Metrarabdotos* as *Escharella micropora;* the type species of *Escharella* Gray, 1848, is not congeneric with those here referred to *Metrarabdotos* (Brown, 1952, p. 337). Namias (1891, p. 497) referred the nominal species *E. monilifera* to *Mucronella* Hincks, 1877, now considered a synonym of *Escharella* (Brown, 1952, p. 337).

Busk (1884, p. 150) placed a species of *Metrarabdotos, M. tenue,* in *Smittia;* the type species of *Smittina* Norman, 1903 (=*Smittia* Hincks, 1877, not Holmgren, 1869) is not congeneric with the species here referred to *Metrarabdotos* (Osburn, 1952, p. 399).

Neviani (1891, p. 125; 1894, p. 667), Almera (1897, p. 31), and de Angelis (1898, p. 24; 1899, p. 40) placed the nominal species *E. monilifera* in *Escharoides* Milne Edwards, 1836, the type species of which is discussed above.

Neviani (1895, p. 238; 1896, p. 122; 1897, p. 587; 1898, pp. 101, 107; 1900a, p. 238; 1900b, p. 61) and Canu (1903, p. 116; 1912, p. 209; 1913, pp. 126, 127) placed the nominal species *E. monilifera* in *Schizoporella* Hincks, 1877, the type species of which is generically distinct from the assemblage here included in *Metrarabdotos* (Lagaaij, 1952, p. 65).

When Canu (1914, p. 472) erected *Metrarabdotos,* he included in it *Eschara heteromorpha* Reuss, 1869, as well as the type species. Canu and Bassler (1920, p. 536) were probably referring to the same species under the binomen *Metrarabdotos polymorphum* (Reuss). This species belongs to *Schizostomella* Canu and Bassler, 1927 (Cheetham, 1966, p. 91).

Canu and Bassler (1935, p. 53), in restudying *Trigonopora vermicularis* Maplestone, 1902, concluded that *Metrarabdotos* is a junior subjective synonym of *Trigonopora* Maplestone, 1902, and their conclusion was followed by Osburn (1940, p. 447; 1952, p. 443), McGuirt (1941, p. 88), Roger and Buge (1947, p. 225), Lagaaij (1952, p. 122), Bassler (1953, p. 214), Marcus (1955, p. 304), Kühn (1955, p. 232), Buge (1957 p. 299), Cheetham (1957, p. 90; 1963, p. 70), Reguant (1960, p. 128; 1961, p. 237), Ghiurca (1961a, p. 726; 1961b, table 1; 1962, table 1), Annoscia (1963, p. 233), and David and Demarcq (1964, p. 155). Brown (1958, p. 64) and Buge and Galopim de Carvalho (1963, p. 138) rejected the synonymy, though apparently on different grounds. In Brown's view the major differentiating characters of *Metrarabdotos* are its sinuate orifice, umbonuloid frontal wall, and perforate "ovicell"; Buge and Galopim de Carvalho described two species of *Metrarabdotos* as having a lyrulate orifice and two as having imperforate "ovicells." Moreover, the frontal wall of *T. vermicularis* appears to be umbonuloid (see discussion above).

The present study has disclosed that the most significant difference between *Metrarabdotos* and *Trigonopora vermicularis* is in the structure of the brooding zooecia. The highly differentiated gonoecia of the former contrast with the hyperstomially ovicelled, but not otherwise modified, brooding zooecia of the latter. The gonoecia of *Metrarabdotos* have been interpreted as hyperstomially ovicelled by Marcus (1955, p. 304) and as entozooecially ovicelled by most other authors.

The diagnosis presented by Buge (1966, p. 40) differs from that set forth here in (1) excluding nonerect forms (although *M.* (*U.*) *unguiculatum* Canu and Bassler was included in the genus by Buge and Galopim de Carvalho, 1963), (2) describing the frontal areolae as occurring in two lateral rows, (3) characterizing the brooding zooecia as entozooecially ovicelled, and (4) interpreting the simple interzooecial communication pores as parietal dietellae.

Subgenus METRARABDOTOS (RHABDOTOMETRA), n. subgen.

Diagnosis.—*Metrarabdotos* having elongate zooecia and orifice with simple distal shelf and a single, median, usually shallow proximal denticle in the short peristome; areolae almost invariably in a single row; avicularia typically paired, dimorphic: (1) ordinary avicularia lateral to secondary orifice, or slightly proximal or distal, directed proximally or transversely inward; (2) special avicularia developed generally on zooecia lateral to gonoecia and rarely at random locations; gonoecium with avicularia, unhooded proximal lip, and strongly convex, usually heavily costulate distal cover margined by graded areolae.

Range.—Uppermost Eocene-lower Miocene (Vicksburg-Tampa), southeastern to south-central United States; middle Oligocene (Stampian), France.

Type species.—*Escharella micropora* Gabb and Horn, 1862.

Taxa included.—*M.* (*R.*) *micropora* (Gabb and Horn, 1862); *M.* (*R.*) *vigneauxi,* n. sp.

Remarks.—This earliest subgenus of *Metrarabdotos* is especially characterized by virtual restriction of special avicularia to zooecia lateral to gonoecia. Its oral denticulation overlaps that of *M.* (*Biavicularium*) and its gonoecial ornamentation that of *M.* (*Porometra*).

METRARABDOTOS (RHABDOTOMETRA) MICROPORA
(Gabb and Horn, 1862)

Diagnosis.—Zooecia medium size; areolae in one row, rarely with additional proximal ones; oral denticle shallow. Ordinary avicularia small, lateral or slightly proximal or distal; special avicularia moderately to strongly differentiated, developed generally on zooecia lateral to gonoecia, on few other zooecia in vicinity of gonoecia. Gonoecia with reflected distal lip and heavily costulate distal surface.

Differs from *M.* (*R.*) *vigneauxi* in having weaker differentiation of special avicularia, shallower oral denticle, and more heavily costulate gonoecia with reflected distal lip.

Occurrence.—This species includes three chronologic-geographic subspecies:

1. ***M.* (*R.*) *micropora micropora:*** Eocene-Oligocene (Shubuta to Chickasawhay Fms.), Alabama to Louisiana.
2. ***M.* (*R.*) *micropora floridanum:*** Eocene-Oligocene (Bumpnose Ls., Marl above Cooper), Florida and Georgia.
3. ***M.* (*R.*) *micropora butlerae:*** Miocene (Tampa Fm.), western Florida.

TABLE 7.—*Zooecial variates in* Metrarabdotos (Rhabdotometra).

For each sampling unit of a species or subspecies, statistical measures are shown in a column for each character in the following order: mean, standard deviation, and sample size. Mean and standard deviation are in millimeters for all characters except na. Four decimal places in mean and standard deviation are given only for purposes of calculation of other statistics.

[See Figure 9 for character symbols and Table 1 for unit symbols.]

Species or subspecies	Unit symbol	Lz	lz	ho	lo	Lav	na
M. (R.) m. floridanum	**A1-3**	0.6637	0.2525	0.1312	0.1190	0.1133	18.55
		0.0741	0.0328	0.0181	0.0147	0.0208	1.88
		42	43	42	43	40	40
	A4	0.6546	0.3027	0.1476	0.1328	0.1361	17.26
		0.0758	0.0319	0.0144	0.0150	0.0388	1.84
		24	24	24	24	21	23
M. (R.) m. micropora	**B**	0.7490	0.2654	0.1355	0.1272	0.0764	17.95
		0.0872	0.0524	0.0130	0.0125	0.0137	2.67
		39	39	39	39	28	38
	C	0.7406	0.2800	0.1329	0.1286	0.0842	19.33
		0.0951	0.0430	0.0153	0.0160	0.0186	3.27
		33	33	33	33	25	33
	D	0.7553	0.2874	0.1386	0.1324	0.0815	21.45
		0.0841	0.0268	0.0215	0.0125	0.0168	2.16
		29	29	29	29	26	29
	E	0.7560	0.2819	0.1356	0.1313	0.0777	19.50
		0.0821	0.0517	0.0158	0.0171	0.0166	2.12
		18	18	18	18	15	18
	F	0.6957	0.2674	0.1336	0.1202	0.0879	19.51
		0.0505	0.0348	0.0202	0.0158	0.0209	1.58
		39	39	39	39	28	35
	G	0.7972	0.2725	0.1310	0.1282	0.0750	22.76
		0.0767	0.0178	0.0233	0.0175	0.0089	3.95
		22	22	22	22	11	21
	H	0.7852	0.3049	0.1556	0.1481	0.0616	23.28
		0.1458	0.0184	0.0189	0.0146	0.0104	0.0340
		9	9	9	9	8	7
M. (R.) m. butlerae	**J**	0.7739	0.2990	0.1579	0.1378	0.0958	20.30
		0.0641	0.0212	0.0134	0.0167	0.0297	1.64
		10	10	10	10	9	10
M. (R.) vigneauxi	**I**	0.7707	0.3148	0.1517	0.1291	0.1001	21.78
		0.0793	0.0201	0.0182	0.0181	0.0099	1.66
		19	19	17	18	17	18

TABLE 8.—*Gonoecial variates and length of special avicularia in* Metrarabdotos (Rhabdotometra). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lg	lg	ho	lo	LAv
M. (R.) m. floridanum	**A**	1.1100	0.5105	0.0508	0.3124	0.2311
		0.1065	0.0453	0.0232	0.0436	0.0527
		5	5	4	5	5
M. (R.) m. micropora	**B**	1.1104	0.5840	0.0616	0.3824	0.1824
		0.0645	0.0407	0.0214	0.0316	0.0212
		14	14	14	14	7
	C	1.1312	0.5530	0.0630	0.3542	0.1083
		0.1191	0.0299	0.0261	0.0287	—
		8	8	8	8	3
	D	1.2700	0.6858	0.0889	0.4064	0.1905
		—	—	—	—	—
		3	3	3	3	3
	E	1.1648	0.5712	0.0470	0.3360	0.1643
		0.0519	0.0419	0.0094	0.0412	—
		5	5	5	5	3
	F	1.0765	0.6154	0.0585	0.3305	0.1643
		0.0563	0.0174	0.0123	0.0391	—
		8	8	8	8	3
	G	1.3420	0.6181	0.0677	0.3133	0.1680
		—	—	—	—	—
		3	3	3	3	1
	H	1.0416	0.5768	0.0896	0.3640	0.1120
		—	—	—	—	—
		1	2	2	2	1
M. (R.) m. butlerae	**J**	1.1648	0.6384	0.0784	0.4144	0.1904
		—	—	—	—	—
		1	1	1	1	1
M. (R.) vigneauxi	**I**	1.1684	0.5080	0.1016	0.3556	0.3238
		—	—	—	—	—
		1	1	1	1	1

METRARABDOTOS (RHABDOTOMETRA) MICROPORA MICROPORA (Gabb and Horn, 1862)

Plate 1, figures 1–4; plate 2, figures 1–4; plate 3, figures 1–4; plate 17, figures 1, 4

Escharella micropora Gabb and Horn, 1862, p. 136, pl. 19, fig. 17; de Gregorio, 1890, p. 242, pl. 40, figs. 8–20; Canu and Bassler, 1920, p. 8; Richards, 1968, p. 22.

Escharella micropora var. *asperulata* de Gregorio, 1890, p. 242, pl. 40, figs. 21, 22.

Escharella micropora de Gregorio (sic); Canu and Bassler, 1920, p. 11.

Metrarabdotos moniliferum (Milne Edwards); Canu and Bassler, 1920, p. 533, pl. 98, figs. 1–10; McGuirt, 1934, p. 28.

Metrarabdotos grande Canu and Bassler, 1920, p. 537, pl. 98, figs. 11–15; Buge and Galopim de Carvalho, 1963, p. 152, fig. 6.

Metrarabdotos monoliferum (sic) (Milne Edwards)?; Cooke, 1926, p. 292.

Metrarabdotus (sic) *monoliferum* (sic) (Milne Edwards); Howe, 1942, p. 269.

Trigonopora sp.; McGuirt, 1941, p. 89, pl. 4, figs. 7, 8, 10.

Trigonopora grandis (Canu and Bassler); McGuirt, 1941, p. 89, pl. 10, figs. 8, 10.

Trigonopora monilifera var. *vicksburgica* Roger and Buge, 1947, p. 228.

Metrarabdotos sp.; Howe, 1948, pl. 1, fig. 22.

Metrarabdotos colligatum Canu and Bassler; Howe, 1948, p. 70, pl. 1, figs. 23, 31.

Trigonopora vicksburgica Roger and Buge; Lagaaij, 1952, p. 126; Cheetham, 1957, pp. 90–93 (part); 1963, p. 70 (part, not pl. 3, fig. 10).

Metrarabdotos vicksburgicum (Roger and Buge); Buge and Galopim de Carvalho, 1963, p. 143, figs. 1–2.

Diagnosis.—Areolae in a single row; ordinary avicularia directed proximally and generally inward; special avicularia strongly differentiated.

Occurrence.—Uppermost Eocene (Vicksburgian) Shubuta Clay, Clarke Co., Mississippi; Red Bluff Formation, Clarke and Washington Cos., Alabama; Oligocene (Vicksburgian), Red Bluff Formation, Wayne Co., Mississippi, Clarke and Washington Cos., Alabama; Mint Spring Marl, Warren and Rankin Cos., Mississippi; Marianna Limestone, Clarke, Washington, and Monroe Cos., Alabama; Glendon Limestone, Jasper Co., Mississippi, and Clarke and Washington Cos., Alabama; Byram Marl, Hinds Co., Mississippi; Chickasawhay Limestone, Washington Co., Alabama.

Material studied.—Probable syntype of *M. micropora* ANSP, labeled "type, Alabama?"; lectotype of *M. grande* (here designated) USNM 649349 (Canu and Bassler, 1920, pl. 98, fig. 12), paralectotypes USNM 649350–649352 (1920, pl. 98, figs. 13-15); USNM 64317 (1920, pl. 98, fig. 11; 15 specimens in zoarial restoration), all from Marianna Limestone, 3 miles southeast of Vosburg, Jasper Co., Mississippi; specimens USNM 649341–649348 (Canu and Bassler, 1920, pl. 98, figs. 2-9); USNM 64316 (Canu and Bassler, 1920, pl. 98, fig. 1; 12 specimens in zoarial restoration), all from Marianna Limestone, 1 mile north of Monroeville, Monroe Co., Alabama; specimen USNM 650785 Shubuta Clay, Shubuta, Clarke Co., Mississippi; 4 specimens USNM 650786–650788, lower Red Bluff Formation, Little Stave Creek, Clarke Co., Alabama; 4 specimens USNM 650789–650792, lower Red Bluff Formation, St. Stephens Quarry, Washington Co., Alabama; 4 specimens USNM 650793–650795, upper Red Bluff Formation, Little Stave Creek; 4 specimens USNM 650796–650799, upper Red Bluff Formation, St. Stephens Quarry; specimen USNM 650800, Red Bluff Formation, Hiwannee, Wayne Co., Mississippi; 2 specimens USNM 650801–650802, Mint Spring Marl, Mint Spring Bayou, Warren Co., Mississippi; 4 specimens USNM 650803–650805, Mint Spring Marl, Brandon Quarry, Rankin Co., Mississippi; 2 specimens USNM 650806–650807, lower Marianna Limestone, St. Stephens Quarry; 2 specimens USNM 650808–650809, lower Marianna Limestone, Little Stave Creek; 5 specimens USNM 650810-650814, upper Marianna Limestone, Little Stave Creek; 2 specimens USNM 650815–650816, Marianna Limestone, 1 mile north of Monroeville; 3 specimens USNM 650817–650819, 2.8 miles south of Stafford Springs, Jasper Co., Mississippi; 2 specimens USNM 650820–650821, Chickasawhay Formation, St. Stephens Quarry.

Description.—*Zoarium* erect, arborescent, repeatedly and unequally branching, originating from a small, encrusting base; branches bilaminate, subcylindrical to compressed, narrow to moderately wide, with zooecia arranged in 5 to 20 longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally generally by intercalation, rarely by bifurcation.

Zooecia irregularly rectangular to claviform, medium size, elongate, marginal zooecia not distinctly broader than central ones.

Frontal wall thin, convex, becoming thick and flat with age, highest at proximolateral corners of peristome. Frontal surface finely granular, with coarser granules on peristome and rarely on midline. Areolae extremely variable in size, irregularly elliptical to polygonal, disposed in a single, evenly spaced row around lateral and proximal margins, numbering 13-22 in *"vicksburgicum"* form, 20-28 in *"grande"* form. Interareolar costules weakly developed as a rule, but commonly strong, reaching nearly to frontal midline.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular to oval, with simple, arcuate, nearly vertical distal shelf. Peristome thin, short, reaching just to distal margin of zooecium, without deep-seated structures, but with a single, median, bluntly tapering, lyrule-like denticle at, or just below, level of proximal lip of secondary orifice. Secondary orifice oval, broadly rounded distally, with broad, poorly defined, proximal sinus, in some zooecia divided by a short mucro projecting over median denticle.

Ordinary avicularia small, paired, rarely single or absent, present on gonoecia as well as zooecia; placed on lateral margins of peristome, at oral midpoint or slightly distally or proximally; rostrum pointed, directed proximally, upward, and inward or, rarely, slightly outward; on heavily calcified portions of zoarium avicularia may be occluded by overlapping frontal wall of distal zooecium.

Special avicularia single or paired with ordinary avicularium; developed commonly on zooecia laterally adjacent to distal part of a gonoecium, rarely on other zooecia in vicinity of gonoecium; rostrum elongated, directed proximally and inward to lateral margin of secondary orifice; chamber extends distally and outward from orifice, not swollen.

Gonoecium one and a half times as long and twice as broad as zooecia. Orifice crescent shaped; distal lip with straight or triangular flange reflected over frontal surface; proximal lip not produced. Distal cover strongly convex, with broadly rounded distal margin and granular surface finely and evenly perforate between costules; areolae evenly spaced around distal and lateral margins, increasing in size distally; costules narrow or wide, sharply raised, granular.

Remarks.—This variable assemblage ranges throughout the Vicksburg of the central Gulf Coast region. Canu and Bassler (1920, pp. 533-538) partitioned it into two morphologic species, in part sympatric. One, which they identified with *M. moniliferum* (Milne Edwards), is characterized by narrow branches, short zooecia, and avicularia; the other, which they named *M. grande,* has wide branches, long zooecia, and no avicularia. Roger and Buge (1947) excluded the first form from *M. moniliferum* and named it *M. vicksburgicum.* The two concepts were retained by them and by Buge and Galopim de Carvalho (1963).

The range of variation included in the two morphologic species is embraced by specimens from the same sample (e.g., pl. 1, figs. 2, 4) and, rarely, even by the same zoarial fragment (e.g., pl. 2, fig. 4). Avicularia, for example, occur on some zooecia of every specimen of the *M. grande* form examined, including the syntypes (e.g., pl. 3, fig. 4) and are lacking from some zooecia of Canu and Bassler's hypotypes of the *"vicksburgicum"* form (pl. 2, fig. 1).

The distal cover of the gonoecium of this subspecies has been interpreted as imperforate (Buge and Galopim de Carvalho, 1963, pp. 144, 152), but all gonoecia examined have small intercostular perforations (pl. 1, figs. 1, 3-4; pl. 2, figs. 2, 4).

The syntype figured by Gabb and Horn (1862, pl. 19, fig. 17), ANSP 83, cannot be found. Gabb and Horn's illustration, especially of the gonoecia, leaves little room for doubt that the specimen is consubspecific with the material described here. Moreover, a probable syntype, ANSP 31285, labeled "type," remains in the Academy collection. This specimen (pl. 3, fig. 3) lacks gonoecia but otherwise agrees with Gabb and Horn's description and with the other material described here.

METRARABDOTOS (RHABDOTOMETRA) MICROPORA BUTLERAE, n. subsp.

Plate 4, figures 1-2

Diagnosis.—Few extra areolae present proximally; ordinary avicularia generally directed transversely inward; special avicularia strongly differentiated.

Occurrence.—Miocene, Tampa Formation, Falling Waters Sink, Washington Co., Florida.

Material studied.—Holotype USNM 650822 and paratypes USNM 650823–650824.

Description.—*Zoarium* erect, arborescent, composed of moderately wide, bilaminate, compressed fronds with zooecia arranged in twelve or more longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation or bifurcation.

Zooecia irregularly rectangular to claviform, medium size, elongate, the marginal zooecia not broader than central ones.

