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EVOLUTIONARY SIGNIFICANCE OF SEXUAL AND ASEXUAL MODES OF PROPAGATION IN NEOGENE SPECIES OF THE BRYOZOAN *METRARABDOTOS* IN TROPICAL AMERICA

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ABSTRACT—Three new Miocene-Pliocene species of the cheilostome bryozoan *Metrarabdotos* from Venezuela are atypical in showing significant evidence that as many as half the colonies originated asexually (clonally) by ''regeneration'' from previously existing colonies, rather than almost exclusively from ancestrular zooids (products of metamorphosis of sexually produced larvae), as is characteristic of the genus. The extremely low proportion of zooids (less than two percent) recognizably committed to producing larvae (ovicelled) in these Venezuelan species agrees with that reported in a variety of Danian (Paleocene) genera in which clonal propagation has been reported to predominate. However, all but two of 17 other living and fossil species of *Metrarabdotos* also have fewer than two percent of their zooids ovicelled, even though all but one of more than 250 colony bases examined originated from ancestrulae. The lack of significant correlation in *Metrarabdotos* between frequencies of ovicelled zooids and of ancestrular colonies suggests that clonal propagation may not have diverted resources from sexual reproduction. This inference is supported by the retention in these species of a level of heritable morphologic variation (estimated by partitioning among-colonies and within-colonies variance in zooid characters) that is commensurate with that estimated for species of *Metrarabdotos* in which propagation was apparently entirely by sexual means. Thus, sexual reproduction throughout the genus was apparently sufficient to maintain the genetic diversity from which speciation could proceed at normal rates. As estimated by both cladistic and nearest-neighbor morphologic-stratigraphic methods, the three Venezuelan species occupy quite different positions in the inferred phylogeny of *Metrarabdotos.* Thus, the elevated level of clonal propagation in these species appears to be a response to local conditions, most probably high productivity associated with upwelling, that promoted more rapid vegetative growth while leaving the level of sexual reproduction unchanged.

INTRODUCTION

MARINE BRYOZOANS typically reproduce sexually, forming motile larvae, each of which attaches and metamorphoses to initiate growth of a new adult genetic individual: a colony. Because a colony grows by budding modular units (zooids), each of which may perform many or all of the colony's vital functions, bryozoan species are also generally capable of another, asexual, means of propagation. By breaking into pieces, either through injury or programmed fission, one colony may give rise to others through the continued growth by budding of subsets of the original modules. Because budding is a clonal process, such propagules are parts of a single genetic individual, even though physically disconnected.

Although all marine bryozoans are thus potentially capable of both sexual and asexual increase, the relative frequency of propagation by fragmentation varies with species (Thomsen and Håkansson, 1995; Håkansson and Thomsen, in press). In some species and higher taxa, budding at fractures may be virtually limited to restoring the contours of otherwise intact colonies (reparative budding). Thomsen and Håkansson (1995) found that fragmentation was the predominant mode of propagation in species with erect growth habits in the Danian (Paleocene) of Denmark. They suggested that, for such species, colony design may have been optimized for allocating resources to vegetative growth rather than to the production of larvae. By limiting the production of motile larvae, such emphasis on propagation by fragmentation could reduce dispersal and thus increase rates of speciation and extinction. However, there is relatively little difference in the dispersal abilities of propagules formed by fragmentation and the extremely brief, largely benthic larval stages characteristic of the great majority of marine bryozoan species (Jackson and Coates, 1986).

On the contrary, propagation by fragmentation is more likely to result in significantly decreased rates of speciation and extinction because of the effects of cloning on genetic variation (Jackson and Coates, 1986). By reducing the incidence of recombination, cloning would decrease the pool of genetic variability from which a new species might be constituted; by increasing the longevity of genotypes, cloning would increase generation times and thus species durations.

The morphology of bryozoans is well suited to evaluating the relative incidence of these modes of propagation and their genetic consequences, in both living and fossil populations. As indices of the relative incidence of sexually and asexually produced colonies, Thomsen and Håkansson (1995) used 1) the proportion of zooids within colonies that possess calcified chambers for brooding embryos (ovicells); and 2) the ratio of colonies originating from metamorphosed larvae (ancestrulae) to those grown from pre-existing fragments. They found a consistent relationship between these indices for a broad spectrum of cheilostome bryozoans in the Maastrichtian and Danian of Denmark. In rearing experiments with two living species of the cheilostome *Stylopoma*, Cheetham et al. (1993) found that the proportion of phenotypic variation that is heritable can be approximated by partitioning among-colonies and within-colonies variance in quantitative traits of zooidal morphology. A similar result was obtained experimentally by Hageman et al. (1999) with the less closely related cheilostome *Electra.* The correspondence between approximations from variance partitioning and heritability estimates obtained with the usual quantitative genetic procedures, using the breeding data, is close enough that tests for the relative importance of selection and drift are virtually identical (Cheetham et al., 1993).

This paper represents a first attempt to combine these two morphologic approaches in order to estimate the effect of asexual propagation on the genetic variance of a clade of living and fossil bryozoans. *Metrarabdotos* Canu, 1914, is one of the most widespread and abundant bryozoan genera in deposits of Neogene age in tropical America. It is also one of the most extensively studied, in large part because of the major collecting efforts over the past two decades by the Dominican Republic Project (Saunders et al., 1986; Cheetham, 1986a) and the Panama Paleontology Project (Jackson et al., 1996; Collins and Coates, 1999; Cheetham et al., 1999). Although much of its taxonomy presently remains in open

nomenclature (Cheetham et al., 1999), species of *Metrarabdotos* have been quantitatively discriminated on the basis of the finest-scale, statistically significant morphologic differences and supported by analogy with genetic differences in related genera (Jackson and Cheetham, 1990, 1994). This study was prompted by new material of *Metrarabdotos* from the Miocene and Pliocene of Venezuela, also collected as part of the Panama Paleontology Project, that is unique in including significant evidence that many colonies originated by growth from pre-existing fragments. In all of the previously examined material of this genus, we have found only one such colony base among more than 250 that clearly originated from groups of ancestrular zooids in the pattern characteristic of the genus. Thus, a comparison of the Venezuelan species with those from other Neogene localities in tropical America should provide an initial assessment of the probable effects of clonal propagation on genetic variation and evolutionary rates in a clade of cheilostome bryozoans.

MATERIAL AND METHODS

Material studied.—Morphologic data for the three Venezuelan species were obtained from Panama Paleontology Project (PPP) collections as follows: *Metrarabdotos* n. sp. 11 (PPP 2535, 2537, 2650); *Metrarabdotos* n. sp. 12 (PPP 2567, 2569); *Metrarabdotos* n. sp. 13 (PPP 2539–2542). The localities from which these collections were made are described in the file locdbas4.dbf on the Panama Paleontology Project website (Collins, 1999), from which the following descriptions were extracted:

PPP 2535: Paraguana Formation, on beach ~200 m south of MARAVEN (Miramar) Clubhouse, Punta Cardon, Paraguana region, Venezuela.
PPP 2537 and PPP 2650: Paraguana Formation, just south of PPP 2535, 2–3 m above beach.
PP 2567: Cubagua Formation, Cañon de las Calderas, Isla Cubagua, Isla Margarita region, Venezuela.
PPP 2569: Cubagua Formation, 2 m west of PPP 2567.
PPP 2539: Cantaure Formation, 36.7 m below surface, well number 1, south of Casa Cantaure (El Hatillo), Paraguana region, Venezuela.
PPP 2540: Cantaure Formation, 6.5 m above PPP 2539, 30.2 m below surface.
PPP 2541: Cantaure Formation, 5.5 m above PPP 2540, 24.7 m below surface.
PPP 2542: Cantaure Formation, 4.6 m above PPP 2541, 20.1 m below surface.

Comparative material of other tropical American Neogene species of *Metrarabdotos* is from Dominican Republic Project localities (NMB, for Naturhistorisches Museum Basel), all of which are described in Saunders et al. (1986): *Metrarabdotos* n. sp. 1 (NMB 17265, 17284, 17286); *Metrarabdotos* n. sp. 2 (NMB 16935, 16936, 16938, 17265); *Metrarabdotos* n. sp. 3 (NMB 15804, 15835, 15837, 15838, 15840, 15842, 15846, 15860, 15863, 15871, 15900, 16191, 16910, 17175); *Metrarabdotos* n. sp. 4 (NMB 15814, 15835, 15836, 15838, 15840, 15842, 15846, 15849, 15860, 15863–15865, 15869, 15871, 15934, 15962, 16810, 16811, 16833, 16910, 17175); *Metrarabdotos* n. sp. 5 (NMB 15901, 16839, 16844, 16986, 16989, 16995); *Metrarabdotos* n. sp. 6 (NMB 15878, 15881, 15882); *Metrarabdotos* n. sp. 7 (NMB 15814, 15835, 15842, 15934, 16910, 17175); *Metrarabdotos* n. sp. 8 (NMB 15860, 15863); *Metrarabdotos* n. sp. 9 (NMB 16824, 16828, 16832, 16961, 16970, 16971, 16973, 16977); *Metrarabdotos* n. sp. 10 (NMB 16818, 16824, 16832, 16835, 16836, 16837, 16838, 16842, 16844, 16961, 16977, 16984); *M. auriculatum* (NMB 15878, 16817, 16824, 16836, 16839, 16843, 16844, 16857, 16913, 16915, 16959, 16961, 16971, 16986, 16995, 17005, 17012, 17019); *M. colligatum* (NMB 15878, 15904, 15915, 16857, 16910, 16912, 16913, 16918, 16922, 16926, 16928, 16929); *M. lacrymosum* (NMB 15860, 16833, 16835, 16836, 16858, 16844).

In addition to the Neogene tropical American *Metrarabdotos* material, we studied the Oligocene species *M. micropora* (from the Marianna Limestone, Monroeville, Alabama), the hypothesized ancestor of the Neogene species, and two living tropical American species, *M. tenue* (from Caroline station 68 northeast of Puerto Rico) and *M. unguiculatum* (from Albatross station D.2363 east of Yucatan). Together with the American Neogene species, these species apparently form a clade (Cheetham, 1968, 1986a); all were included in the analyses of species distinctions and phylogenetic relationships in *Metrarabdotos* described below.

