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PHYLOGENY OF GENUS *CUPULADRIA* (BRYOZOA, CHEILOSTOMATA) IN THE NEOGENE OF TROPICAL AMERICA

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ABSTRACT—We used 57 morphometric characters to discriminate 17 extant and fossil *Cupuladria* species and analyzed their phylogenetic relationships in relation to extant *Discoporella* species. Data were gathered from 496 extant and fossil *Cupuladria* specimens ranging in age from early Miocene to Recent and distributed from the Caribbean to tropical eastern Pacific. A first series of discriminant analyses distinguished three morphological groups: *Cupuladria* with vicarious avicularia, *Cupuladria* without vicarious avicularia, and *Discoporella*. Further discriminant analyses identified 17 species of *Cupuladria*. Cladistic analyses of these three groups yielded four equally parsimonious trees. All of the consensus trees exhibited the same topology, dividing the 25 tropical American cupuladriids into four distinct monophyletic clades, including *Discoporella*, and are consistent with previous molecular phylogenies except that there are no molecular data for the C_{V2} clade. Diversification of species was higher in the C_{V1} and C_{V2} clades than C_{NV} clade, and involved mostly Caribbean species. *Cupuladria* with vicarious clade 1 (C_{V1}) includes: *C. monotrema*, *C. pacificiensis*, *C. exfragminis*, *C. cheethami*, *C. biporosa*, and four new species: *C. pervagata*, *C. floridensis*, *C. colonensis* and *C. dominicana*. *Cupuladria* with vicarious clade 2 (C_{V2}) includes: *C. multesima*, *C. incognita*, and three new species *C. collyrida*, *C. veracruxiensis* and *C. planissima*. *Cupuladria* clade without vicarious (C_{NV}) includes: *C. surinamensis*, *C. panamensis*, and one new species *C. gigas*. The stratigraphic occurrence of species is consistent with cladogram topology within clades. However hypothesized cladistic relations among clades are the reverse of their stratigraphic occurrence with younger clade C_{NV} appearing as the hypothetical ancestor of the two older clades C_{V1} and C_{V2}. More extensive collections of early to middle Miocene specimens of *Cupuladria* and *Discoporella* will be required to resolve this apparent paradox.

INTRODUCTION

CUPULADRIID BRYOZOANS in the genera *Cupuladria* and *Discoporella* are among the most diverse and abundant bryozoans in tropical American seas where they have dominated shallow-water faunas since the early Miocene (Cheetham et al., 1999; Cheetham and Jackson, 2000; O'Dea et al., 2004). This great abundance and diversity have made cupuladriids a model system for studies of diversification and extinction, life history evolution, systematics, and paleoceanographic analysis (O'Dea and Jackson, 2002; Dick et al., 2003; O'Dea et al., 2004, 2007, 2008; Herrera-Cubilla et al., 2006, 2008; O'Dea, 2006; O'Dea and Jackson, 2009; Jagadeeshan and O'Dea, 2012). In particular, the striking responses of cupuladriid faunas to the gradual isolation of the tropical eastern Pacific from the Caribbean by the uplift of the Isthmus of Panama, and attendant major changes in oceanographic conditions, have provided deep insight into the role of environmental change in driving major ecological and evolutionary events.

In the course of these studies, it has become apparent that cupuladriid species diversity based upon both morphometric and genetic analyses is several times greater than reported previously (Dick et al., 2003; Herrera-Cubilla et al., 2006, 2008; O'Dea and Jackson, 2009); a pattern previously demonstrated for other cheilostome bryozoans (Cheetham, 1986; Jackson and Cheetham, 1990, 1994; Cheetham and Jackson, 1996; Cheetham et al., 2007) and marine invertebrates generally (Knowlton, 1993; Knowlton and Jackson, 1994). Phylogenetic studies, however, have been restricted to molecular analyses of living species with no contribution from the fossil record.

In this paper we develop a first phylogeny of the genus *Cupuladria* based on morphometric analysis of 17 living and fossil species of *Cupuladria* and eight extant species of *Discoporella*. The 17 *Cupuladria* species include all those described by Herrera-Cubilla et al. (2006) plus additional living and fossil species from the Gulf of Mexico, Greater Antilles, Honduras, Nicaragua, Panama, Colombia, and Guyana in the western Atlantic; and Mexico, Panama, and Colombia in the eastern Pacific. Morphological techniques comparable to those in our previous studies were used for species discrimination (Herrera-Cubilla et al., 2006, 2008). We used the same morphologically based approach for cladistic analysis developed by Cheetham et al. (2006, 2007). Extant *Discoporella* species (Herrera-Cubilla et al., 2008) were added to the cladistic analyses to help delineate overall generic relations within the family Cupuladriidae, but further study is required to discriminate fossil *Discoporella* species. We also visually fitted the cladogram topology to the stratigraphic ranges of species to compare their hypothesized times of divergence with the first occurrence of species in the fossil record.

COLLECTIONS

All the specimens were collected from Neogene to Recent marine deposits in the Caribbean and tropical eastern Pacific. The stratigraphic provenance of fossil *Cupuladria* examined is summarized in Figure 1. Eighty-one percent were collected by the Panama Paleontological Project (PPP) in Panama, Costa Rica, Honduras and Nicaragua, currently housed at the

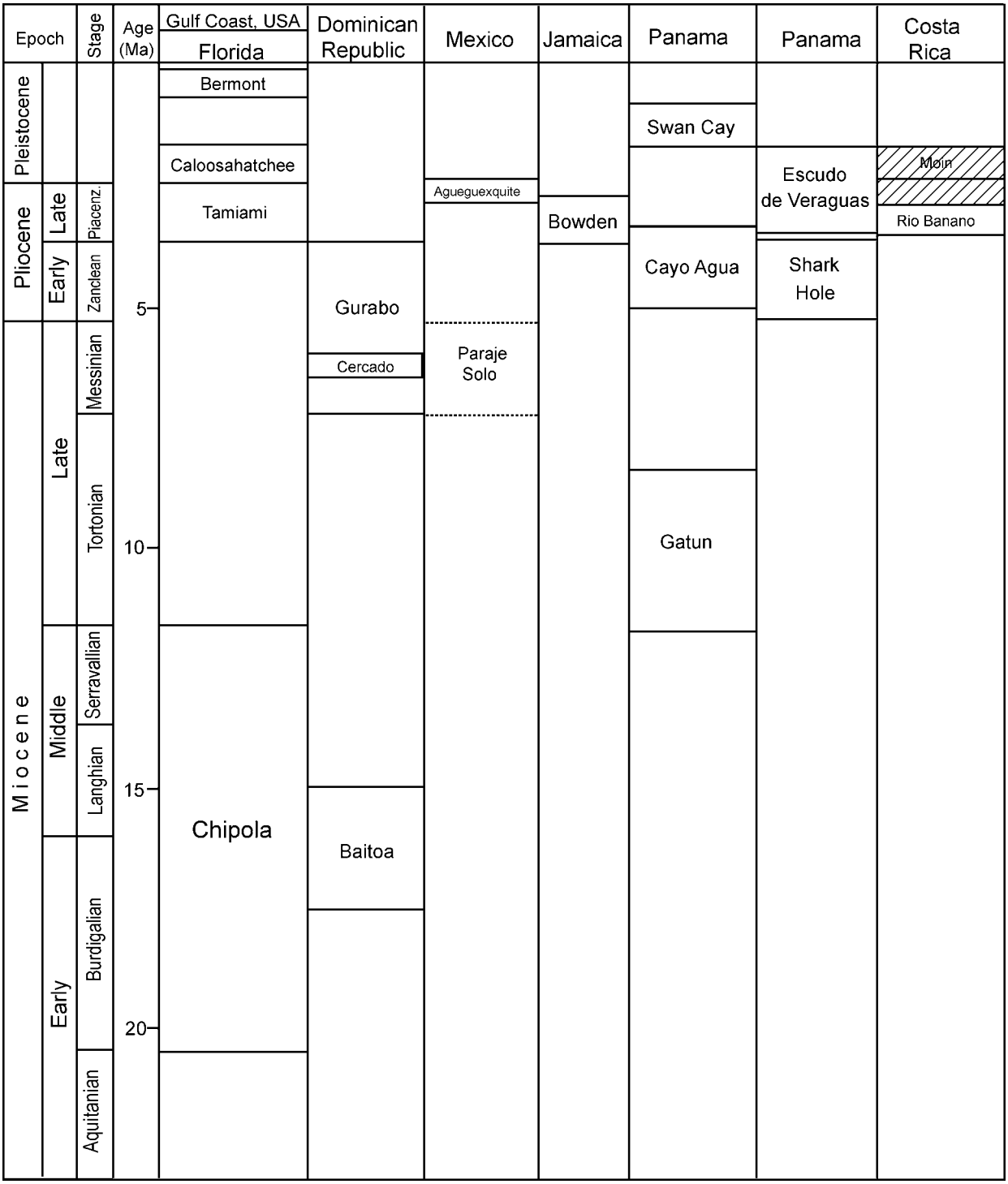

FIGURE 1—Neogene correlation chart, showing formations in tropical America from which *Cupuladria* was collected. Modified after Cheetham et al., 2007, according to Graham, 1976, Coates et al., 2005, and McNeill et al., 2012.

Smithsonian Tropical Research Institute in Panama. The remainder were obtained from the following museum collections: Neogene Paleontology of the Northern Dominican Republic Project (DR) and additional collections, Department of Paleobiology, National Museum of Natural History, Washington DC; Department of Palaeontology, the Natural History Museum, London; Section of Fossil Protists and Invertebrates, Louisiana State University, Museum of Natural Science; Department of Marine Invertebrates, Museum of Comparative Zoology, Harvard University; Invertebrate Paleontology Division, Florida Museum of Natural History (FLMNH), University of Florida; and Museo de Historia Natural Marina de Colombia, Instituto de Investigaciones Marinas y Costeras. The museum collections include specimens from Florida, the Gulf of Mexico, the Greater Antilles, Caribbean Colombia, Guyana, and the eastern Pacific coast of Mexico.

Data for PPP fossil localities are in electronic file, LOCDBAS4.DBF, dated 20 April 2005, available on the PPP

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World Wide Web site (Collins, 2005) and Coates (1999a, 1999b). Locality data for the DR Project samples are published in Saunders et al. (1986). Locality data for extant (SURVEY) specimens collected by the PPP along both coasts of Panama between 1995 and 1998 are published in Herrera-Cubilla et al. (2006, 2008). Locality data are also available for specimens borrowed from FLMNH on its Invertebrate Paleontology Database on the FLMNH World Wide Web site, dated 10 May 2010. Additional locality data are provided in the specimen descriptions in the Systematic Paleontology section.

TAXONOMIC CHARACTERS

We used a combination of traditional zooidal characters and non-traditional colonial characters as in our previous studies (Fig. 2; Herrera-Cubilla et al., 2006, 2008). Characters include primary information on zooidal dimensions such as width and length; colony-level characters such as size, shape, and dry weights of whole colonies; and 'shape' or ratio characters calculated between various pairs of the original measured characters. We used the term vicarious avicularium following Cook and Chimonides (1994, p. 254), who defined them as "large avicularia which replace and autozooid, but do not replace the distal zooidal avicularian subunit" (vibraculum). "The zoecial vibracula, although apparently inserted between the zooecia at the frontal surface . . .are not strictly interzooecial, nor are they adventitious or dependent" (Cook, 1965a, p. 156). Some new characters including autozooids (Zcp), vicarious avicularia with closure plates (Vcp), and kenozooids at the margin of the colony (Ken) (Fig. 3) were scored 0 or 1 on an individual-colony basis. All measurements were re-scaled as in previous studies log10(1+variable). Table 1 contains the full set of 57 morphological characters used for discrimination of taxa and subsequent cladistic analysis.

DISCRIMINATION OF SPECIES

All multivariable analyses for the morphometric discrimination of species were performed with PASW statistical software (SPSS Inc., 2009). A total of 20 separate discriminant analyses described below are numbered sequentially as DA1, DA2 . . . DA20.

Extant species of Cupuladria *and* Discoporella.—We used a sequence of two discriminant analyses to examine the morphological distances among species of *Cupuladria* and *Discoporella* for 15 extant species of the two genera from both sides of the Isthmus of Panama previously described by Herrera-Cubilla et al. (2006, 2008). The analyses were based on 54 of the 57 morphometric characters listed in Table 1, including most of the characters used in earlier analyses plus ten new characters related to the vicarious avicularia and their vibracula. The three characters Zcp, Vcp and Ken were not included because they are only present in fossils. The 54 characters were measured or scored from 258 colonies that were entered as 'groups' into a linear discriminant analysis (DA).

The initial DA1 clearly separated the 15 previously described species into two groups: *Cupuladria* species with vicarious avicularia (henceforth termed "vicarious *Cupuladria*") and *Cupuladria* species without vicarious (henceforth "non-vicarious *Cupuladria*") along with *Discoporella* species (above and below in Fig. 4.1). The two groups were different at $p<0.0001$ with 100 percent of colonies correctly classified and jackknife values of 98.5 percent (Table 2). Characters with the highest coefficients in the DA were: Cw, Ch, Rahw, Vl, VOwVOl, and RaVawVw. We then ran a second DA2 to resolve further the cluster of non-vicarious *Cupuladria* plus *Discoporella* cluster (Fig. 4.2). This analysis clearly separated all the *Discoporella* species (above), from the non-vicarious *Cupuladria* species (below), at $p<0.0001$, 99.1 percent of colonies were correctly classified versus 90.9 percent jackknife (Table 2). The first three discriminant functions account for 92 percent of the total variance. Characters with highest coefficients were: Cw, Graden, Aw, AwAl, RaOlZl, and RaAloAl. The linear pattern exhibited by non-vicarious *Cupuladria* is due to the contribution of Cw, Graden and Aw that have the highest coefficients along the DF1.

Recent and fossil Cupuladria *species*.—Having thus confirmed the strong differences between *Cupuladria* and *Discoporella*, and between vicarious and non-vicarious *Cupuladria*, we next performed an extensive second series of DA to discriminate extant and fossil species of vicarious and non-vicarious *Cupuladria*. Here we used a modification of our earlier methods (Herrera-Cubilla et al., 2006, 2008) to incorporate part of the methodology used by Cheetham et al. (2006, 2007).

A subset of 91 well-preserved colonies of extant and fossil *Cupuladria* was chosen subjectively to maximize the range of morphological, geographic, and stratigraphic variation (present) in the whole dataset (see Cheetham et al., 2006, 2007). The principal criteria for this preliminary selection included differences among species observed previously plus variations in colony size and shape, closure plates of autozooids and vicarious avicularia, evidence for determinate growth, shape of the basal sectors, and numbers of pores. These 91 colonies were entered as 'groups' in a third discriminant analysis (DA3) based on all of the 52 characters observed for *Cupuladria* (opesiules, pores, related to the nearly complete cryptocyst of *Discoporella* and basal granules are absent in *Cupuladria*; see Table 1 for details). DA3 distinguished two clusters of vicarious (N=70) and non-vicarious colonies (N=21) (Fig. 5), just as for recent colonies of *Cupuladria* (Herrera-Cubilla et al., 2006, fig. 2). The clusters were different at $p<0.0001$, success of classification was 100 percent versus 97 percent jackknifed. The first three discriminant functions account for 99.9 percent of the total variance. The characters with the highest coefficients were the Vl, Vw, VAl, VOwVOl, OwOl, RaAloOl. Separation of vicarious from non-vicarious *Cupuladria* along DF2 is due to VAwo, Vw, and VOwVOl which have in rank order the highest coefficients.