Frontal wall thin, moderately convex, highest at proximolateral corners of peristome. Frontal surface finely granular, with coarser granules developed along midline. Areolae large, elliptical, disposed in a single, evenly spaced row around proximal and lateral margins, numbering usually 17-22; few areolae of second row developed proximally on some zooecia. Interareolar costules weak, limited to periphery.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular to oval; distal shelf simple, nearly vertical, arcuate.

Peristome without deep-seated structures, but with a single, median, bluntly tapering, or rarely bifid, lyrule-like denticle at, or just below, level of proximal lip of secondary orifice. Secondary orifice oval, broadly rounded distally, interrupted proximally in a broad, shallow, poorly defined median notch. Peristome thin, short, not differentiated from frontal surface, inclined proximally, reaching just to distal margin of zooecium.

Ordinary avicularia small, paired, present on gonoecia as well as zooecia; placed on lateral margins of peristome at midline of secondary orifice; rostrum short, pointed, directed transversely orally or slightly distally or slightly proximally on zooecia, proximally on gonoecia.

Special avicularia single or paired with ordinary one, developed on zooecia distolaterally adjacent to a gonoecium; rostrum elongate, directed proximally and inward to lateral margin of secondary orifice; chamber extending distally and outward from orifice, not swollen.

Gonoecium one and a half times as long and twice as broad as zooecia. Orifice crescent shaped; distal lip a triangular flange reflected over frontal surface of gonoecium; proximal lip not produced. Distal cover semielliptical, with broadly rounded distal margin and strongly convex, granular surface finely and evenly perforate between costules. Areolae evenly spaced around distal and lateral margins, increasing in size distally. Costules narrow, sharply raised, granular.

Remarks.—This subspecies is named in honor of Miss E. A. Butler of the Sinclair Oil Company.

METRARABDOTOS (RHABDOTOMETRA) MICROPORA FLORIDANUM, n. subsp.

Plate 4, figures 3–5; plate 5, figures 1–4

Trigonopora vicksburgica Roger and Buge; Cheetham, 1957, pp. 90, 93 (part); 1963, p. 70 (part), pl. 3, fig. 10.

Diagnosis.—Areolae in a single row; ordinary avicularia directed proximally and generally inward; special avicularia moderately differentiated.

Occurrence.—Uppermost Eocene (Vicksburgian), Bumpnose Limestone, Jackson and Polk Cos., Florida; Oligocene (Vicksburgian), marl above Cooper Marl, Pulaski Co., Georgia.

Material studied.—Holotype USNM 650825 and 4 paratypes USNM 650826, Smith's quarry, 5½ miles northwest of Marianna, Jackson Co., Florida; paratypes USNM 650827–650828 and FGS 5392, Marianna Lime Products quarry, 6 miles northwest of Marianna, Jackson Co., Florida; paratypes USNM 650829–650831, Avon Park Rifle Range well (FGS well 381), depth 320 feet, Polk Co., Florida; 6 paratypes USNM 650832–650833, Ocmulgee River, 3 miles below highway bridge at Hawkinsville, Pulaski Co., Georgia.

Description.—*Zoarium* erect, arborescent; branches subcyclindrical to compressed, bilaminate, with zooecia arranged in as many as 20 longitudinal rows, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation.

Zooecia rectangular, small, elongate, the marginal ones not broader than central ones.

Frontal wall thin, moderately convex in young zooecia; thick, flat in old ones. Surface finely granular, with few coarser granules medially and strong interareolar costules peripherally. Areolae large, subcircular, disposed in a single, evenly spaced row of 14-22.

Orifice steeply inclined distally, placed deep in peristome, small, oval, with simple, shallow distal shelf. Peristome thin on young zooecia, thick on old ones, highest at proximolateral corners of secondary orifice, reaching just to distal margin of zooecium. Secondary orifice rounded-triangular with deep proximal notch having a single median denticle.

Ordinary avicularia large, paired, present on gonoecia as well as zooecia; placed on lateral margins of secondary orifice at mid-point or slightly distally, with rostrum directed proximally, upward and usually inward; crossbar rarely preserved.

Special avicularia developed on zooecia of random position and more regularly on zooecia lateral to gonoecia; feebly differentiated from ordinary ones, with rostrum attenuated and chamber usually swollen.

Gonoecium twice as long and twice as broad as zooecia. Orifice crescent shaped, with reflected distal lip and unhooded proximal lip. Distal cover strongly convex with rounded, gothic-arch-shaped distal margin outlined by a row of areolae increasing in size distally; surface finely perforate between raised costules.

Remarks.—This species resembles *M.* (*R.*) *micropora micropora* and occurs in part in contemporaneous deposits. The two subspecies were geographically isolated; *M.* (*R.*) *m. floridanum* was restricted to Florida and Georgia while *M.* (*R.*) *micropora* inhabited more westerly areas. The former apparently migrated northward from Florida (Eocene-early Oligocene) to Georgia (middle Oligocene), when it occurs in Byram equivalents (Herrick, Pickering, and Sachs, 1967).

Neither this subspecies nor *M.* (*R.*) *m. micropora* occurs in the middle Oligocene Marianna Limestone in western Florida. A superficially similar species, probably referable to *Smittoidea* Osburn, apparently replaced *M.* (*R.*) *m. floridanum* in that area after deposition of the Bumpnose Limestone; a barrier of unknown nature prevented *M.* (*R.*) *micropora* from reaching Florida. Glawe (1968, in press) postulated such a barrier to explain speciation in the *Pecten perplanus* stock.

Specimens from Florida are poorly preserved; the paratype illustrated by Cheetham (1963, pl. 3, fig. 10; FGS 5392) does not preserve gonoecial perforations, though the holotype does.

METRARABDOTOS (RHABDOTOMETRA) VIGNEAUXI, n. sp.

Plate 5, figure 5; plate 6, figure 2

Diagnosis.—Zooecia medium size; areolae in one row; oral denticle deep set. Ordinary avicularia small, lateral, directed proximally and slightly inward; special avicularia strongly differentiated, developed on zooecia lateral to gonoecia. Gonoecia with straight distal lip and only slightly raised costules on distal surface.

Differs from *M.* (*R.*) *micropora* in having stronger avicularian dimorphism, deeper oral denticle, more consistently inwardly directed avicularia, and larger gonoecia with weaker costulation and straight distal lip.

Occurrence.—Oligocene (Stampian), borehole (depth 132.65–155.97 m.), Biganos (Landes), France.

Material studied.—Holotype USNM 650834 and 3 paratypes USNM 650835–650836.

Description.—*Zoarium* erect, arborescent, composed of compressed, bilaminate fronds with zooecia arranged in 17 or more longitudinal rows, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation or bifurcation.

Zooecia claviform, medium size to large, elongate, the marginal zooecia no broader than more central ones.

Frontal wall thin, convex, highest at proximolateral corners of peristome. Frontal surface finely granular with few tubercles on midline. Areolae small, circular to elliptical, disposed in a single, evenly spaced row of 19-24. Interareolar costules rudimentary, limited to periphery.

Orifice steeply inclined distally, buried in peristome, subcircular, with simple distal shelf. Peristome thin, short, not differentiated from frontal surface, inclined proximally, reaching just to distal margin of zooecium, with single, short, pointed, median, lyrule-like denticle placed just below proximal lip. Secondary orifice oval, broadly rounded distally, with deep or shallow, median sinus proximally.

Ordinary avicularia small, paired, present on gonoecia as well as zooecia; placed on lateral margins of peristome at midpoint of secondary orifice; rostrum pointed, directed proximally and slightly inward.

Special avicularia strongly differentiated, paired with ordinary ones; developed on zooecia laterally adjacent to distal part of gonoecium; rostrum elongated, directed proximally and inward to lateral margin of secondary orifice; chamber extends distally and outward from orifice, not swollen.

Gonoecium about one and a half times as long and twice as broad as zooecia. Orifice crescent shaped; distal lip partly obscured by matrix in holotype, but appears to be straight, proximal lip unhooded. Distal half of gonoecium semielliptical, with rounded distal margin and markedly convex, granular surface, finely and evenly perforate between costules. Areolae in a single, evenly spaced row, larger distally. Costules narrow, only slightly raised, forming a pattern radiating distolaterally from median line.

Remarks.—This species is named in honor of Professor Michel Vigneaux of l'Université de Bordeaux.

Subgenus METRARABDOTOS (BIAVICULARIUM), n. subgen.

Diagnosis.—*Metrarabdotos* having elongate zooecia and orifice with pouch-like distal shelf and one, two, or three deep-set denticles in the slightly elongate peristome; areolae commonly multiplied proximally; avicularia typically paired, dimorphic: (1) ordinary avicularia usually lateral and small; (2) special avicularia strongly differentiated, developed at variable locations in zoarium; gonoecium usually without avicularia and with subequal areolae and unhooded proximal lip.

Range.—Middle Miocene–Recent, southeastern and south-central United States to Brazil.

Type species.—*Smittia tenuis* Busk, 1884.

Taxa included.—*M.* (*B.*) *chipolanum,* n. sp.; *M.* (*B.*) *tenue* (Busk), 1884; *M.* (*B.*) *lacrymosum* Canu and Bassler, 1919.

Remarks.—This subgenus is the least homogeneous one in *Metrarabdotos;* it lacks any diagnostic character state shared by all constituent species. Greatly differentiated special avicularia occur in nearly all constituent taxa in axillary position and in few in gonoecial position and thus almost form a unifying feature. It overlaps *M.* (*Rhabdotometra*) in oral denticulation and gonoecial ornamentation and *M.* (*Porometra*) in oral denticulation and presence of marginal special avicularia.

Trigonopora monilifera (Milne Edwards); Barbosa (1967, p. 78, fig. 2), from the Miocene of the Amazon region of Brazil, probably belongs to this subgenus; its oral denticulation and gonoecial structure are unknown.

TABLE 9.—*Zooecial variates in* Metrarabdotos (Biavicularium). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lz	lz	ho	lo	Lav	na
M. (B.) chipolanum	**K**	0.8422	0.3595	0.1960	0.1512	0.0952	24.30
		0.0772	0.0245	0.0219	0.0343	0.0158	2.11
		10	10	10	10	8	10
M. (B.) t. colligatum	**N**	0.7077	0.2960	0.1750	0.1430	0.0879	17.64
		0.0724	0.0301	0.0177	0.0224	0.0187	1.89
		44	38	44	44	31	44
M. (B.) t. auriculatum	**L1**	0.8078	0.3388	0.1904	0.1582	0.1083	23.14
		0.1416	0.0266	0.0199	0.0111	0.0183	3.29
		8	8	8	8	6	7
	L2-4	0.8085	0.3505	0.1934	0.1566	0.1129	21.21
		0.0481	0.0269	0.0191	0.0165	0.0187	2.36
		44	37	44	45	28	42
M. (B.) t. tenue	**L_1**	0.7408	0.3631	0.1961	0.1565	0.0815	17.66
		0.0741	0.0388	0.0225	0.0186	0.0220	1.99
		48	44	50	50	36	32
M. (B.) lacrymosum	**O**	0.7298	0.2989	0.1783	0.1442	0.1861	16.18
		0.0906	0.0341	0.0122	0.0121	0.0532	2.25
		28	28	28	28	26	28

TABLE 10.—*Gonoecial variates and length of special avicularia in* Metrarabdotos (Biavicularium). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lg	lg	ho	lo	LAv
M. (B.) chipolanum	K	1.1648	0.5936	—	0.3360	0.2352
		—	—	—	—	—
		2	2	0	2	2
M. (B.) t. colligatum	N	1.1370	0.5920	0.1308	0.4141	0.3671
		0.1037	0.0248	0.0519	0.0515	0.1166
		10	10	10	10	9
M. (B.) t. auriculatum	L	1.1666	0.5697	0.1228	0.3756	0.3914
		0.0760	0.0460	0.0194	0.0192	0.0720
		7	7	3	7	17
M. (B.) t. tenue	L_1	1.0753	0.6054	0.0825	0.4212	0.4491
		0.0560	0.0583	0.0513	0.0233	0.0911
		6	6	6	6	11
M. (B.) lacrymosum	O	0.9525	0.5309	0.0472	0.3632	0.5842
		0.1000	0.0396	0.0164	0.0355	—
		5	5	4	5	2

METRARABDOTOS (BIAVICULARIUM) CHIPOLANUM, n. sp.

Plate 6, figures 1, 3–4

Diagnosis.—Zooecia large, slightly broader on zoarial margins; areolae in one row; peristome extends slightly beyond distal margin of zooecium; oral denticle single. Ordinary avicularia small, lateral, directed proximally, absent from gonoecia; special avicularia developed usually on axillary zooecia and rarely on those adjacent to gonoecia or on zoarial margins. Gonoecia with upturned distal lip and lightly costulate distal cover.

Differs from *M.* (*B.*) *tenue* in having a single row of areolae, unidenticulate orifice, and less distally placed avicularia; from *M.* (*B.*) *lacrymosum* in having larger zooecia, unidenticulate orifice, ordinary avicularia placed laterally to orifice and directed proximally, and gonoecia without avicularia.

Occurrence.—Miocene (Alum Bluff), Chipola Formation, Florida highway 73 bridge over Tenmile Creek, 4.8 miles north of Clarksville, Calhoun Co., Florida.

Material studied.—Holotype USNM 650837 and 2 paratypes USNM 650838–650839.

Description.—*Zoarium* erect, arborescent, composed of bilaminate compressed fronds, with zooecia arranged in seven or more longitudinal rows on each side, those in adjacent rows alternating in position. Number of rows increases distally by intercalation or bifurcation.

Zooecia rhomboidal to claviform, large, elongate, those on zoarial margins slightly broader than more central ones.

Frontal wall thin, moderately convex, highest at proximolateral corners of peristome. Frontal surface finely granular, with coarse, irregularly spaced tubercles along midline and on peristome. Areolae large, elliptical, disposed in a single, evenly spaced row of 19-25 around lateral and proximal margins. Interareolar costules weak, limited to periphery.

Orifice steeply inclined distally, deeply placed in peristome, large, circular to oval; distal shelf concave frontally, with upturned proximal margin. Peristome thin, short, usually reaching slightly beyond distal margin of zooecium, with bluntly tapering or bifid denticle, placed about midway between primary and secondary orifices. Secondary orifice large, oval, broadly rounded distally, with broad, shallow, poorly defined notch proximally.

Ordinary avicularia small, usually paired, rarely single or absent on zooecia, placed on lateral margins of peristome, with rostrum directed proximally.

Special avicularia single or paired with ordinary ones; developed usually on axillary zooecia and rarely on marginal zooecia or zooecia distolateral to gonoecium; rostrum elongated, curving proximally and outward around lateral margin of secondary orifice; chamber swollen, extending distally from orifice.

Gonoecium one and a half times as long and broad as zooecia. Orifice crescent shaped; distal lip broken, but small remnant upturned; proximal lip not produced. Distal cover semielliptical, with broadly rounded distal margin; surface not preserved, but remnants display single, evenly spaced row of uniformly small areolae between which are weak costules.

Remarks.—*Trigonopora colligata* var. *catahoulana* McGuirt (1941, p. 90, pl. 3, figs. 9, 12; pl. 4, figs. 1, 2), described from the *Heterostegina* zone (Miocene) in a well in Acadia Parish, Louisiana, may be conspecific with *M.* (*B.*) *chipolanum.* Unfortunately, diagnostic characters, including special avicularia and gonoecia, are not shown on McGuirt's illustrations, and the syntypes are not in the Louisiana State University Geology Museum (H. V. Andersen, personal communication). Core samples from the same zone, on file with the Louisiana Geological Survey, Baton Rouge, failed to yield comparable material.

This species and *M.* (*B.*) *lacrymosum* Canu and Bassler fit least comfortably of any into the subgenus *M.* (*Biavicularium*).

METRARABDOTOS (BIAVICULARIUM) TENUE (Busk, 1884)

Diagnosis.—Zooecia medium size, those on zoarial margins broader; areolae include a partial second row proximally; peristome terminal at distal margin of zooecium; oral denticles two or three, but constant within a subspecies. Ordinary avicularia small, slightly to distinctly distolateral, directed proximally and usually outward, absent from gonoecia; special avicularia developed usually on some zooecia on margins of zoaria and on axillary zooecia and rarely on zooecia lateral to gonoecia. Gonoecia with slightly upturned distal lip and slightly convex distal surface showing weak, peripheral costules.

Differs from *M.* (*B.*) *lacrymosum* in having small, proximally directed ordinary avicularia and gonoecia without avicularia; from *M.* (*B.*) *chipolanum* in having additional areolae, more than one oral denticle and more distally placed avicularia.

Occurrence.—This species includes three chronologic-geographic subspecies:

1. ***M.* (*B.*) *tenue colligatum:*** Miocene (Cercado Fm.), Dominican Republic.
2. ***M.* (*B.*) *tenue auriculatum*** Miocene (Tamiami Fm.), southern Florida; Pliocene (Waccamaw Marl) South Carolina; Pliocene (Caloosahatchee Marl), southern Florida.
3. ***M.* (*B.*) *tenue tenue:*** Recent, Puerto Rico to central Brazil.

METRARABDOTOS (BIAVICULARIUM) TENUE COLLIGATUM
Canu and Bassler, 1919

Plate 7, figures 2–3; plate 17, figures 2–3

Metrarabdotos colligatum Canu and Bassler, 1919, p. 95, pl. 4, figs. 3–12; 1923, p. 162, pl. 4, figs. 3–12; Buge and Galopim de Carvalho, 1963, p. 146, fig. 3.

Diagnosis.—Zoarial branches moderately expanded; orifices tridenticulate; special avicularia developed on zooecia lateral to gonoecia and on marginal zooecia, but not consistently on either; gonoecia large.

Occurrence.—Miocene (Cercado Fm.), Rio Mao and Rio Cana, Dominican Republic.

Material studied.—Lectotype (here designated) USNM 68677 (Canu and Bassler, 1919, pl. 4, fig. 7), paralectotypes USNM 650840 (1919, pl. 4, figs. 3, 6, 10; 1923, pl. 4 figs. 3, 6, 10), USNM 650841 (1919, pl. 4, figs. 4, 6, 8, 11; 1923, pl. 4, figs. 4, 6, 11), USNM 650842 (1919, pl. 4, figs. 5, 6, 9; 1923, pl. 4, figs. 5, 6, 8, 9), specimen USNM 650843 (Canu and Bassler, 1923, pl. 4, fig. 7), 9 specimens USNM 650844–650851, all from Cercado de Mao, Rio Mao Bluff 3, Dominican Republic; specimen USNM 650852, Rio Cana, Dominican Republic.

Description.—*Zoarium* erect, arborescent, branching, originating from a small, encrusting base from which the main stem hooks around in a nearly right-angle bend. Branches subcylindrical at first, becoming bilaminate, compressed fronds with zooecia arranged in up to 20 longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation.

Zooecia rhomboidal to rectangular, medium size, elongate, those on zoarial margins distinctly broader than more central ones.

Frontal wall thin, markedly convex, highest at proximolateral corners of peristome. Frontal surface finely granular, with coarse, irregularly spaced tubercles along midline and on peristome. Areolae large, elliptical, disposed in an evenly spaced row of 15-24 around proximal and lateral margins, a few of which may be included in an inner row proximally. Interareolar costules weakly developed, limited to periphery.

Orifice steeply inclined distally, placed deeply in peristome, large, subcircular to oval, with pouch-like distal shelf. Peristome thin, short, just reaching distal margin of zooecium, with three deep-set proximal denticles, one median, bluntly tapering, and lyrule-like, the others lateral, paired. Secondary orifice large, oval, broadly rounded distally, with broad, rarely deep notch proximally.

Ordinary avicularia small, usually paired, rarely single or absent on zooecia, lacking on gonoecia; placed on distolateral margins of secondary orifice, directed proximally and slightly outward; crossbar usually preserved.

Special avicularia single or paired with ordinary ones, with elongate, subspatulate rostrum directed proximally and usually slightly inward; chamber swollen, extending distally beyond zooecial margin; crossbar rarely preserved; developed in two locations: usually present on zooecia lateral to gonoecia; more rarely present on zooecia of marginal rows.

Gonoecium twice as long and one and a half times as broad as zooecia. Orifice crescent shaped; distal lip slightly upturned; proximal lip not produced. Distal cover semielliptical, with rounded gothic-arch-shaped distal margin and moderately convex surface finely and evenly perforate between narrow, granular, raised costules. Areolae evenly spaced around distal and lateral margins, uniformly small.

Remarks.—The specimen illustrated by Canu and Bassler (1919) on their plate 4, figure 12, has not been placed in the Smithsonian collections.