To broaden the comparison of sexual versus asexual modes of propagation beyond the tropical American *Metrarabdotos* clade, we included the European Pliocene species *Metrarabdotos moniliferum* (from the Coralline Crag, Sutton, Suffolk, England), the type species of *Metrarabdotos*, and two less closely related species. *Cigclisula porosa* (from NMB 16834, 16918, 16926, 16935, 16938, 17269) and *Gemelliporella punctata* (from NMB 16928) occur in abundance in the same tropical American Neogene deposits as most of the *Metrarabdotos* species, which they resemble in (erect) colony form. These species were not included in the analyses of species distinctions and phylogenetic relationships in *Metrarabdotos* described below.

All of the specimens studied are deposited in the Bryozoa collection of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., where the figured specimens are catalogued under USNM numbers.

Discrimination of species.—Species identities of the Venezuelan specimens were determined empirically by a series of multivariate statistical procedures modified from those used in Cheetham (1986a) and Jackson and Cheetham (1994). These procedures require specimens showing all 46 of the characters on which the original multivariate analysis of *Metrarabdotos* was based (Appendix 1; Cheetham, 1986a, 1987; Cheetham and Hayek, 1988). A further requirement is that each specimen include at least five ordinary autozooids on which the first 15 characters are preserved and at least one zooid for each of the other 31 characters (from special avicularia and ovicelled zooids) (Cheetham and Hayek, 1988). As is typical of fossil specimens of erect cheilostomes, most are fragments representing small parts of the original colonies (Cheetham et al., 1981). This, compounded by the imperfect preservation of the great majority of specimens, limited this part of the analysis to 10 specimens eventually assigned to *Metrarabdotos* n. sp. 11, one to *Metrarabdotos* n. sp. 12, and three to *Metrarabdotos* n. sp. 13.

In a departure from procedures used previously, each of the 14 specimens was initially entered into a canonical discriminant function analysis (SPSS 6.1, Norusis, 1994) as an independent ''group,'' based on the 15 autozooidal characters, with specimens of the other species of *Metrarabdotos* all grouped as in Cheetham (1986a). The resulting matrix of F-values between all pairs of groups was examined for any values in which the probability of identity was 0.001 or greater. Such pairs were combined directly, rather than through an intervening cluster analysis (Cheetham, 1986a; Jackson and Cheetham, 1994). The discriminant analysis was repeated with the new groupings, and, after five repetitions, the Venezuelan specimens were in five groups, each distinct from the other *Metrarabdotos* species. Then a second series of discriminant analyses was run, using the mean values for each specimen of the 15 autozooidal characters plus the other 31 characters, and pairs of groups with F-values not significant at 0.001 were combined as before. After three repetitions, the Venezuelan specimens were grouped into the three distinct species.

Estimation of phylogenetic relationships.—The phylogenetic affinities of the three Venezuelan species were estimated by both nearest-neighbor morphologic-stratigraphic (stratophenetic) and cladistic methods. For the former, we calculated morphologic distances (square root of Mahalanobis D^2) between all pairs of tropical American *Metrarabdotos* species, including the three new Venezuelan species, from the matrix of F-values obtained in the final discriminant analysis based on all 46 characters. These distances, and the stratigraphic ranges updated with the occurrence data in Cheetham et al. (1999), were used to reconstruct the tree, as in Cheetham (1986a). In this procedure, morphologic characters are weighted in proportion to their contribution to the overall statistical distinctiveness of species (Cheetham and Hayek, 1988). As in the previous studies, the oldest species, *M. micropora*, was placed at the root of the tree.

For the cladogram, each of the characters is coded individually, and here we used the matrix of coded character states based on Duncan's multiple range test (Norusis, 1994) in Jackson and Cheetham (1994). We assigned ordered states to the three Venezuelan species based on the mean values of the 33 characters (Appendix 1) in which statistically significant gaps had been found (Jackson and Cheetham, 1994). Unlike the approach based on Mahalanobis distances, this procedure makes no use of the 13 characters in which gaps were not found. With the three species added, the new cladogram was calculated with the ''implicit enumeration'' procedure of the program Hennig86, which is certain to find all trees of minimum length (Farris, 1988). As in the stratophenetic tree, *Metrarabdotos micropora* was placed at the root by designating it as the ''outgroup,'' in accordance with results obtained by Jackson and Cheetham (1994) showing that this procedure produces trees more consistent with stratigraphic data than other approaches to outgroup selection for this genus. Multiple most-parsimonious trees were reduced to a single consensus tree with the ''nelsen'' command in Hennig86, as in Jackson and Cheetham (1994).

It should be noted that the morphologic characters (ovicell frequency, frequency of ancestrular and regenerated bases, and branch thickening gradients) used to compare reproductive modes, were not included in the character matrices used for either species discrimination or phylogeny reconstruction.

Colony bases.—The sexual origin of a *Metrarabdotos* colony is readily recognized if the distinctive ancestrular complex characteristic of the genus (Cook, 1973, fig. 1) is preserved at the base of the colony. However, from topology it can be shown that, in the fragmentary material characteristic of the vast majority of fossil *Metrarabdotos* species, pieces of branches should outnumber colony bases by orders of magnitude (Cheetham et al., 1981; Cheetham and Hayek, 1983). Thus, the absence of ancestrular colony bases in any species of *Metrarabdotos* in which specimens with ovicells are found can be attributed to sampling bias.

Colony bases originating asexually by new growth (''regeneration'') from previously existing colonies lack the ancestrular complex, but may mimic those of sexually produced colonies in other ways. For example, in *Metrarabdotos* the extrazooidal deposits that add support to the colony base while obscuring zooidal orifices (Boardman and Cheetham, 1973, fig. 18; Cheetham, 1986b, fig. 1), may be present in both kinds of bases. Such asexually produced new growths can be distinguished from the simple healing of injuries by their markedly different polarity or proportions from the underlying part of the original (''parent'') colony (Thomsen and Håkansson, 1995, fig. 2, D and E). In many cases, growth from more than one locus on a single piece of the original colony may produce multiple subcolonies or ''shoots,'' in contrast to the single erect structure arising from an ancestrular base. Even though not all such specimens show definite evidence of separation from the ''parent'' colony (Ostrovsky, 1997), they are morphologically and functionally analogous to the ''colonial buds'' described in free-living cheilostomes (Marcus and Marcus, 1962).

It is important to note here a major difference in morphology affecting regeneration in cheilostomes and cyclostome Bryozoa, such as those described by Ostrovsky (1997). Unlike the situation in cyclostomes with open communication between zooids, breakage through the body cavity of a cheilostome zooid does not expose the interiors of adjacent zooids to the environment, because of the solid plugs of cells in their communication pores. According to Banta (1969), cuticle deposited over these plugs can then allow them to swell into the empty zooidal cavity and ''heal'' the wound through reparative budding of a new zooid within the remnant of the old. Even without reparative budding, the cheilostome would not be open to the environment in the same way as a cyclostome (Ostrovsky, 1997). Thus, the resources remaining in a fragment of a colony can be concentrated in new growth directions, rather than in repairing the pattern of the fragment from which the new growth originates.

Estimation of ovicell frequency.—The extrazooidal skeletal deposits, mentioned above, that characterize the proximal parts of erect colonies in *Metrarabdotos*, obscure zooidal outlines and orifices, thus making accurate counts of the number of zooids in those parts of colonies impossible. Such counts, for both ovicelled and nonovicelled zooids, therefore were made only on specimens representing parts of colonies in which all zooidal outlines are observable and orifices are open. This procedure could overestimate ovicell frequencies if zooids in first-formed (proximal) parts of colonies are less likely to be ovicelled and more likely to be obscured by extrazooidal calcification. However, such a bias is likely to be similar for all species.

Ovicells were readily counted directly on all qualifying specimens in all species. However, in order to make the task of estimating the very large number of nonovicelled zooids more manageable, we based counts on the mean number of zooids per specimen in up to seven specimens in each of three size classes (those retained on sieves of 2 mm, 1 mm, and 0.5 mm mesh). Each size class ordinarily included some specimens consisting of both ovicelled and nonovicelled zooids and many others consisting entirely of nonovicelled zooids. The total number of nonovicelled zooids was then calculated as the sum of the products of these mean values and the total number of specimens in each size class.

Branch thickening gradients.—The ontogenetic thickening of zooidal frontal skeletons and their eventual transformation into extrazooidal deposits produce a gradient of branch thickening from the growing tips of erect colonies proximally toward the colony base (Boardman and Cheetham, 1973, fig. 18; Cheetham, 1986b, fig. 1). The thickening gradient is a mechanical design factor that could be related to the incidence of propagation by fragmentation (Cheetham and Thomsen, 1981; Cheetham, 1986b). We therefore estimated branch thickening gradients using specimens in which zooids at the distal ends exhibit morphology characteristic of early stages of ontogeny (Boardman and Cheetham, 1973, fig. 18). The gradient of thickening was calculated as the coefficient of linear regression of the thickness of the branch (dependent variable) on the distance from the distal end of the branch (independent variable) (Cheetham et al., 1981). The thickening coefficients were scaled as percent of branch length.

Estimation of heritable variation.—For each species of *Metrarabdotos*, we used the 15 autozooidal characters employed in species discrimination (characters 1–15 in Appendix 1) in a single-classification ANOVA to partition among-colonies and within-colonies variance components (Cheetham et al., 1994). (Measurements of the other 33 characters are too few per specimen for this part of the analysis.) The justification for using this method

to estimate heritable variation is based on the analysis of phenotypic variance from breeding data in two species of the cheilostome *Stylopoma* (Cheetham et al., 1993, 1994, fig. 1). In calculating mean heritabilities for each species, we omitted characters invariant within that species, but included any zeroes (or negative values) obtained for characters that do vary within colonies (Cheetham et al., 1994). For the species of *Cigclisula* and *Gemelliporella* included for purposes of comparison, only a subset of five of the 15 autozooidal characters used in *Metrarabdotos* was available for heritability estimates. Because possession of ovicells and special avicularia was not a requirement for these calculations, each ANOVA in both the *Metrarabdotos* species and those of the other two genera was based on five zooids in each of five specimens in order to equalize degrees of freedom.