The 70 colonies with vicarious avicularia and 21 colonies without vicarious avicularia were treated separately in a series of hierarchical cluster analyses using the average linkage method based on Euclidean distances to obtain discrete groups to begin the process of discriminating morphospecies in each group. The resulting clusters were next tested for stability in a series of DA to determine whether the groups were significantly different from each other and whether each colony was correctly assigned to its group (Jackson and Cheetham, 1994; Herrera-Cubilla et al., 2006, 2008). The resulting groups, or morphospecies, thus discriminated were used to classify batches of colonies randomly selected from the whole dataset that were entered unassigned in a second series of DAs. Correctness of classification was determined by whether a colony was assigned to its higher probability group, given the function coefficients calculated by the DA. After each DA, the process of combining groups, reassigning colonies to their highest probability groups, or leaving incorrectly classified colonies unassigned for entry in the next DA, was made manually. Classification of colonies was cross-validated by first order or higher order jackknifing. These methods are equal to those employed in previous studies (including Cheetham et al., 2006, 2007).

Colonies with vicarious avicularia.—Hierarchical cluster analysis of 70 colonies with vicarious avicularia based on 52 characters yielded 20 discrete groups with a Similarity Coefficient ≤ 0.03 plus four outliers (5.7% of total specimens). Three rounds of DAs (DA4–DA6) reduced the 20 clusters of vicarious

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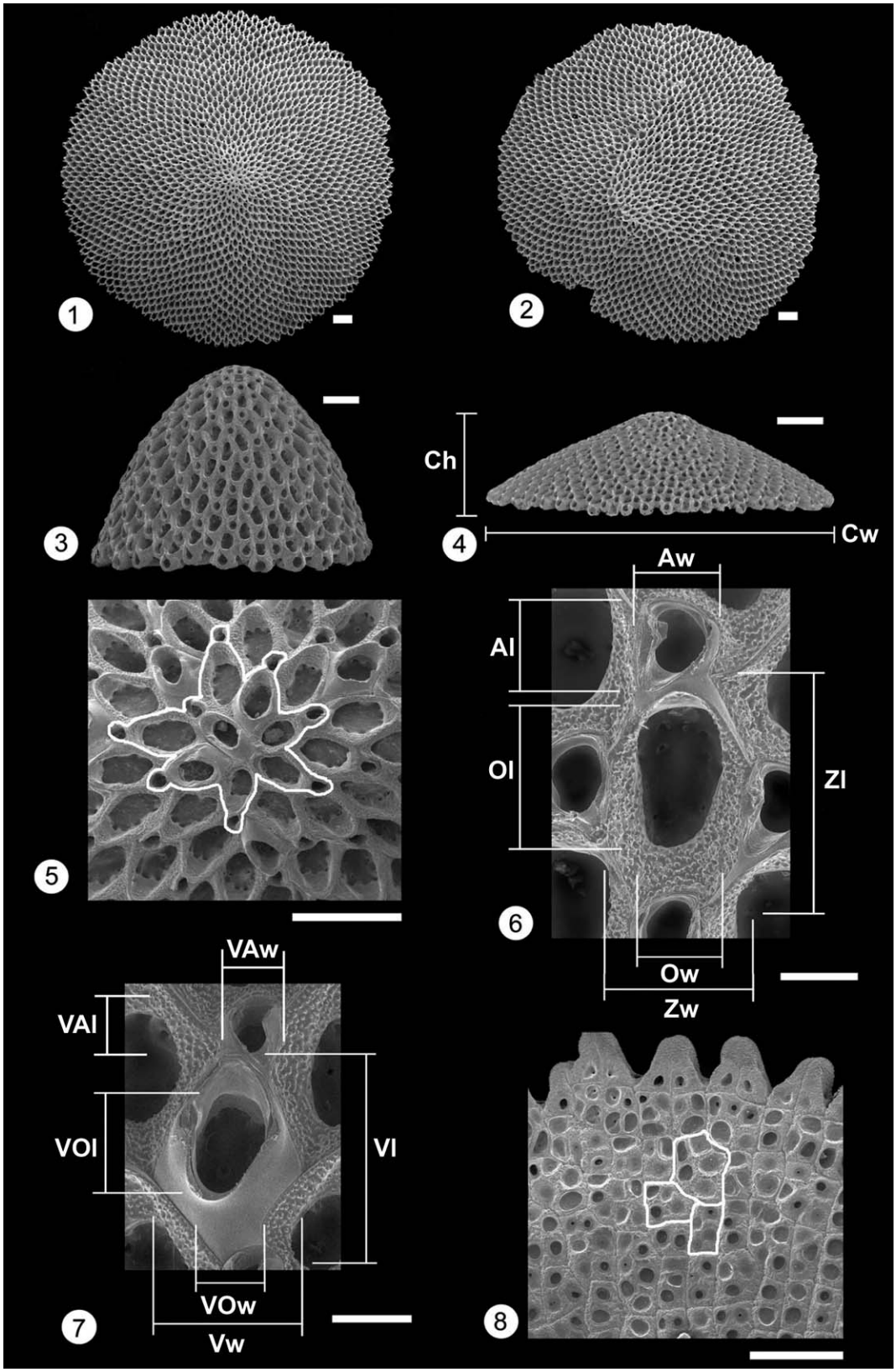

FIGURE 2—Morphological characters used for discriminant and cladistic analyses of extant and fossil cupuladriids. *1–8* characters for *Cupuladria* after Herrera-Cubilla et al., 2006: *1–4*, colony size, shape and mode of reproduction; *1–2*, *4*, *C. biporosa* Canu and Bassler, 1923: *3*, *C. panamensis*; *5–8*, *C. biporosa*: *5*, ancestrula and early astogeny (outlined); *6*, *7*, characters of autozooid and vicarious avicularium; *8*, basal sectors (outlined) and pores. Colonies bar scale=1 mm, colony modules bar scale=100 μm.

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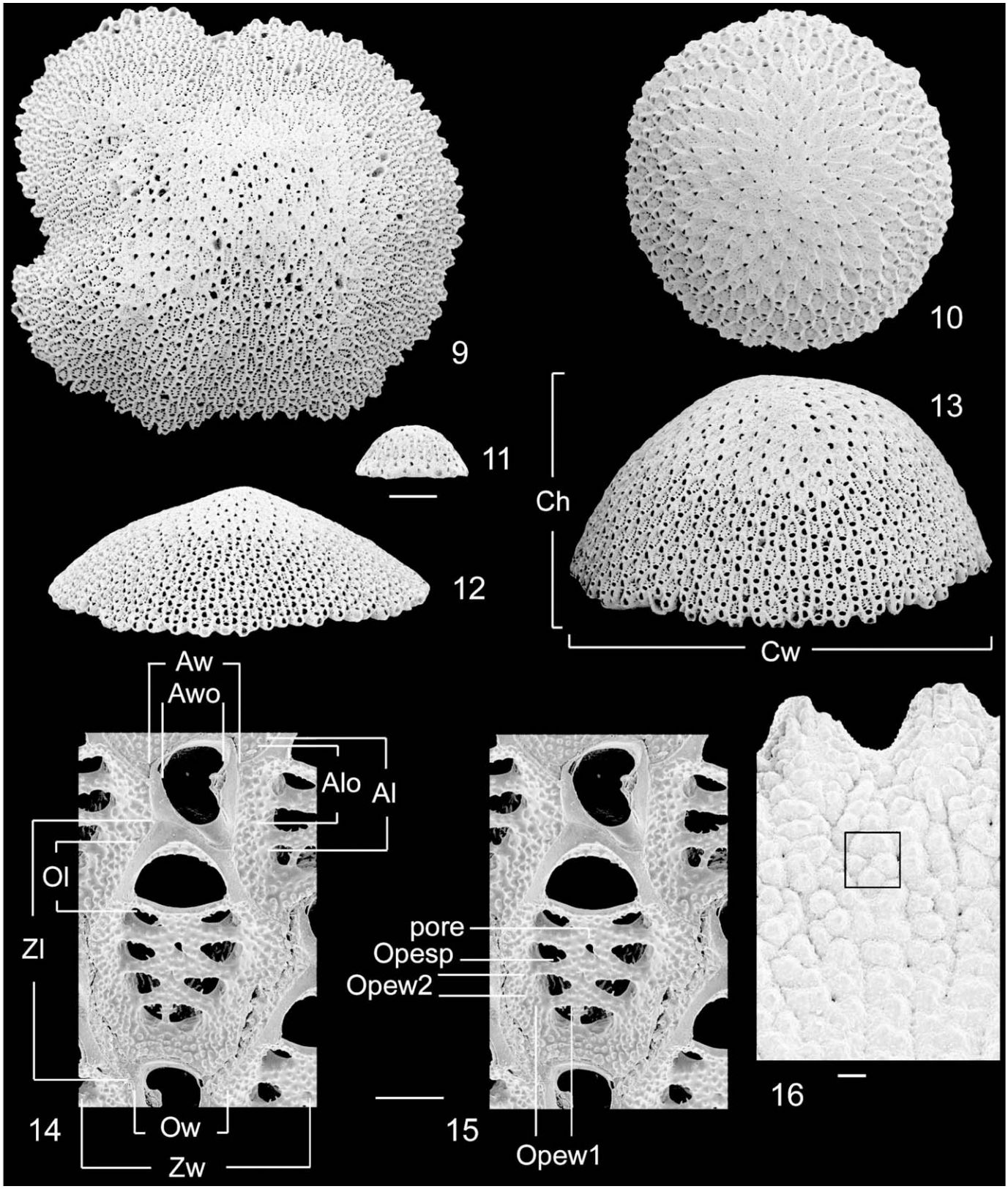

FIGURE 2—9–16 characters for *Discoporella* after Herrera-Cubilla et al., 2008: *9*, *13*, *D. cookae* (clonal origin): *10*, *D. scutella*; *11*, *D. triangula*; *12*, *D. bocasdeltoroensis* (aclonal origin); *14–16*, *D. marcusorum*; *14*, *15*, characters of autozooid and vibraculum avicularium; *16*, basal granular density. Colonies bar scale=1 mm, colony modules bar scale=100 μm.

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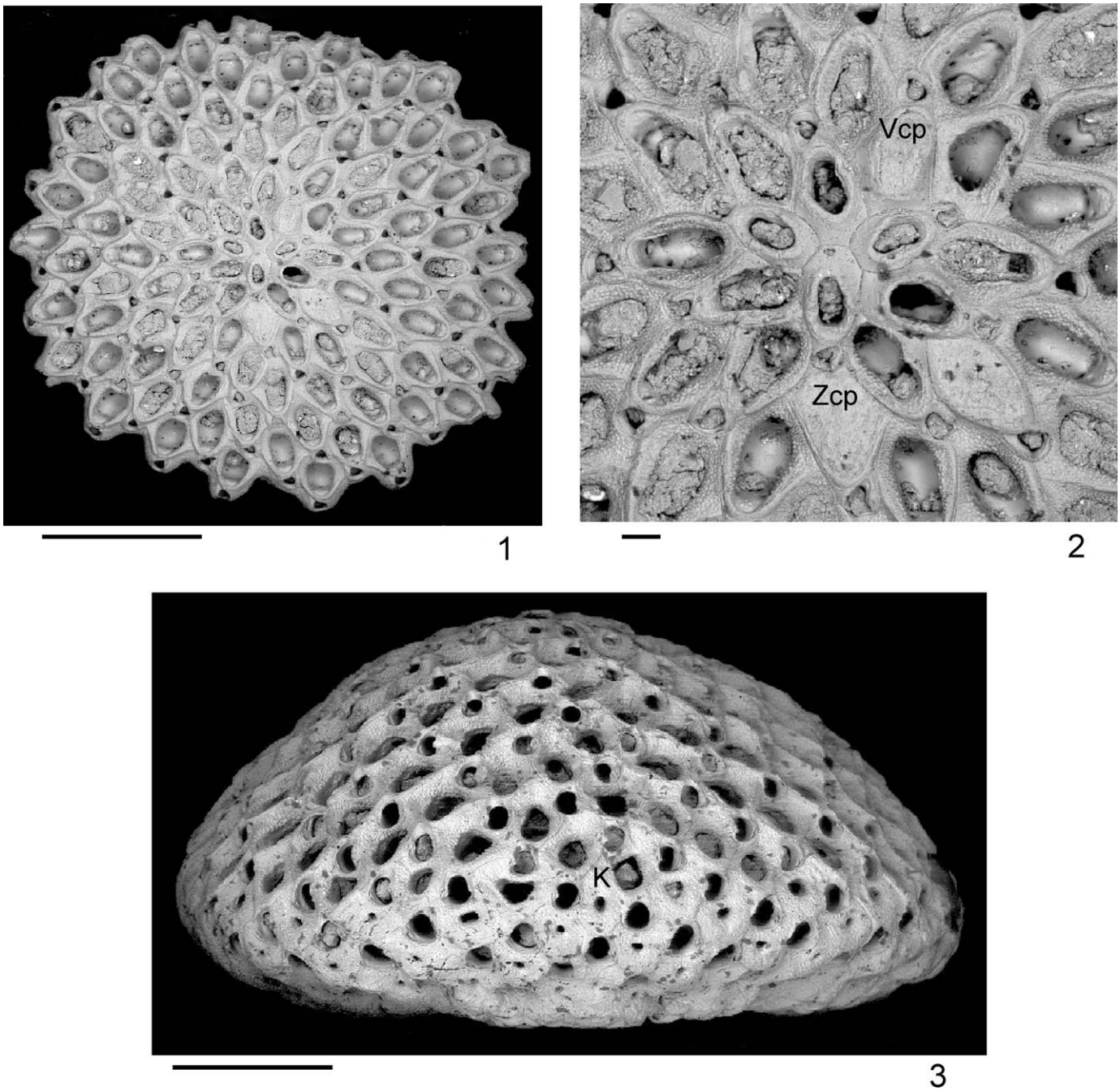

FIGURE 3—Autozooids and vicarious avicularia with closure plates, kenozooids. *1*, *2 Cupuladria veracruxiensis* n. sp., autozooids and vicarious avicularia with closure plates; *3*, *C. collyrida*, holotype, USNM542561, kenozooids at the colony margin. Colonies bar scale=1 mm, colony modules bar scale=100 μm. For details on these characters see Table 1.

specimens to 14 morphospecies. All the groups were different at $p<0.0001$ and 100 percent of vicarious morphospecies were correctly classified versus 99 percent jackknifed. Next, to initiate the process of classification of the remaining specimens, three batches of vicarious colonies were entered un-assigned into consecutive DAs. The first batch of 80 specimens were added to DA6, and then submitted to three rounds of additional DA (DA7–DA9) whereby 99 percent of the cases were correctly classified versus 94 percent jackknifed. Addition of a second batch of 59 specimens including fossils 4 Ma yielded 98 percent of the cases correctly classified versus 94 percent jackknifed (DA10). Finally the third batch of 22 colonies, including fossils from Florida and recent specimens from the Caribbean coast of Colombia, yielded 98 percent of the cases correctly classified versus 93 percent jackknifed (DA11) for all 231 vicarious colonies (Fig. 6, Table 3). The characters with the highest coefficients were in rank order: Rahw, Ch, RaZV, Psec, Cw, Ol, Csur, RaAloAl, and Asec (see Table 1 for details).