Buge and Galopim de Carvalho (1963) followed Canu and Bassler (1919; 1923) in attributing inconstancy of avicularia and lack of median oral denticle to this subspecies.

Louisiana Miocene specimens identified by McGuirt with *M.* (*B.*) *tenue colligatum* (as *Trigonopora colligata* var. *catahoulana* McGuirt) are seemingly related to *M. chipolanum.* Material of Vicksburgian age from Mississippi identified by Howe (1948, p. 70) with *M. colligatum* is referable to *M.* (*R.*) *micropora.*

M. (*B.*) *tenue colligatum* resembles *M.* (*B.*) *t. auriculatum* in zoarial form and in having special avicularia on zooecia lateral to gonoecia; its salient features are tridenticulate orifices, lack of special avicularia on axillary zooecia, and large gonoecia.

METRARABDOTOS (BIAVICULARIUM) TENUE AURICULATUM Canu and Bassler, 1923

Plate 7, figures 1, 4; plate 8, figures 1–2

Metrarabdotos auriculatum Canu and Bassler, 1923, p. 164, pl. 31, figs. 1–9; Buge and Galopim de Carvalho, 1963, p. 149, fig. 5.

Trigonopora ariculatum (sic) Canu and Bassler; Eppert, 1966, p. 59.

Diagnosis.—Zoarial branches moderately expanded; orifices bidenticulate; special avicularia developed on zooecia lateral to gonoecia, on marginal zooecia, and on axillary zooecia, but not consistently on any; gonoecia small.

Occurrence.—Miocene (Choctawhatchee), Tamiami Formation, Collier and Sarasota Cos., Florida; Pliocene, Waccamaw Marl, Horry

Co., South Carolina; Caloosahatchee Marl, De Soto and Monroe Cos., Florida.

Material studied.—Lectotype (here designated) USNM 68679 (Canu and Bassler, 1923, pl. 31, fig. 2) and paralectotypes USNM 650853 (1923, pl. 31, figs. 1, 3), USNM 650854–650856 (1923, pl. 31, figs. 7-9), USNM 650857 (not figured), all from Shell Creek, De Soto Co., Florida; paralectotypes USNM 68680 (1923, pl. 31, fig. 1), USNM 650858–650860 (1923, pl. 31, figs. 4-6); USNM 650861 (not figured) all from Monroe Co., Florida; specimen USNM 650862, Intracoastal Canal, 15 miles northeast of Myrtle Beach, Horry Co., South Carolina; specimen USNM 650863 quarry west of Florida Highway 29, Sunniland, Collier Co., Florida.

Description.—*Zoarium* erect, arborescent, originating in a small encrusting base which gives rise to a subcylindrical stem which passes in turn into compressed, bilaminate fronds with zooecia arranged in up to 20 longitudinal rows on each side, zooecia in adjacent rows alternating in position. Number of zooecial rows increases distally by bifurcation or intercalation.

Zooecia claviform, medium size, elongate, those on zoarial margins distinctly broader than more central ones.

Frontal wall thin and convex in young zooecia thicker and flat in old ones. Surface finely granular with large tubercles on midline and an especially large pair on either side of secondary oral sinus. Areolae small, circular, evenly spaced around lateral and proximal margins, numbering 16-27, one to four of which occur within peripheral ring at proximal end of most zooecia; distal areolae occluded by frontal thickening in old zooecia which take on false boundaries and appear to change shape.

Orifice steeply inclined distally, deeply placed in peristome, large, circular, with a concave, pouch-like distal shelf. Peristome only slightly inclined, generally reaching distal margin of zooecium, long but obscured by thickened frontal wall; proximal interior having a pair of deep-set, pointed, lateral denticles that nearly meet proximally. Secondary orifice large, oval to pyriform, evenly rounded distally, broadly and deeply notched proximally.

Ordinary avicularia small, usually paired, rarely single or absent on zooecia, lacking on gonoecia, commonly occluded on frontally thickened zooecia; placed on lateral margins of secondary orifice slightly distal to midpoint; rostrum pointed, curved around lateral margin of orifice, directed proximally and usually slightly outward; crossbar usually preserved.

Special avicularia strongly differentiated from ordinary ones; rostrum subspatulate, directed proximally, chamber swollen, extended distally beyond orifice; crossbar rarely preserved; developed in three positions: usually on axillary zooecia, frequently on marginal zooecia, and more rarely on zooecia distolaterally adjacent to gonoecia.

Gonoecium one and a half times as long and broad as zooecia. Orifice crescent shaped, with slightly upturned distal lip and unhooded proximal lip. Distal cover semielliptical, with rounded, gothic-arch-shaped distal margin and a border of small, subequal areolae; surface granular between small, evenly spaced perforations, the granules tending to develop into feeble costules peripherally.

Remarks.—*M.* (*B.*) *tenue auriculatum* resembles *M.* (*B.*) *t. colligatum* in zoarial form and in having special avicularia on zooecia lateral to gonoecia; it is similar to *M.* (*B.*) *t. tenue* in having bidenticulate orifices, special avicularia on axillary zooecia, and small gonoecia. It is, thus, intermediate between the two subspecies but closer to the latter.

Though Canu and Bassler (1923, p. 165) reported that this taxon occurs in the Waccamaw Marl on the Waccamaw River, Horry Co., South Carolina, specimens from that locality have not been found. The specimens listed above from the Intracoastal Canal northeast of Myrtle Beach, South Carolina, are from nearby.

METRARABDOTOS (BIAVICULARIUM) TENUE TENUE (Busk, 1884)

Plate 8, figures 3–4; plate 9, figures 1–3

Smittia tenuis Busk, 1884, p. 150, pl. 20, fig. 1.
Metrarabdotos tuberosum Canu and Bassler, 1928b, p. 91; pl. 8, figs. 3, 4; Buge and Galopim de Carvalho, 1963, p. 180.
Trigonopora tenuis (Busk); Osburn, 1940, p. 447.
Trigonopora gulo Marcus, 1955, p. 304, pl. 7, figs. 71–77.
Metrarabdotos tenue (Busk); Rucker, 1967, p. 831.

Diagnosis.—Zoarial branches narrow; orifices bidenticulate; special avicularia developed on axillary and marginal zooecia, but not consistently on either; gonoecia small.

Occurrence.—Recent, Atlantic off Puerto Rico (10-120 fms.), off British Guiana (50 fms.), off Recife, Bahia, and Victoria, Brazil (10-20 fms.).

Material studied.—Holotype BM (NH) 87. 12. 9. 596 (Challenger Coll.) and specimen USNM (Z) 9232, off Bahia, Brazil; specimen USNM (Z) 9759, Atlantic off San Juan, Puerto Rico

(50 fms.); 4 specimens USNM (Z) 9817, 11934–11936, Caroline sta. 68 off northeast coast of Puerto Rico; specimen USNM 8568 (holotype of *M. tuberosum*), Atlantic off Recife, Brazil, Albatross sta. 2758 (20 fms.).

Description.—*Zoarium* erect, arborescent, originating in a small, encrusting base which gives rise to a subcylindrical stem which passes, in turn, into compressed, bilaminate fronds with zooecia arranged in up to 15 longitudinal rows on each side; zooecia in adjacent rows alternate in position; number of zooecial rows increases distally by bifurcation or intercalation.

Zooecia claviform, medium size, elongate, those on zoarial margins distinctly broader than more central ones.

Frontal wall thin and convex in young zooecia, thicker and flat in old ones, covered by a cuticular-epithelial membrane light purple in dried specimens. Surface beneath membrane finely granular with large tubercles, including a very large proximal-oral pair, on midline. Areolae small, circular, evenly spaced around lateral and proximal margins, numbering 13-21, one to four of which occur within peripheral ring at proximal ends of most zooecia; distal areolae occluded by frontal thickening in old zooecia which take on false boundaries and appear to change shape.

Orifice steeply inclined distally, deeply buried in peristome, large, circular, with a very concave, pouch-like distal shelf. Peristome only slightly inclined, generally reaching distal margin of zooecium, long but obscured in frontal thickening; proximal interior having a pair of deep-set, pointed, lateral denticles that nearly meet proximally. Secondary orifice large, oval to pyriform, evenly rounded distally, broadly and deeply notched proximally.

Ordinary avicularia small, usually paired, rarely single or absent on zooecia, lacking on gonoecia; commonly occluded on frontally thickened zooecia; placed on distolateral margin of secondary orifice, in some zooecia nearly meeting distally; rostrum pointed, curved around lateral margin of orifice, directed proximally and outward; crossbar complete; mandible simple, pointed, occluding with rostral palate.

Special avicularia single or paired with ordinary one; chamber swollen, extended distally beyond orifice; crossbar complete; mandible bilobed, the rounded outer lobe occluding with rostral palate, the pointed inner lobe occluding with inner margin of peristome; developed in two positions, usually on axillary zooecia and frequently on marginal zooecia.

Gonoecium one and a half times as long and broad as zooecia; orifice crescent shaped, with slightly upturned distal lip and unhooded but slightly produced proximal lip. Distal cover semielliptical, with rounded, gothic-arch-shaped distal margin and a border of small, subequal areolae; surface granular between small, evenly spaced perforations, the granules tending to align as feeble costules peripherally.

Remarks.—The nomenclature of this subspecies was confused by Busk's (1884, p. 150) attributing median suboral avicularia to it. The holotype is a fragment from the proximal part of a zoarium and thus shows modifications that accompany frontal thickening, but possesses distolateral ordinary avicularia and greatly enlarged special avicularia on some axillary zooecia. Osburn (1940, p. 447), who examined the U. S. National Museum material from Puerto Rico listed above, identified it with *M. tenue,* but Marcus (1955, p. 304) described consubspecific material from Brazil as *T. gulo. M. tuberosum* Canu and Bassler, also described from Brazil, is consubspecific with *M. (B.) tenue tenue.*

M. (B.) tenue tenue resembles *M. (B.) t. auriculatum* in having bidenticulate orifices, special avicularia on axillary zooecia, and small gonoecia; its salient features are narrow-branched zoaria and lack of special avicularia on zooecia lateral to gonoecia.

METRARABDOTOS (BIAVICULARIUM) LACRYMOSUM
Canu and Bassler, 1919

Plate 9, figure 5; plate 12, figure 1

Metrarabdotos lacrymosum Canu and Bassler, 1919, p. 96, pl. 3, figs. 1–10; 1923, p. 164, pl. 8, figs. 1–10; Buge and Galopim de Carvalho, 1963, p. 148, fig. 4.

Diagnosis.—Zooecia medium size; those on zoarial margins not distinctly broader; areolae in one row; peristome terminal at distal margin of zooecium; orifice tridenticulate. Ordinary avicularia medium size, proximolateral, directed distally and inward on zooecia, proximally and inward on gonoecia. Special avicularia developed on axillary zooecia only. Gonoecia with distal lip upturned, proximal lip unhooded, distal cover convex, costulate.

Differs from *M. (B.) chipolanum* in having smaller zooecia, tridenticulate orifice, larger, distally directed ordinary avicularia, and gonoecia with avicularia; from *M. (B.) tenue* in having larger, distally directed ordinary avicularia; and gonoecia with avicularia.

Occurrence.—Pliocene, Bowden Marl, Bowden, Jamaica.

Material studied.—Lectotype (here designated) USNM 68678 (Canu and Bassler, 1919, pl. 3 fig. 10; 1923, pl. 8, fig. 10) and paralectotypes, USNM 650864 (1919, pl. 3, fig. 2; 1923, pl. 8, fig. 2), USNM 650865 (1919, pl. 3, figs. 3, 4; 1923, pl. 8, figs. 3, 4); USNM 650866–650870 (1919, pl. 3, figs. 5-9; 1923, pl. 8, figs. 5-9); specimen USNM 650871; specimens BM(NH) D.41123, 34309–34312; all from Bowden, Jamaica.

Description.—*Zoarium* erect, arborescent, branching repeatedly and unequally, originating in a small, encrusting base which gives rise to subcylindrical stems which pass, in turn, into bilaminate, compressed branches composed of zooecia arranged in as many as twelve longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation or bifurcation.

Zooecia irregularly polygonal to claviform, medium size, elongate.

Frontal wall thin, convex, highest at proximolateral corners of peristome. Frontal surface finely granular, lacking tubercles. Areolae circular to elliptical, disposed in a single, evenly spaced row of 11-20 around proximal and lateral margins. Interareolar costules peripheral, rudimentary.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular to oval; distal shelf deep, pouch-like. Peristome with three deeply seated proximal denticles, one median, bluntly tapering, lyrule-like, others lateral, paired. Secondary orifice oval, broadly rounded distally, with distinct sinus proximally. Peristome thin, not well differentiated from frontal surface, just reaching distal margin of zooecium.

Ordinary avicularia usually paired, rarely single or absent on zooecia and gonoecia, medium size, placed on peristome proximolateral to orifice; rostrum long, pointed, directed distally and inward to midpoint of lateral margin of secondary orifice on zooecia, directed proximally and inward on gonoecia; crossbar rarely preserved.

Special avicularia single, rostrum subspatulate, produced, directed proximally and inward, curved around proximal lip of orifice; crossbar not preserved; chamber extended distally beyond orifice; developed on axillary zooecia.

Gonoecium one and a third times as long and twice as broad as zooecia. Orifice crescent shaped; distal lip upturned; proximal lip slightly produced, unhooded. Distal surface semielliptical, with broadly rounded distal margin, outlined by a row of small, subequal areolae; perforate between weak, peripheral costules.

Remarks.—Buge and Galopim de Carvalho (1963, p. 149) described the orifice of this species as rimulate; Canu and Bassler (1919, p. 96; 1923, p. 164) referred to a "rounded and perforated sinus." Both descriptions probably were based on the secondary rather than the primary orifice.

Special avicularia and avicularia on the gonoecia have not been previously recorded.

This species and *M.* (*B*) *chipolanum,* n. sp., fit least comfortably into the subgenus *M.* (*Biavicularium*).

Subgenus METRARABDOTOS (UNIAVICULARIUM), n. subgen.

Diagnosis.—*Metrarabdotos* having orifice tridenticulate or bidenticulate, the denticles simple, lamellar, or repeated, placed in elongate peristome; distal oral shelf pouch-like; avicularium monomorphic, usually single, large, curved, present or absent on gonoecium; distal cover of gonoecium convex, costulate or tuberculate.

Range—Upper Miocene-Recent, Caribbean and Gulf of Mexico to Brazil; Recent, west coast of Panama, West Africa.

Type species.—*Metrarabdotos unguiculatum* Canu and Bassler, 1928.

Taxa included.—*M.* (*U.*) *kugleri,* n. sp.; *M.* (*U.*) *unguiculatum* Canu and Bassler, 1928.

TABLE 11.—*Zooecial variates in* Metrarabdotos (Uniavicularium). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lz	lz	ho	lo	Lav	na
M.* (*U.*) *kugleri	P	0.6832	0.2997	0.1465	0.1434	0.1944	17.33
		0.0574	0.0236	0.0144	0.0117	0.0446	0.62
		25	25	25	25	20	15
M.* (*U.*) *u. pacificum	Z	0.7112	0.4699	0.1796	0.1500	0.1968	24.00
		0.0598	0.0419	0.0146	0.0125	0.0280	—
		21	21	21	21	8	2
M.* (*U.*) *u. unguiculatum	Y	0.8453	0.5486	0.1984	0.1738	0.3602	17.75
		0.1328	0.0754	0.0337	0.0244	0.0622	2.57
		66	66	66	66	39	56
M.* (*U.*) *u. cookae	Y_1	0.8652	0.5834	0.2095	0.1651	0.3166	22.44
		0.0998	0.0571	0.0270	0.0123	0.0599	2.00
		16	16	16	16	14	16

TABLE 12.—*Gonoecial variates in* Metrarabdotos (Uniavicularium). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lg	lg	ho	lo
M. (U.) kugleri	P	0.8512	0.5040	—	0.3472
		0.1080	0.0513	—	0.0194
		3	3	0	3
M. (U.) u. pacificum	Z	0.9969	0.6032	0.0508	0.3492
		0.0090	0.0090	0.0180	0.0090
		2	2	2	2
M. (U.) u. unguiculatum	Y	1.1065	0.7302	0.0762	0.4397
		0.1053	0.0311	0.0378	0.0365
		8	8	8	8
M. (U.) u. cookae	Y_1	1.0604	0.7239	0.1270	0.4699
		0.0269	0.0898	0	0.0359
		2	2	2	2

Remarks.—Loss of avicularian dimorphism, virtual suppression of one ordinary avicularium, and enlargement of the remaining one have made this a distinctive subgenus. The gonoecium, however, has retained many of the characters of *M.* (*Rhabdotometra*), and the oral denticulation overlaps that of *M.* (*Biavicularium*) and *M.* (*Porometra*).

METRARABDOTOS (UNIAVICULARIUM) KUGLERI, n. sp.

Plate 9, figure 4

Diagnosis.—Zoarium bilaminate with narrow branches. Zooecia medium size, elongate, broader on zoarial margins; peristome terminal at distal margin of zooecium; orifice with three proximal denticles. Avicularium lateral, directed proximally and inward, present on both zooecia and gonoecia. Gonoecia with straight distal lip; distal cover costulate, margined by graded areolae.

Occurrence.—Miocene, San José calcareous silt member, Manzanilla Formation, Manzanilla Bay coast, Trinidad (van den Bold, 1963, p. 364, loc. 17).

Material studied.—Holotype USNM 650872 and 13 paratypes USNM 650873–650874.

Description.—*Zoarium* erect, arborescent, with bilaminate branches composed of zooecia arranged in as many as eight longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally by bifurcation or intercalation.

Zooecia rectangular to claviform, medium size, elongate, broader on zoarial margins.

Frontal wall thin, strongly convex, highest on lateral margins of peristome; surface finely granular with few larger granules on midline. Areolae large, circular, evenly spaced in a single row of usually 16-18 around proximal and lateral margins. Interareolar costules weak.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular, with pouch-like distal shelf. Peristome thin, not well differentiated from frontal surface, inclined proximally, just reaching distal margin of zooecium; interior with a pair of short, weak, deep-set proximolateral denticles flanking a median one. Secondary orifice subcircular, with broadly U-shaped sinus proximally.

Avicularium on zooecia usually single, commonly absent, rarely paired (especially on marginal zooecia); on gonoecia single; large, placed on either right or left lateral margin of secondary orifice; rostrum raised, produced, pointed, straight or curving medially, directed proximally and inward to proximal lip of secondary orifice; crossbar commonly preserved.

Gonoecium slightly longer than and nearly twice as broad as zooecia. Orifice crescent shaped; distal lip with straight, granular flange; proximal lip not hooded. Distal surface semielliptical, with broadly rounded margin and moderately convex surface finely and evenly perforate between costules; areolae evenly spaced around distal and lateral margins, increasing in size distally; costules narrow, sharply raised, forming a pattern radiating distolaterally from median line.

METRARABDOTOS (UNIAVICULARIUM) UNGUICULATUM

Canu and Bassler, 1928

Diagnosis.—Zoarium basically unilaminate, encrusting but commonly rising in irregular tubes. Zooecia medium size to large, broad, with much thinner frontal walls than other species; peristome usually extends beyond distal margin of zooecium; orifice with paired proximolateral denticles which may be simple, lamellar, or repeated. Avicularium proximolateral, directed distally and inward, absent on gonoecia. Gonoecia having orifice with upturned distal lip; distal cover tuberculate, margined by subequal areolae.

Occurrence.—This species includes three geographic subspecies:

1. ***M.* (*U.*) *unguiculatum pacificum:*** Recent, west coast of Panama.
2. ***M.* (*U.*) *unguiculatum unguiculatum:*** Recent, Gulf of Mexico, Caribbean, off Guianas and Brazil.
3. ***M.* (*U.*) *unguiculatum cookae:*** Recent, off Ghana, ? off Cape Verde Islands.

METRARABDOTOS (UNIAVICULARIUM) UNGUICULATUM PACIFICUM (Osburn, 1952)

Plate 11, figures 1–2

Trigonopora pacifica Osburn, 1952, p. 443, pl. 58, fig. 9.

Diagnosis.—Zooecia proportionately smaller in all dimensions, including orificial and avicularian, than those of other subspecies; oral denticles simple.

Occurrence.—Recent, off Secas Islands, Panama (12 fms.).

Material studied.—Two paratypes AHF 95.

Description.—*Zoarium* encrusting, unilaminate, forming pavements on mollusk shell; zooecia arranged in radiating, longitudinal rows which increase in number distally by intercalation, those in adjacent rows alternating in position.