RESULTS

Characteristics and affinities of Venezuelan species.—The three new species of *Metrarabdotos* from Venezuela (Fig. 1) are morphologically heterogeneous and probably not closely related to each other. In overall morphology based on all 46 characters used in the discriminant analysis (Appendix 1), these species differ by 27.01 to 32.59 units (mean, 29.88; all units = square root of Mahalanobis D^2); this value is not much less than the mean difference of 37.23 among all species of tropical American Neogene *Metrarabdotos* (Fig. 2). Each of the three Venezuelan species, however, is closer in morphology (differences less than 20) to one or more species from the Dominican Republic and other areas in the Caribbean.

Metrarabdotos n. sp. 11, from the Lower Pliocene Paraguana Formation, is most similar to *M. auriculatum* (difference 10.47), but also resembles *Metrarabdotos* n. sp. 9, *Metrarabdotos* n. sp. 10, and *M. tenue* (differences 14.22, 14.97, and 17.89, respectively). These species are widely distributed in Upper Miocene and Pliocene deposits in tropical America (Cheetham et al., 1999), forming a morphologically distinctive group (Fig. 2). As in other species in this group, autozooidal orifices in *Metrarabdotos* n. sp. 11 have only lateral denticles (Fig. 1.9); the denticles are more closely spaced in *Metrarabdotos* n. sp. 11, even though the orifices are larger than those of other species in this group. Also like other species in this group, *Metrarabdotos* n. sp. 11 lacks avicularia on ovicelled zooids (Fig. 1.2). Lateral-oral avicularia on ordinary autozooids closely match those in *M. auriculatum* in position, but are smaller and more variable in orientation (Fig. 1.1). Enlarged (special) avicularia on zooids at row bifurcations, on branch margins, and adjacent to ovicells are generally similar to those in *M. auriculatum* (Fig. 1.1, 1.2). *Metrarabdotos* n. sp. 11 has longer, narrower zooids than other species in this group, although even longer and narrower zooids are known in other, more distantly related species, e.g., *Metrarabdotos* n. spp. 3 and 4.

Metrarabdotos n. sp. 12, from the Lower Pliocene Cubagua Formation, shows close similarity (difference 19.46) to only one species, *Metrarabdotos* n. sp. 7, known only from the Upper Miocene in the Dominican Republic (Cheetham et al., 1999). Orifices in both species have both median and lateral denticles, but the latter are more widely spaced in *Metrarabdotos* n. sp. 12, in correlation with its wider orifice (Fig. 1.10). Like those of *Metrarabdotos* n. sp. 7, ovicelled zooids in *Metrarabdotos* n. sp. 12 have paired lateral-oral avicularia (Fig. 1.4). Also as in *Metrarabdotos* n. sp. 7, zooids on branch margins have greatly enlarged avicularia directed distally (Fig. 1.5), in contrast to the enlarged avicularia adjacent to ovicells, which are directed proximally (Fig. 1.4), as in most species of *Metrarabdotos.* The lengths and widths of zooids are about the same in the two species.

Metrarabdotos n. sp. 13, from the upper Lower Miocene Cantaure Formation, is most similar to *Metrarabdotos* n. sp. 1 (difference 14.36), which is known only from the upper Lower or lower Middle Miocene of the Dominican Republic and Haiti (Cheetham et al., 1999). *Metrarabdotos* n. sp. 13 is somewhat less similar (difference 16.10) to *Metrarabdotos* n. sp. 5 from the Upper Miocene of the Dominican Republic. All three species have small zooids and orifices with both median and lateral denticles (Fig. 1.11). However, ovicelled zooids bear avicularia in *Metrarabdotos* n. sp. 13 (Fig. 1.7) and *Metrarabdotos* n. sp. 1, but lack avicularia in *Metrarabdotos* n. sp. 5. The lateral-oral avicularia on ordinary autozooids in *Metrarabdotos* n. sp. 13 are placed more distally than those in the other two species (Fig. 1.6, 1.11).

Based on overall differences in morphology (square root of Mahalanobis D^2) and stratigraphic occurrence, the three Venezuelan species appear to occupy quite different positions in the inferred phylogeny of *Metrarabdotos* (Fig. 2). *Metrarabdotos* n. sp. 13 is just once removed from the Oligocene *M. micropora,* the hypothesized ancestor of the tropical American Neogene species, whereas *Metrarabdotos* n. sp. 11 and *Metrarabdotos* n. sp. 12 are four and six nodes, respectively, farther removed. The distances between these nodes are generally small, ranging from 10.47 to 22.87 (mean 15.92). Moreover, none of the Venezuelan species shows much similarity to any of the species lying on the right side of the tree in Figure 2, from which they are separated by much greater differences (e.g., 44.19 between *Metrarabdotos* n. sp. 1 and *Metrarabdotos* n. sp. 2).

In general, the affinities for the Venezuelan species suggested by overall morphologic similarity and stratigraphic occurrence (*Metrarabdotos* n. sp. 13 with *Metrarabdotos* n. sp. 1; *Metrarabdotos* n. sp. 12 with *Metrarabdotos* n. sp. 7; *Metrarabdotos* n. sp. 11 with *M. auriculatum*) are confirmed by the cladistic arrangement shown in Figure 3. Also, the numbers of nodes separating them from the root of the tree (*M. micropora,* the designated ''outgroup'') are similar. However, the placement in Figure 3 of the species representing the branch on the right side of the tree in Figure 2 with respect to *Metrarabdotos* n. sp. 12 (as well as *Metrarabdotos* n. spp. 6–9) is subject to criticism on grounds of stratigraphic incongruence, as in Jackson and Cheetham (1994). It should be noted that, with reference to the tree in Jackson and Cheetham (1994), the addition of the three Venezuelan species actually reduced the number of most parsimonious solutions from four to two, while increasing length and decreasing consistency by almost 10 percent.

Sexual and asexual reproductive morphology.—All fossil and living species of *Metrarabdotos* have modified autozooids with greatly widened orifices opening into the brood chambers (ovicells), which are as large as the zooids themselves (Fig. 4.1). Although ovicelled zooids can be clustered within parts of branches (Fig. 4.1), they are generally more evenly scattered throughout all but the most proximal branches in the few large intact colonies we have examined (e.g., the Recent specimen of *M. tenue* illustrated in Cheetham, 1968, pl. 9, fig. 1).

In living species, larvae are large when extruded through the orifices of the ovicelled zooids and, upon metamorphosis, produce a characteristic tetrad of ancestrular zooids (Cook, 1973), rather than a single ancestrula as in many cheilostomes with smaller ovicells and larvae. The tetrad, whose formation was described by Cook (1973) in one of the three known encrusting species of *Metrarabdotos,* can be recognized in erect species as well (Fig. 4.2, 4.3, 4.5, 4.6). In very young colonies, such as that in Figure 4.2 and 4.3, the primary, distal, and two distolateral members of the tetrad are visible in frontal view. Succeeding zooids are budded distally from the tetrad in an erect orientation, with basal walls back to back, rather than entirely in contact with the substratum. In older colonies, such as that in Figure 4.4–4.6, the frontal sides of the ancestrular zooids, as well as the erect ones, become obscured by succeeding extrazooidal deposits (Fig. 4.4).