Colonies without vicarious avicularia.—Only 30 characters were used to cluster the 21 specimens without vicarious avicularia, since all the characters related with vicarious avicularia were absent. This analysis yielded five discrete groups with a Similarity Coefficient ≤ 0.09 plus two outliers (9.5% of total specimens). Four subsequent rounds of DA (DA12–DA15)

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TABLE 1—Full set of morphological characters used in the discrimination of taxa and cladistic analysis.

Abbreviation	Character name
1. Cw[1αβ]	Colony diameter
2. Ch[1αβ]	Colony height
3. Rahw[1αβ]	Colony height-diameter ratio
4. Csur[1αβ]	Colony surface area
5. Ci[1αβ]	Calcification index
6. RaZV[1αβ]	Autozooid-vicarious avicularium ratio and mode of reproduction: fraction of the eight units, from the first generation of the colony, that are autozooids. In the absence of an ancestrula (e.g., origin by fragmentation) we scored as the integer 2.
7. Zl[1αβ]	Autozooid length
8. Zw[1αβ]	Autozooid width
9. ZwZl[1αβ]	Autozooid width-length ratio
10. Ol[1αβ]	Opesia length
11. Ow[1αβ]	Opesia width
12. OwOl[1αβ]	Autozooid opesia width-length ratio
13. Al[1αβ]	Autozooid vibraculum length
14. Aw[1αβ]	Autozooid vibraculum width
15. AwAl[1αβ]	Autozooid vibraculum width-length ratio
16. Alo[1αβ]	Autozooid vibraculum opesia length
17. Awo[1αβ]	Autozooid vibraculum opesia width
18. AwoAlo[1αβ]	Autozooid vibraculum opesia width-length ratio
19. RaOlZl[1αβ]	Ratio opesia length-autozooid length
20. RaOwZw[1αβ]	Ratio opesia width-autozooid width
21. RaAlZl[1αβ]	Ratio autozooid vibraculum length-autozooid length
22. RaAwZw[1αβ]	Ratio autozooid vibraculum width-autozooid width
23. RaAloAl[1αβ]	Ratio autozooid vibraculum opesia length-autozooid vibraculum length
24. RaAwoAw[1αβ]	Ratio autozooid vibraculum opesia width-autozooid vibraculum width
25. RaAloOl[1αβ]	Ratio autozooid vibraculum opesia length-autozooid opesia length
26. RaAwoOw[1αβ]	Ratio autozooid vibraculum opesia width-autozooid opesia width
27. Zcp[2β]	Presence/absence of closure plates in autozooids
28. Vcp[2β]	Presence/absence of closure plates in vicarious avicularia
29. Nope[1α]	Number of opesiules
30. Opew[1α]	Opesiule maximum average diameter (calculated on Opew1 and Opew2 measured on the bigger opesiule found per autozooid)
31. Opesp[1α]	Opesiule median number of spines per autozooid
32. Npor[1α]	Number of pores in autozooid frontal shield
33. NV[1αβ]	Number of vicarious avicularia
34. Vl[1αβ]	Length of vicarious avicularium
35. Vw[1αβ]	Width of vicarious avicularium
36. VwVl[2αβ]	Vicarious avicularium width-length ratio
37. VOl[1αβ]	Length of the vicarious avicularium opesia
38. VOw[1αβ]	Width of the vicarious avicularium opesia
39. VOwVOl[2αβ]	Vicarious avicularium opesia width-length ratio
40. VAl[1αβ]	Vicarious avicularium vibraculum length
41. VAw[1αβ]	Vicarious avicularium vibraculum width
42. VAwVAl[2αβ]	Vicarious avicularium vibraculum width-length ratio
43. VAlo[2αβ]	Vicarious avicularium vibraculum opesia length
44. VAwo[2αβ]	Vicarious avicularium vibraculum opesia width
45. VAwoVAlo[2αβ]	Vicarious avicularium vibraculum opesia width-length ratio
46. RaVOlVl[1αβ]	Ratio vicarious avicularium opesia length-vicarious avicularium length
47. RaVOwVw[1αβ]	Ratio vicarious avicularium opesia width-vicarious avicularium width
48. RaVAlVl[1αβ]	Ratio vicarious avicularium vibraculum length-vicarious avicularium length
49. RaVAwVw[1αβ]	Ratio vicarious avicularium vibraculum width-vicarious avicularium width
50. RaVAloVAl[2αβ]	Ratio vicarious avicularium vibraculum opesia length-vicarious avicularium vibraculum length
51. RaVAwoVAw[2αβ]	Ratio vicarious avicularium vibraculum opesia width-vicarious avicularium vibraculum width
52. RaVAloVOl[2αβ]	Ratio vicarious avicularium vibraculum opesia length-vicarious avicularium opesia length
53. RaVAwoVOw[2αβ]	Ratio vicarious avicularium vibraculum opesia width-vicarious avicularium opesia width
54. Asec[1αβ]	Basal sector area
55. Psec[1αβ]	Number of pores per sector
56. Graden[1α]	Basal granule density near the margin on the basal side of the colony
57. Ken[2β]	Presence/absence of kenozooids in the margin of the colony

[1] Characters used in Herrera-Cubilla et al. (2006, 2008).
[2] Characters added in this study.
[α] Characters used in the first series of discriminant analyses.
[β] Characters used in the second series of discriminant analyses.

reduced the five clusters of non-vicarious specimens to four putative morphospecies with 100 percent of colonies correctly classified versus 95 percent jackknifed. Next, 55 of the remaining non-vicarious colonies were added unassigned to the colonies from DA15. After four rounds of DA (DA16–DA19), one species group represented by only two fossil specimens was merged into another group from which it was not different at $p<0.0001$. This reduced the number of groups discriminated to three with 100 percent of cases correctly classified versus 99 percent jackknifed. Next a second batch of 30 colonies was submitted to the same procedure bringing the total to 106 for the last DA20 resulting in 99.1 percent of colonies correctly classified versus 99.1 percent jackknifed (Fig. 7, Table 3). The characters with the highest coefficients were in rank order: Csur, Cw, Ch, and Rahw (see Table 1 for details).

The 14 vicarious and three non-vicarious groups (hereafter morphospecies or species) of *Cupuladria* are considered equivalent to biological species distinguished in previous studies of different cheilostome genera using similar morphometric methods for which genetic data was also available (Jackson and Cheetham, 1990, 1994; Herrera-Cubilla et al., 2006, 2008).

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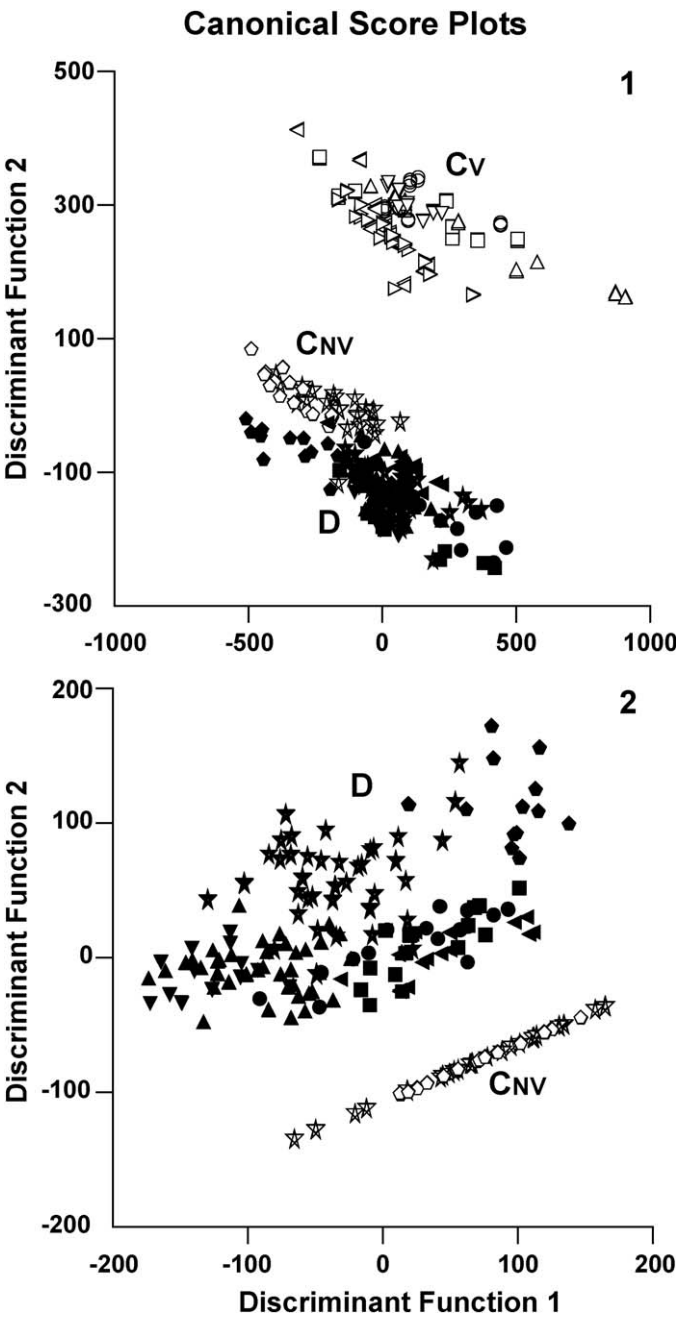

FIGURE 4—Canonical score plots done on 15 species of extant *Cupuladria* and *Discoporella* described in Herrera-Cubilla et al., 2006, 2008. All colonies were entered as 'groups'. *1*, first discriminant analysis (DA1) separates vicarious *Cupuladria* species (above) from non-vicarious *Cupuladria* and *Discoporella* species (below); *2*, second discriminant analysis (DA2) separates non-vicarious *Cupuladria* (below) from *Discoporella* (above). The species are: □ *C. biporosa*, ○ *C. cheethami*, △ *C. exfragminis*, ▽ *C. pacificiensis*, ◁ *C. multesima*, ▷ *C. incognita*, ☆ *C. surinamensis*, ⌂ *C. panamensis*, ■ *D. scutella*, ● *D. peltifera*, ▲ *D. terminata*, ▼ *D. triangula*, ◀ *D. bocasdeltoroensis*, ★ *D. marcusorum*, ⬟ *D. cookae*.

TABLE 2—Results of linear discriminant analysis done on 15 species of *Cupuladria* and *Discoporella* described in A. Herrera-Cubilla et al. (2006, 2008). The analysis was based on a total of 54 rescaled characters, and all colonies were entered as "groups". For details see text.

Cupuladria vs. *Discoporella*: DA1		
Difference between groups:		
N=258, Wilks' Lambda=0.000, Chi-square=53,006.86, $p<0.0001$		
DF	Eigen value	Cumulative
1	70,981.27	43.1
2	46,116.34	71.1
3	34,583.30	92.0
4	6,107.37	95.7
Percent of cases correctly classified: 100%		
Jackknifed classification: 98.5%		
Cupuladria without vicarious vs. *Discoporella*: DA2		
Difference between groups:		
N=192, Wilks' Lambda=0.000, Chi-square=18,402.96, $p<0.0001$		
DF	Eigen value	Cumulative
1	10,386.56	64.3
2	5,630.72	99.2
Percent of cases correctly classified: 99.1%		
Jackknifed classification: 90.9%		

CLADISTIC ANALYSIS

We constructed cladistic phylogenies for 25 cupuladriid species, including all 17 recent and fossil *Cupuladria* species discriminated above plus eight recent *Discoporella* species. The later include the seven species previously described from Panama (Herrera-Cubilla et al., 2008) and *Discoporella* sp. nov. P1 (from Jagadeeshan and O'Dea, 2012). The 57 morphological characters listed in Table 1 were coded for cladistic analysis using the same procedure as in earlier studies of cheilostome phylogeny (Jackson and Cheetham, 1994; Cheetham et al., 2006, 2007).

We used analysis of variance (ANOVA) on the 496 colonies distributed among 26 taxa, including the outgroup, to test for the statistical ability of each of the characters to distinguish among the species. These included all 231 vicarious and 106 non-vicarious *Cupuladria* specimens used for species discrimination plus 156 specimens of *Discoporella* and three of *Antropora*. All the ANOVAs yielded F-values significant at $p<0.0001$.

We then used the post-hoc Duncan's Multiple Range Test (DMRT) to identify which of the species-groups have means that do not differ at the default significance level of $p<0.05$ to

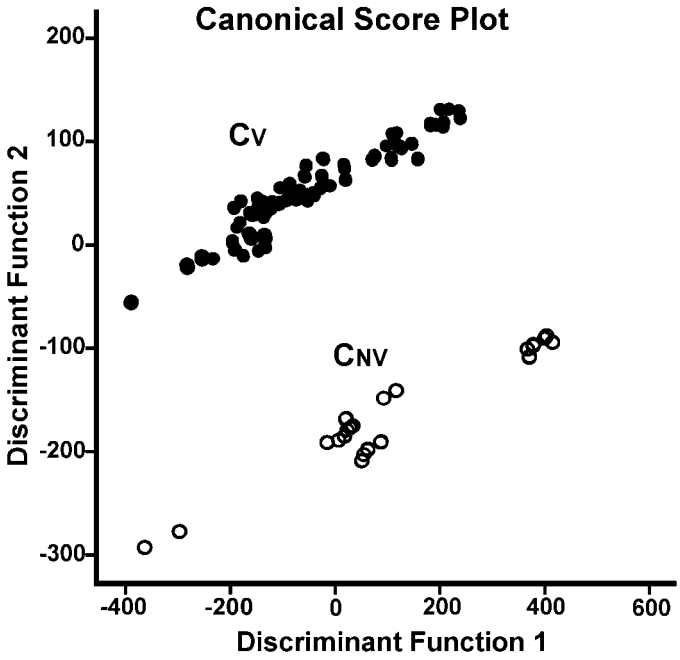

FIGURE 5—Canonical score plot for 91 extant and fossil colonies of *Cupuladria* entered as 'groups' based on 52 characters. Colonies with vicarious avicularia (solid circles), colonies without vicarious avicularia (open circles). See text for details.