Zooecia irregularly rectangular to claviform, medium size, broad. *Frontal wall* thin, convex, covered by a cuticular-epithelial membrane light magenta in dried specimens. Surface (beneath membrane) coarsely tuberculate, margined by a single row of evenly spaced, circular areolae, numbering 23-25, between which tubercles align as distinct costules reaching almost to midline.

Orifice steeply inclined distally, deeply placed in peristome, oval, with pouch-like distal shelf. Peristome thin, not differentiated from frontal surface, slightly produced, reaching just beyond distal margin of zooecium; interior with a pair of deep-set proximolateral denticles. Secondary orifice oval with well-developed proximal sinus.

Avicularium adventitious, large, monomorphic, single or absent, placed on right or left proximolateral slope of peristome; rostrum bluntly pointed, curved outward, directed distally and inward to distolateral corner of secondary orifice, crossbar complete, mandible feebly chitinized, single lobed, slightly curved, pointed, occluding with rostral palate.

Gonoecium short, wide, without avicularium; orifice crescent shaped with upturned distal lip and protruding, but not hooded, proximal lip; distal cover slightly convex, semicircular distally, margined by a row of small, subequal areolae; surface finely perforate between coarse tubercles aligned as costules peripherally.

Remarks.—Osburn's (1952, p. 443) separation of this subspecies from *M.* (*U.*) *unguiculatum* s. s. was based on zooecial and avicularian size (a proportionate, and, therefore, single-character difference), avicularian position (not significantly different), and perforation of the distal gonoecial cover (incorrectly described as imperforate in *M.* (*U.*) *unguiculatum* by Canu and Bassler, 1928a, p. 128). The differences in zooecial size and oral denticulation, coupled with the geographic isolation from *M. unguiculatum* s. s., makes it likely that the two are distinct at the subspecific level. *M.* (*U.*) *u. pacificum* seems to have retained more primitive features than has either of the other subspecies of *M.* (*U.*) *unguiculatum.*

METRARABDOTOS (UNIAVICULARIUM) UNGUICULATUM UNGUICULATUM Canu and Bassler, 1928

Plate 10, figures 1–4; plate 17, figure 5; plate 18, figures 1–2

Metrarabdotos unguiculatum Canu and Bassler, 1928a, p. 128, pl. 23, figs. 6–9; Canu and Bassler, 1928b, p. 92, pl. 8, fig. 9; Buge and Galopim de Carvalho, 1963, p. 181, figs. 3, 4.

Trigonopora unguiculata (Canu and Bassler); Osburn, 1940, p. 447; Marcus, 1955, p. 304, pl. 6, fig. 70.

Diagnosis.—Zooecia proportionately large in all dimensions including orificial and avicularian; oral denticles lamellar.

Occurrence.—Recent, Gulf of Mexico, west of Florida (30 fms.), Straits of Florida (56 fms.); Caribbean, east of Yucatan (21-25 fms.); western Atlantic off Bahia, Espiritu Santo, and Victoria, Brazil (18-27 fms.).

Material studied.—Lectotype (here designated) USNM (Z) 7556 (Canu and Bassler, 1928a, pl. 23, figs. 6, 7) and paralectotypes USNM (Z) 11937-11938 (1928a, pl. 23, figs. 8-9), and USNM (Z) 11939 (1928a, not figured), all from Albatross sta. D. 2363, east of Yucatan; specimen USNM (Z) 8571 (Canu and Bassler, 1928b, pl. 8, fig. 9), off Bahia, Brazil; specimens USNM (Z) 11940, 11941, Albatross sta. D.2362, east of Yucatan; 5 specimens, USNM (Z) 7554, 11942–11945, Albatross sta. D.2405, west of Florida.

Description.—*Zoarium* encrusting; usually unilaminate but with sporadic areas having a superficial layer of frontally budded, irregularly oriented zooecia; pavement-like, but almost invariably rising in erect, irregularly tubular, convoluted branches. Zooecia arranged in trifurcating pattern in area of ancestrula but in longitudinal rows more distally, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation or, more rarely, bifurcation.

Zooecia irregularly rectangular to claviform, large, broad.

Frontal wall thin, strongly convex, highest at lip of secondary orifice, covered by a cuticular-epithelial membrane light magenta in dried specimens. Surface (beneath membrane) tuberculate, especially medially, margined laterally and proximally by a single row of evenly spaced, large, elliptical areolae numbering 14-24; more distal areolae tend to be divided by a longitudinal septum as calcification increases; interareolar costules strong, reaching almost to midline on proximal part of frontal.

Orifice steeply inclined distally, deeply placed in peristome, oval, with pouch-like distal shelf. Peristome thin, elongate, tubular, inclined proximally, extending beyond distal margin of zooecium enough to hide proximal areolae of next zooecium from frontal view; interior with a pair of strong, pointed, proximolateral denticles which may almost meet and continue up the peristome nearly to secondary orifice as a pair of lamellae; secondary orifice oval with a broad, shallow sinus limited laterally by the lamellar denticles.

Avicularium usually single, commonly lacking, rarely paired; placed on either right or left side of peristome, lateral and slightly proximal to secondary orifice; rostrum raised, attenuated, bluntly pointed, curved strongly outward, directed distally and inward to distal margin of secondary orifice; crossbar complete; mandible moderately chitinized, single lobed, strongly curved, pointed, occluding with rostral palate.

Gonoecium one and a third times as long and broad as zooecia; distalmost pair of frontal areolae larger than others but not forming avicularia; orifice crescent shaped, with upturned distal lip just visible in frontal view under produced but unhooded proximal lip; distal cover semielliptical with broadly rounded distal margin marked by a row of small, subequal areolae; surface convex, finely perforate between coarse tubercles which tend to be aligned in irregular costules peripherally.

Remarks.—Lack of perforation of the gonoecial cover implied by the descriptions and illustrations of Canu and Bassler (1928a), Marcus (1955), and Buge and Galopim de Carvalho (1963) has not been substantiated by the present study. Gonoecial avicularia (Canu and Bassler, 1928a, p. 128; Buge and Galopim de Carvalho, 1963,

p. 183) are lacking on the syntypes and all other specimens examined.

This subspecies resembles *M.* (*U.*) *u. cookae* in all features but its lamellar oral denticles and shallow secondary sinus; the difference from *M.* (*U.*) *u. pacificum* is greater.

This subspecies is the only one in the genus which has yielded material suitable for observation of early astogeny (Figures 1, 2; pl. 10, fig. 1).

METRARABDOTOS (UNIAVICULARIUM) UNGUICULATUM COOKAE, n. subsp.

Plate 11, figures 3–4

?Metrarabdotos unguiculatum Canu and Bassler; Calvet, 1931, p. 112; Buge and Galopim de Carvalho, 1964, p. 656.

Metrarabdotos unguiculatum Canu and Bassler; Redier, 1965, p. 388; Cook, 1967, p. 346, pl. 1, fig. d.

Diagnosis.—Zooecia proportionately large in all dimensions including orificial and avicularian; oral denticles repeated.

Occurrence.—Recent, off Accra, Ghana (25 fms.); off Cape Verde Islands (50 fms.) (Calvet, 1931).

Material studied.—Holotype USNM (Z) 11946 and 4 paratypes USNM (Z) 11947–11950, Accra, Ghana.

Description.—*Zoarium* encrusting, unilaminate, rising in erect, irregularly tubular branches; zooecia arranged in longitudinal rows, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation.

Zooecia irregularly rectangular to claviform, large, broad.

Frontal wall thin, strongly convex, highest at lip of secondary orifice, covered by cuticular-epithelial membrane light magenta in dried specimens. Surface (beneath membrane) coarsely tuberculate, margined by a single row of large, elliptical areolae, numbering 19-26, of which the more distal ones tend to be divided by a longitudinal septum as calcification increases. Peripheral tubercles tend to be aligned as costules which extend almost to midline on proximal part of frontal.

Orifice steeply inclined distally, placed deeply in peristome, oval, with pouch-like distal shelf. Peristome thin, elongate, tubular, inclined proximally, extending enough beyond distal margin of zooecium to hide proximal areolae of next zooecium from frontal view; interior with two pairs of pointed, proximolateral denticles developed one above the other. Secondary orifice oval with deep, narrow proximal sinus.

Avicularium usually single, commonly absent, rarely paired; placed on lateral margin of peristome slightly proximal to secondary orifice; rostrum raised, produced, bluntly pointed, curved strongly outward, directed distally and inward to distal margin of secondary orifice; crossbar complete; mandible moderately chitinized, single lobed, pointed, curved, occluding with rostral palate.

Gonoecium one and a third times as long and broad as zooecia; orifice crescent shaped, with upturned distal lip and produced, but unhooded, proximal lip. Distal cover semielliptical, with broadly rounded distal margin outlined by a row of small, subequal areolae; surface convex, finely perforate between coarse tubercles which tend to be aligned peripherally as costules.

Remarks.—This subspecies differs from its western Atlantic counterpart in the denticulation of its elongate peristome and the sinuation of its secondary orifice.

The name is derived in honor of Miss P. L. Cook of the British Museum (Natural History).

Subgenus METRARABDOTOS (POROMETRA), n. subgen.

Diagnosis.—*Metrarabdotos* having both bidenticulate and tridenticulate orifices in the same zoarium; areolae in a single row; distal oral shelf pouch-like; avicularia typically paired, dimorphic: (1) ordinary avicularia medium size, lateral to proximolateral, directed proximally and inward; (2) special avicularia moderately to strongly differentiated, developed on zooecia lateral to gonoecia and usually on marginal zooecia; gonoecium with avicularia and moderately convex or flat distal cover with weak, peripheral costules and subequal areolae.

Range.—Middle Miocene-Pliocene, central Europe and Mediterranean to Sierra Leone.

Type species.—*Trigonopora helvetica* Roger and Buge, 1947.

Taxa included.—*M.* (*P.*) *helveticum* (Roger and Buge, 1947); *M.* (*P.*) *maleckii*, n. sp.

Remarks.—*M. canui* Buge and Galopim de Carvalho, 1963, from the Miocene of Portugal, may belong to this subgenus; the form of the gonoecial cover, presence of special avicularia on zooecia lateral to gonoecia, and apparent absence of special avicularia from axillary zooecia are suggestive of affinity to *M.* (*P.*) *maleckii.*

M. girondicum Duvergier, 1924, from the Miocene of southern France, appears to belong to this subgenus, but the peculiar preservation of the syntypes (see p. 63) makes definite assignment impossible.

M. girondicum tarraconense (Reguant, 1960), from the Miocene of Spain, cannot be assigned with certainty to this subgenus because of the poor preservation of its type specimens.

TABLE 13.—*Zooecial variates in* Metrarabdotos (Porometra). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lz	lz	ho	lo	Lav	na
M. (P.) h. helveticum	$T_1$1	0.7061	0.2836	0.1924	0.1416	0.1034	20.13
		0.0836	0.0192	0.0187	0.0514	0.0169	2.32
		47	33	46	46	29	45
	$T_1$2	0.7009	0.2782	0.1703	0.1384	0.0931	19.70
		0.0929	0.0120	0.0168	0.0126	0.0142	2.41
		21	11	17	19	9	10
	$T_1$3	0.7098	0.2889	0.1997	0.1531	0.1067	20.40
		0.0788	0.0157	0.0129	0.0111	0.0125	2.38
		18	16	18	18	15	15
M. (P.) h. canariense	R_1	0.7477	0.2945	0.1538	0.1291	0.1064	19.16
		0.0578	0.0361	0.0220	0.0146	0.0166	1.46
		31	21	28	30	16	25
	S	0.8473	0.3094	0.1708	0.1490	0.0832	18.13
		0.0801	0.0400	0.0178	0.0218	0.0192	1.86
		20	16	20	20	7	16
M. (P.) h. thomasi	R	0.6753	0.2408	0.1554	0.1166	0.0795	21.13
		0.0324	0.0185	0.0152	0.0112	0.0162	1.25
		17	14	16	17	10	15
M. (P.) maleckii	T1	0.8136	0.3365	0.1622	0.1439	0.0889	24.00
		0.0718	0.0357	0.0181	0.0078	0.0180	2.40
		15	12	13	15	4	9
	T2	0.7345	0.2975	0.1642	0.1390	0.0903	20.80
		0.0601	0.0285	0.0208	0.0102	0.0195	2.57
		18	14	14	18	9	10
	T3	0.7341	0.3229	0.1729	0.1391	0.0917	21.53
		0.0872	0.0138	0.0195	0.0105	0.0085	2.37
		20	14	18	20	9	17

TABLE 14.—*Gonoecial variates and length of special avicularia in* Metrarabdotos (Porometra). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lg	lg	ho	lo	LAv
M. (P.) h. helveticum	**T_1**	0.9366	0.5921	—	0.4635	0.1919
		0.0394	0.0214	—	0.0225	0.0377
		8	8	0	8	18
M. (P.) h. canariense	**R_1**	1.3208	0.6731	0.1397	0.3810	0.2307
		—	—	—	—	0.0863
		1	1	1	1	12
	S	—	—	—	—	0.1960
		—	—	—	—	0.0296
		—	—	—	—	4
M. (P.) h. thomasi	**R**	1.0005	0.4480	0.0672	0.3061	0.1744
		0.0453	0.0336	—	0.0233	0.03706
		3	3	1	3	7
M. (P.) maleckii	**T_2**	1.1176	0.5715	0.1016	0.3937	—
		0.1257	0.0381	—	0.0127	—
		2	3	1	3	—

M. vinassai Panzera, 1932, from the Miocene of Libya, may also belong to *M.* (*Porometra*), but gonoecia are lacking on all specimens known.

M. (*Porometra*) is especially characterized by its gonoecial ornamentation; its variable oral denticulation in the same zoarium is not found in other subgenera.

METRARABDOTOS (POROMETRA) HELVETICUM

(Roger and Buge, 1947)

Diagnosis.—Zooecia elongate, those on zoarial margins broader; ordinary avicularia small to medium size, lateral or slightly proximal, directed proximally and commonly slightly inward; special avicularia moderately to strongly differentiated, developed usually on zooecia lateral to gonoecia and almost invariably on zooecia on margins of zoaria. Gonoecia with upturned distal lip, unhooded proximal lip; distal surface moderately convex to flat.

Differs from *M. maleckii* in having marginal special avicularia, flatter gonoecia with weaker costulation, and more expanded zoaria.

Occurrence.—This species includes three chronologic-geographic subspecies:

1. ***M. (P.) helveticum helveticum:*** Miocene (Helvetian), France north of the Aquitaine and Rhone Basins.
2. ***M. (P.) helveticum canariense:*** Miocene-Pliocene, Canary Islands to Rhodes.
3. ***M. (P.) helveticum thomasi:*** Miocene or Pliocene, Sierra Leone.

METRARABDOTOS (POROMETRA) HELVETICUM HELVETICUM (Roger and Buge, 1947)

Plate 12, figures 2-5; plate 17, figures 6-7

Eschara monilifera Milne Edwards; Michelin, 1847, p. 327, pl. 78, figs. 10 a, b.

Schizoporella monilifera (Milne Edwards); Canu, 1913, p. 127.

Metrarabdotos moniliferum (Milne Edwards); Canu, 1917, p. 146; Canu and Lecointre, 1927, pl. 8, figs. 6, 7; 1928; p. 59; Balavoine, 1948, p. 436; Vigneaux, 1949, p. 90, pl. 8, fig. 13.

Metrarabdotos moliniferum (sic) Canu; Gillard, 1936, p. 191.

Trigonopora monilifera var. *helvetica* Roger and Buge, 1947, p. 228.

Metrarabdotos moniliferum var. *helveticum* (Roger and Buge); Buge, 1948, p. 75.

Trigonopora helvetica Roger and Buge; Lagaaij, 1952, p. 126; Buge, 1957, p. 299; Buge, 1964, p. 165 (part).

Metrarabdotos helveticum (Roger and Buge); Buge and Galopim de Carvalho, 1963, p. 154, figs. 7-9 (part); ? Buge and Galopim de Carvalho, 1964, p. 653.

Metrarabdotos canui Buge and Galopim de Carvalho, 1963, p. 170, pl. 2, fig. 2 (part—not pl. 2, figs. 1, 3).

Diagnosis.—Zoarial branches moderately expanded; orifices nearly all tridenticulate; gonoecium small, with a flat distal cover.

Occurrence.—Miocene (Faluns of Helvetian age), France north of the Aquitaine and Rhone Basins, ? Portugal.

Holotype.—MNHN (Paris) specimen from Pont-Levoy illustrated by Canu and Lecointre (1927, pl. 8, fig. 6).

Material studied.—Ten specimens USNM 60540, 650875–650883, Pont-Levoy (Loir-et-Cher); 3 specimens USNM 89263, Le Hagineau (Maine-et-Loire); 5 specimens USNM 89261, La Placette, Ferrière-l'Arcon (Indre-et-Loire).

Description.—*Zoarium* erect, arborescent, repeatedly and unequally branching, originating in a small, encrusting base which gives rise to a narrow, subcylindrical stem which, in turn, gives way to moderately expanded, bilaminate, compressed, flabellate fronds. Zooecia arranged in 6 rows on stems and 6 to more than 20 rows on each side of a branch, those in adjacent rows alternating in position. Number of zooecial rows increases distally usually by intercalation, rarely by bifurcation.

Zooecia rectangular to club shaped, medium size, elongate, the marginal zooecia about one and a half times as broad as the more central ones.

Frontal wall thin, strongly convex, slightly raised on lateral margins in young zooecia; thick, flat in old ones. Surface finely granular, with a few tubercles on midline near peristome. Areolae small to large, circular to elliptical, disposed in a single, evenly spaced row of 16-25. Interareolar costules weak to moderate.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular to oval, with a deep, pouch-like distal shelf. Peristome thin, not differentiated from frontal surface, extending just to distal margin of zooecium; denticles deeply set, consisting of a proximolateral pair of pointed denticles and in nine tenths of the zooecia on most specimens, a third, median, blunt one; rarely the three denticles almost meet to form a pair of pores. Secondary orifice subcircular, with a well-defined proximal sinus limited laterally in some zooecia by a pair of incipient lateral denticles above those nearer the level of the primary orifice.

Ordinary avicularia paired, present on both zooecia and gonoecia, on some zooecia occluded by advancing frontal calcification; small to medium size, placed on lateral margins of peristome, usually at midpoint, frequently slightly proximally, rarely slightly distally; rostrum pointed, directed proximally and usually slightly inward; pivotal bar rarely preserved.

Special avicularia single or paired with an ordinary one; chamber extended distally beyond orifice; rostrum directed proximally and slightly inward to lateral margin of orifice and with pivotal bar usually preserved; developed usually on zooecia laterally adjacent to distal part of gonoecium, the rostrum produced but the chamber not swollen, and almost invariably on marginal zooecia, the rostrum produced and the chamber swollen.

Gonoecium one and a half times as long and twice as wide as zooecia. Orifice crescent shaped, with slightly upturned, granular distal lip and unhooded proximal lip. Distal cover nearly flat, with rounded gothic-arch-shaped distal margin outlined by a single row of small, subequal areolae; surface finely and evenly perforate between narrow, weak, peripheral costules.

Remarks.—As defined here, the occurrence of this subspecies comprises all recorded populations of *Metrarabdotos* from deposits of Helvetian age in France north of the Aquitaine and Rhone Basins including those considered referable to *M. helveticum* by Buge (1957) and Buge and Galopim de Carvalho (1963) and the following records referred by the latter to *M. canui:* *Le Hagineau, Maine-et-Loire; *La Placette (Ferrière-l'Arcon), Indre-et-Loire; Bossée, Indre-et-Loire; Charnizay, Indre-et-Loire; Cléré-le-Pines, Indre-et-Loire (specimens from the two localities marked with an asterisk were included in the present study).

Predominance of tridenticulate over bidenticulate orifices and the almost invariable presence of special avicularia on the marginal zooecia make this assemblage homogeneous enough to assign to the single subspecies.

M. (*P.*) *helveticum helveticum* resembles *M.* (*P.*) *h. canariense* in having strongly differentiated avicularia and *M.* (*P.*) *h. thomasi* in having small gonoecia. The salient features of *M.* (*P.*) *h. helveticum* are the preponderance of tridenticulate orifices, the width of its zoarial branches, and the flatness of its gonoecia.

METRARABDOTOS (POROMETRA) HELVETICUM CANARIENSE, n. subsp.