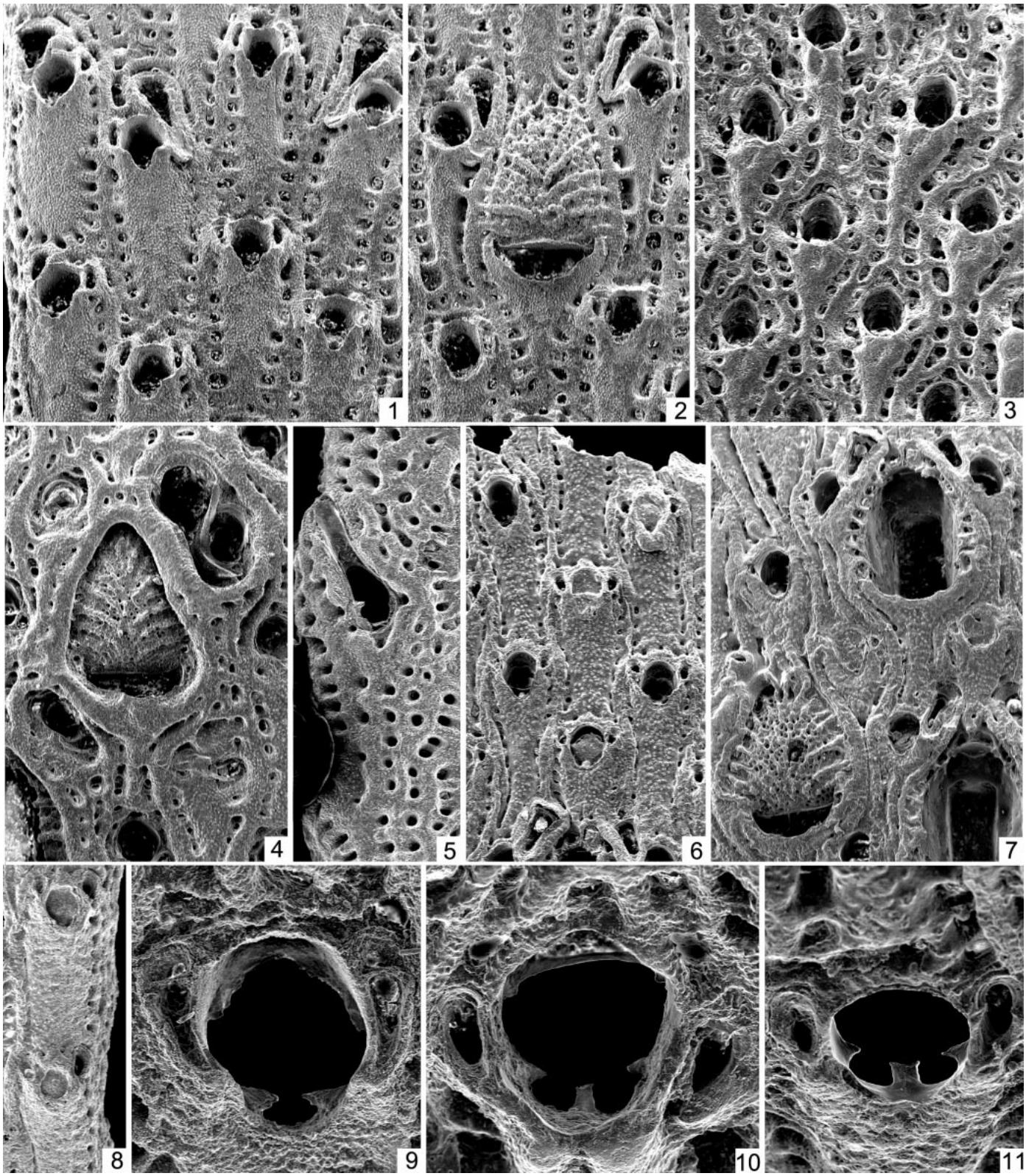

FIGURE *1*—Distinguishing morphology of Venezuelan species of *Metrarabdotos*. *1, 2, 9, Metrarabdotos* n. sp. 11, Paraguana Formation, Lower Pliocene, locality PPP 2535; *1,* autozooids with ordinary avicularia, zooids on branch margin (on left) with enlarged avicularia, and zooids at row bifurcations (left and right of center) also with enlarged avicularia, USNM 509417; *2,* zooid with ovicell and adjacent autozooids, two of which have enlarged avicularia, USNM 509417; *9,* detail of autozooid orifice and ordinary avicularia, USNM 509418. *3–5, 10, Metrarabdotos* n. sp. 12, Cubagua Formation, Lower Pliocene, locality PPP 2569; *3,* autozooids with ordinary avicularia, USNM 509419; *4,* zooids in more heavily calcified part of colony, one with ovicell and one with enlarged avicularium adjacent to ovicell, USNM 509420; *5,* zooids on margin of very heavily calcified

The ancestrular tetrad is then discernible only in basal view, near one end of the encrusting base, which enlarges by growth of the extrazooidal deposits (Fig. 4.5, 4.6).

We found colony bases with recognizable ancestrular morphology in 13 of 19 erect species of *Metrarabdotos* examined (Table 1), including all three of the Venezuelan species (Fig. 5.1, 5.2). Failure to find such bases in the other six species (Table 1) is most probably related to the topologic relationship in which the number of branches far exceeds the number of bases, as noted above.

With the exception of a single colony of *Metrarabdotos* n. sp. 10 from the Dominican Republic (Table 1), significant evidence of growth by regeneration (Fig. 5.3–5.6) was found only in the three Venezuelan species. Examples of new growth from old colony branches in these species include both reparative budding at fractures (Fig. 5.6) and frontal budding on intact branch surfaces (Fig. 5.5), both showing significant departures from the growth directions in the pre-existing branch. Even in the earliest stages of new growth (Fig. 5.5), complete reversals in budding directions of zooids are evident. As growth progresses (Fig. 5.6), the number of zooidal rows remains less than in the branches from which the new structure emanates, giving the new branch a significantly less flattened cross section, comparable to that in the proximal part of a sexually produced colony (Fig. 5.1). Extrazooidal supporting skeleton appears at a relatively early stage of the new growth (Fig. 5.6), initially contrasting with the absence of such material in the part of the branch from which the new growth emanates. As the extrazooidal skeleton thickens with further growth of the new branch so that its zooidal orifices become sealed (Fig. 5.3, 5.4), the frontal surfaces of zooids in adjacent parts of the old fragment may also become sealed (Fig. 5.4). This relationship suggests that zooids in the fragment continued to contribute to growth of the new colony, rather than expending resources on mending the fragment itself. In some cases, multiple erect growths emanate from a single fragment (Fig. 5.3), and an incipient second new structure is visible even in the early stage of growth shown in Figure 5.6. The similarity in external morphology between these specimens and the colony bases preserving the ancestrular tetrad (compare Fig. 5.4 with Fig. 4.4) strongly suggests that much, if not all, of the regeneration in the three Venezuelan species was directed toward asexual propagation.

Relation between asexual propagation and larval output.—Apparently unlike any other species of *Metrarabdotos,* the three Venezuelan species may have produced fully a third to a half of all new colonies by asexual growth, judging by the evidence of regeneration (Table 1, Fig. 6). This and the extremely low frequency of ovicells in these species (0.4–1.4 percent) suggest a tradeoff between sexual and asexual propagation, as hypothesized for erect cheilostomes in the Danian (Paleocene) of Denmark (Thomsen and Håkansson, 1995). However, the fact that ovicells are typically rare throughout *Metrarabdotos* (0.01–7.66 percent), despite absence of evidence for asexual propagation in the majority of species (Table 1, Fig. 6), weakens such a relationship. The frequency of ovicells and the incidence of regeneration are negatively correlated for the genus as a whole, but the correlation is nonsignificant ($r = -0.3196$, $P > 0.10$, 11 degrees of freedom). For the three species with the most abundant larvally produced colony bases, *M. colligatum, Metrarabdotos* n. sp. 9, and *Metrarabdotos* n. sp. 10, the incidence of ovicells (0.75–1.72 percent) is scarcely greater than in the Venezuelan species (Table 1). Moreover, the encrusting species *M. unguiculatum* has only 1.24 percent of its zooids ovicelled, far short of the level in encrusting Danian cheilostomes (8.0–25.3 percent; Thomsen and Håkansson, 1995). In contrast, the distantly related erect species *Gemelliporella punctata,* which occurs with species of *Metrarabdotos* at many Caribbean Neogene localities including those in Venezuela, has ovicell frequencies (22 percent) near the upper end of the range for encrusting Danian cheilostomes. This percentage far exceeds that in any species of *Metrarabdotos,* even though asexual generation of colony bases is also common in *G. punctata* (Table 1, Fig. 6). (However, the morphology of colony bases in *G. punctata* is complicated by the ability of this species to form extensive sheets of encrusting zooids from which multiple erect shoots can arise.)

Relation between asexual propagation and colony design.—Compared to erect species of many other cheilostome genera (Cheetham, 1986b), branch thickening gradients in the three Venezuelan *Metrarabdotos* species are rather weak (1.3–2.6 percent of branch length; Table 1, Fig. 6), suggesting that they could be more easily fragmented than co-occurring erect species such as *Cigclisula porosa* and *Gemelliporella punctata* (thickening 3.6–4.4 percent of branch length). However, again, this is a general characteristic of *Metrarabdotos,* including the many species in which evidence for propagation from fragments is unknown (Table 1, Fig. 6, mean thickening rate 1.3 percent). The greater than average material strength of *Metrarabdotos* skeletons compensates for the slender construction of its branches (Cheetham and Thomsen, 1981). Moreover, the thickening gradients in *Metrarabdotos* n. spp. 12 and 13 are the highest recorded for the genus (Table 1, Fig. 6), resulting in a slight positive but nonsignificant correlation with regeneration ($r = 0.4753$, $P > 0.10$, 11 degrees of freedom). Thus the Venezuelan species may have been built to resist fragmentation as well as or better than those in which regeneration is rare or absent.

Relation between asexual propagation and genetic variation.—As estimated by partitioning within- and among-colonies components of variance in the 15 autozooidal characters, heritable variation appears not to be less in the three Venezuelan species, on average, than in species of *Metrarabdotos* lacking evidence of asexual propagation, or in the other two erect genera (Table 2, Fig. 6). For *Metrarabdotos* n. spp. 11 and 13, the mean among-colonies components are actually higher than in any other species (53 percent). Compared to the species with which they show the greatest similarity in overall morphology, these means of among-colonies variances represent increases of 46 percent (over *M. auriculatum*) and 21 percent (over *Metrarabdotos* n. sp. 1). On the other hand, the mean value in *Metrarabdotos* n. sp. 12 (26 percent) is almost 30 percent below the mean for *Metrarabdotos* as a whole (37 percent) and 27 percent below that for *Metrarabdotos* n. sp. 7, but it is 60 percent above the minimum value in the genus (16 percent in *Metrarabdotos* n. sp. 8). Moreover, the magnitudes of among-colonies variances vary from character to character as well as species to species, and the values for three characters in *Metrarabdotos* n. sp. 12 exceed the mean values for the genus (Table 2). Compared with the species to which they show

←

branch, one with enlarged avicularium, USNM 509420; *10,* detail of autozooid orifice and ordinary avicularia, USNM 509419. *6–8, 11, Metrarabdotos* n. sp. 13, Cantaure Formation, Lower Miocene, locality PPP 2541; *6,* autozooids with ordinary avicularia, USNM 509421; *7,* three zooids with ovicells (two on right broken) and adjacent autozooids, some with enlarged avicularia (two of which also appear at the bottom of *6*) USNM 509421; *8,* autozooids on branch margin with slightly enlarged avicularia, USNM 509421; *11,* detail of autozooid orifice and ordinary avicularia, USNM 509421. *9–11* (zooid interiors darkened to emphasize orifice morphology), ×200; all others, ×50.