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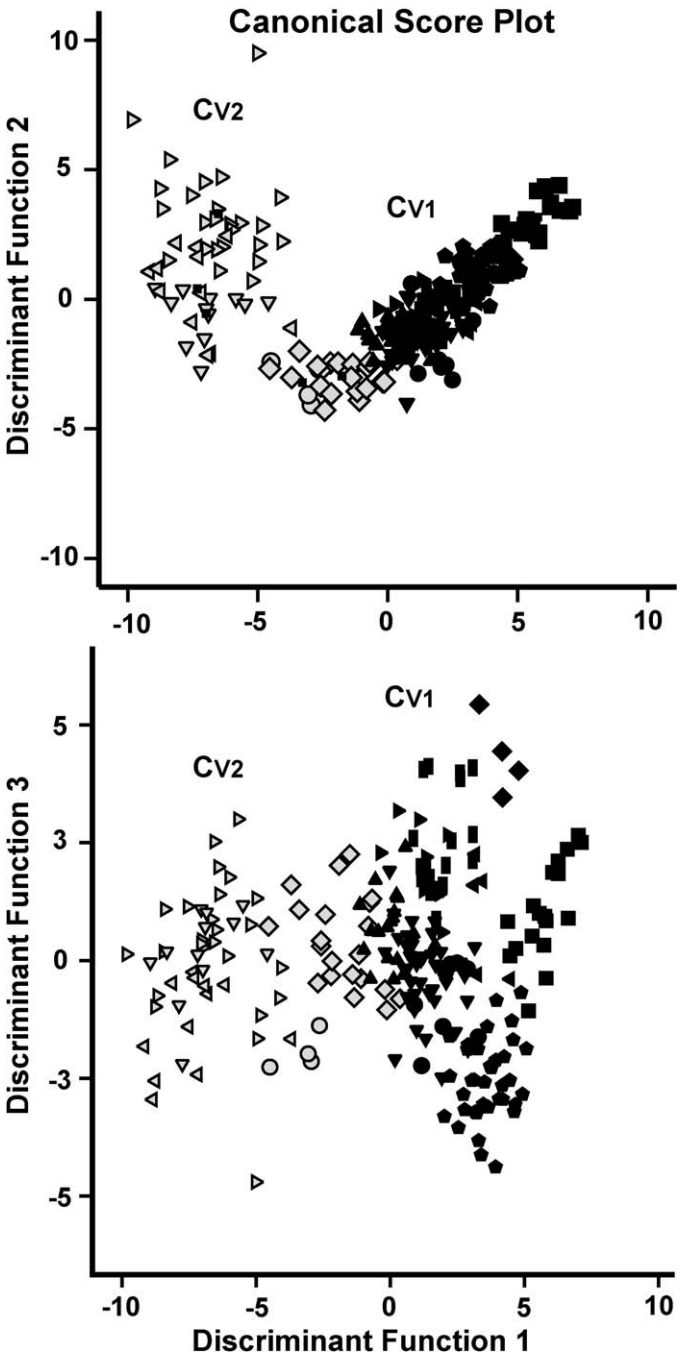

FIGURE 6—Canonical score plots for extant and fossil Vicarious *Cupuladria*. The species are: ● *C. monotrema*, ▲ *C. pacificiensis*, ▼ *C. pervagata*, ◀ *C. cheethami*, ▶ *C. biporosa*, ⬟ *C. exfragminsis*, ■ *C. floridensis*, ◆ *C. colonensis*, ▮ *C. dominicana*, ○ *C. collyrida*, ◇ *C. veracruxiensis*, ▷ *C. incognita*, ▽ *C. planissima*, ◁ *C. multesima*, ■ Group centroid.

form homogeneous subsets (SPSS Inc., 2009). Coded states of each character were assigned rank-order values from zero to nine, with the difference between successive states (ranks) equal to two for non-overlapping subsets or one with an overlap of one. This procedure is analogous to gap coding but based upon ranges rather than gaps (Cheetham et al., 2007, p. 15, fig. 7). We used letters to assign rank-order values for the few characters for which the number of character subsets exceeded 10 (see online Supplemental Data file). All of the coded characters

TABLE 3—Results of linear discriminant analysis done on total extant and fossil *Cupuladria* species with and without vicarious. For details see text.

Cupuladria species with vicarious:
DA11
Difference between groups:
N=231, Wilks' Lambda=0.000, Chi-square=1,907.15, $p<0.0001$

DF	Eigen value	Cumulative Variance
1	17.19	61.6
2	3.98	75.9
3	2.45	84.6
4	1.86	91.3
5	1.16	95.4

Percent of cases correctly classified: 97.9%
Jackknifed classification: 93.2%

Cupuladria species without vicarious:
DA20
Difference between groups:
N=106, Wilks' Lambda=0.079, Chi-square=257.25, $p<0.0001$

DF	Eigen value	Cumulative Variance
1	4.50	77.7
2	1.29	100.0

Percent of cases correctly classified: 99.1%
Jackknifed classification: 99.1%

successfully separated species into one or more subsets in the following DMRTs (Appendix 1).

The oldest known specimens of cupuladriids consist of badly worn fragments unsuitable for morphological measurements and are therefore inadequate to use as the outgroup for cladistic analysis. These specimens (NHM, D-41382-4) collected from the Eocene Bartonian, Bende-Ameki Formation, Nigeria Africa, have features similar to both *Cupuladria* and *Discoporella* (Fig. 8). They resemble *Cupuladria* on the frontal surface in lacking a bar forming subopercular opesia, denticles, or spines. In

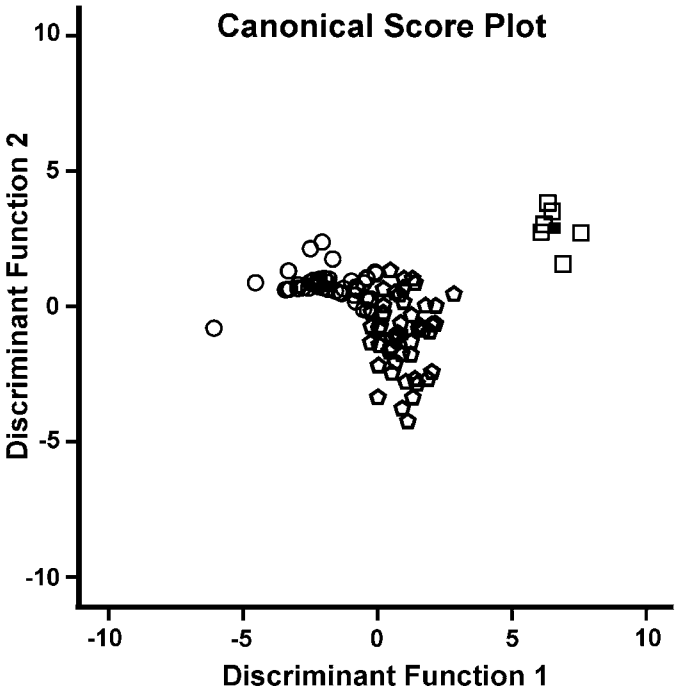

FIGURE 7—Canonical score plot for extant and fossil non-Vicarious *Cupuladria*. The species are: ○ *C. surinamensis*, ⬠ *C. panamensis*, □ *C. gigas*, ■ Group centroid.

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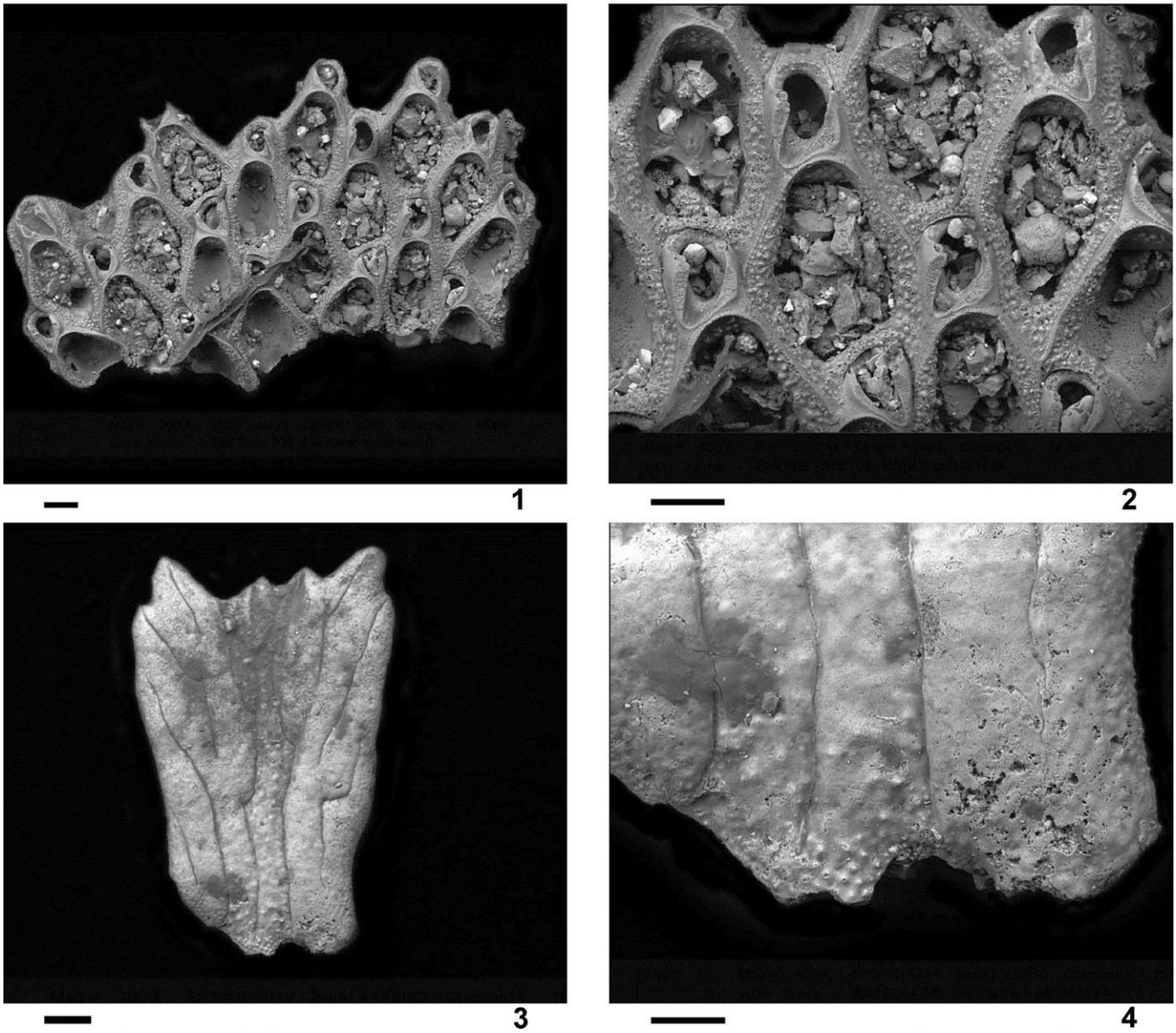

FIGURE 8—Cupuladriid specimen from Ameki formation Nigeria Africa middle Eocene, in the department of Paleontology's collection of the NHM. The morphology shows a *Cupuladria* 'like' specimen in frontal view and *Discoporella* basal view. Photo courtesy of P. D. Taylor.

contrast, they resemble *Discoporella* on the basal surface of the colony in the possession of tubercles and grooves. A similar mix of characters occurs in specimens of roughly the same age from Egypt: *Cupuladria numulitophila* n.sp (early Eocene, Priabonian, Maadi Fm., Gabal Homret Shaibun east of Beni Suef), and *Cupuladria fayumensis* n. sp (early Eocene, Priabonian, Qasr el-Sagha Fm., Fayum area) (Ziko A., 1985) that also occur only as worn fragments unsuitable for morphological analysis.

Because of this lack of suitable fossil material, we used the extant encrusting anascan *Antropora leucocypha*, Marcus, 1937 (Calloporidae) from the Perlas Archipelago in the Gulf of Panama as the outgroup for cladistic analysis. Its most important trait is the presence of internal brooding chambers (Marcus, 1937; Cook, 1968; Winston, 1982), which also occur in the Cupuladriidae.

Hastings (1930, p. 709, fig. 17) described the position of an internal sac-bearing embryo in *Antropora tincta*, but was unable to conclude if such sac represented a true ovicell (for a discussion on the similarity between *A. leucocypha* and *A. tincta* see the systematic paleontology section). Tilbrook (1998) also described seven species of *Antropora* with small indistinct or vestigial endozooidal ovicells. Subsequently, Ostrovsky and colleagues demonstrated that cupuladriids incubate embryos within an internal sac or immersed ovicell and concluded that cupuladriids are nested within calloporids based upon their type of internal brooding and simple zooidal morphology (Ostrovsky et al., 2009).

Cladograms were calculated from the characters coded by DMRT entered as ordered states in PAUP* 4.0b10 (Swoford, 2000). The routine Branch and Bound search was used to look for the most parsimonious trees.

Four equally parsimonious trees were obtained (Fig. 9) with length 485, consistency index 0.59, and retention index 0.86. Nine of the 57 characters were uninformative for parsimony (C*i*,

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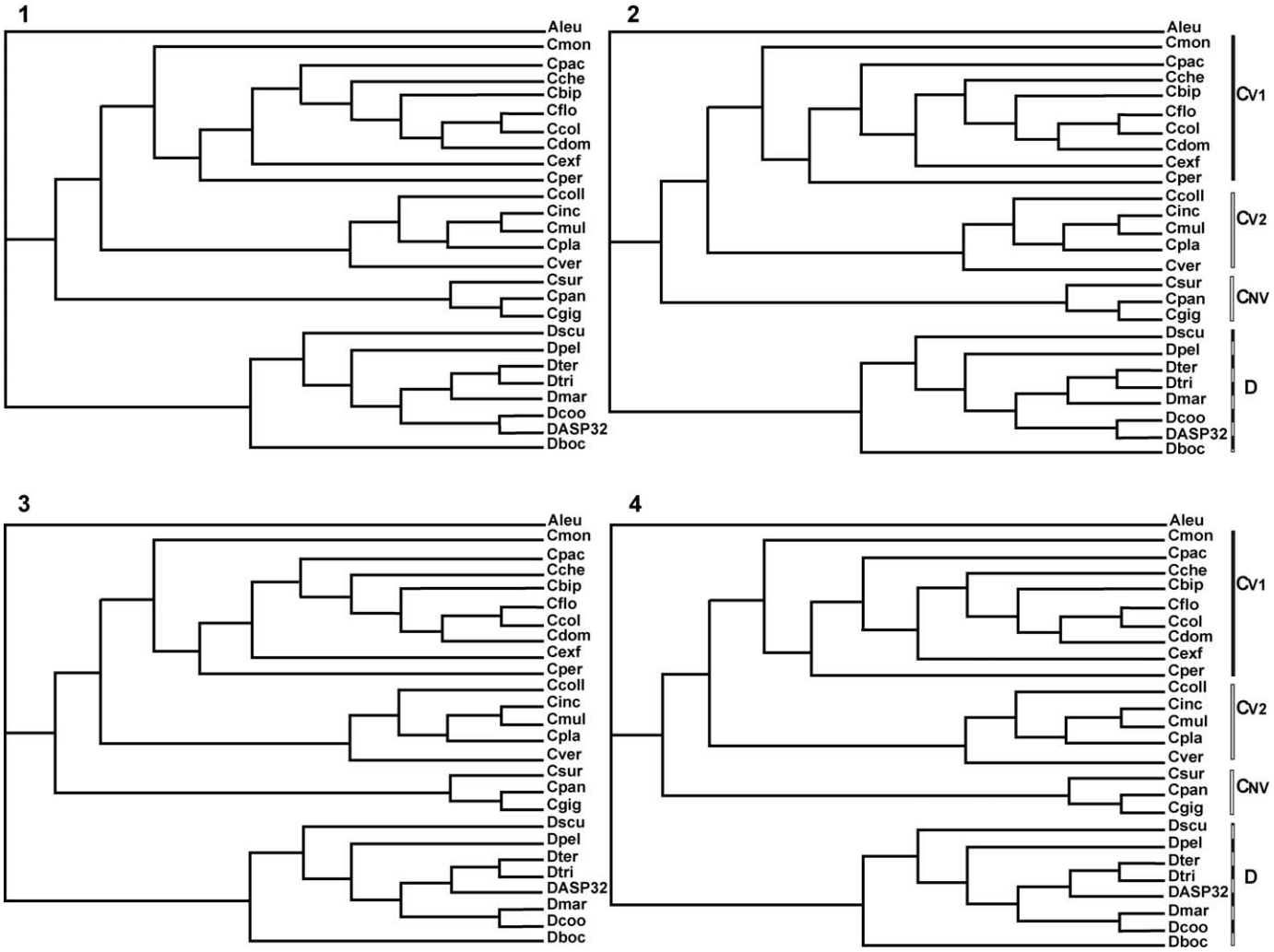

FIGURE 9—Four equally parsimonious trees obtained with branch and bound search routine in PAUP*, and routed to *A. leucocypha* (Calloporidae, Anasca); length 485, consistency index 0.59, and retention index 0.86. Species are grouped in four monophyletic groups: vicarious *Cupuladria* clade 1(C_{V1}), vicarious *Cupuladria* clade 2(C_{V2}), non-vicarious *Cupuladria* clade (C_{NV}), and *Discoporella* (D).