Plate 13, figures 2-4

Eschara monilifera Milne Edwards; Manzoni, 1877b, p. 66; Pergens, 1887a, p. 27.
Metrarabdotos moniliferum (Milne Edwards); Dartevelle, 1937, p. 105.

Diagnosis.—Zoarial branches slightly expanded; orifices mostly bidenticulate; ordinary avicularia small; gonoecia large, with a convex distal surface.

Occurrence.—Miocene, Monte San Roque, Las Palmas, Grand Canary Island; Pliocene, Rodhos, Island of Rhodes.

Material studied.—Holotype BM(NH) D.9294, paratypes BM(NH) D.9283, D.9292, D.9348, D.9349, Grand Canary Island; 6 paratypes USNM 650884–650885, Rhodes.

Description.—*Zoarium* erect, arborescent, repeatedly and unequally branching, originating from a small, encrusting base which gives rise to bilaminate, compressed fronds with zooecia arranged in 6 to 15 rows on each side of a branch, those in adjacent rows alternating in position. Number of zooecial rows increases distally by bifurcation or intercalation.

Zooecia club shaped, medium size to large, elongate, the marginal zooecia slightly broader than the more central ones.

Frontal wall thin, convex, sharply raised on lateral margins in young zooecia; thick and flat in old ones. Surface (recrystallized in Canaries specimens) finely granular, with tubercles on midline of a few zooecia. Areolae of moderate size, elliptical to circular, disposed in a single, evenly spaced row of 15-22 on central zooecia, 17-21 on marginal ones. Interareolar costules weak, peripheral.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular to oval, with nearly vertical, pouch-like distal shelf. Peristome thin, not differentiated from frontal surface, extending just to distal margin of zooecium; denticles pointed, deeply seated, consisting of a proximolateral pair and, in less than one half the zooecia observed, a third median one. Secondary orifice oval, broadly rounded distally, with poorly defined sinus proximally.

Ordinary avicularia paired, present on both zooecia and gonoecia; on some zooecia occluded by advancing frontal calcification; small; placed on lateral margins of peristome, usually at midpoint, frequently slightly proximally, rarely slightly distally; rostrum pointed, directed proximally and slightly inward, terminating just short of proximal lip; pivotal bar preserved on some avicularia.

Special avicularia single or paired with an ordinary one; chamber extended distally beyond zooecial orifice; rostrum directed proximally and usually slightly inward to proximal lip of orifice; developed on zooecia laterally adjacent to distal part of gonoecium, the rostrum produced but the chamber not swollen, and on marginal zooecia, the rostrum produced and the chamber swollen.

Gonoecium nearly twice as long and over twice as wide as zooecium. Orifice crescent shaped, with granular, upturned distal lip and unhooded proximal lip. Gonoecial cover moderately convex, with rounded gothic-arch-shaped distal margin outlined by a single row of small, subequal areolae; surface finely and evenly perforate between narrow, weak costules.

Remarks.—This subspecies resembles *M.* (*P.*) *h. helveticum* in having strongly differentiated avicularia and *M.* (*P.*) *h. thomasi* in having only slightly expanded zoarial branches, small ordinary avicularia, and convex gonoecial cover. The salient features of *M. h. canariense* are the dominance of bidenticulate orifices and its large gonoecia.

METRARABDOTOS (POROMETRA) HELVETICUM THOMASI, n. subsp.

Plate 13, figure 1

Diagnosis.—Zoarial branches slightly expanded; orifices half bidenticulate; ordinary avicularia small; gonoecium small with a convex distal surface.

Occurrence.—Miocene or Pliocene, borehole near Benguema, Sierra Leone, depth 85-100 feet.

Material studied.—Holotype USNM 650886 and 6 paratypes USNM 650887.

Description.—*Zoarium* erect, arborescent, branching, originating in a small, encrusting base which gives rise to a narrow, subcylindrical stem which, in turn, gives way to compressed, bilaminate, lobate fronds. Zooecia arranged in 4 longitudinal rows on stem and up to ten rows on each side of a branch, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation.

Zooecia rectangular to club shaped, medium size, elongate; zooecia of the two rows on each margin of a branch about twice as wide as those more centrally placed.

Frontal wall thin, convex, with sharply raised lateral margins in young zooecia; thick, flat in older ones. Surface finely granular, especially on midline, without tubercles. Areolae of moderate size, circular to elliptical, evenly disposed in a single row of 18-22 in central zooecia, up to 24 in marginal ones. Interareolar costules weak, peripheral.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular, with nearly vertical pouch-like distal shelf. Peristome thin, not differentiated from frontal surface, extending just to distal margin of zooecium; denticles pointed, deeply seated, consisting of a pair of proximolateral ones and, in approximately half the zooecia, a third median one. Secondary orifice oval, broadly rounded distally, with poorly defined sinus proximally.

Ordinary avicularia generally paired, rarely single or absent, on some zooecia occluded by advancing frontal calcification; present on gonoecia; small, placed on lateral margins of secondary orifice; usually at midpoint, frequently slightly proximally, rarely slightly distally; rostrum pointed, directed proximally and usually slightly inward, terminating short of proximal lip.

Special avicularia single or paired with an ordinary one; chamber extended distally beyond zooecial orifice; rostrum directed proximally and inward to midpoint of lateral margin of orifice; developed on zooecia laterally adjacent to distal part of gonoecium, the rostrum produced but the chamber not swollen; and on marginal zooecia, the rostrum produced and the chamber swollen.

Gonoecium about one and a half times as long and twice as wide as zooecium; orifice crescent shaped, with granular, upturned distal lip and unhooded proximal lip. Gonoecial cover moderately convex, with rounded gothic-arch-shaped distal margin outlined by a single row of small, subequal areolae; surface finely and evenly perforate between narrow, weak costules.

Remarks.—This subspecies resembles *M.* (*P.*) *h. helveticum* in having small gonoecia and *M.* (*P.*) *h. canariense* in having only slightly expanded zoarial branches, small ordinary avicularia, and gonoecia with convex distal surface. The salient features of *M.* (*P.*) *h. thomasi* are the approximately equal frequency of bidenticulate and tridenticulate orifices and the moderate differentiation of avicularia.

The name of this subspecies is derived to honor the late H. Dighton Thomas.

METRARABDOTOS (POROMETRA) MALECKII, n. sp.

Plate 14, figures 1-5

Eschara punctata Philippi; Reuss, 1848, p. 69, pl. 8, figs. 25a, b; Reuss, 1851, p. 164.

Eschara monilifera Milne Edwards; Manzoni, 1877a, p. 59, pl. 5, fig. 20; pl. 6, fig. 21; Pergens, 1887c, p. 18; Koch, 1900, p. 134.

Schizoporella monilifera (Milne Edwards); Canu, 1913, p. 126.

Metrarabdotos moniliferum (Milne Edwards); Canu and Bassler, 1924, p. 682; Malecki, 1951, p. 488; 1952, p. 197, pl. 11, fig. 13; Ghiurca, 1961a, p. 726; 1961b, table 1.

?*Trigonopora monilifera* (Milne Edwards); Kühn, 1955, p. 232.

Metrarabdotos helveticum (Roger and Buge); Buge and Galopim de Carvalho, 1963, p. 154 (part).

Metrarabdotos canui Buge and Galopim de Carvalho, 1963, p. 170, pl. 2, fig. 1 (part—not pl. 2, figs. 2, 3); Ghiurca and Florei, 1966, p. 16, pl. 3, fig. 7.

Diagnosis.—Zoarium with narrow branches. Ordinary avicularia not uncommonly lacking over large areas of zoaria, small, lateral to secondary orifice, directed proximally; special avicularia possibly present on zooecia lateral to gonoecia. Gonoecia with distal surface moderately convex, finely and evenly perforate between weak, peripheral costules.

Differs from *M. helveticum* in lacking marginal special avicularia, in having more convex gonoecia with stronger costulation, and less expanded zoarial branches.

Occurrence.—? Burdigalian (Miocene); Eggenburg, Austria (Kühn, 1925; 1955). Leithakalk (Miocene); Grzybóm, Poland; Palecznica, Sosnowka, Poland (Malecki, 1951; 1952); Zidlochovice, Czechoslovakia; Tara-Chio'arului (Baia-Mare), Rumania (Koch, 1900; Ghiurca, 1961a, 1961b); Baden (Canu, 1913) and Eisenstadt, Austria (Reuss, 1848; Manzoni, 1877a; Canu and Bassler, 1924; Buge and Galopim de Carvalho, 1963); Tasmajdan (Belgrade), Yugoslavia (Pergens, 1887c).

Material studied.—Holotype USNM 60579 and paratypes USNM 650888–650889, Eisenstadt, Austria; 8 paratypes USNM 650890–650891, Zidlochovice, Czechoslovakia, and 9 paratypes USNM 650892–650894, Grzybóm, Poland.

Description.—*Zoarium* erect, arborescent, branching, composed of narrow bilaminate compressed fronds, with zooecia in six to ten longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally by intercalation.

Zooecia claviform, medium size, elongate, the marginal zooecia about one and a half times as broad as the more central ones.

Frontal wall thin, strongly convex, raised on lateral margins in young zooecia; thick, flat in old ones. Surface finely granular with large tubercles on midline. Areolae small, circular, disposed in a single, evenly spaced row of 16-27. Interareolar costules weak, peripheral.

Orifice steeply inclined distally, deeply placed in peristome, small, subcircular to oval, with a deep, pouch-like distal shelf. Peristome thin, with an indistinct depression separating it from frontal surface, extending just to distal margin of zooecium; denticles deep set, consisting of a proximolateral pair and frequently a third median single one. Secondary orifice subcircular, with a poorly defined proximal sinus.

Ordinary avicularia generally paired, not uncommonly lacking over large areas of a zoarial fragment, possibly present on gonoecia; small, placed on lateral margins of secondary orifice at midpoint; rostrum pointed, directed proximally; pivotal bar not preserved.

Special avicularium possibly present on zooecium lateral to gonoecium, absent on zooecia on zoarial margins.

Gonoecium one and a half times as long and twice as wide as zooecium, orifice crescent shaped, with unhooded proximal lip. Gonoecial cover convex, with rounded gothic-arch-shaped distal margin outlined by a row of possibly subequal areolae; surface finely and evenly perforated between narrow, weak, peripheral costules.

Remarks.—Poor preservation of the specimens of this species from all three localities makes their interpretation difficult. Only one specimen (USNM 650892) displays gonoecia; it is recrystallized and covered with matrix (pl. 14, fig. 5), but a gonoecial special avicularium and gonoecial avicularia may be present.

Austrian specimens have many tridenticulate orifices, whereas Polish and Czechoslovakian specimens are bidenticulate.

Occurrences of this species were included by Buge and Galopim de Carvalho (1963) in *M. canui* and *M. helveticum.*

Subgenus METRARABDOTOS (METRARABDOTOS) Canu, 1914

Diagnosis.—*Metrarabdotos* having bidenticulate orifice with pouch-like distal shelf; elongate peristome; avicularia typically paired, dimorphic: (1) ordinary avicularia medium size, proximolateral; (2) special avicularia moderately to strongly differentiated, developed on zooecia lateral to gonoecia and less consistently on marginal and axillary zooecia; gonoecium with avicularia, hooded proximal lip and slightly convex to flat distal cover margined by subequal areolae.

Range.—Uppermost Miocene-Pliocene, ? Pleistocene, England, France, and the Low Countries.

Type species.—*Eschara monilifera* Milne Edwards, 1836.

Taxa included.—*M.* (*M.*) *nysti* (Lagaaij, 1952), *M.* (*M.*) *moniliferum* (Milne Edwards, 1836).

M. elegans Buge and Galopim de Carvalho, 1963, *M. lecointrei* Buge and Galopim de Carvalho, 1963, and *M. teixeirai* Buge and Galopim de Carvalho, 1963, all from the Pliocene of Portugal and Morocco, may belong to *M.* (*Metrarabdotos*). The first of the three has ordinary avicularia oriented like those of *M.* (*M.*) *nysti,* whereas the other two have them oriented like those of *M.* (*M.*) *moniliferum.* Special avicularia are not known in any of the three.

TABLE 15.—*Zooecial variates in* Metrarabdotos (Metrarabdotos). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lz	lz	ho	lo	Lav	na
M.* (*M.*) *moniliferum	U	0.8513	0.3170	0.1690	0.1408	0.1317	18.19
		0.0694	0.0354	0.0291	0.0167	0.0305	1.82
		39	33	38	38	25	27
	V	0.8477	0.2954	0.1799	0.1372	0.1318	19.13
		0.1309	0.0300	0.0149	0.0156	0.0293	1.59
		17	16	15	16	13	16

TABLE 16.—*Gonoecial variates and length of special avicularia in* Metrarabdotos (Metrarabdotos). *Conventions as in Table 7. Four decimal places in mean and standard deviation are given for purposes of calculation only.*

Species or subspecies	Unit symbol	Lg	lg	ho	lo	LAv
M. (M.) moniliferum	**U**	1.3328	0.6981	—	0.4741	0.2256
		0.0582	0.0282	—	0.0065	0.0416
		3	3	0	3	7
	V	1.1032	0.6272	—	0.4704	0.2501
		0.1188	0.0158	—	—	—
		2	2	0	1	3

METRARABDOTOS (METRARABDOTOS) NYSTI (Lagaaij, 1952)

Trigonopora nysti Lagaaij, 1952, p. 125, pl. 14, figs. 5-6.
Metrarabdotos nysti (Lagaaij); Buge and Galopim de Carvalho, 1963, p. 169.

Diagnosis.—Zoarium with moderately expanded branches. Peristome produced slightly beyond distal margin of zooecium. Ordinary avicularia directed slightly distally and inward on zooecia, proximally and inward on gonoecia; special avicularia developed on zooecia lateral to gonoecia and almost invariably on zooecia of marginal rows. Gonoecial distal cover slightly convex, with weak, irregular, peripheral costules.

Differs from *M.* (*M.*) *moniliferum* in having ordinary avicularia directed distally on zooecia, special avicularia present on almost all marginal zooecia, and more convex gonoecial cover without costulation, and in lacking special avicularia on axillary zooecia.

Occurrence.—Miocene (Lower Diestian), Antwerp, Bercham-lez-Anvers, and Deurne-Sud, Belgium.

Material studied.—Holotype IRSN (Brussels) 26 and paratypes IRSN (Brussels) 27, Houzeau Coll.

Remarks.—The major features of this species can be determined from Lagaaij's (1952) remarks and figures; the special avicularia, however, have not been described previously.

METRARABDOTOS (METRARABDOTOS) MONILIFERUM (Milne Edwards, 1836)

Plate 15, figures 1-4

Eschara monilifera Milne Edwards, 1836, p. 327, pl. 1, figs. 1, 1a-d; Wood, 1844, p. 16; Busk, 1859, p. 68, pl. 11, figs. 1-3; Bell and Bell, 1872, pp. 206, 212; Vine, 1884, p. 202; Lorie, 1885, p. 128, pl. 3, fig. 8; F. W. Harmer, 1896, p. 777; Kendall, 1931, p. 419.
Escharellina monilifera (Milne Edwards); d'Orbigny, 1852, p. 448; Couffon, 1907, p. 171.

Eschara triaperta Couffon, 1905, p. 167, fig. 1.

Metrarabdotos moniliferum (Milne Edwards); Canu, 1920, pp. 213, 214; Canu, 1925, p. 765; Buge, 1945, p. 541; Buge and Calopim de Carvalho, 1963, p. 165, figs. 15-17.

Trigonopora monilifera var. *monilifera* (Milne Edwards); Roger and Buge, 1947, p. 225.

Trigonopora monilifera (Milne Edwards) Lagaaij, 1952, p. 122, pl. 14, figs. 2-4; Bassler, 1953, p. 214, fig. 162-3.

Diagnosis.—Zoarium with greatly expanded, foliaceous branches. Peristome terminal at distal margin of zooecium. Ordinary avicularia directed proximally and inward on both zooecia and gonoecia; special avicularia developed usually on zooecia lateral to gonoecia, almost invariably on axillary zooecia, and rarely on marginal zooecia. Gonoecia with flat, noncostulate distal cover.

Differs from *M.* (*M.*) *nysti* in having ordinary avicularia directed proximally on both zooecia and gonoecia, in lacking special avicularia on most marginal zooecia and having them on axillary zooecia, and in having flatter gonoecial covers without costulation.

Occurrence.—Pliocene (Coralline Crag), Gedgrave, Sudbourne, Aldeburgh, Sutton, Suffolk; Pliocene (Scaldisian), the Low Countries; Pliocene (Redonian), France; Pleistocene (Red Crag), Essex (probably reworked); Pleistocene (Poederlian) the Netherlands (probably reworked).

Material studied.—Ten specimens BM(NH) B.1649 (Busk Coll.), illustrated by Busk (1859), all from Gedgrave, Sudbourne, Suffolk; 4 specimens USNM 650895–650898, Sudbourne Hall, Sudbourne, Suffolk; 4 specimens USNM 650899–650902, Crag Pit Farm, Aldeburgh, Suffolk; specimen USNM 60344, Sutton, Suffolk; 3 specimens USNM 650903–650905, Walton-on-the-Naze, Essex; 7 specimens BM(NH) D.35145 (F. W. Harmer Coll.), Antwerp, Belgium.

Description.—*Zoarium* erect, arborescent, repeatedly and unequally branching, originating in a large or small encrusting base completely sealed by frontal thickening; branches at first subcylindrical with the zooecia arranged radially but becoming bilaminate and expanding in short distances to lobate or convoluted fronds with zooecia arranged in more than 30 longitudinal rows, those in adjacent rows alternating in position. Number of zooecial rows increases usually by bifurcation, rarely by intercalation.

Zooecia irregularly rectangular to claviform, large, elongate, the marginal zooecia usually broader than the more central ones.

Frontal wall thin, strongly convex in young zooecia; thick, flat in older ones. Surface finely granular with few coarser granules or tubercles on midline of young zooecia, becoming longitudinally ridged and losing boundaries and areolae on very old ones. Areolae of moderate size, irregularly polygonal, disposed in a single, evenly spaced row of 15-22; interareolar costules rudimentary, peripheral.

Orifice slightly inclined distally, deeply placed in peristome, small, oval, with pouch-like, deep-set distal shelf. Peristome thin on young zooecia, thick on old ones, its proximal part protuberant and spout-like, vertical or slightly inclined, reaching just to distal margin of zooecium; interior with a pair of strong, deep-set proximolateral denticles. Secondary orifice oval with poorly defined proximal sinus.

Ordinary avicularia paired on both zooecia and gonoecia, medium size, placed on lateral or proximolateral slopes of peristome, with rostrum pointed and directed proximally, upward, and inward, those of a pair nearly meeting on proximal lip of secondary orifice and accentuating its spout-like appearance; crossbar rarely preserved.

Special avicularia single or paired with an ordinary one, with rostrum produced and directed proximally and inward, and chamber swollen; developed in three positions, usually on zooecia lateral to gonoecia, almost invariably on axillary zooecia and rarely on zooecia on zoarial margins.

Gonoecium one and a half times as long, twice as broad as zooecia. Orifice crescent shaped, with straight distal lip completely hidden in frontal view by a greatly projecting, proximal lip with faint longitudinal ridges. Distal cover flat, with rounded, gothic-arch-shaped distal margin outlined by a row of small, subequal areolae; surface finely and evenly perforate, without costules.

Remarks.—Under this specific name, a heterogeneous assemblage of citations grew up in the literature from its first introduction in 1836 to the present. Many of them refer to material patently not related to *M.* (*M.*) *moniliferum* and a few (e.g., Stoliczka, 1862; Reuss, 1864; Waters, 1881; Gottardi, 1886; Pergens, 1887b, p. 5; 1889; MacGillivray, 1895; Ghiurca, 1962; Malecki, 1963) probably not assignable to *Metrarabdotos.* Records of this species from the Miocene, Pliocene, and Pleistocene of Italy (e.g., Seguenza, 1879; Namias, 1891; Neviani, 1891; 1894; 1895; 1896; 1898; 1900a; 1900b; 1900c; Annoscia, 1963), of the Iberian Peninsula (e.g., Almera, 1897; de Angelis, 1898; 1899; Reguant, 1961; Galopim de Carvalho, 1966), of Sardinia (e.g., Neviani, 1897), and of North Africa (e.g., Fuchs, 1883, Canu, 1912; Buge and Galopim de Carvalho, 1963; Buge, 1964) cannot at present be evaluated.