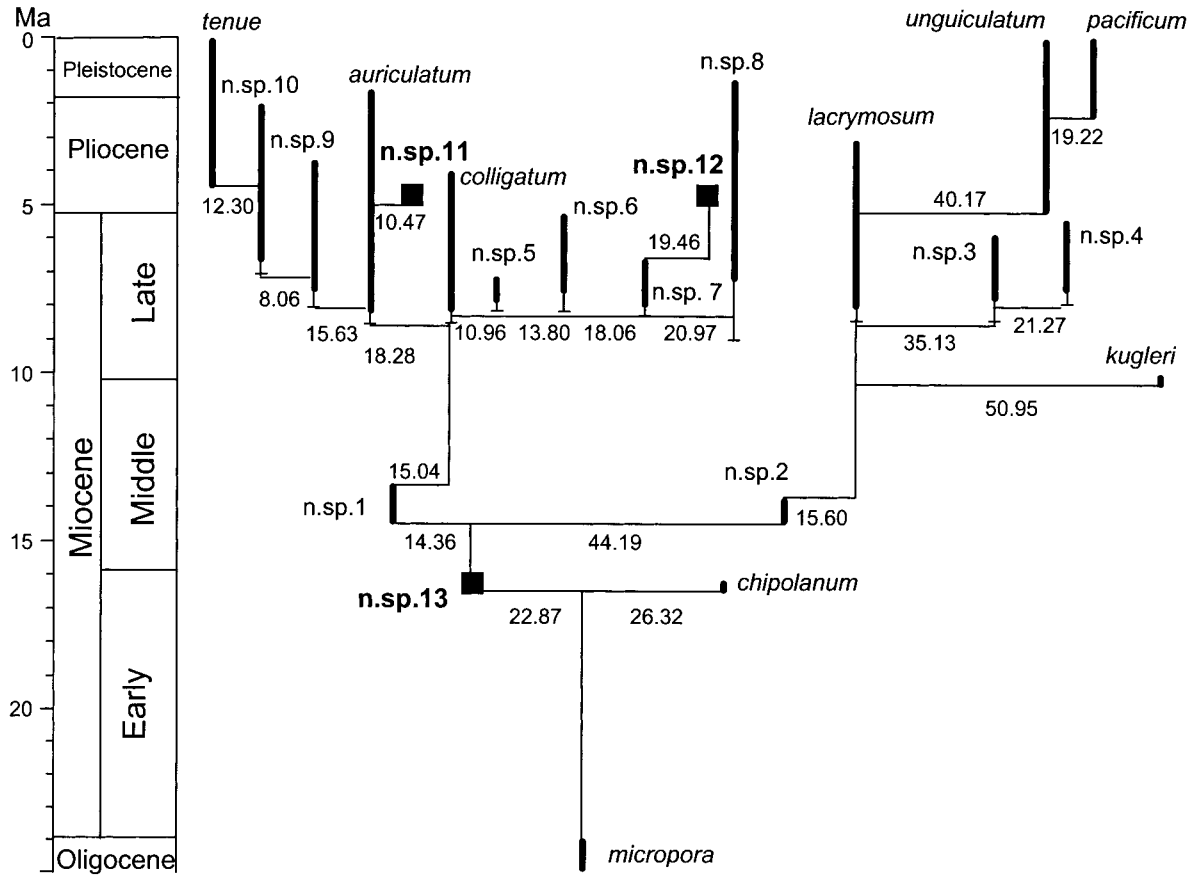

FIGURE 2—Hypothesized phylogenetic relationships of tropical American species of *Metrarabdotos* (Venezuelan species in boldface) based on minimum morphologic and stratigraphic distances. Species ranges (heavy lines) are modified from Cheetham (1986a) with new data in Cheetham et al. (1999). Minimum morphologic distances are square root of Mahalanobis D^2 based on all 46 characters in Appendix 1.

the greatest similarity in overall morphology, the Venezuelan species all show a balance between characters with increased and decreased levels of among-colonies variance: *Metrarabdotos* n. sp. 11, eight increases and four decreases from *M. auriculatum*; *Metrarabdotos* n. sp. 12, six increases and six decreases from *Metrarabdotos* n. sp. 7; and *Metrarabdotos* n. sp. 13, six increases, five decreases, and one no change from *Metrarabdotos* n. sp. 1.

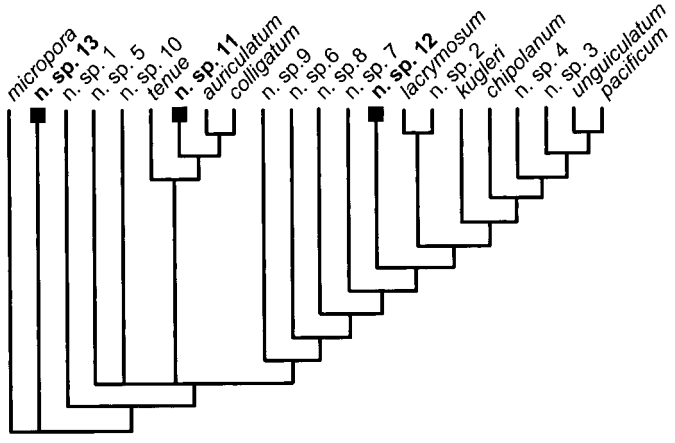

FIGURE 3—Hypothesized phylogenetic relationships of tropical American species of *Metrarabdotos* (Venezuelan species in boldface) based on strict consensus of two cladistically most parsimonious trees of length 278, consistency index 46, retention index 69, obtained with the character matrix in Appendix 2 and rooted on *M. micropora.*

Low estimates of mean genetic variation for *Metrarabdotos* n. sp. 12 and some other species (Table 2) could be related in part to limited sampling. For all species, at least some specimens came from the same sample and thus could represent the same colony. In addition, samples as close together as those from which *Metrarabdotos* n. sp. 12 was obtained (2 m apart) could also include fragments from the same colony. In the living encrusting species *M. unguiculatum,* basing calculations on two patches of zooids in a single colony reduced the mean ''among-colonies'' variance component from 35 percent (near the mean value for the genus) essentially to zero (Table 2). However, none of the *Metrarabdotos* species shows mean values this low, and at least two (*Metrarabdotos* n. spp. 3 and 4) with mean values lower than those of *Metrarabdotos* n. sp. 12 were obtained from samples hundreds of thousands of years apart.

DISCUSSION

Thomsen and Håkansson (1995) suggested that erect species of cheilostomes may divert resources from sexual reproduction into vegetative growth and clonal propagation, based on the high incidence of regeneration from colony fragments (62–98 percent of colony bases) and the low frequency of ovicelled zooids (0.5–3.4 percent) in a variety of genera in the Danian (Paleocene) of Denmark. The incidence of regenerative growth in the three Venezuelan Neogene species of *Metrarabdotos* (36–53 percent), all of which are erect, approaches that in the

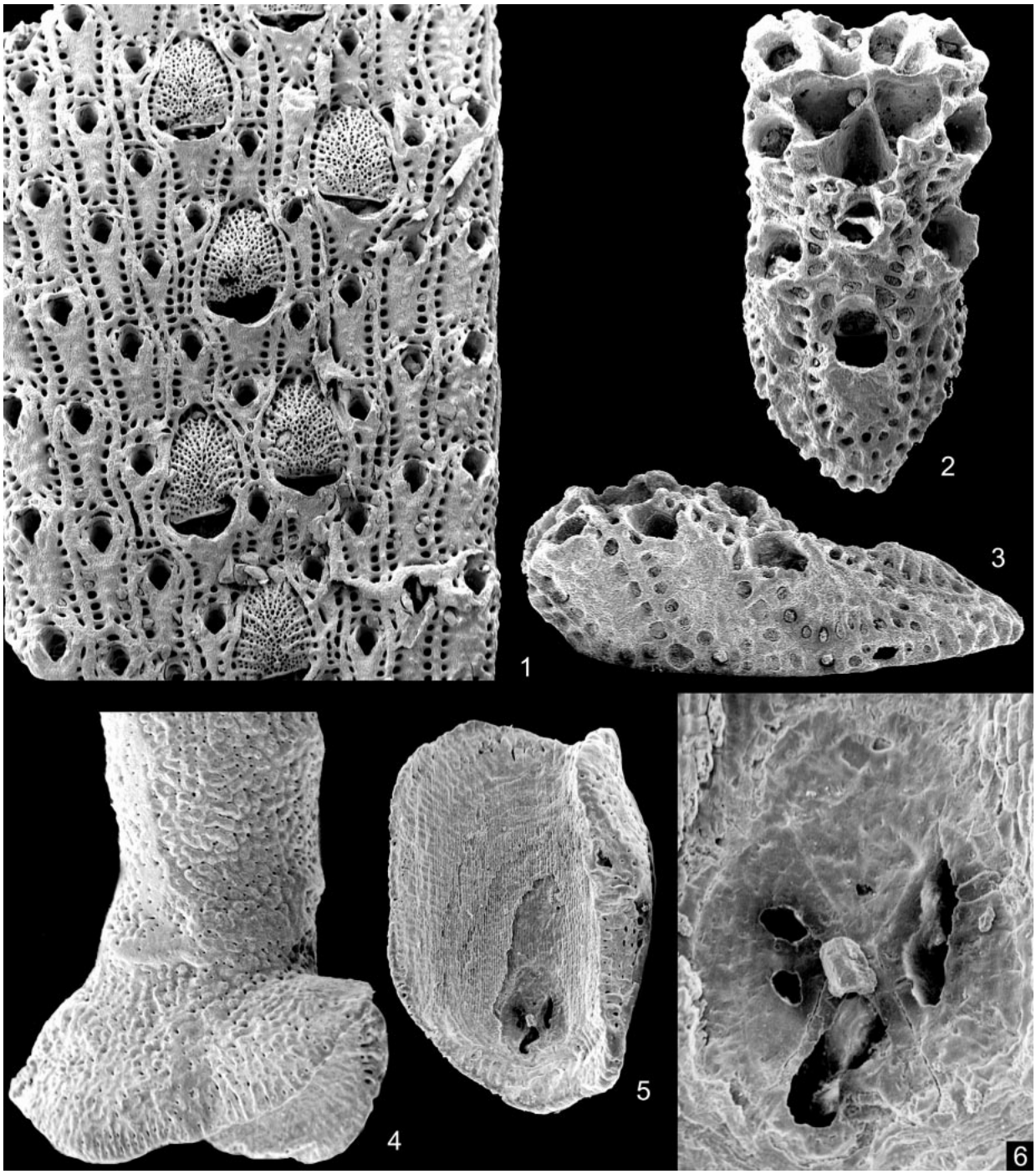

FIGURE 4—Sexual reproductive morphology in *Metrarabdotos colligatum*, Cercado Formation, Upper Miocene, Rio Mao, Dominican Republic. *1*, Ovicelled zooids and surrounding ordinary autozooids, USNM 509422, locality NMB 16918; *2, 3*, frontal and lateral views of ancestrular zooids and succeeding erect zooids forming base of young colony, USNM 509423, locality NMB 16928; *4, 5*, lateral and basal views of older colony in which ancestrular and erect zooids are completely enveloped in extrazooidal calcification; *6*, detail of *5* showing basal walls of ancestrular tetrad surrounded by extrazooidal skeleton with bioimmurated brick-like pattern of cells of the encrusted seagrass, USNM 509424, locality NMB 16918. *1*, ×25; *2, 3*, ×50; *4, 5*, ×20; *6*, ×100.