ZwZl, Aw, AwAl, RaAlZl, RaAwZw, RaAloAl, RaAwoOw, Vcp). All four trees divided the 25 tropical American cupuladriids into four distinct morphological clades that are well supported by the discriminant analysis (Figs. 4–7), as well as the bootstrap support tree based on 1,000 pseudoreplicates of the original cladistic data illustrated in Figure 11A. The extant and fossil *Cupuladria* clades are: non-vicarious *Cupuladria* (C_{NV}), *Cupuladria* clade 2 (C_{V2}), and *Cupuladria* clade 1 (C_{V1}); and beneath the extant *Discoporella* species (D). *Discoporella* is paraphyletic to *Cupuladria*. Within *Cupuladria*, C_{V1} and C_{V2} are sister groups both of which are apparently derived from the C_{NV} clade.

We used the command 'ConTree' to calculate strict, semi strict and 50 percent majority-rule consensus trees that had the same topology. The strict consensus tree (Fig. 10) closely resembles the bootstrap support tree (Fig. 11A) with good support for the grouping ($C_{NV} + [C_{V1} + C_{V2}]$). The C_{NV} clade is strongly supported. In contrast, the C_{V1} clade collapses into a five branched unresolved politomy, but with reasonably good support for (*C. cheethami* + [*C. biporosa* + [*C. dominicana* + [*C. floridensis* + *C. colonensis*]]]). The C_{V2} clade retains its previous topology but is less well supported than the C_{NV} clade.

Twelve of the 48 characters informative for parsimony with a consistency index between 0.7–1.0 and the lowest frequency of change were chosen for their potential ability to distinguish morphologically defined clades. The basal node of the C_{NV} versus C_{V1} and C_{V2} clades reflects differences in area of the basal sectors (Asec). The basal node of the C_{V1} and C_{V2} clades is defined by differences in the size of the opesia of vicarious avicularia (VOw) as well as the shape and strength of the vicarious avicularium vibraculum and its opesia (VAwVAl, VAwoVAlo, RaVAwVw, RaVAloVAl, RaVAwoVAw, RaVAloVOl). Relevant characters for the *Discoporella* clade include those related to the hydrostatic mechanism (RaOlZl), colony strength (Zcp), autozooid size (Zw), and autozooid vibraculum strength (RaAwoAw).

We visually fit the strict consensus cladogram to the stratigraphic ranges of tropical American *Cupuladria* species (Fig. 10). Black circles represent data from this study. Gray circles indicate occurrences from O'Dea and Jackson, 2009. Open triangles indicate occurrences from Canu and Bassler (1923). The stratigraphic congruence within each of the groups of *Cupuladria* is largely consistent with cladogram topology. However, the hypothesized ancestry of the non-vicarious clade

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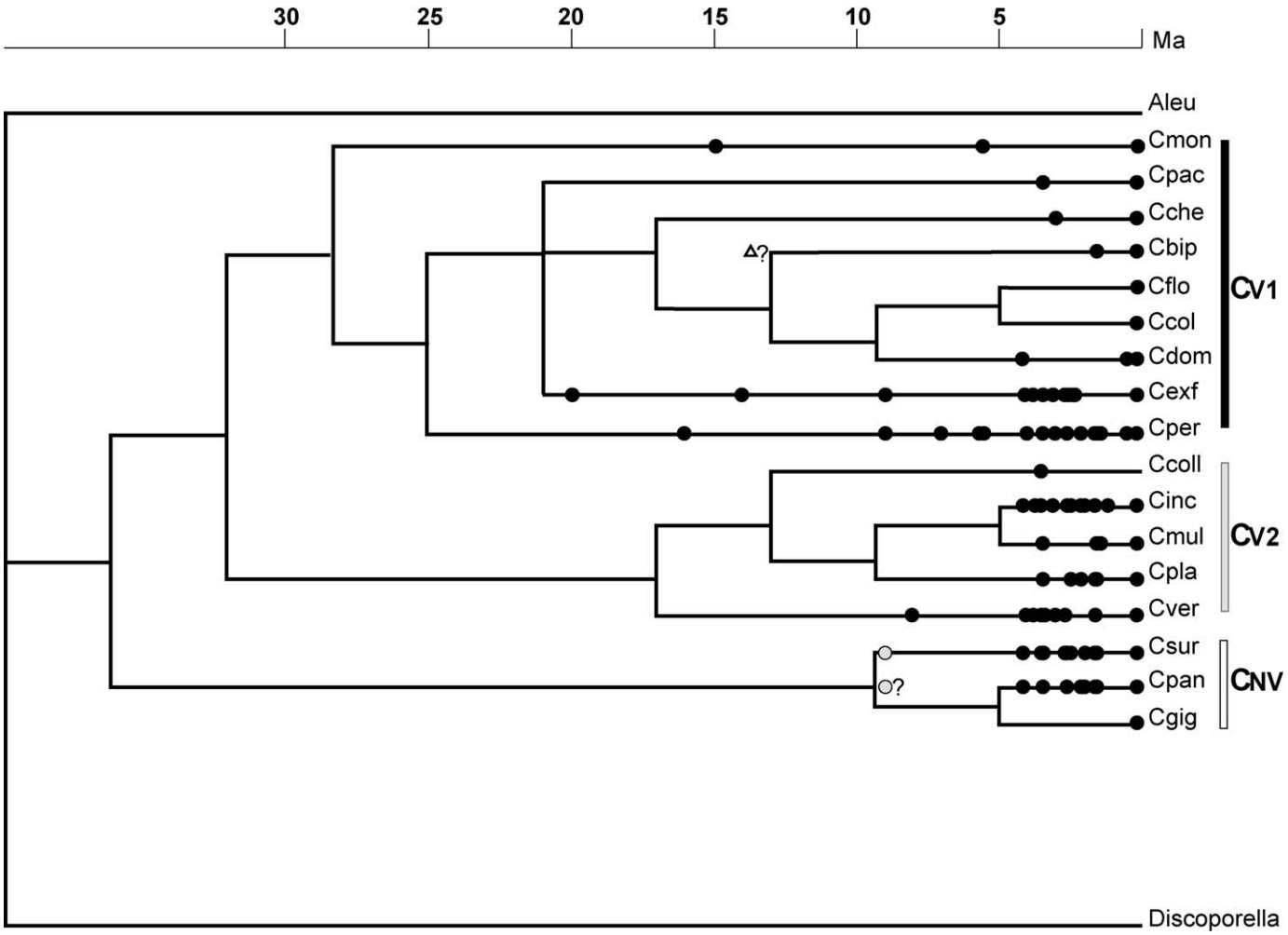

FIGURE *10*—Strict consensus tree cladogram visually fitted to the stratigraphic ranges of tropical American *Cupuladria* species.

of *Cupuladria* (C_{NV}) in relation to the two vicarious *Cupuladria* clades (C_{V1} and C_{V2}) is stratigraphically inconsistent.

DISCUSSION

Morphological characters.—Cupuladriid autozooids are responsible for feeding and reproduction whereas autozooidal vibracula serve to support and position the colony as well as to provide limited locomotion (Cook, 1965a, 1965b; McKinney and Jackson, 1989). The function of vicarious avicularia is difficult to assess since they have not been observed in motion, however our personal observations of their placement in damaged portions of colonies and the shape of their setae suggests they may be involved in regeneration and defense (see also Cook, 1965b). All of the characters with a consistency index of 1 are related to regeneration, defense, the hydrostatic mechanism of the autozooids, and the strength of the colony and autozooids vibracula.

Characters related to vicarious avicularia were especially useful to discriminate species and delineate cladistic relationships among the vicarious *Cupuladria* clades. Avicularia have evolved many times across a broad spectrum of cheilostome taxa (Winston, 1984; Cheetham et al., 2006) and bryozoologists distinguish several types based on their position and shape (Winston, 1984). Vicarious avicularia in cupuladriids replace an autozooid in position, and they appear to arise by intramural budding in both the C_{V1} and C_{V2} clades. In the former, they have been observed in proximity to damaged portions of colonies where they may act to maintain colonial integrity. In contrast, in C_{V2} they appear during early astogeny and are generally restricted to the central part of the colony.

Other morphological characters of particular interest include the area of basal sectors (Asec) that has a consistency index of only 0.7 but a high coefficient in the final discriminant analysis of vicarious *Cupuladria* species (DA11). The shape of the basal sectors also changes noticeably from rectangular in the C_{V1} clade to radial in the C_{V2} clades (except *C. veracruxiensis*) and the C_{NV} clade. In general, the basal sectors are also related in *Cupuladria* to occurrence of kenozooidal chambers. These change in the number of internal layers from 1 to 2 in $C_{V1,}$ 3 to 6 in $C_{V2,}$ and just 1 in C_{NV} (Herrera-Cubilla et al., 2006). Both basal sectors and kenozooidal chambers are absent in *Discoporella*.

The ratio of opesia-autozooid length (RaOlZl) is important cladistically because *Discoporella* autozooids have a nearly complete cryptocyst except for a number of opesiules along each side, while those in *Cupuladria* have a wide open front. This difference in cryptocyst development and size of opesia may be related to egg size, which is larger in *Cupuladria* than in *Discoporella* (Cook, 1965b). Recent measurements of the diameter of the embryos of *C. exfragminis* and *D. marcusorum* yielded 0.223 mm and 0.157 mm (Ostrovsky et al., 2009; figs. 2, 4, respectively). However we did not find significant difference in autozooid area between the species of *Cupuladria* and

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Discoporella used in this work (N=25, Mann-Whitney U=67, Z=–0.058, p=0.954). Differences in Zl and Zw were also not significant. Other useful characters within the C_{NV} and *Discoporella* clades are: autozooid size (Zw), closure plates in autozooids (Zcp), which in *Discoporella* occurs at the center of the colony, and the strength of the autozooidal vibraculum (RaAwoAw).

Only three of the nine characters uninformative for parsimony were among the characters with highest coefficient in DAs for species discrimination. These include Aw, AwAl, and RaAloAl in DA2 done to further resolve the non-vicarious *Cupuladria* plus *Discoporella* clusters. This last character was also among those with highest coefficient in the final DA11 performed to classify vicarious *Cupuladria* colonies.

Cladistic analyses of morphological versus molecular characters.—The results of both the discriminant (Figs. 4–7) and cladistic (Figs. 9–11) analyses yielded a subdivision of tropical American cupuladriids which is in good agreement with two previous molecular phylogenetic analyses with respect to separation of genera and major clades within genera (Dick et al., 2003; Jagadeeshan and O'Dea, 2012). There are discrepancies, however, in the resolution of topologies between the two types of analyses that appear to reflect differences in the numbers of taxa studied. We examined 25 species whereas the two previous studies included 10 and 14 species respectively. For example, we analyzed three species within the C_{NV} clade whereas Dick et al. (2003, fig. 4) analyzed only *C. surinamensis*, Cadée, 1975, that appeared at the basal node of the *Discoporella* clade. The topology of this clade was better resolved by Jagadeeshan and O'Dea (2012, fig. 2) who also included *C. gigas* in their analysis. Similarly, Jagadeeshan and O'Dea sampled only *C. incognita*, Herrera-Cubilla et al. 2006, from the C_{V2} clade resulting in its placement as a sister species of *C. exfragminis*, whereas the phylogeny based on morphological characters placed these two species in two distinct clades.

Correspondence between phylogeny and the fossil record.—The relationships among sister clades in both the molecular and morphologically based phylogenies are stratigraphically incongruent by 20 Ma (compare Figs. 10 and 11). This is despite quantitative estimates of the probability of completeness of the fossil record of nearly 100 percent and near maximum probability of the occurrence of ancestors of PA=0.5 (Foote, 1996; Cheetham and Jackson, 1998, 2000). Resolution of this issue will require cladistic reexamination of eight or more Eocene to Recent principally eastern Atlantic species traditionally assigned to *Cupuladria* but intermediate in a number of characters between *Discoporella* and *Cupuladria* (Lagaaij, 1963; Cook, 1965a, 1965b, 1985; Boardman et al., 1970; Cadée, 1975). As we have seen, the oldest cupuladriid known (NHM D41382-4, Bende Ameki, Nigeria, middle Eocene) resembles *Cupuladria* on the frontal surface in lacking the development of a cryptocyst, denticles, or spines, but possesses tubercles and grooves on the basal surface of the colony similar to *Discoporella* (Fig. 8). The other seven species also have basal grooves with tubercles and varyingly complete development of a cryptocyst. All of them also appear to lack vicarious avicularia, which is consistent with our results (Fig. 10).

In contrast, the fossil record of the C_{V1} clade extends back to the early Miocene Chipola Formation along the northern coast of the Gulf of Mexico and that of the C_{V2} clade to the (?) late Miocene Paraje Solo Formation, Veracruz, Mexico (Fig. 10). Diversification was slow until the early Pliocene, although this may be at least partially an artifact of the sparseness of the Miocene fossil record as for other well-studied clades (Jackson and Cheetham, 1994; Cheetham and Jackson, 1995). The fossil record of eastern Pacific cupuladriids is also scanty and unstudied. Nevertheless, it is of great interest that the only two recent species of *Cupuladria* encountered in our very extensive eastern Pacific dredge samples have a Caribbean fossil record that extends back to the Pliocene for *C. pacificiensis* and to the early Miocene for *C. exfragminis* (Fig. 10).