UNNAMED SUPERFAMILY

Remarks.—The family Adeonidae Hincks, after removal of the umbonuloid genus *Metrarabdotos,* includes only genera having lepralioid-microporelloid development of the frontal wall and subjacent ascus (Harmer, 1902, p. 332-336). Consequently, the Adeonidae cannot be placed in the superfamily Umbonulacea or in any other taxon of the division Ascophora Imperfecta Harmer. Though Harmer did not specify fully the taxonomic contents of the two divisions of Ascophora he proposed (Hastings, *in* Harmer, 1957, p. 722), his statements (1957, p. 645, 805) about the frontal wall in Adeonidae leave no doubt about his intention to include this taxon in the division Ascophora Vera together with Schizoporellidae Jullien, Microporellidae Hincks, and other families. Unfortunately, Harmer did not make superfamilial groupings within his divisions. As pointed out by Harmer (1957, p. 788), the way in which brood chambers (gonoecia) have developed in Adeonidae, by direct modification of zooecia, sets this family apart; further research will probably disclose that the gap is great enough for separate superfamilial status.

Vigneaux (1949, pp. 16, 18) assigned most of the genera of Adeonidae to the superfamily Lepraliellacea Vigneaux; however, for two of them, *Bracebridgia* MacGillivray and *Smittistoma* Canu, and the genus *Metrarabdotos* he proposed the family Smittistomatidae (nom. correct. pro Smittistomidae) which he placed in the superfamily Smittinacea Levinsen. Morphologically, the adeonids are not very similar to the type genera of any of the five ascophoran superfamilies proposed by Vigneaux.

Adeonidae, as exemplified by the middle Eocene species *Schizostomella crassa* (Canu) discussed below, differ from Umbonulacea in having a single-layered frontal wall margined distally as well as laterally and proximally by areolae, gonoecia modified from zooecia, ascopores commonly on gonoecia and less commonly on zooecia, and avicularia, where present, without crossbars for the mandible.

Family ADEONIDAE Hincks, 1884

Genus SCHIZOSTOMELLA Canu and Bassler, 1927

SCHIZOSTOMELLA CRASSA (Canu, 1908)

Plate 16, figure 1; plate 18, figures 3-5

Schizostoma crassum Canu, 1908, p. 70, pl. 8, figs. 6-8.

Occurrence.—Eocene (Lutetian), Paris Basin.

Material examined.—Two specimens, USNM 65778, 650906, Chaussy (Seine-et-Oise); 2 specimens USNM 65780, 650907, Cahaignes (Eure), France.

Remarks.—This species, the type by original designation of *Schizostomella,* resembles some species of *Metrarabdotos* in having an erect, bilaminate zoarium, zooecia with frontal areolae and proximally notched orifices, lateral adventitious avicularia, and gonoecia. The following remarks are a necessary supplement to Canu's (1908) description and illustrations of the species.

The zooecia and gonoecia of *S. crassa* differ from those of *Metrarabdotos* in several important respects. The frontal wall is composed of a single layer (pl. 18, fig. 5) margined by a row of areolae which continue around the distal margin (pl. 18, fig. 4). The primary orifice of the zooecia is sinuate and that of the gonoecia is separated from a proximal ascopore (pl. 16, fig. 1); moreover, there is no distal oral shelf (pl. 18, fig. 5). The avicularia develop from areolae (pl. 18, fig. 4), but from those about the middle of lateral rows, and they occur on the distal covers of gonoecia as well as laterally on zooecia and gonoecia (pl. 16, fig. 1). Interzooecial communication pores occur near the base of lateral walls (pl. 18, fig. 3) and the areolae originate much nearer the basal walls. Finally, the gonoecia differ from zooecia primarily in enlargement of the oral region (pl. 16, fig. 1; pl. 18, fig. 3) and lack the distinctive ornamentation of the distal cover shown by *Metrarabdotos.*

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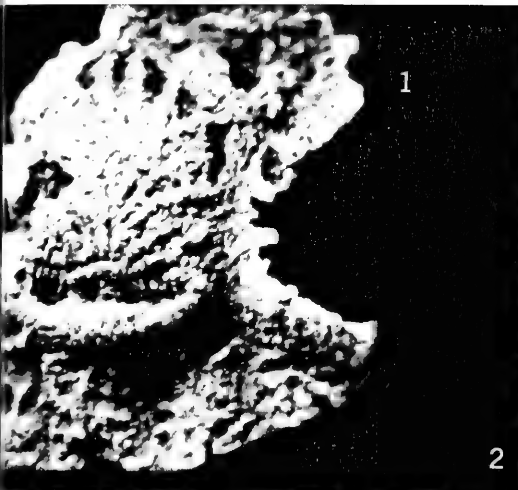
PLATES

PLATE 1

[All figures ×50; specimens coated with ammonium chloride]

FIGS. **1–4.**—***Metrarabdotos* (*Rhabdotometra*) *micropora micropora*** (Gabb and Horn). **1,** Frontal view of specimen USNM 650785 showing nearly complete gonoecium having moderately costulate distal cover; basal marl bed, Shubuta Clay at type locality, Mississippi. **2,** Frontal view of specimen USNM 650788 showing thin-walled zooecia having lateral oral avicularia; lower Red Bluff Formation, Little Stave Creek, Alabama. **3,** Frontal view of specimen USNM 650791 showing thick-walled zooecia having slightly distal ordinary avicularia; moderately differentiated special avicularia occur on zooecia distolateral to gonoecium having moderately costulate distal cover; lower Red Bluff Formation, St. Stephens quarry, Alabama. **4,** Frontal view of specimen USNM 650787 showing feebly differentiated special avicularia on zooecia distolateral to gonoecia; gonoecial covers heavily costulate; lower Red Bluff Formation, Little Stave Creek, Alabama.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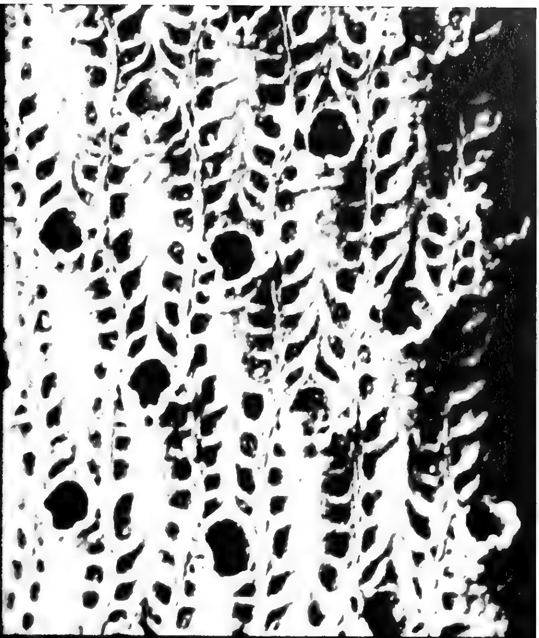
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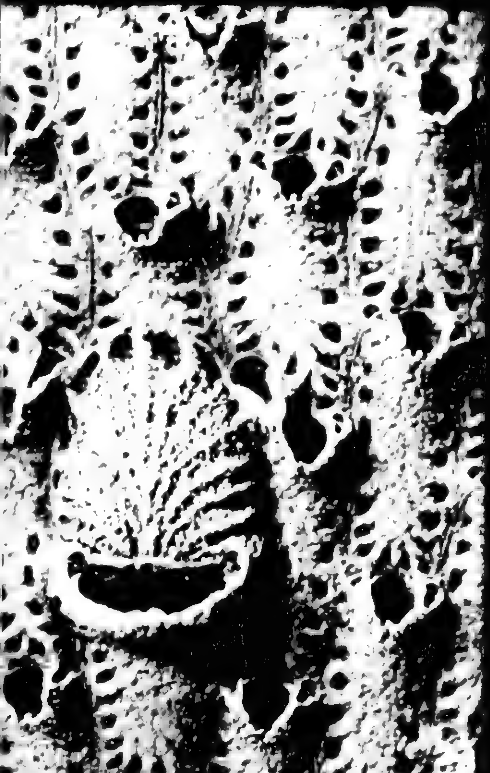
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PLATE 2

[Specimens coated with ammonium chloride]

FIGS. **1–4.—*Metrarabdotos* (*Rhabdotometra*) *micropora micropora*** (Gabb and Horn). **1,** Frontal view of Canu and Bassler's hypotype USNM 649341 showing thick-walled zooecia having ordinary avicularia occluded, ×50; Marianna Limestone, Monroeville, Alabama. **2,** Frontal view of specimen USNM 650802 showing thick-walled zooecia having slightly distal ordinary avicularia; moderately differentiated special avicularia occur on zooecia distolaterally adjacent to gonoecia; gonoecial covers heavily costulate but preserving intercostular perforations; ×50; Mint Spring Marl at type locality, Mississippi. **3,** Zoarial fragment, USNM 650807, ×12.5. **4,** Frontal view of same specimen showing thick-walled zooecia having slightly distal avicularia and mucronate secondary orifices and gonoecium with moderately costulate distal cover, ×50. Lower Marianna Limestone, St. Stephens quarry, Alabama.

PLATE 3

[All figures ×50; specimens coated with ammonium chloride]

FIGS. **1–4.—*Metrarabdotos (Rhabdotometra) micropora micropora*** (Gabb and Horn). **1,** Frontal view of specimen USNM 650820 showing two gonoecia with extreme costulation of distal cover. **2,** Frontal view of specimen USNM 650821 showing zooecia having distally placed ordinary avicularia. Chickasawhay Limestone, St. Stephens quarry, Alabama. **3,** Frontal view of specimen in collection of Academy of Natural Sciences of Philadelphia, probably a syntype, showing thick-walled zooecia having mucronate secondary orifices and slightly distally placed avicularia; labeled "Alabama?". **4,** Frontal view of lectotype of *M. grande* (USNM 649349) showing thick-walled zooecia one-third of which have avicularia occluded; Marianna Limestone, Vosburg, Mississippi.


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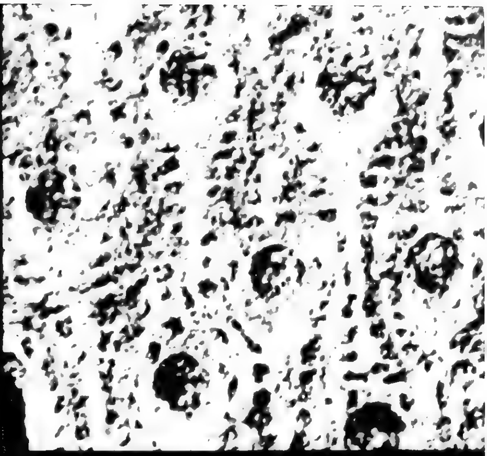
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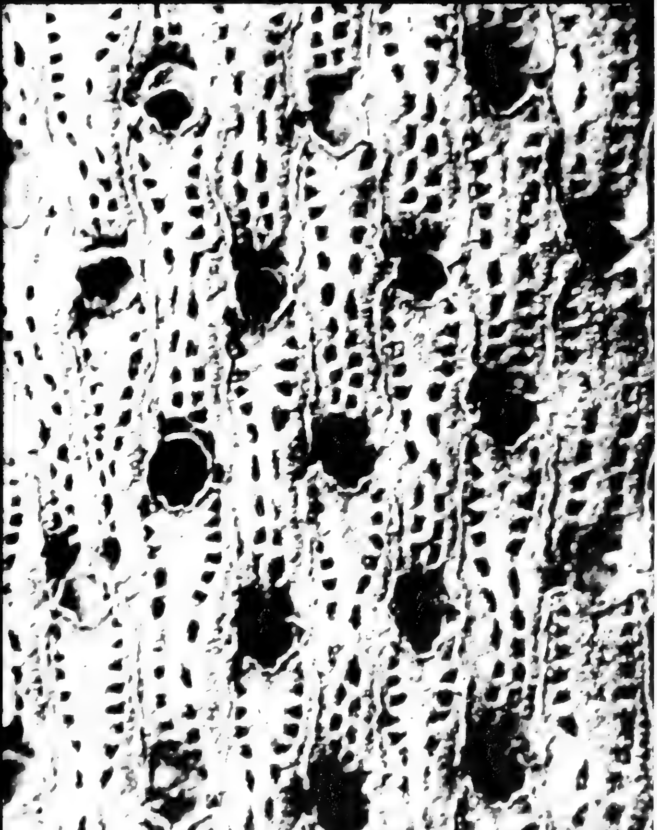
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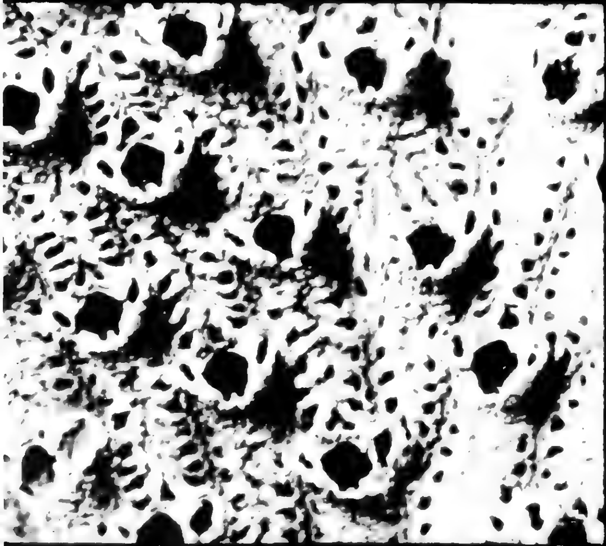
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PLATE 4

[All figures ×50; specimens coated with ammonium chloride]

FIGS. **1–2.**—***Metrarabdotos* (*Rhabdotometra*) *micropora butlerae*,** n. subsp. **1**, Frontal view of paratype USNM 650823 showing gonoecium having slightly costulate distal cover and distolateral zooecia having well-differentiated special avicularia. **2**, Frontal view of holotype USNM 650822 showing gonoecium having even weaker costulation and zooecia having ordinary avicularia directed transversely inward. Tampa Formation, Falling Waters Sink, Florida.

FIGS. **3–5.**—***Metrarabdotos* (*Rhabdotometra*) *micropora floridanum*,** n. subsp. **3**, Frontal view of holotype USNM 650825 showing gonoecium having heavily costulate distal cover with well-preserved intercostular perforations and left distolateral zooecium having weakly differentiated special avicularium; Bumpnose Limestone, Smith's quarry, Florida. **4**, Frontal view of paratype USNM 650827 showing thick-walled, small zooecia having relatively large ordinary avicularia. **5**, Frontal view of paratype FGS 5392 showing thinner walled, poorly preserved zooecia, and heavily costulate gonoecia. Bumpnose Limestone, Marianna Lime Products Company quarry, Florida.

PLATE 5

[Specimens coated with ammonium chloride]

Figs. **1–4.**—***Metrarabdotos* (*Rhabdotometra*) *micropora floridanum*,** n. subsp. **1**, Zoarial fragment, paratype USNM 650829, ×12.5. **2**, Frontal view of paratype USNM 650831 showing small zooecia, ×50. Bumpnose Limestone, Avon Park well, Florida. **3**, Frontal view of paratype USNM 650832 showing small zooecia, ×50. **4**, Frontal view of another part of same specimen showing gonoecium having heavily costulate distal cover and distolateral zooecia having feebly differentiated special avicularia; ×50. Vicksburgian marl above Cooper Marl, Hawkinsville, Georgia.

Fig. **5.**—***Metrarabdotos* (*Rhabdotometra*) *vigneauxi*,** n. sp. Frontal view of holotype USNM 650834 showing gonoecium having moderately costulate distal cover and distolateral zooecia having strongly differentiated special avicularia; ×50; Stampian, Biganos, France.

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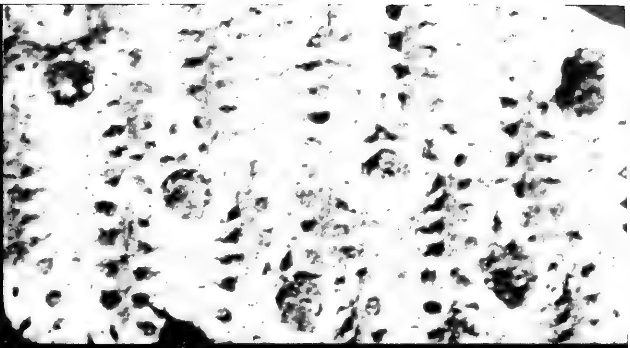

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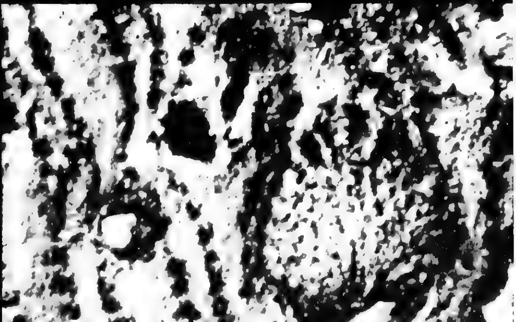

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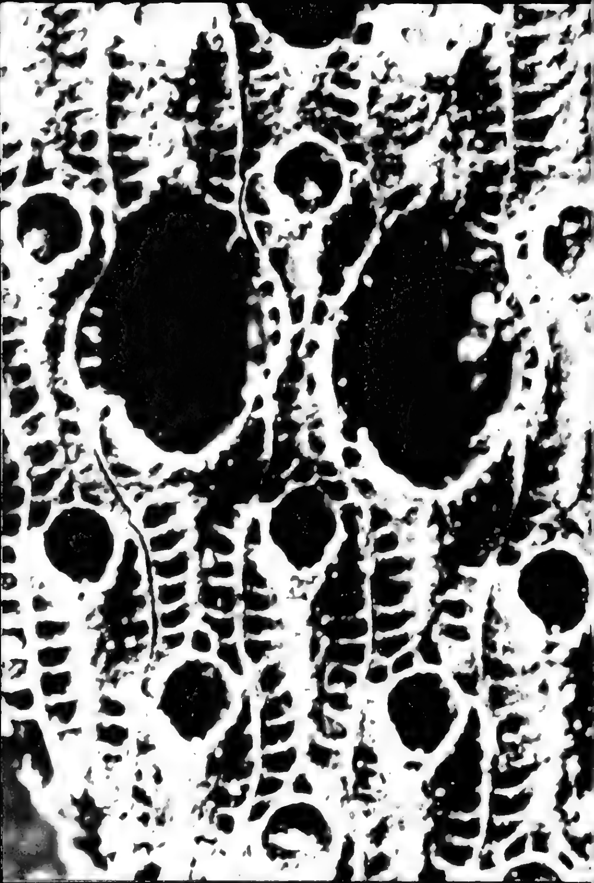

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PLATE 6

[All figures ×50; specimens coated with ammonium chloride]

FIGS. **1, 3–4.**—***Metrarabdotos* (*Biavicularium*) *chipolanum*,** n. sp. **1,** Frontal view of holotype USNM 650837 showing zooecia having lateral ordinary avicularia and axillary zooecium having moderately differentiated special avicularium. **3,** Frontal view of another part of same specimen showing axillary zooecia lacking special avicularia. **4,** Frontal view of paratype USNM 650838 showing two gonoecia in which distal covers are broken; deep-set median denticle is visible in orifices of proximal zooecia. Chipola Formation, Tenmile Creek, Florida.

FIG. **2.**—***Metrarabdotos* (*Rhabdotometra*) *vigneauxi*,** n. sp. Frontal view of paratype USNM 650835 showing zooecia having lateral avicularia; Stampian, Biganos, France.

PLATE 7

[All figures ×50; specimens coated with ammonium chloride]

FIGS. **1, 4.**—***Metrarabdotos* (*Biavicularium*) *tenue auriculatum*** Canu and Bassler. **1,** Frontal view of lectotype USNM 68679 showing zooecia having ordinary avicularia and axillary zooecia having strongly differentiated special avicularia; Caloosahatchee Marl, Shell Creek, Florida. **4,** Frontal view of specimen USNM 650862 showing heavily calcified zooecia and gonoecia; strongly differentiated special avicularia occur on zooecia distolateral to gonoecium at lower right; Waccamaw Marl, 15 miles northeast of Myrtle Beach, South Carolina.

FIGS **2–3.**—***Metrarabdotos* (*Biavicularium*) *tenue colligatum*** Canu and Bassler. **2,** Frontal view of lectotype USNM 68677 showing zooecia having distal avicularia, the one on left distolateral margin of gonoecium having well-differentiated special avicularium; Cercado Formation, Cercado de Mao, Dominican Republic. **3,** Oblique-marginal view of specimen USNM 650852 showing zooecia of marginal row having strongly differentiated special avicularia and wing-like marginal expansion of frontal wall; Cercado Formation, Rio Cana, Dominican Republic.