Danian species, and the proportion of zooids committed to producing larvae (0.4–1.4 percent) is even lower. As a corollary, Thomsen and Håkansson (1995) further suggested that colonies of erect species may be designed to enhance fragmentation and thus clonal propagation, much like the ''colonial budding'' in some species of free-living cheilostomes (Marcus and Marcus, 1962). However, the similarities between the Neogene species of *Metrarabdotos* from Venezuela and Danian erect cheilostomes seem unlikely to have a common evolutionary basis, for three reasons:

1) The low frequency of ovicells in *Metrarabdotos* characterizes all species, whether erect or encrusting, and thus appears to

TABLE 1—Incidence of ovicells and of colony bases initiated from ancestrulae or by regeneration, and branch thickening gradients in 20 species of *Metrarabdotos* (n. spp. 11-13 from Venezuela), *Cigclisula porosa*, and *Gemelliporella punctata*. N = number of colony fragments in which zooids and ovicells have functional orifices; ancest. = ancestrulae; regen. = regeneration; df = degrees of freedom.

		Colony fragments							
			Ovicells		Colony bases		Branch thickening		
Species	N	Zooids	Number	Percent	Ancest.	Regen.	Gradient	df	*P*
M. n. sp. 11	396	48,647	212	0.436	48	55	0.0133	34	<0.01
M. n. sp. 12	386	39,066	315	0.806	5	4	0.0265	18	<0.001
M. n. sp. 13	126	8,697	118	1.357	7	4	0.0253	24	<0.05
M. n. sp. 10	118	24,118	416	1.725	46	1	0.0232	44	<0.001
M. n. sp. 5	49	7,396	47	0.365	2	0	0.0054	26	<0.05
M. n. sp. 9	110	4,934	47	0.953	46	0	0.0070	36	>0.1
M. auriculatum	152	20,418	213	1.043	31	0	0.0186	86	<0.001
M. n. sp. 6	35	2,169	26	1.200	9	0	0.0151	2	>0.1
M. colligatum	149	19,758	258	1.306	109	0	0.0127	62	<0.001
M. n. sp. 2	23	1,949	31	1.591	11	0	0.0084	9	>0.3
M. n. sp. 1	21	2,198	42	1.911	3	0	0.0162	8	>0.2
M. tenue	162	15,737	1,205	7.657	1	0	0.0139	21	<0.001
M. n. sp. 3	166	9,245	1	0.011	0	0	0.0038	42	>0.1
M. n. sp. 4	398	25,680	8	0.031	0	0	0.0035	46	>0.1
M. lacrymosum	36	7,090	82	1.157	0	0	0.0193	22	>0.05
M. n. sp. 7	9	345	4	1.159	0	0	0.0140	18	<0.05
M. n. sp. 8	20	655	8	1.221	0	0	0.0073	8	>0.1
M. micropora	93	9,434	153	1.622	0	0	0.0080	108	<0.001
M. moniliferum	19	3,798	179	4.713	2	0	0.0187	12	<0.01
M. unguiculatum	8	2,020	25	1.238	0	0	(encrusting; not applicable)		
C. porosa	33	1,204	99	8.223	45	0	0.0356	9	<0.05
G. punctata	18	811	176	21.702	24	8	0.0438	10	<0.01

be a pan-generic phylogenetic constraint, rather than an adaptation to a particular mode of life or set of environmental circumstances. In seven of the nine erect species of *Metrarabdotos* in which only ancestrular colonies have been found, fewer than two percent of zooids are ovicelled. Ovicell frequencies in both of the exceptions, the living Caribbean species *M. tenue* (eight percent) and the Pliocene European species *M. moniliferum* (five percent), are much less than those in some erect cheilostome genera such as *Gemelliporella* (22 percent).

2) The slender branches of erect *Metrarabdotos* colonies likewise appear to result from a phylogenetic constraint, shared by all species including the encrusting ones, that limits the rate of extrazooidal thickening on frontal surfaces of zooids. The fact that two of the three Venezuelan species have the highest rates of branch thickening known in the genus argues strongly against adaptation for a diminished ability to resist breakage.

3) Perhaps most significantly, the apparently undiminished level of heritable variation in morphologic characters in the Venezuelan species of *Metrarabdotos* suggests that output of sexually produced larvae continued unabated, despite whatever additional resources were necessary for asexual propagation. Thus, the presence or absence of clonal propagation in *Metrarabdotos* seems unlikely to have affected rates of speciation and extinction. A similar conclusion was reached by Jackson and Coates (1986) for scleractinian corals, based on the average durations of clonal and aclonal species.

Unlike ovicell frequency and colony design, the incidence of regeneration, and thus asexual propagation, in *Metrarabdotos*

TABLE 2—Among-colonies variance components (heritability estimates) for 15 traits of zooid morphology (characters 1–15 in Appendix 1) in Venezuelan and other species of *Metrarabdotos*, compared with those for five traits in two other genera. Traits left blank for *Metrarabdotos* species are invariant in those species. LZ, zooid length; WZ, zooid width; LO, orifice length; WO, orifice width; LD, distance between lateral denticles; LAVS, LAVL, length of smaller, larger avicularium; PAVS, PAVL, position of smaller, larger avicularium; O1AVS, O1AVL, lateral-medial orientation of smaller, larger avicularium; 02AVS, 02AVL, distal-proximal orientation of smaller, larger avicularium; NA, number of areolae; ND, number of denticles.

	Metrarabdotos									
	Venezuelan species			16 other erect species			*unguiculatum*			
Trait	n. sp. 11	n. sp. 12	n. sp. 13	Min.	Max.	Mean	Different colonies	Same colony	*Cigclisula porosa*	*Gemelliporella punctata*
LZ	0.7243	0.3783	0.7548	0.0589	0.8683	0.5810	0.5202	−0.2436	−0.0041	0.6171
WZ	0.3384	0.7532	−0.1541	0.1550	0.9469	0.5502	0.7249	−0.2220	0.5220	0.4198
LO	0.5803	0.4559	0.6016	−0.0845	0.9487	0.5742	0.3171	0.3182	−0.0853	0.6601
WO	0.5773	0.6838	0.5391	0.1111	0.7728	0.4087	0.5899	−0.0417	0.6618	0.5584
LD	0.6108	0.5688	0.6613	−0.0610	0.8647	0.5442	0.1385	0.2000	0.2593	0.0732
LAVS	0.6512	−0.0755	0.6326	−0.1277	0.7260	0.2839		0.0000		
LAVL	0.6298	0.2453	0.6760	−0.1024	0.7719	0.4057	0.0622	−0.0069		
PAVS	0.2500	0.1709	0.7500	−0.0606	0.7000	0.1922				
O1AVS	0.6849	−0.1017	0.4615	−0.0606	0.7669	0.1514				
O2AVS		−0.0526		−0.0606	0.5645	0.0797				
PAVL	0.2500	0.1071	0.7500	−0.0870	0.9095	0.2213	0.0476	−0.1364		
O1AVL	0.3625	0.0000	0.3478	0.0000	0.2500	0.0782	0.0476	−0.1364		
O2AVL				0.0000	1.0000	0.1671	0.9524	−0.1364		
NA	0.6603	0.2240	0.3933	−0.0913	0.7767	0.5150	0.1068	−0.0039		
ND				−0.0156	0.3351	0.0852				
Mean	0.5266	0.2583	0.5345	0.1650	0.5151	0.3572	0.3507	−0.0372	0.2707	0.4657