This apparent lack of a uniquely eastern Pacific clade of *Cupuladria* has two important implications. First, the radiation of *Cupuladria* in tropical America appears to have occurred almost entirely within the Caribbean and Gulf of Mexico, as was also the case for the cheilostomes *Metrarabdotos* and *Stylopoma*. Second, the two pairs of most closely related species on opposite sides of the Isthmus of Panama diverged within the Caribbean, long before the final isolation of the two oceans 3.5 Ma, and became allopatric only after the two Pacific species had finally gone extinct within the Caribbean. *Discoporella marcusorum* and *D. cookae* exhibit a similar evolutionary history (O'Dea and Jackson, 2009). Extinction in both cases did not occur until the late Pliocene, about 2 Ma after final closure of the Seaway and the collapse in Caribbean planktonic productivity (O'Dea et al., 2007; O'Dea and Jackson, 2009). The predominantly clonal life histories of eastern Pacific species of cupuladriids are closely tied to the high productivity in the eastern Pacific (O'Dea et al., 2004, 2008).

SYSTEMATIC PALEONTOLOGY

Order CHEILOSTOMATIDA Busk, 1852
Suborder FLUSTRINA Smitt, 1867
Superfamily CALLOPOROIDEA Norman, 1903
Family CALLOPORIDAE Norman, 1903
Genus ANTROPORA Norman, 1903
ANTROPORA LEUCOCYPHA Marcus, 1937

1937 *Crassimarginatella leucocypha* MARCUS, p. 46.
1982 *Antropora leucocypha* (Marcus); WINSTON, p. 123.

Description.—Colony encrusting gastropod shells, pink to magenta in color, unilaminar to bilaminar. Autozooids irregularly oval, cryptocyst very narrow distally, slightly wider and crenulated proximally. Triangular spaces between autozooids, avicularia not observed and ovicell endozooidal.

Material.—USNM593679-593681, La Guarda channel. See Appendix 2 for morphological measurements.

Occurrence.—La Guarda channel, Las Perlas Archipelago, Gulf of Panama, Panama.

Remarks.—*Antropora leucocypha* was originally described from the Atlantic, but is very similar to the eastern Pacific (EP) species *A. tincta* from which can only be distinguish by the frequency of kenozooids, size of avicularia and shape of the avicularian mandible (Cook, 1968; Winston, 1982). According to PPP and DR records, its stratigraphic range is from middle Miocene to the present with occurrence in both the western Atlantic and Pacific.

Family CUPULADRIIDAE Lagaaij, 1952
Genus CUPULADRIA Canu and Bassler, 1919
CUPULADRIA MONOTREMA (Busk, 1884)

1994 *Cupuladria monotrema* (Busk), COOK AND CHIMONIDES, p. 261.

Description.—Colonies are conical, with maximum observed diameter 6.8 mm, the central area of the colony is occupied mostly by vicarious avicularia up to the fifth astogenetic generation, but occasionally autozooids are present. Vicarious avicularia opesia auriform, and gymnocyst well developed. Cryptocyst of autozooids in central area straight sided, lateral septula not visible, while cryptocyst of autozooids in periphery descend steeply. The autozooids are hexagonal in shape, and the

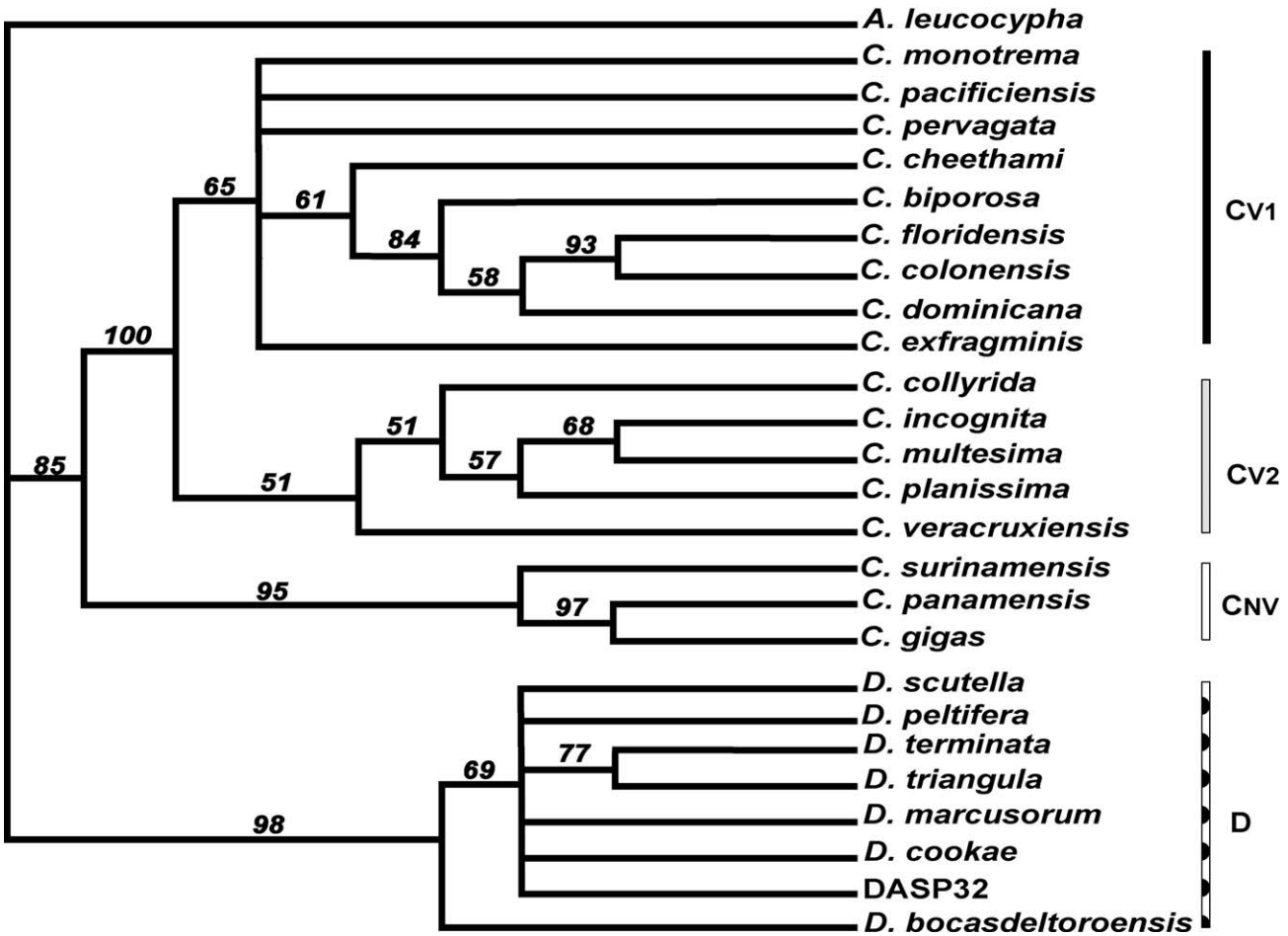

FIGURE 11—Comparison between molecular versus morphological phylogenies of Cupuladriidae. A, this study, bootstrap support tree, based on 1000 pseudoreplicates of the original cladistic data.

basal sectors are rectangular with one but occasionally two pores per basal sector.

Material.—USNM593682, PPP1284; USNM593683, NMB15962; USNM593684–593688, Guyana shelf, Luymes CICAR 23 st. 54. See Appendix 2 for morphological measurements.

Occurrence.—?Middle Miocene, east Deer I., Bocas del Toro, Panama. Messinian to Zanclean, Gurabo Formation, Rio Gurabo, Dominican Republic. Recent, Guyana shelf, Guyana.

CUPULADRIA PACIFICIENSIS Herrera-Cubilla et al., 2006
Figures 12, 13

1950 *Cupuladria canariensis* OSBURN, p. 33, pl. 3, figs. 2, 3 (in part?).

Description.—Colonies conical, with a maximum observed diameter of 7.6 mm, the central area of the colony is occupied mostly by autozooids. In general cryptocyst of autozooids descend moderately but septula still visible, autozooids are hexagonal in shape. Vicarious avicularia are scattered through the zone of astogenetic change (Herrera-Cubilla et al., 2006), with gymnocyst well developed, opesia auriform in shape. The basal sectors are rectangular with 3–6 pores per basal sector. In the central area of the colony of few fossil specimens have been observed autozooids and vicarious avicularia with closure plates, and autozooids whose cryptocysts are thickened by secondary calcification.

Types.—Hypotype USNM542592, PPP334.

Material.—USNM593689–593694, PPP365, 635, 639, 2038, 2026; USNM593695, GM98–69, 9°18.6′ Lat., 80°20′ Lon., Gulf de los Mosquitos, Bocas del Toro, Panama; USNM593696, SB95–9, 9°31′ Lat., 78°44.3′ Lon., San Blas, Panama; USNM593697, SB95–11, 9°30.2′ Lat., 78°54.9′ Lon., San Blas, Panama; USNM593698–593699, SB95–20, 9°36.9′ Lat., 78°59.2′ Lon., San Blas, Panama; USNM593700, GC97–65, 7°10.9′ Lat., 81°39.9′ Lon., Gulf of Chiriqui, Panama; USNM593701, GP97–1, 8°36.1′ Lat., 78°34.9′ Lon., Gulf of Panama, Panama; USNM593702, GP97–9, 7°32.8′ Lat., 78°10.6′ Lon., Gulf of Panama, Panama; USNM593703–593704, BT98–19, 9°22.5′ Lat., 82°10′ Lon., Bocas del Toro, Panama; USNM523170–523172 designated by Herrera-Cubilla et al., 2006.

See Appendix 2 for morphological measurements.

Occurrence.—Early Pliocene, Cayo Agua Formation, Punta Norte to Punta Tiburon, Bocas del Toro, Panama. Late Pliocene, Escudo de Veraguas Formation, northern coast, Bocas del Toro, Panama; late Pliocene, Moin Formation, Lomas del Mar, eastern sequence, Limon, Costa Rica; late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica. Recent, Gulf of Panamá and Chiriquí EP.

Remarks.—The vicarious avicularia vibracula opesia width (VAwo) are less than 0.1 mm and the ratio autozooid vibracula opesia length-autozooid vibracula length (RaAloAl) less than 0.75 mm like in *C. exfragminis*, *C. biporosa* and *C. cheethami*. Three Caribbean specimens of late Pliocene age were discriminated as *C. pacificiensis* probably because the process of extinction did not occur until that time (see Discussion). However

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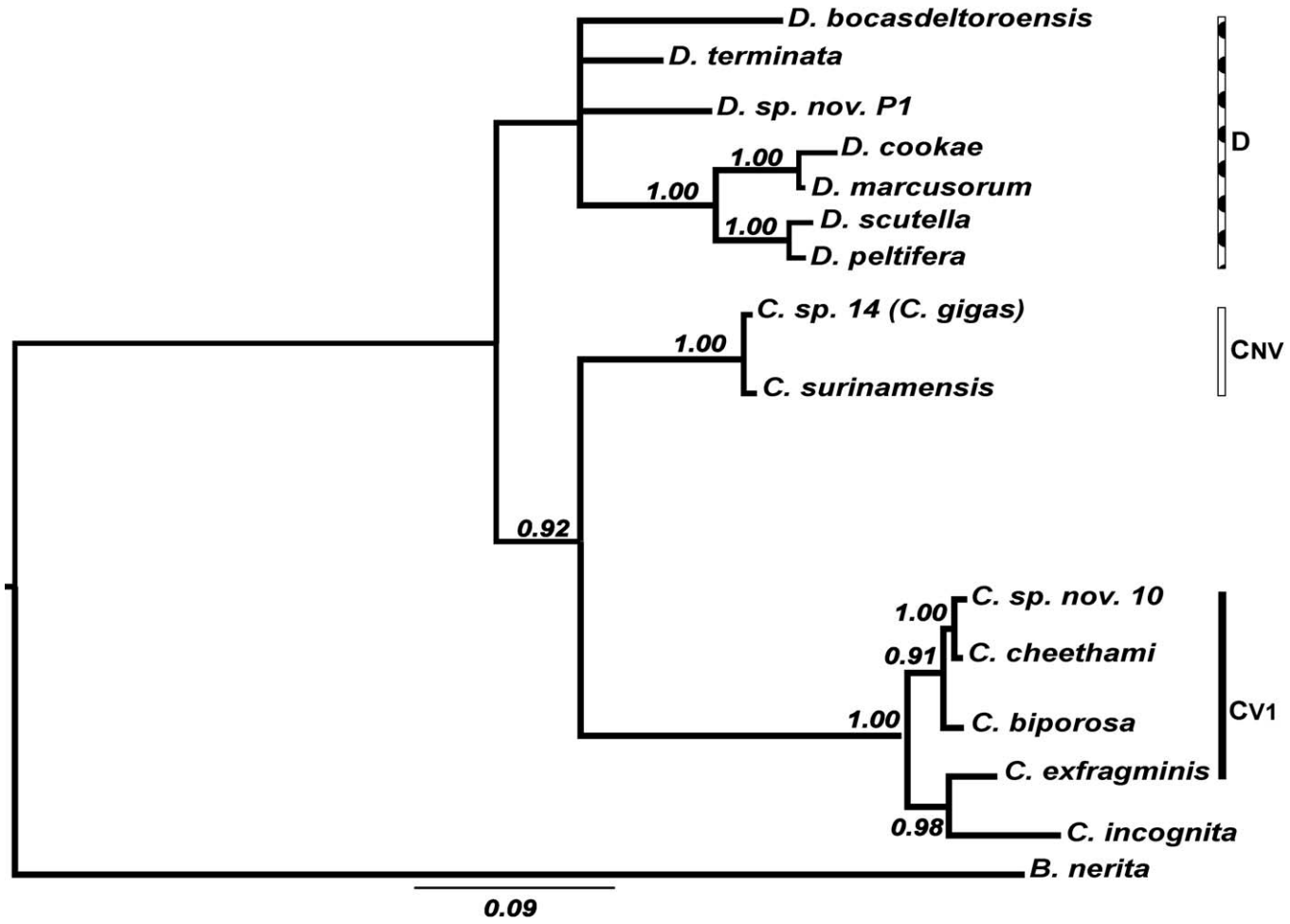

FIGURE 11—B, Bayesian inference phylogeny (Jagadeeshan and O'Dea, 2012).

five recent specimens could not be discriminated from their cognate species from the opposite ocean, a difficulty also encountered in a previous study (Herrera-Cubilla et al., 2006).

CUPULADRIA EXFRAGMINIS Herrera-Cubilla et al., 2006
Figures 14–19

1950 *Cupuladria canariensis* OSBURN, p. 33, pl. 3, figs. 2, 3 (in part?).

Description.—Colonies have an irregular conical shape, with a maximum observed diameter of 9.3 mm, the central area of the colony is occupied mostly by autozooids. In general cryptocyst of autozooids descend moderately but septula still visible, autozooids are hexagonal. Vicarious avicularia are scattered through the zone of astogenetic change with gymnocyst well developed, opesia auriform in shape, and like in *C. pacificiensis* VAwo are less than 0.1 mm. The basal sectors are rectangular with 2–5 pores per basal sector. Closure plates are absent in autozooids and vicarious avicularia in all specimens examined. One of five specimens from the Chipola formation possesses a few autozooids thickened by secondary calcification.

Types.—Hypotypes USNM542593 NMB17830; USNM542594, PPP204; USNM542595, PPP1306.