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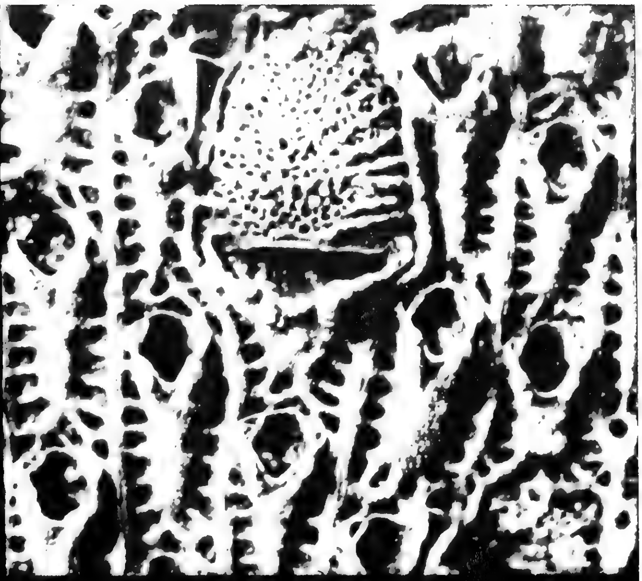

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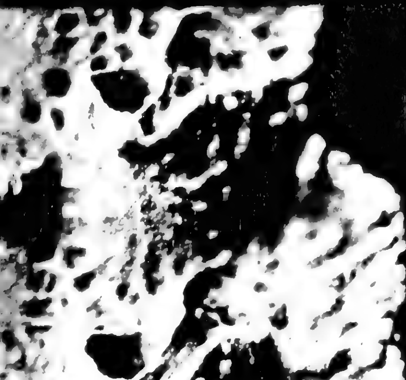

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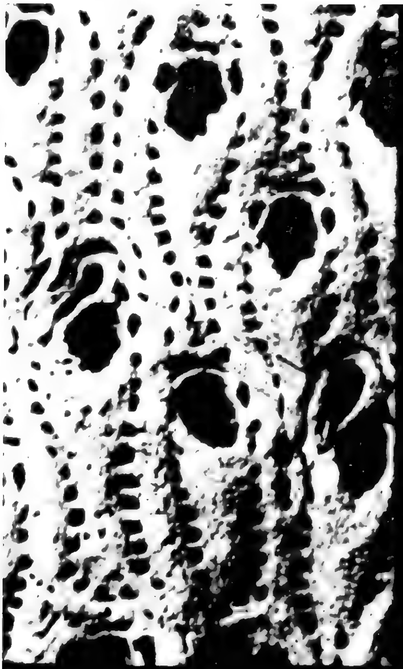

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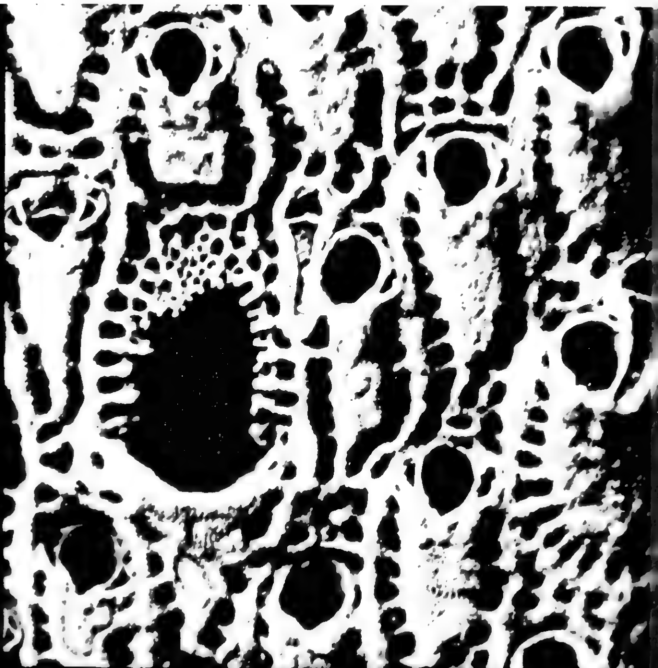

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PLATE 8

[All figures ×50; specimens coated with ammonium chloride]

FIGS. **1–2.**—***Metrarabdotos (Biavicularium) tenue auriculatum*** Canu and Bassler. **1,** Frontal view of specimen USNM 650863 showing zooecia having only slightly distally placed ordinary avicularia and false boundaries along areolae of adjacent zooecia; axillary zooecia have moderately differentiated special avicularia; Tamiami Formation, Sunniland, Florida. **2,** Frontal view of specimen USNM 650862 showing zooecia having laterally placed ordinary avicularia; zooecium on right distolateral margin of gonoecium has a well-differentiated special avicularium, and one marginal zooecium has a special avicularium; Waccamaw Marl, 15 miles northeast of Myrtle Beach, South Carolina.

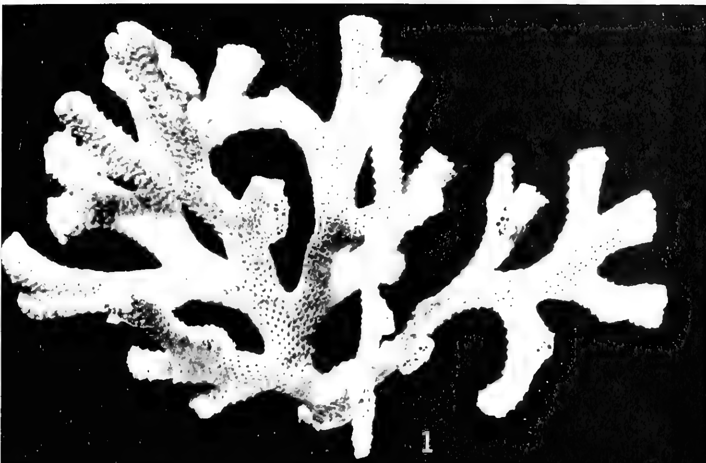
FIGS. **3–4.**—***Metrarabdotos (Biavicularium) tenue tenue*** (Busk). **3,** Frontal view of specimen USNM (Z) 11935 with membrane partly removed to show zooecia having distally placed avicularia and marginal zooecium having special avicularium with bilobed mandible. **4,** Frontal view of another part of the same specimen with epifrontal membrane removed entirely to show gonoecium and adjacent zooecia; one marginal zooecium has special avicularium with subspatulate rostrum. Recent, off Puerto Rico.

PLATE 9

FIGS. **1–3.**–***Metrarabdotos* (*Biavicularium*) *tenue tenue*** (Busk). **1,** Nearly complete zoarium, USNM (Z) 11934, ×2. **2,** Frontal view of a marginal and parts of adjacent zooecia of specimen USNM (Z) 9817 showing a special avicularium with bilobed mandible (in occludent position) and antirostral membrane; ×50; specimen lightly coated with ammonium chloride. **3,** Frontal view of growing edge of same specimen showing anasciform distal zooecia having broken frontal membranes overarched at proximal ends by epifrontal membrane; distal oral shelf is visible in second zooecium from left in distal ring; ×50; specimen lightly coated with ammonium chloride. Recent, off Puerto Rico.

FIG. **4.**—***Metrarabdotos* (*Uniavicularium*) *kugleri,*** n. sp. Frontal view of holotype USNM 650872 showing gonoecium having avicularium, costulate distal cover, and straight distal lip and zooecia having single, large avicularium or lacking one altogether, ×50; specimen coated with ammonium chloride; Manzanilla Formation, Manzanilla Bay, Trinidad.

FIG. **5.**—***Metrarabdotos* (*Biavicularium*) *lacrymosum*** Canu and Bassler. Frontal view of lectotype USNM 68678 showing gonoecia having costulate distal cover and avicularia, zooecia having distally directed ordinary avicularia, and axillary zooecium having strongly differentiated, special avicularium with subspatulate rostrum; ×50; specimen coated with ammonium chloride; Bowden Marl, Bowden, Jamaica.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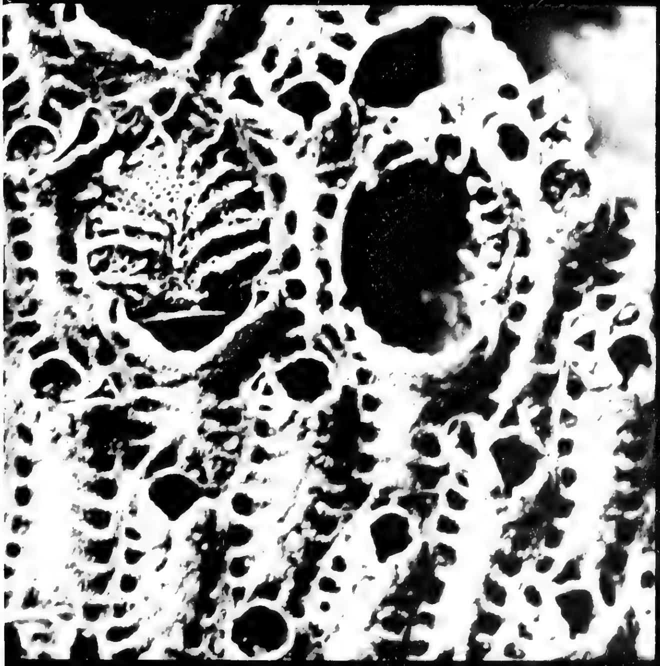
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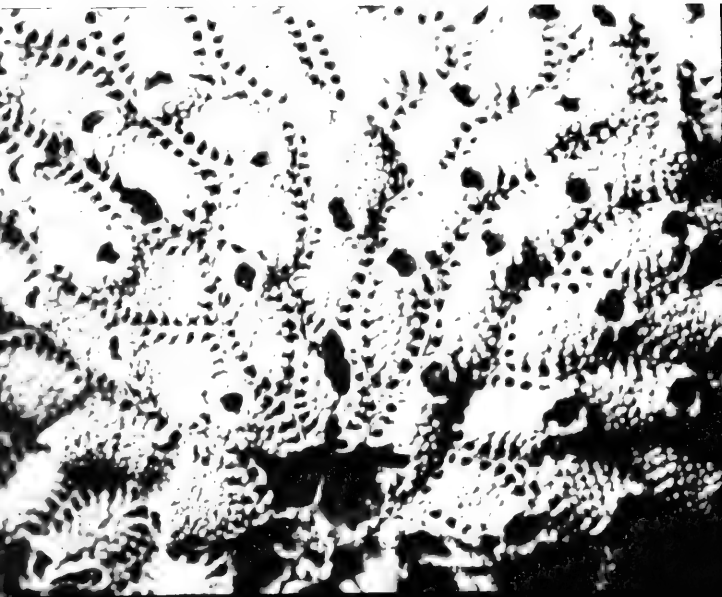

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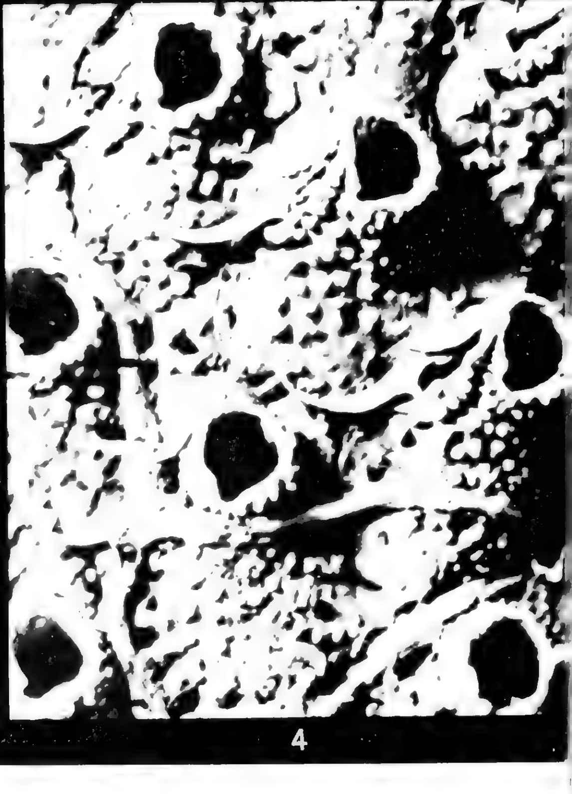

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PLATE 10

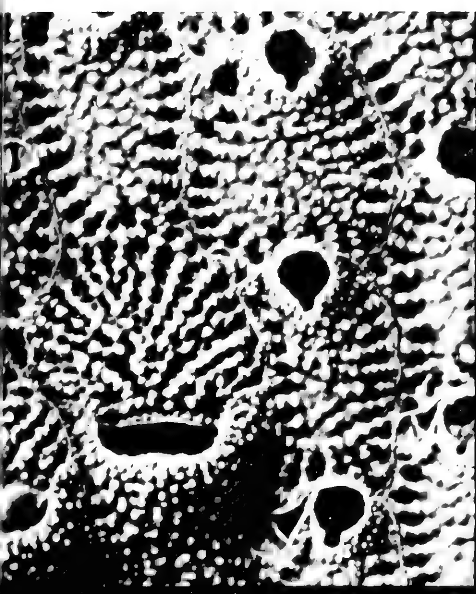
GS. **1–4.**—***Metrarabdotos* (*Uniavicularium*) *unguiculatum unguiculatum*** Canu and Bassler. **1,** Frontal view of specimen USNM (Z) 11940, an encrusting zoarium, showing broken ancestrula and zooecia of first six generations (budding pattern shown in Figure 1 in the text), ×25; specimen coated with ammonium chloride; Recent, east of Yucatan. **2,** Nearly complete zoarium USNM (Z) 11942 having several tubular offshoots formed by frontal budding (center) or coalescence of unilaminate fronds (near top); zooecia oriented in several directions; ×2; Recent, west of Florida. **3,** Frontal view of Canu and Bassler's hypotype USNM (Z) 8571 showing zooecia within four rings of growing edge of an encrusting zoarium; most distal zooecia have only basal and wedge-shaped lateral walls, in the latter of which communication pores are visible; next-to-distal zooecium on right has distal wall and proximal part of frontal wall including communication pores in areolae and buttresses between them; next-to-distal zooecium on left has primary layer of frontal wall complete including peristome, interareolar buttresses, on the proximal of which tubercles of superficial material have appeared, and enlarged, multiple areola to left of orifice forming precursor of avicularium; more proximal zooecia have avicularia, paired on zooecium at center, extensively developed, tuberculate superficial frontal layer which has topped the frontal margin of the lateral wall at lower left, and elongate peristome with sinus deflected toward avicularium; avicularia, complete on two proximal zooecia, have mandibular bar attached antirostrally to a cryptocyst-like lamina bearing a pore off center; ×50; specimen coated with ammonium chloride; Recent, off Brazil. **4,** Frontal view of specimen USNM (Z) 7554 showing zooecia having epifrontal membrane and avicularian mandibles intact (mandible at upper right in occludent position); proximal zooecium at center has mandible overgrown by chitinous tube of an epibiont; ×50; specimen coated with ammonium chloride, Recent, west of Florida.

PLATE 11

[All figures ×50; specimens coated with ammonium chloride]

FIGS. **1–2.—*Metrarabdotos* (*Uniavicularium*) *unguiculatum pacificum*** (Osburn). **1,** Frontal view of paratype AHF-95 showing small, broad zooecia, about half of which have avicularia, and two gonoecia. **2,** Frontal view of another part of the same specimen showing zooecia, only two of which have avicularia. Recent, west coast of Panama.

FIGS. **3–4.—*Metrarabdotos* (*Uniavicularium*) *unguiculatum cookae,*** n. subsp. **3,** Frontal view of holotype USNM (Z) 11946 showing gonoecium and zooecia having single avicularia or none. **4,** Frontal view of paratype USNM (Z) 11948 showing zooecia having single or paired avicularia. Recent, off Accra, Ghana.



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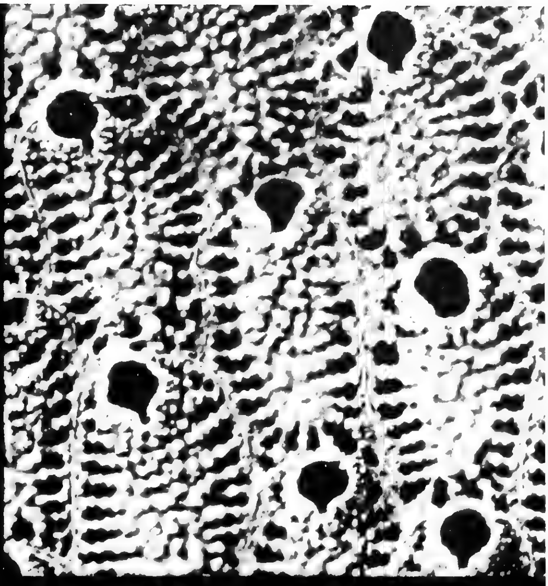

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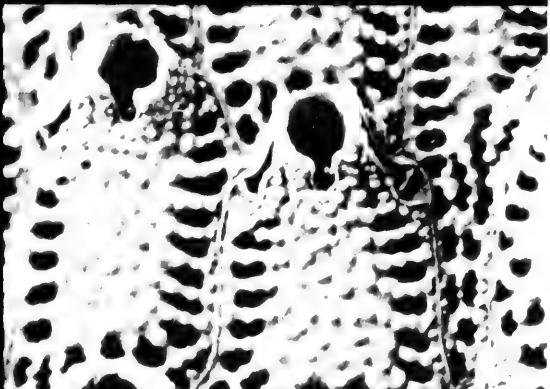

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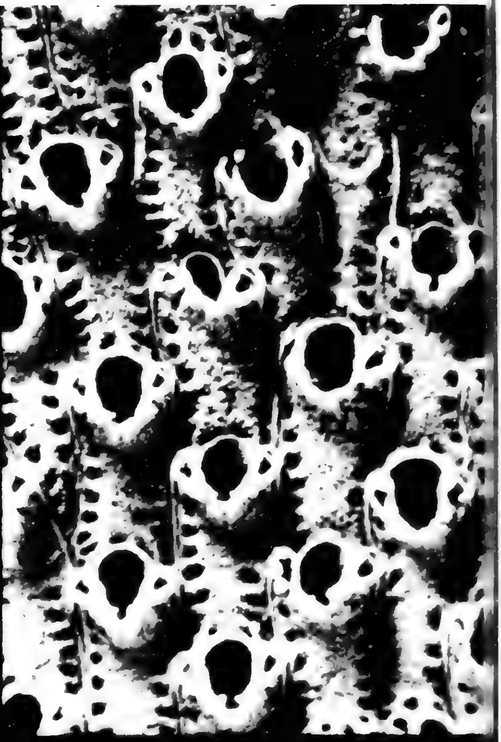

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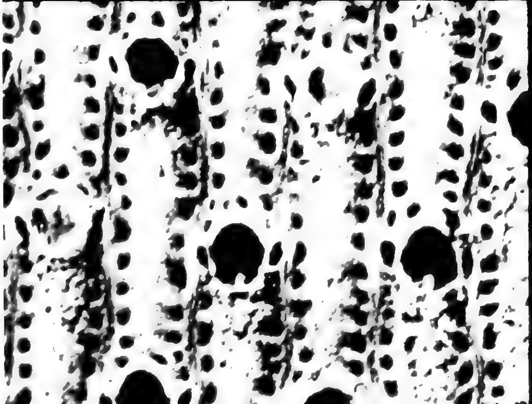

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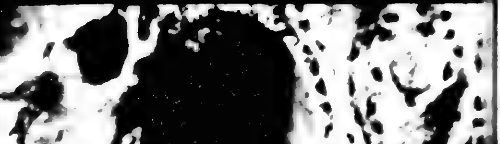

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PLATE 12

[All figures ×50; specimens coated with ammonium chloride]

FIG. 1.—***Metrarabdotos* (*Biavicularium*) *lacrymosum*** Canu and Bassler. Frontal view of specimen USNM 650871 (topotype) having distally directed ordinary avicularia; Bowden Marl, Bowden, Jamaica.