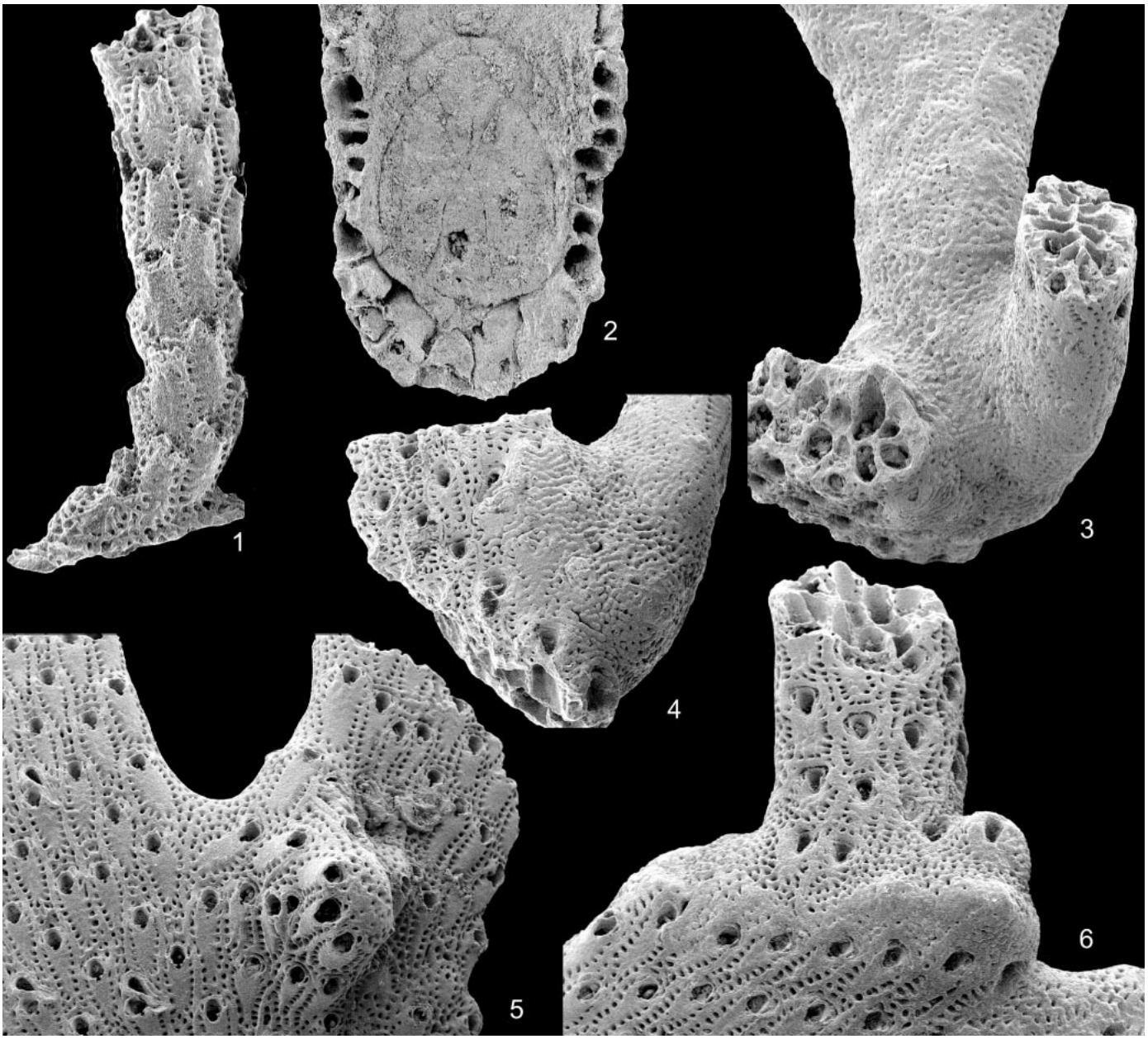

FIGURE 5—Sexual and asexual reproductive morphology in *Metrarabdotos* n. sp. 11, Paraguana Formation, Lower Pliocene, Venezuela. *1*, Lateral view of young colony showing ancestrular tetrad and succeeding erect zooids before development of obscuring extrazooidal calcification, USNM 509425; *2*, basal view of similar colony, USNM 509426, locality PPP 2650; *3*, erect basal parts of two colonies arising toward top and right sides of pre-existing fragment (on lower left, shown in transverse section); *4*, other side of same specimen with zooids of original fragment in frontal view on left giving rise to extrazooidal calcification supporting new colony base on right, USNM 509427, locality PPP 2537; *5*, frontal view of flat branched fragment with frontally budded and contrastingly oriented zooids initiating new growth, USNM 509428; *6*, frontal view of flat branched fragment with subcylindrical, differently oriented new growth originating along an oblique fracture, with a narrow band of extrazooidal calcification (note smaller incipient new growth at the right margin of the fracture), USNM 509429, locality PPP 2650. *1*, ×25; *2*, ×75; all others, ×20.

shows no evidence of being a phylogenetic constraint uniting the three species in which it occurs in significant proportions. The three Venezuelan species are separated by as many as six nodes in the stratophenetic tree and seven nodes in the cladistic tree, i.e., at least half the number of nodes separating the most divergent species in either tree. Thus, the elevated level of regenerative growth in these species is most probably a response to local conditions, through either separate (convergent) adaptation in the three lineages or through an ecophenotypic modification of which other species might be potentially capable. However, unlike the Carboniferous stenolaemate bryozoan *Archimedes* (McKinney, 1983), many species of *Metrarabdotos* were obviously capable of achieving abundance and wide distributions without deviating from strict adherence to the sexual mode of propagation.

The Neogene deposits in which species of *Metrarabdotos* have been found in abundance in tropical America are typically associated with reef corals or with free-living corals characteristic of seagrass environments (Budd et al., 1996; Collins et al., 1999).

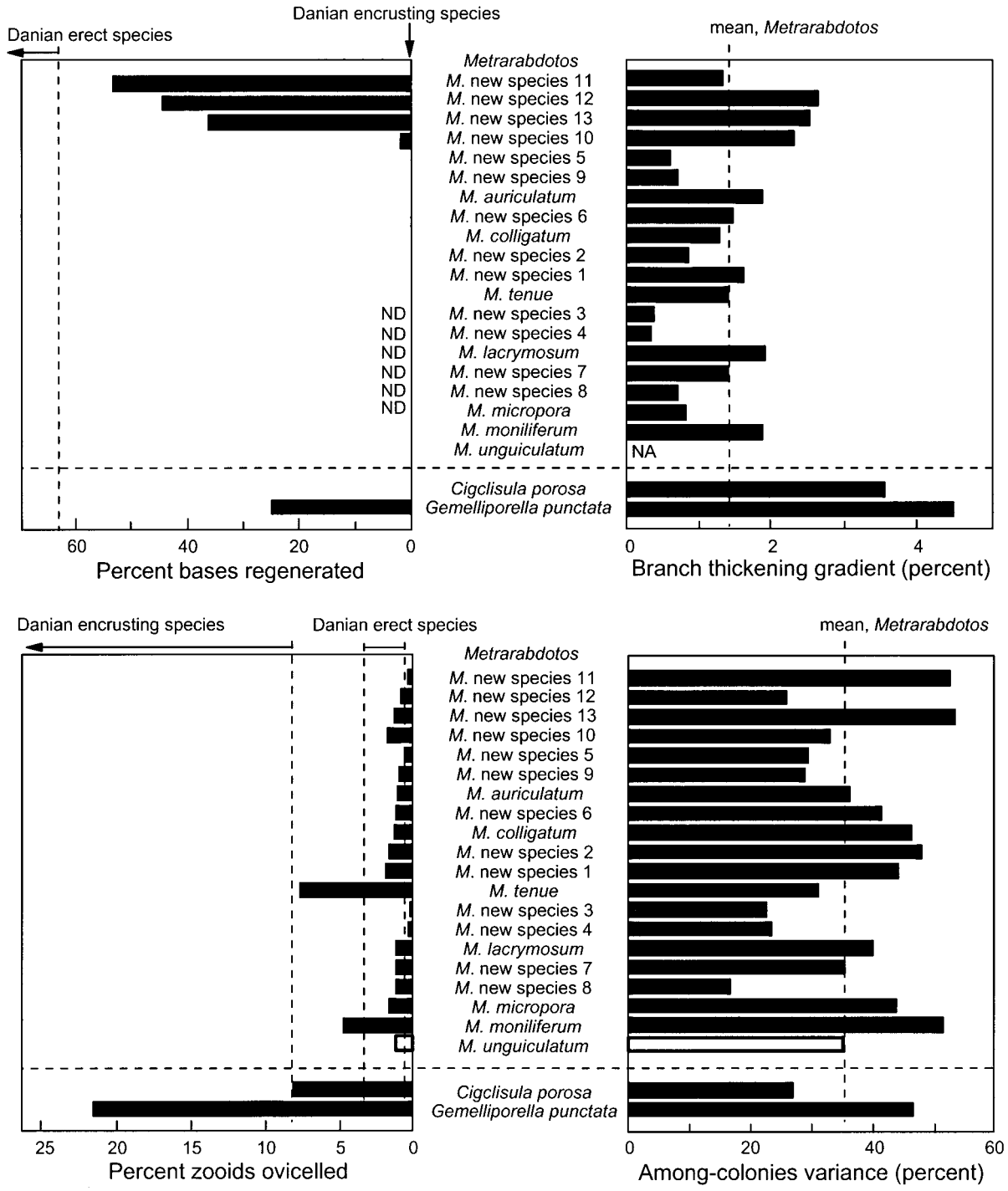

FIGURE 6—*Left*, incidence of apparently asexually produced colonies (above) and brooding (ovicelled) zooids (below) in *Metrarabdotos* and species of two other Neogene erect genera compared with those properties in erect and encrusting Danian (Paleocene) species (Thomsen and Håkansson, 1995); ND, no data. *Right*, rates of branch thickening (above, as percent of branch length) and mean among-colonies variance components (below) in *Metrarabdotos* and species of two other Neogene erect genera; NA, not applicable. Black bars, erect species; white bars, encrusting.

Colonies of *Metrarabdotos* and other genera from coral-rich deposits in the Dominican Republic commonly preserve evidence of growth on seagrass (Fig. 4.5; Cheetham and Jackson, 1996). However, ancestrular colonies of the three Venezuelan species (e.g., Fig. 5.1, 5.2) show no evidence of growth on seagrass, and corals are virtually absent from all the Venezuelan localities.

Instead, Venezuelan Miocene and Pliocene sediments from the Araya Peninsula (in the vicinity of where *Metrarabdotos* n. sp. 12 was collected) contain abundant otoliths and shark teeth characteristic of the fauna of regions of strong upwelling with nutrient enrichment and high primary production (Aguilera and Aguilera, in press). There are abundant, exceptionally large scallops, oysters, and pinnid bivalves scattered through all three formations where *Metrarabdotos* was collected, also suggesting high primary

productivity. Thus, the Venezuelan *Metrarabdotos* species may have grown faster than those from other areas in tropical America, producing larger colonies that were more easily fragmented despite their atypically robust branches. Although the skeletons of erect species of *Metrarabdotos* commonly include laminated frontal structures that thicken as a colony grows older (Cheetham et al., 1969), it is unknown how the periodicity of laminations correlates within or among colonies. Isotope chemistry might be the only way to quantify the growth rates of *Metrarabdotos* colonies in these contrasting environments.

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APPENDIX 1

Character states for tropical American *Metrarabdotos*

The full set of 46 morphologic characters listed below was used in discriminating species of tropical American *Metrarabdotos* and constructing the hypothetical relationships shown in Figure 2. Each of the subset of 33 characters preceded by an asterisk (*) furnished two or more nonoverlapping ranges of values in Duncan's multiple range tests, and thus was coded for use in constructing the hypothesis of relationship shown in Figure 3. The one-digit codes for states in each character in this subset vary from a simple linear sequence (e.g., 0, 1, 2, 3) to a nonlinear series (e.g., 0, 1, 4, 6), depending on the relative continuity or discontinuity of species means (Jackson and Cheetham, 1994).