Material.—USNM593705, Chipola Formation, Shoal River, FL, U.S.A; USNM593706–593712, PPP1306, 350, 345, 204, 69, 65; USNM593713, NMB18105; USNM593714, Solarte I., western Tip, Bocas del Toro, Panama; USNM593715–USNM593716, PPP68, 2169; USNM593717, Shell creek De Soto Co., FL, U.S.A; USNM593718, Bastimentos I., Bocas del Toro, Panama; USNM593719–593720, NMB18388, 18084; USNM593721, PPP3257; USNM593722, GP97–1, 8°36.1′ Lat., 78°34.9′ Lon., Gulf of Panama, Panama; USNM593723–593724, GC97–89, 8°0.03′ Lat., 82°2.3′ Lon., Gulf of Chiriqui, Panama; USNM593725, Caroline Sta. 56, Sto. Domingo, Dominican Republic; USNM523173–523175 designated by Herrera-Cubilla et al. (2006).

Other material.—UF44633, Chipola formation, Tenmile crek 02, Florida U.S.A; UF53535, Richardson Rd. Shell Pit 01B, Florida, U.S.A; UF47715, 49626 Macasphalt Shell Pit, Florida, U.S.A.; UF51907, 27564 Bermont Formation, Leisey Shell Pit, Florida, U.S.A.; LSUMG-I9314, E Destin FL. U.S.A. (Gulf of Mexico); MHNMC IB88, 11°19′86″ Lat., 74°5′ 28″ Lon. 20 m depth, Caribe, Colombia; MHNMC IB96, 9°41′47″ Lat., 76°5′71″ Lon., 71 m depth, Caribe, Colombia.

See Appendix 2 for morphological measurements.

Occurrence.—Early Miocene, Chipola Formation, Tenmile Creek 02, Florida, U.S.A. middle Miocene, Chipola Formation, Shoal River, Florida, U.S.A. Late Miocene, Gatun Formation, Sabanita to Payardi, Colon, Panama. Early Pliocene, Cayo Agua Formation, Punta Piedra Roja, western sequence, Bocas del Toro, Panama. Late Pliocene, Solarte I., western tip, Bocas del Toro, Panama; late Pliocene, Cayo Agua Formation, Punta Norte to Punta Tiburon, Bocas del Toro Panama, late Pliocene, Escudo de Veraguas Formation, northern coast, Bocas del Toro, Panama;

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late Pliocene, Bastimentos I., Bocas del Toro Panama; late Pliocene, Rio Banano Formation, Limon, Costa Rica; late Pliocene, Moin Formation, Pueblo Nuevo, Limon, Costa Rica, late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica; late Pliocene to early Pleistocene, Macasphalt Shell Pit, Florida, U.S.A. Pliocene, Tamiami Formation, Richardson Rd. Shell Pit 01B, Florida, U.S.A.; Pliocene, Shell creek, DeSoto Co., Florida, U.S.A. Pleistocene, Bermont Formation, Leisey Shell Pit, Florida, U.S.A.; Pleistocene, Bermont Formation, South Bay 04, Florida, U.S.A. Recent Gulf of Panama and Chiriqui EP.

Remarks.—Like in *C. pacificiensis* four Caribbean specimens from late Pliocene to Pleistocene were discriminated as *C. exfragminis*, probably for the same reasons pointed above. As well as four Recent specimens from the same region, finding the same difficulty to discriminate them from their cognate species.

Cupuladria pervagata new species
Figures 20, 21

Diagnosis.—Autozooids have the ratio autozooid vibracula opesia length-autozooid vibracula length (RaAloAl) $\geq$0.75 mm. Colonies are conical, average height diameter ratio 0.19 mm, average diameter 5.7 mm.

Description.—Colonies are conical, with maximum observed diameter of 7.7 mm. The central area of the colony is formed mostly by autozooids and in the majority of the colonies examined their cryptocysts are not thickened by secondary calcification. In general cryptocyst of autozooids descend moderately but septula still visible. Vicarious avicularia are scattered throughout the zone of astogenetic change with gymnocyst well developed, opesia auriform in shape and VAwo less than 0.1 mm (for details see text). Basal sectors are rectangular or irregular in shape with 2–5 pores per sector.

Etymology.—Pervagata, Latin "widespread, common" with reference to its widespread geographical and stratigraphical distribution.

Types.—Holotype, USNM542565, BT98–19, 9°22.5′ Lat., 82°10′ Lon., Bocas del Toro; Panama; Paratypes: USNM542566, CMN95–5, 14°30′ Lat., 82°29′ Lon., Cayos Miskitos, Nicaragua; USNM542567, PPP709; USNM542568, PPP196; USNM542569, PPP1306; USNM542570, NMB16942.

Material.—USNM593726, NMB16935; USNM593727, PPP1306; USNM593728–593730, NMB17175, 15863, 15864; USNM593731–593736, PPP379, 350, 334, 709, 69, 311; USNM593737, NMB18105; USNM593738, PPP370, USNM593739–593740, 593742, Bowden Formation, Jamaica; USNM593741, Puerto Limon, Costa Rica; USNM593743–593747, PPP634, 2038, 2024, 631, 944; USNM593748, GM98–90, 8°57.4′ Lat., 80°50′ Lon., Bocas del Toro, Panama; USNM593749–593750, BT98–19, 9°22.5′ Lat., 82°10′ Lon., Bocas del Toro; Panama; USNM593751–593752, Eolis station FL U.S.A.; USNM593753, CMN95–5, 14°30′ Lat., 82°29′ Lon., Cayos Miskitos, Nicaragua; USNM593754, CMN95–11, 14°29′ Lat., 82°47.4′ Lon., Cayos Miskitos, Nicaragua; USNM593755, PB99–225, 9°39.1′ Lat. 79°37.9′ Lon., Colon, Panama.

Other material.—BZ5603 Basal Moin Formation Puerto Limon, Costa Rica; UF57526, Caloosahatchee Formation, Florida, U.S.A.; UF51907 Bermont Formation, South Bay 04, Florida, U.S.A.; MHNMC–IB88, 11°19′86″ Lat., 74°5′28″ Lon., Caribbean Colombia.

See Table 4 for morphological measurements.

Occurrence.—Middle Miocene, Baitoa Formation, Rio Yaque Norte, Dominican Republic. Late Miocene, Gatun Formation, Sabanita to Payardi, Colon, Panama; late Miocene, Cercado Formation, Rio Mao, Dominican Republic; Messinian to Zanclean, Gurabo Formation, Rio Gurabo, Dominican Republic. Early Pliocene, Shark Hole Point Formation, Valiente Peninsula, Bruno Bluff to Plantain Cay, Bocas del Toro, Panama; early Pliocene, Cayo Agua Formation, Punta Piedra Roja, western sequence, Bocas del Toro, Panama; early Pliocene, Cayo Agua Formation, Punta Norte, western side, Bocas del Toro, Panama; early Pliocene, Cayo Agua Formation, Punta Norte to Punta Tiburon, Bocas del Toro, Panama. Late Pliocene, Escudo de Veraguas Formation, northern coast, Bocas del Toro, Panama; late Pliocene, Cayo Agua Formation, Bocas del Toro, Panama; late Pliocene, Solarte Island., western tip, Bocas del Toro, Panama; late Pliocene, Rio Banano Formation, Santa Rita, Limon, Costa Rica; late Pliocene, Moin Formation; Lomas del Mar, eastern sequence, Limon, Costa Rica; late Pliocene, Moin Formation, Pueblo Nuevo Cemetery, Limon, Costa Rica; late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica. Pliocene, Puerto Limon, Costa Rica; Pliocene, basal Moin Formation, Puerto Limon, Costa Rica; Pliocene, Bowden

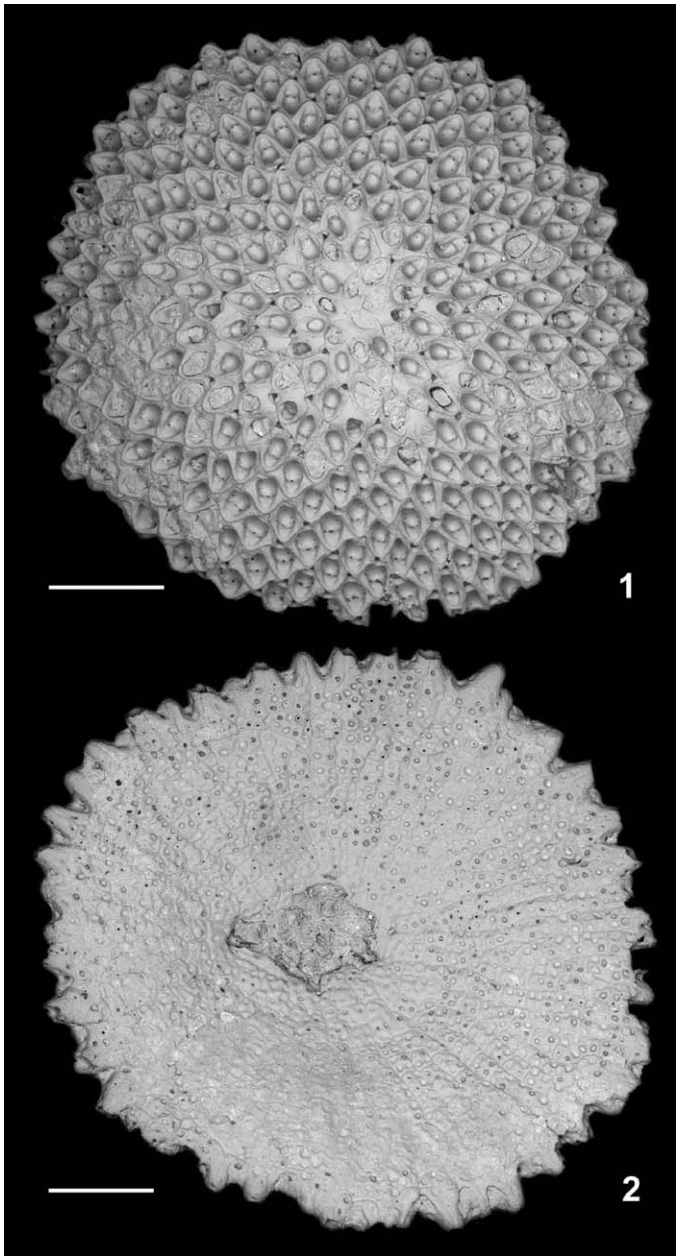

Figure *12*—*Cupuladria pacificiensis*. *1*, *2*, hypotype, USNM542592, PPP334, Cayo Agua Formation, early Pliocene, Bocas del Toro, Panama: *1*, colony frontal view; *2*, colony basal view. Scale bar=1 mm.

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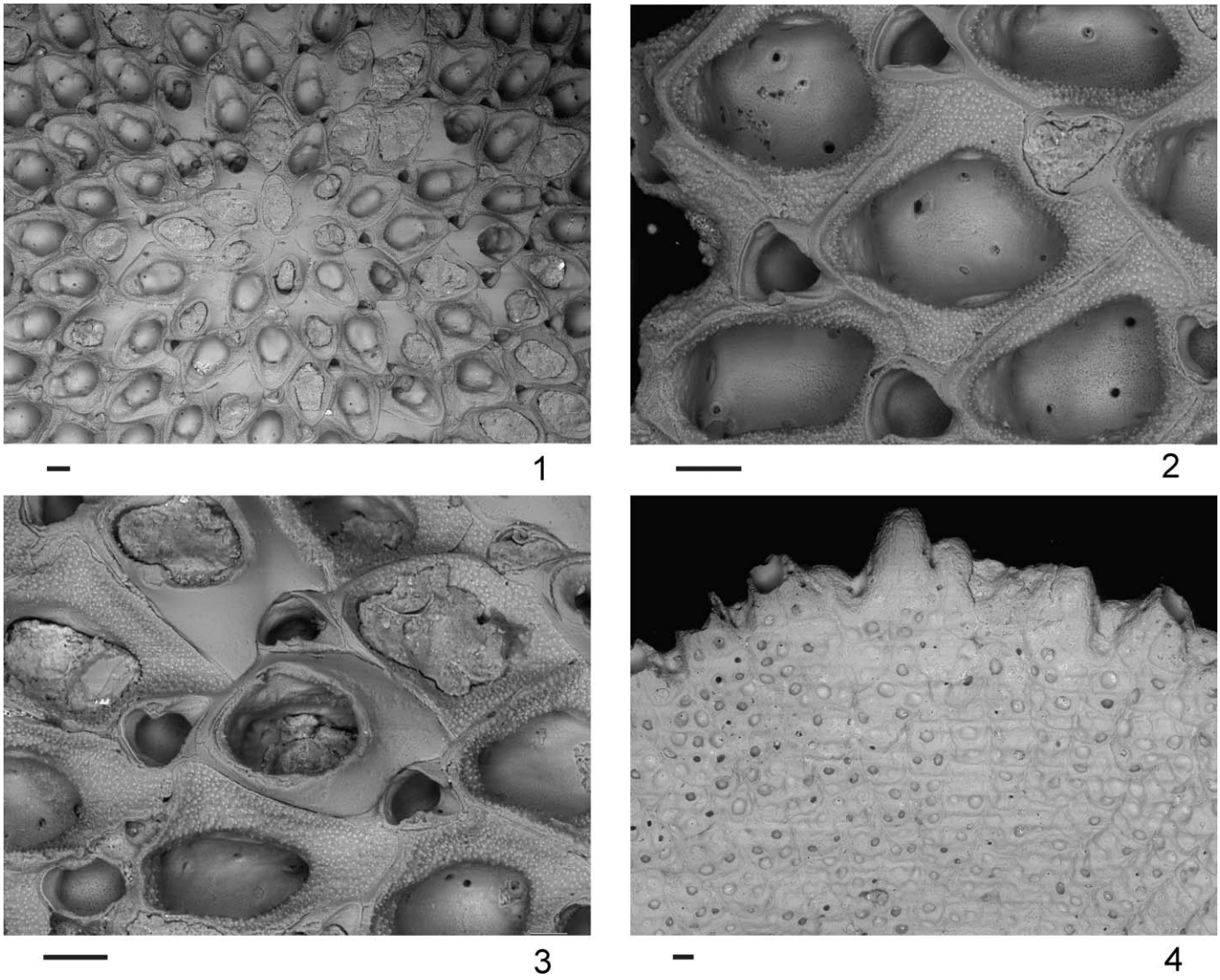

FIGURE 13—*Cupuladria pacificiensis*. *1–4*, hypotype, USNM542592, PPP334, Cayo Agua Formation, early Pliocene, Bocas del Toro, Panama: *1*, colony center showing autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

Formation, Jamaica. Pleistocene, Caloosahatchee Formation, Florida, U.S.A.; Pleistocene, Bermont Formation, south bay 04, Florida, U.S.A. Recent from Florida to Caribbean Colombia.