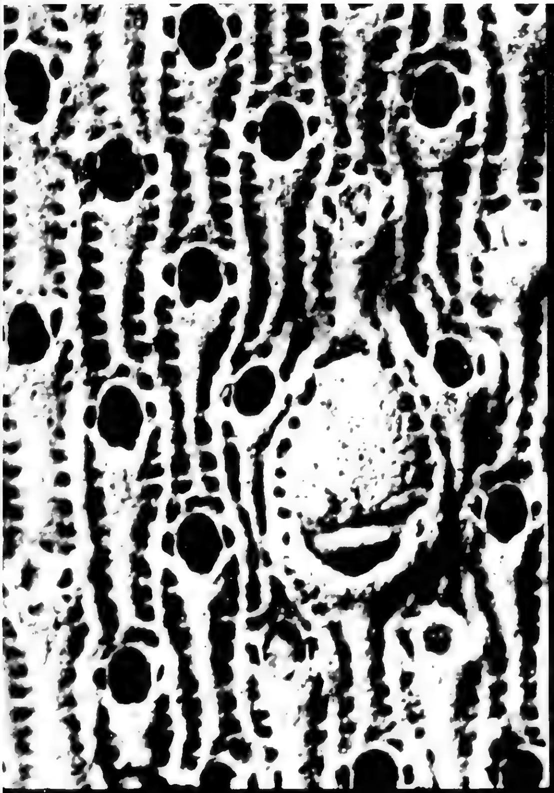
FIGS. 2–5.—***Metrarabdotos* (*Porometra*) *helveticum helveticum*** (Roger and Buge). **2,** Marginal view of specimen USNM 60540 showing marginal zooecia of both rows having well-differentiated special avicularia. **3,** Frontal view of specimen USNM 650877 showing small zooecia having lateral avicularia and most having lateral oral denticles visible. **4,** Frontal view of specimen USNM 650876 showing larger zooecia most of which have only the median oral denticle visible. **5,** Frontal view of specimen USNM 650875 showing two gonoecia with broken distal covers, zooecia distolateral to gonoecia having moderately differentiated special avicularia, and several zooecia having lateral oral denticles visible. Helvetian, Pont-Levoy, France.

PLATE 13

[All figures ×50; specimens coated with ammonium chloride]

FIG. **1.—*Metrarabdotos (Porometra) helveticum thomasi,*** n. subsp. Frontal view of holotype USNM 650886 showing small gonoecium, zooecia having lateral ordinary avicularia, and zooecia distolateral to gonoecium having well-differentiated special avicularia; Miocene or Pliocene, Sierra Leone.

FIGS. **2–4.—*Metrarabdotos (Porometra) helveticum canariense,*** n. subsp. **2,** Frontal view of holotype BM (NH) D.9294 showing large gonoecium, zooecia having lateral ordinary avicularia, and zooecia distolateral to gonoecium having strongly differentiated special avicularia. **3,** Frontal view of paratype BM (NH) D.9292 showing zooecia having lateral ordinary avicularia. Miocene, Grand Canary Island. **4,** Frontal view of paratype USNM 650884 showing zooecia, including an axillary one, having ordinary avicularia and marginal zooecia, on right, having moderately differentiated special avicularia; Pliocene, Rhodes.



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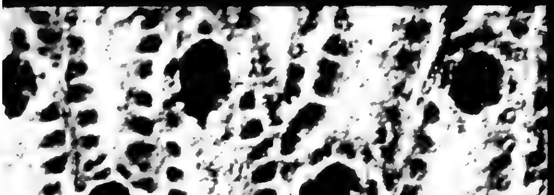

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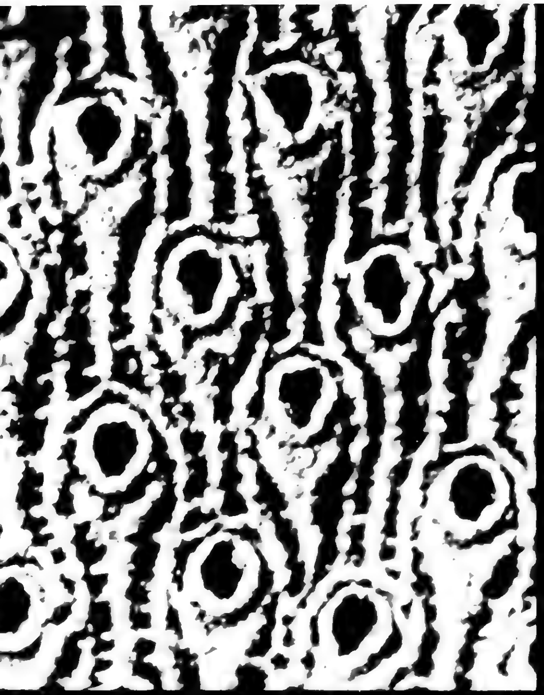

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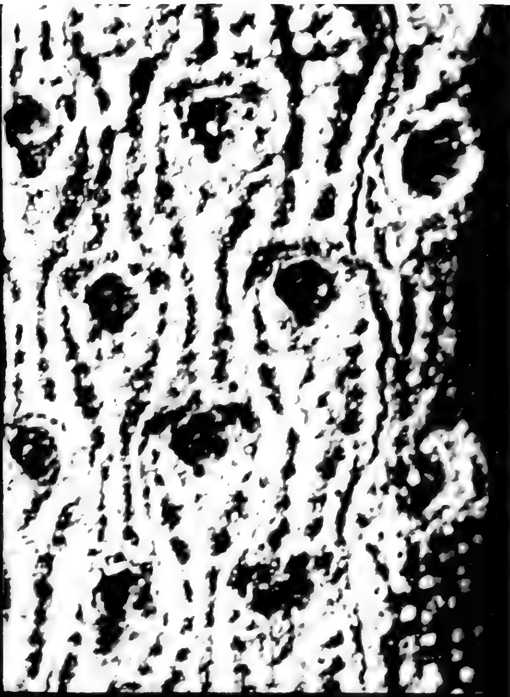

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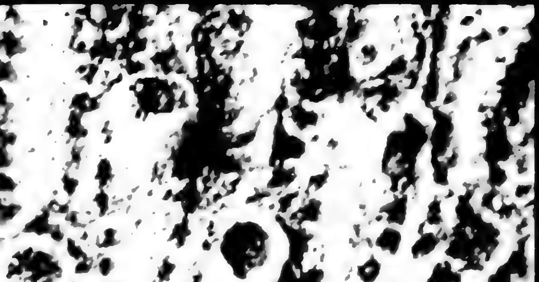

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PLATE 14

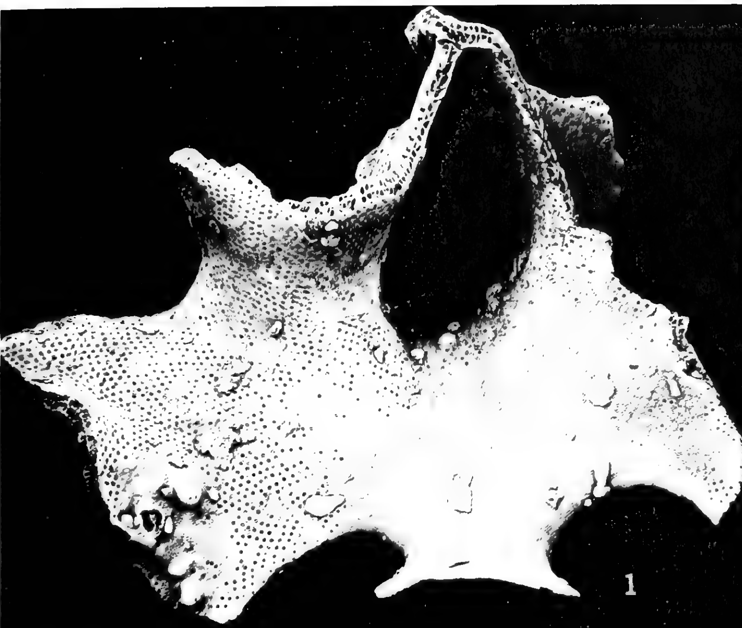
[All figures ×50; specimens coated with ammonium chloride]

Figs. **1–5.—*Metrarabdotos* (*Porometra*) *maleckii*,** n. sp. **1,** Frontal view of holotype USNM 60579 showing thick-walled zooecia lacking ordinary avicularia; Leithakalk, Eisenstadt, Austria. **2,** Frontal view of paratype USNM 650890 showing thinner walled zooecia having ordinary avicularia; marginal zooecia lack special avicularia; Leithakalk, Zidlochovice, Czechoslovakia. **3,** Frontal view of paratype USNM 650893, broken transversely in fossilization, showing zooecia, all but the proximal one just inside right margin, lacking avicularia; Leithakalk, Grzybóm, Poland. **4,** Frontal view of paratype USNM 650889, severely recrystallized, showing zooecia having lateral ordinary avicularia; Leithakalk, Eisenstadt, Austria. **5,** Frontal view of paratype USNM 650892, poorly preserved, showing most of a gonoecium; Leithakalk, Grzybóm, Poland.

PLATE 15

[Specimens coated with ammonium chloride]

FIGS. 1–4.—***Metrarabdotos* (*Metrarabdotos*) *moniliferum*** (Milne Edwards). **1,** Large, nearly complete, foliaceous zoarium, USNM 60344, having broad, encrusting base; proximal zooecia have been sealed frontally and their boundaries have been obliterated; ×2; Coralline Crag, Sutton, Suffolk. **2,** Proximal fragment of a less robust zoarium, USNM 650897 (topotype); ×15. **3,** Frontal view of specimen USNM 650895 (topotype) showing two gonoecia having noncostulate distal covers and broken hood-like proximal lips; zooecia have slightly proximally placed ordinary avicularia; axillary zooecium and zooecia distolateral to gonoecia have special avicularia; ×50. **4,** Marginal view of same specimen showing some of the rare zooecia which possess special avicularia; ×50. Coralline Crag, Sudbourne, Suffolk.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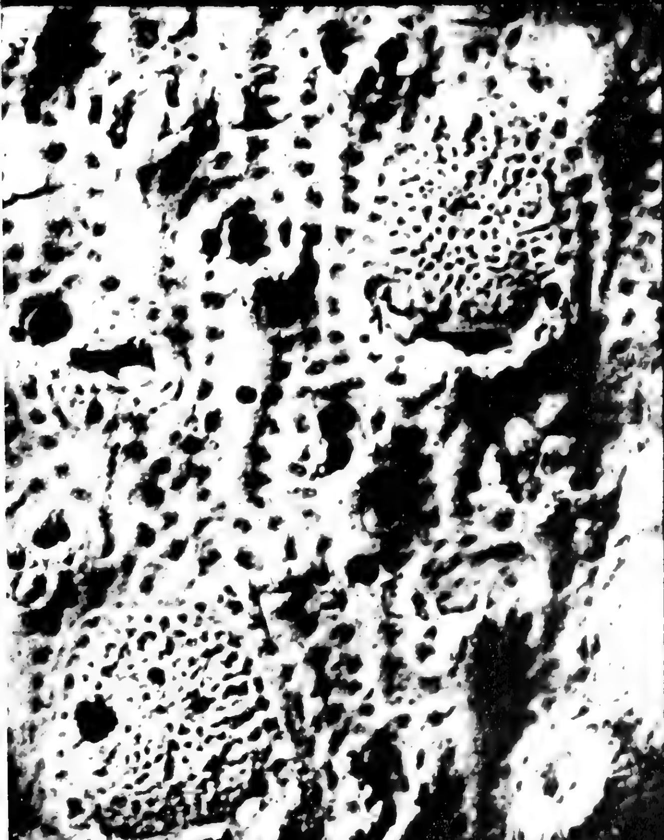
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PLATE 16

[All figures ×50; specimens coated with ammonium chloride]

FIG. **1.—*Schizostomella crassa*** (Canu). Frontal view of specimen USNM 65778 showing all or parts of five gonoecia having distal covers imperforate except for marginal areolae, an ascopore, and distal avicularium as well as lateral ones; zooecia have complete circlet of areolae, sinuate primary orifice and lateral avicularia, lacking crossbars, developed from areolae near middle of lateral rows; Lutetian, Chaussy, France.

FIG. **2.—*Escharoides aliferus*** (Reuss). Frontal view of specimen USNM 65765 showing all or parts of six ovicelled zooecia having elongate, marginally areolate, faintly costulate, finely perforate hyperstomial ovicells; left distal zooecium has avicularian chambers at early stage of development crowding areolae toward frontal midline; distal oral spines and shallow median oral denticle are prominent on several zooecia; avicularia have crossbars and pointed rostra; Lutetian, Parnes, France.

FIG. **3.—*Escharoides laticella*** (Canu and Bassler). Frontal view of specimen USNM 650784 showing all or parts of eight ovicelled zooecia; ovicells, avicularia, and orifices differ slightly from those of *E. aliferus;* distal oral shelf is visible in zooecium with broken ovicell at right; Moodys Marl, Jackson, Mississippi.

FIG. **4.—*Escharoides coccineus*** (Abildgaard). Frontal view of specimen USNM (Z) 9462 showing zooecia having ovicells, avicularia, and orifices still less like those of *E. aliferus;* Recent, Shetland Islands.

FIGS. **5–6.—*Trigonopora vermicularis*** Maplestone. **5**, Oblique-marginal view of specimen USNM 650780 showing one zooecium and parts of five others, two of which have hyperstomial ovicells; areolae margin ovicell and lateral and proximal boundaries of zooecial frontal, which shows two-layered structure at secondary orifice; median proximal oral denticle, paired distolateral avicularia with crossbars, and reflected distal lip of ovicelled zooecium are similar to those of *Metrarabdotos.* **6**, Frontal view of specimen USNM 650781 showing ovicelled zooecium and parts of other, nonovicelled ones; ovicell lacks perforation, except for marginal areolae and irregular lateral fenestrae. Janjukian, Anticline Creek, Victoria, Australia.

PLATE 17

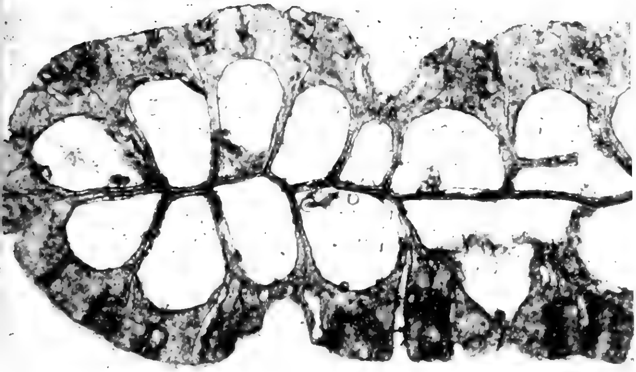
[All figures ×50]

FIGS. **1, 4.**—***Metrarabdotos* (*Rhabdotometra*) *micropora micropora*** (Gabb and Horn). **1,** Transverse view of specimen USNM 650812 showing thin, separate basal walls of zooecia in the two zoarial laminae; thin, separate lateral walls of zooecia of adjacent rows; and thick, continuous frontal walls of zooecia of both laminae; two-layered frontal structure not preserved; upper Marianna Limestone, Little Stave Creek, Alabama. **4,** Longitudinal view of specimen USNM 650794 showing two gonoecia and part of a third all having continuous cavities nearly filled with matrix, thin basal and distal walls, thicker frontal walls and finely perforate distal covers, reflected distal lips and projecting, but not hooded proximal lips; distal part of gonoecium is recumbent upon distal zooecium; two distal gonoecia oppose; proximal one is single; two-layered frontal structure not preserved; upper Red Bluff Formation, Little Stave Creek, Alabama.

FIGS. **2–3.**—***Metrarabdotos* (*Biavicularium*) *tenue colligatum*** Canu and Bassler. **2,** Longitudinal view of specimen USNM 650850 showing thin basal, lateral, and distal walls and thick, two-layered frontal wall; primary frontal layer joins lateral walls by interareolar buttresses; lateral walls perforated by simple pores. **3,** Frontal part of longitudinal view of same specimen showing thick, lamellar superficial layer of frontal overlying thin, primary layer; outer lamellae seal oral region. Cercado Formation, Cercado de Mao, Dominican Republic.

FIG. **5.**—***Metrarabdotos* (*Uniavicularium*) *unguiculatum unguiculatum*** Canu and Bassler. Tangential view of specimen USNM (Z) 11943 showing two zooecia and parts of others; thin lateral and distal walls and the primary layer of the frontal wall, which forms peristome and avicularium, contrast with thicker superficial layer; areolae are limited to lateral and proximal margins of zooecia; Recent, west of Florida.

FIGS. **6–7.**—***Metrarabdotos* (*Porometra*) *helveticum helveticum*** (Roger and Buge). **6,** Oblique tangential view, deepening distally to show development of oral shelf from distal wall and areolae from lateral walls; specimen USNM 650881. **7,** Longitudinal view of specimen USNM 650882 showing alternating zooecia having thin basal, lateral, and distal walls, thick, frontal wall with lateral and proximal areolae, distal oral shelf, and lateral communication pores. Helvetian, Pont-Levoy, France.



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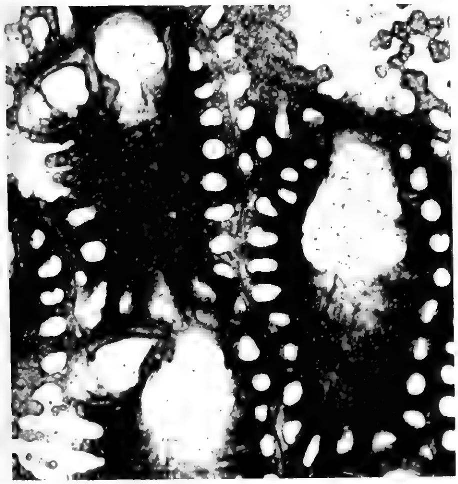

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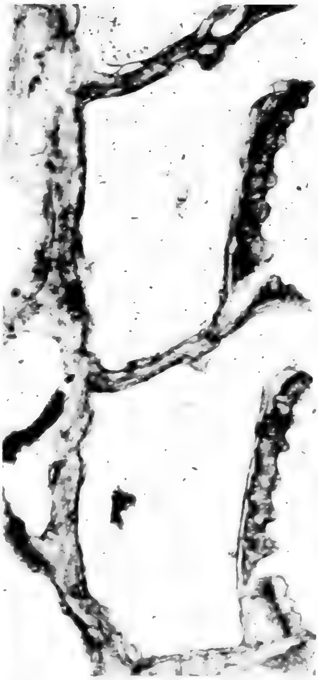

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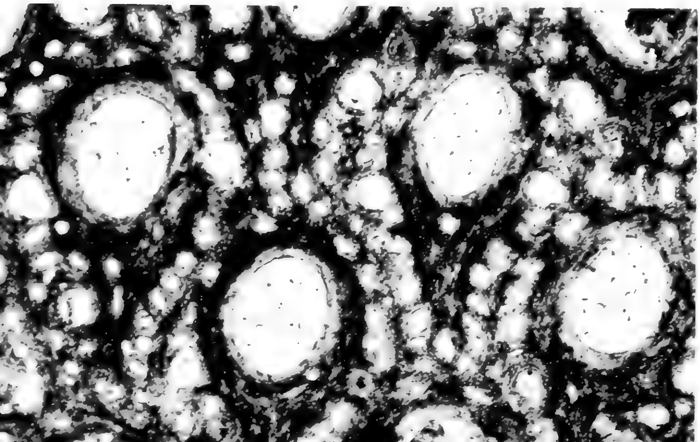

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PLATE 18

Figs. **1–2.—*Metrarabdotos (Uniavicularium) unguiculatum unguiculatum*** Canu and Bassler. **1,** Tangential view of specimen USNM (Z) 11944 showing interareolar buttresses formed from primary layer of frontal wall, avicularium formed by merging distal areolae, and prominent distal oral shelf; ×50. **2,** Longitudinal view of same specimen showing distal oral shelf and two-layered frontal wall, the superficial layer nonlamellar; ×50. Recent, west of Florida.

Figs. **3–5.—*Schizostomella crassa*** (Canu). **3,** Longitudinal view of specimen USNM 650906 showing a pair of opposing gonoecia, part of a third unopposed gonoecium, and zooecia in opposing pairs; gonoecia are not recumbent upon distal zooecia, and their distal covers are imperforate; zooecial communication pores are placed almost at basal wall; ×50; Lutetian, Chaussy, France. **4,** Tangential view of specimen USNM 65780 showing zooecia having single-layered frontal wall, the crown of areolae continuing around distal margin of zooecium, scattered areolae within peripheral row, and avicularia, without crossbars, generated from areolae near midlength in lateral row; ×100. **5,** Longitudinal view of specimen USNM 650907 showing thin basal and distal walls and thick, but single-layered frontal wall with areolae; ×100. Lutetian, Cahaignes, France.