Ordinary feeding zooids

**1) Length (mm).*—Coded states: 0 = 0.6050–0.7143, 1 = 0.7950, 2 = 0.8300, 4 = 1.0150, 5 = 1.0750, 6 = 1.1300.

**2) Width (mm).*—Coded states: 0 = 0.2700–0.3356, 2 = 0.3850, 4 = 0.4300–0.4650, 6 = 0.6100.

**3) Orifice length (mm).*—Coded states: 0 = 0.1200–0.1676, 2 = 0.1900–0.1950.

**4) Orifice width (mm).*—Coded states: 0 = 0.1100–0.1357, 2 = 0.1520, 4 = 0.1700.

**5) Distance between lateral denticles (mm).*—Coded states: 0 = 0.0355–0.0866, 2 = 0.1525.

**6) Shorter avicularium length (mm).*—Coded states: 0 = 0–0.0100, 1 = 0.0200, 2 = 0.0400, 3 = 0.0614–0.1156.

**7) Longer avicularium length (mm).*—Coded states: 0 = 0.0171, 1 = 0.0400, 2 = 0.0700, 3 = 0.0786–0.1505, 5 = 0.2268–0.2500.

**8) Shorter avicularium placement (lower values proximal, higher distal).*—Coded states: 0 = 1.0375–1.400, 2 = 2.0000–2.4200, 4 = 2.9333–2.9667.

**9) Shorter avicularium orientation 1 (lower values inward, higher outward).*—Coded states: 0 = 1.0000–1.3267, 1 = 1.5875, 2 = 1.7000–2.0000, 4 = 2.9200–2.9333.

**10) Shorter avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000–1.0857, 2 = 1.5000, 4 = 1.7500, 6 = 1.9333–2.0429, 8 = 2.6500, 9 = 2.9333–2.9500.

**11) Longer avicularium placement (values as for character 8).*—Coded states: 0 = 1.000–1.3750, 2 = 2.0500–2.5600, 4 = 2.9667–3.0000.

**12) Longer avicularium orientation 1 (values as for character 9).*—Coded states: 0 = 1.0000–2.0000, 2 = 2.9000–2.9611.

**13) Longer avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000–1.1500, 2 = 1.5667–1.6500, 4 = 2.1571, 6 = 2.7500, 8 = 2.9500–3.0000.

**14) Number of areolae.*—Coded states: 0 = 15.00–19.00, 1 = 20.00, 2 = 21.90–22.50, 3 = 23.50, 4 = 25.83, 5 = 28.00.

**15) Number of denticles (lowest values median only, highest lateral only).*—Coded states: 0 = 1.0000, 2 = 2.0000–2.1143, 4 = 2.9222–3.0000.

Axillary zooids at row bifurcations

**16) Shorter avicularium length (mm).*—Coded states: 0 = absent, 1 = 0.0400, 2 = 0.0688–0.1144.

17) Longer avicularium length (mm).

18) Shorter avicularium placement (values as for character 8).

19) Shorter avicularium orientation 1 (values as for character 9).

**20) Shorter avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000–1.5000, 2 = 2.0000, 4 = 2.7750–2.9563.

**21) Longer avicularium placement (values as for character 8).*—Coded states: 0 = 1.0–1.5, 2 = 2.0–3.0.

22) Longer avicularium orientation 1 (values as for character 9).

**23) Longer avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000–1.0500, 2 = 1.5000, 4 = 2.0000, 6 = 2.7500, 7 = 2.8688, 8 = 3.0000.

Zooids on margins of branches

24) Shorter avicularium length (mm).

25) Longer avicularium length (mm).

26) Shorter avicularium placement (values as for character 8).

27) Shorter avicularium orientation 1 (values as for character 9).

**28) Shorter avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000–2.0000, 1 = 2.2857, 2 = 2.5438–2.6500.

**29) Longer avicularium placement (values as for character 8).*—Coded states: 0 = 1.0000–1.4000, 1 = 1.7857, 2 = 2.1250, 3 = 2.5000–3.0000.

30) Longer avicularium orientation 1 (values as for character 9).

**31) Longer avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000–2.1571, 2 = 2.7167–3.0000.

Zooids adjacent to ovicells

**32) Shorter avicularium length (mm).*—Coded states: 0 = absent, 1 = 0.0587, 2 = 0.0700–0.1122.

33) Longer avicularium length (mm).

**34) Shorter avicularium placement (values as for character 8).*—Coded states: 0 = 1.0000, 1 = 1.5229, 2 = 1.5750–2.0000, 3 = 2.3125, 4 = 2.6400–3.0000.

35) Shorter avicularium orientation 1 (values as for character 9).

**36) Shorter avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000–1.2000, 2 = 2.0000, 3 = 2.3833, 4 = 2.5500.

**37) Longer avicularium placement (values as for character 8).*—Coded states: 0 = 1.0–2.0, 2 = 2.6–3.0.

38) Longer avicularium orientation 1 (values as for character 9).

**39) Longer avicularium orientation 2 (values as for character 8).*—Coded states: 0 = 1.0000, 2 = 2.0000, 3 = 2.2500, 4 = 2.5000, 5 = 2.7125.

Ovicelled zooids

40) Ovicell length (mm).

**41) Ovicell width (mm).*—Coded states: 0 = 0.4825–0.6200, 2 = 0.7250.

**42) Orifice width (mm).*—Coded states: 0 = 0.3300–0.4194, 2 = 0.4275, 4 = 0.5050.

**43) Diameter proximal areola on ovicell (mm).*—Coded states: 0 = 0.0223–0.0308, 1 = 0.0343, 2 = 0.0375, 3 = 0.0420, 4 = 0.0445.

**44) Diameter distal areola on ovicell (mm).*—Coded states: 0 = 0.0250–0.0323, 1 = 0.0393, 2 = 0.0450–0.0454, 4 = 0.0560.

**45) Shorter avicularium length (mm).*—Coded states: 0 = 0–0.0225, 2 = 0.0633–0.0850.

**46) Longer avicularium length (mm).*—Coded states: 0 = 0–0.0169, 2 = 0.0425, 4 = 0.0733–0.0950, 6 = 0.1200.

APPENDIX II

Character matrix for tropical American *Metrarabdotos*. Characters coded as in Appendix 1 for the hypothesis of relationship in Figure 3.

	Characters																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	20	21	23	28	29	31	32	34	36	37	39	41	42	43	44	45	46
unguiculatum	4	6	2	4	0	0	5	2	2	6	0	0	6	2	4	0	2	0	6	0	0	2	0	2	2	0	3	2	4	4	4	0	0
n. sp. 3	5	4	0	0	0	3	3	4	0	9	4	0	8	4	2	0	2	2	4	2	3	2	0	2	2	0	2	0	0	0	0	0	0
n. sp. 4	6	4	0	0	0	0	0	2	2	6	2	0	4	5	2	0	2	2	4	1	3	0	0	2	2	0	2	0	0	0	0	0	0
n. sp. 2	0	0	0	0	0	3	3	0	0	8	0	0	8	0	2	2	4	0	8	0	2	0	2	2	4	0	2	0	2	0	0	0	2
lacrymosum	0	0	0	0	0	3	3	0	0	9	0	0	8	0	2	2	4	0	7	2	0	2	1	1	3	0	5	0	0	0	0	2	4
chipolanum	1	2	2	2	2	1	1	2	2	4	2	0	2	3	0	1	0	2	2	0	3	0	0	2	2	0	2	0	0	2	0	0	0
auriculatum	0	0	0	0	0	3	3	4	4	0	4	2	0	0	4	2	0	2	0	0	3	0	2	4	0	2	0	0	0	0	0	0	0
n. sp. 1	0	0	0	0	0	3	3	2	2	0	2	0	0	0	2	2	0	2	0	0	3	0	2	4	0	2	0	0	0	0	0	2	4
colligatum	0	0	0	0	0	3	3	4	4	0	4	2	0	0	2	2	0	2	0	0	3	0	2	4	0	2	0	0	0	0	0	0	0
kugleri	0	0	0	0	0	0	2	2	2	6	2	0	2	0	2	0	2	2	4	0	3	0	0	2	2	2	0	0	0	3	0	0	6
n. sp. 6	0	0	0	0	0	3	3	0	0	0	0	0	0	0	2	2	0	0	0	0	3	0	2	2	0	2	0	0	0	0	2	0	0
n. sp. 7	0	0	0	0	0	3	3	0	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	2	2	0	0	0	0	1	2	2	4
micropora	0	0	0	0	0	3	3	4	0	0	4	0	0	0	0	2	0	2	0	0	3	0	2	4	0	2	0	0	0	0	0	2	4
n. sp. 5	0	0	0	0	0	3	3	2	1	0	2	0	0	0	2	2	0	2	0	0	3	0	2	3	0	2	0	0	0	0	0	0	0
tenue	0	0	0	0	0	2	3	2	2	2	2	0	0	0	4	2	0	2	0	0	3	0	2	4	0	2	0	0	0	0	0	0	0
n. sp. 10	0	0	0	0	0	3	3	2	0	0	2	0	0	0	4	2	0	2	0	0	3	0	2	4	0	2	0	0	0	0	0	0	0
n. sp. 8	2	0	0	0	0	3	3	0	0	0	0	0	0	1	4	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	4
n. sp. 9	0	0	0	0	0	3	3	0	0	0	0	0	0	0	4	2	0	2	0	0	3	0	2	2	0	2	0	0	0	0	0	0	0
pacificum	0	4	0	2	0	0	5	2	2	6	0	0	8	2	4	0	2	0	8	0	0	2	0	2	2	0	4	0	0	0	1	0	0
n. sp. 11	0	0	2	2	0	3	3	3	3	1	2	1	1	1	4	2	0	2	2	0	3	0	2	4	0	2	1	0	0	0	1	0	0
n. sp. 12	0	0	0	2	0	3	3	0	0	1	0	0	0	0	2	0	2	0	2	0	2	0	0	3	1	0	1	0	0	0	0	2	4
n. sp. 13	0	0	0	0	0	3	3	4	0	0	4	0	0	2	2	2	0	2	0	0	3	0	2	4	0	2	0	0	0	0	0	2	4