Remarks.—*Cupuladria pervagata* has a widespread stratigraphic range and geographic distribution in the Caribbean Neogene, and is part of the C_{V1} group. *Cupuladria pervagata* is morphologically similar to *C. pacificiensis* and *C. biporosa*. Its colony size is similar to *C. pacificiensis* but is flatter in shape. Recent specimens of both species have a central area of the colony formed mostly by autozooids whose cryptocysts are not thickened by secondary calcification, but this feature has been observed only sporadically in fossils. Autozooids and vicarious avicularia with closure plates also occur sometimes in fossil specimens, as has been observed in other species of the C_{V1} and C_{V2} clades (see Table 4 and Appendix 2). Autozooids and vicarious opesia size and basal sector area are similar in the two species, although the number of pores per sector is 3–6 in C. *pacificiensis* versus 2–5 in *C. pervagata*. The main difference between the two species is in the ratio of the length of the opesia of autozooid vibracula to the length of autozooid vibracula (RaAloAl). This character showed a high coefficient to discriminate species in DA11 (see above). The ratio for *C. pervagata* is $\geq$0.75 mm (similar to *C. monotrema*, *C. dominicana*, *C. colonensis* and *C. floridensis*) versus 0.67 for *C. pacificiensis*. This feature may be related to the strength of the vibracula mechanism of living cupuladriid colonies, which show a high degree of coordination to maintain them above the sediment surface and to right themselves when turned upside down (Cook, 1963; Cook and Chimonides, 1978; Winston, 1988). *Cupuladria pervagata* corresponds to C. sp. nov. aff. biporosa in the PPP collection of cupuladriids from the SWC analyzed in O'Dea and Jackson, 2009.

CUPULADRIA CHEETHAMI Herrera-Cubilla et al., 2006

Description.—Colonies are conical, with maximum observed diameter of 9.1 mm. The central area of the colony is formed mostly by autozooids. In general cryptocyst of autozooids descend moderately but septula still visible. Vicarious avicularia are scattered throughout the zone of astogenetic change with gymnocyst well developed, opesia auriform in shape and VAwo less than 0.1 mm (for details see text). Autozooids are hexagonal.

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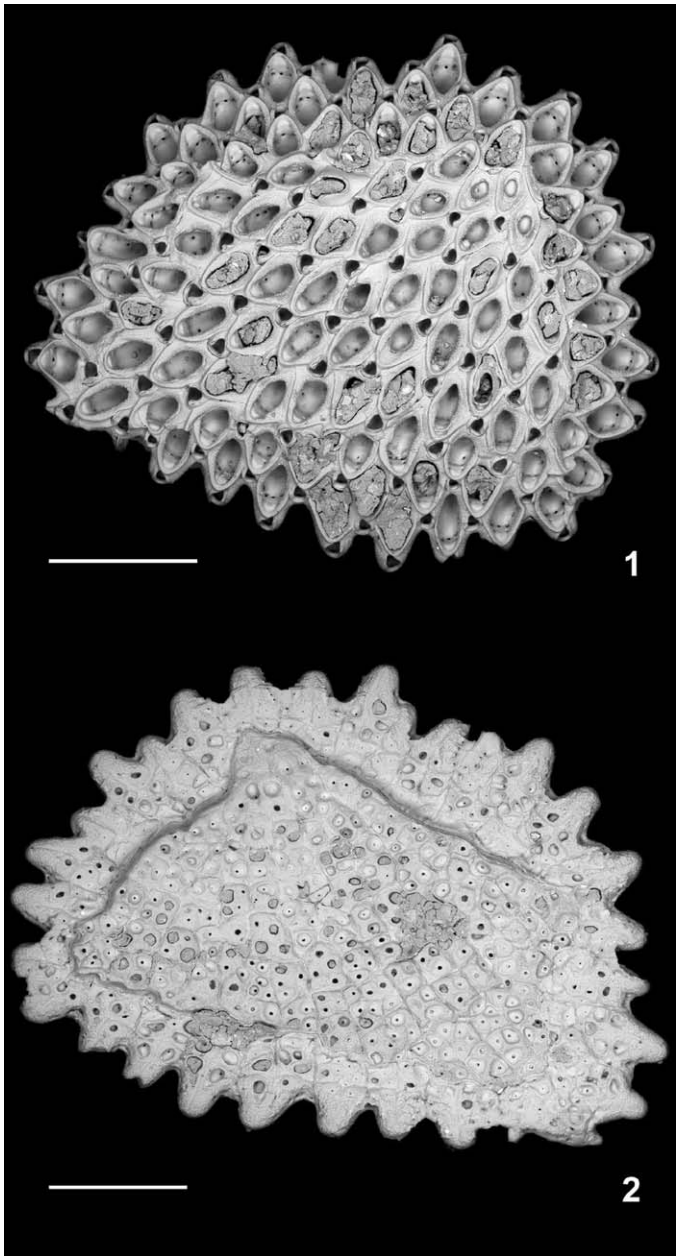

FIGURE *14*—*Cupuladria exfragminis*. *1*, *2*, UF44633, Chipola Formation, early Miocene, Florida, U.S.A.: *1*, colony frontal view; *2*, colony basal view. Scale bar=1 mm.

The autozooids and vicarious avicularia of this species are notably longer than any other species in the C_{V1} clade. Basal sectors are rectangular in shape with 3–4 pores per sector. In none of the specimens examined have been observed autozooids and vicarious avicularia with closure plates.

Material.—USNM593756, PPP210; USNM593757, CMN95–9, 14°42′ Lat., 82°54′ Lon., Cayos Miskitos, Nicaragua; USNM523167–523169 designated by Herrera-Cubilla et al., 2006. See Appendix 2 for morphological measurements.

Occurrence.—Late Pliocene, Solarte Island western tip, Bocas del Toro, Panama. Recent, Panama and Central America.

CUPULADRIA BIPOROSA Canu and Bassler, 1923

1923 *Cupuladria biporosa* CANU AND BASSLER, p. 9, pl. 47, figs. 1, 2, Miocene, Santo Domingo.

1965b *Cupuladria biporosa* (Canu and Bassler), COOK, p.203, pl. 1, figs. 2, 4, 6.

Description.—Colonies are conical, with maximum observed diameter of 12 mm. The central area of the colony is formed mostly by autozooids that are thickened by secondary calcification, although not completely closed, cryptocyst straight sided and septula not visible. Vicarious avicularia are scattered throughout the zone of astogenetic change with gymnocyst well developed, opesia auriform in shape and VAwo less than 0.1 mm (for details see text). Autozooids are hexagonal. Basal sectors are rectangular in shape with 3–5 pores per sector. In none of the specimens examined have been observed vicarious avicularia with closure plates.

Material.—USNM593758, PPP963; USNM593759, BT99–130, 9°28.43′ Lat., 82°20′ Lon., Bocas del Toro, Panama; USNM593760–593761, LC98–29, 9°9.4′ Lat., 81°00′ Lon., Laguna de Chiriqui, Bocas del Toro, Panama; USNM593762–593763, SB95–18, 9°31.9′ Lat., 78°56.5′ Lon., San Blas, Panama; USNM593764, Pepperfish key, Gulf of Mexico, 29°23′00″ Lat.; 83°41′45″ Lon. U.S.A.

See Appendix 2 for morphological measurements.

Occurrence.—Late Pliocene, Moin Formation, Lomas del Mar, eastern sequence, Limon, Costa Rica. Recent, from Gulf of Mexico to Panama.

Remarks.—Seventy percent of the colonies identified as *C. biporosa* have the cryptocyst of the autozooids of the central area thickened by secondary calcification. Cook (1965b) was the first to discuss this feature, commenting that thickening was observed sometimes in colonies of this species. We have also sporadically observed thickening (one to two colonies) in fossil specimens of: *C. pacificiensis*, *C. exfragminis*, and *C. pervagata*; and in one recent specimen of *C. dominicana*.

CUPULADRIA FLORIDENSIS new species
Figures 22, 23

Diagnosis.—Autozooids have the largest ratio autozooid vibracula opesia length-autozooid vibracula length (RaAloAl) of 0.78 mm; and vicarious the largest ratio vicarious avicularia vibracula opesia length-vicarious avicularia vibracula length (RaVAloVAl) of 0.76 mm in average. Colonies are large with a dome shape, average height to diameter ratio 0.28 mm, average diameter 13.4 mm.

Description.—Colonies have a maximum observed diameter of 18.4 mm. The central area of the colony is formed mostly by autozooids, cryptocyst descend moderately but septula still visible. Vicarious avicularia are scattered throughout the zone of astogenetic change with gymnocyst well developed, opesia auriform in shape, and VAwo $\geq$0.1 mm (for details see text). Autozooids are hexagonal. Basal sectors are rectangular in shape with 3–5 pores per sector.

Etymology.—The name floridensis refers to state of Florida U.S.A., where the first specimens were found.

Types.—Holotype USNM542571, New Orleans off coast, 28°32′ Lat., 93°24′42″ Lon., LA U.S.A.; Paratypes: USNM542572 Dry Tortugas, Florida keys, FL, U.S.A.; USNM542573 Nassau, Bahamas; USNM542574 Punta San Blas, Colon, Panama.

Material.—USNM593765–593767, Dry Tortugas, Florida keys, FL, U.S.A.; USNM593768–593769, New Orleans off coast, 28°32′ Lat., 93°24′42″ Lon., LA, U.S.A.; USNM593770, Albatross Station 2823.

Other material.—MCZ100101, Florida keys, 25°13′18″ Lat., 80°12′42″ Lon., FL. U.S.A.; LSUMG-I9314, E Destin, Gulf of Mexico, FL, U.S.A.; NHM.1971.3, 18°41′60″ Lat., 110°57′ 0″ Lon. Mexico; MHNMC IB88, 11°19′ 86″ Lat., 74°5′ 28″ Lon., Caribbean, Colombia; MHNMC IB96, 9°41′47″ Lat., 76°5′71″ Lon., Caribbean, Colombia.

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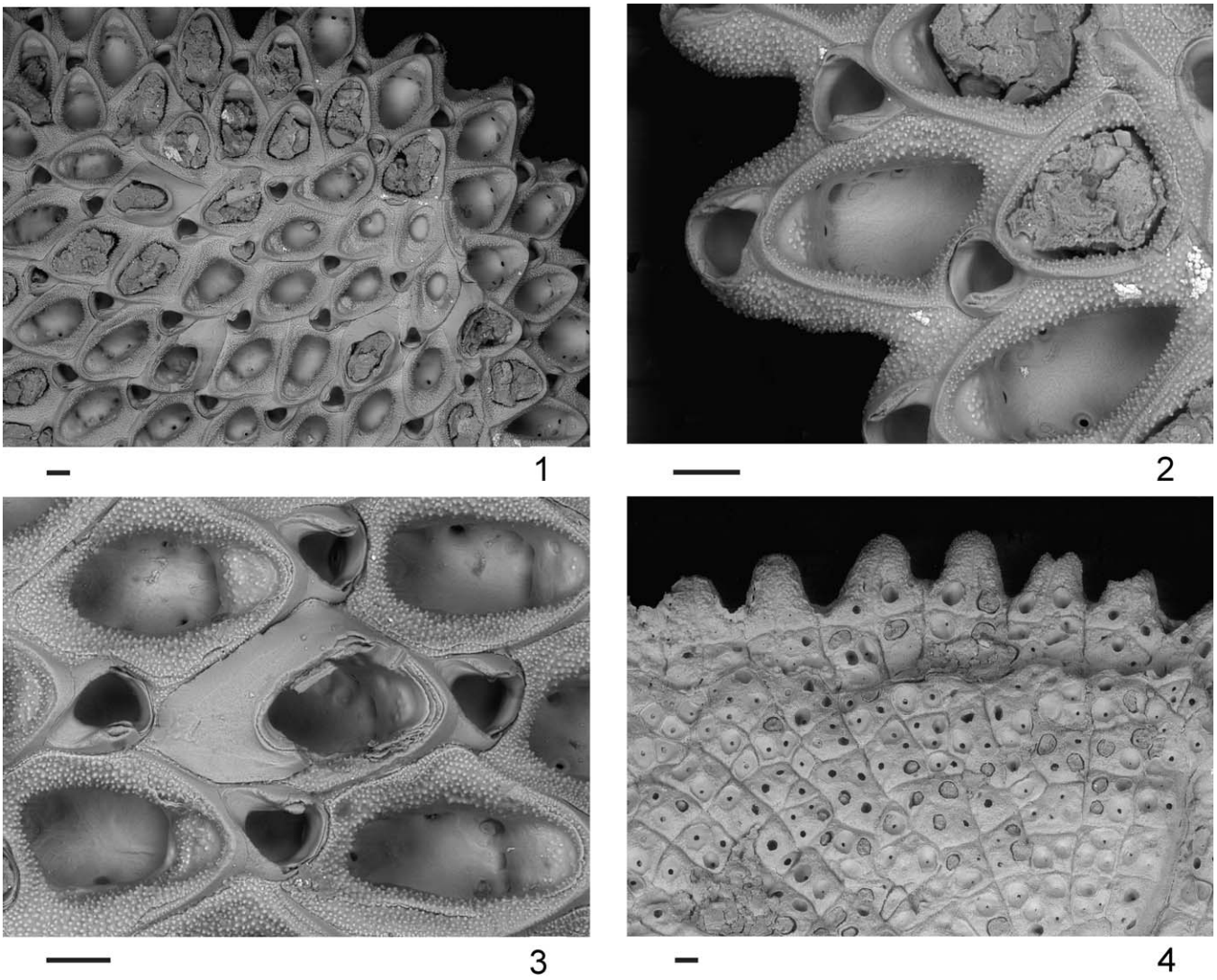

FIGURE 15—*Cupuladria exfragminis*. *1–4*, UF44633, Chipola Formation, early Miocene, Florida, U.S.A.: *1*, close-up of the colony showing autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

See Table 4 for morphological measurements.

Occurrence.—Recent from Gulf of Mexico to Colombia.

Remarks.—This species like *C. colonensis* and *C. dominicana* has a VAwo ≥0.1 mm (for details see text); and the diagnostic characters mentioned above such as RaAloAl have been important in the discrimination of species; while those related to the strength of the vicarious avicularia vibracula such as RaVAloVAl have been important to define this clade (see text). Besides along with *C. dominicana* have the largest ratio autozooid vibracula opesia width-autozooid opesia width (RaAwoOw) of 0.68 mm in average, in comparison to *C. colonensis* which is 10 percent smaller.

Three specimens collected from Mexico eastern Pacific were discriminated as *C. floridensis*.

CUPULADRIA COLONENSIS new species
Figures 24, 25

Diagnosis.—Autozooids have the ratio autozooid vibracula opesia width-autozooid opesia width (RaAwoOw) of 0.62 mm in average. Colonies are large and conical with average height to diameter ratio 0.27 mm, average diameter 16.9 mm.

Description.—Colonies conical with maximum observed diameter 18.1 mm. The central area of the colony is formed mostly by autozooids, cryptocyst descend moderately but septula still visible. Vicarious avicularia are scattered throughout the zone of astogenetic change with gymnocyst well developed, opesia auriform in shape, and VAwo ≥0.1 mm (for details see text). Autozooids are hexagonal. Basal sectors rectangular or irregular with 3–4 pores per sector.

Etymology.—The name colonensis refers to the Province of Colon where the large specimens were found.

Types.—Holotype USNM542575, Punta San Blas, Colon, Panama, Paratypes: USNM542576 Dry Tortugas, Florida keys, FL, U.S.A.; USNM542577 Pepperfish key, 29°23′00″ Lat.; 83°41′45″ Lon, Gulf of Mexico, FL, U.S.A.

Material.—USNM593771, Pepperfish key, Gulf of Mexico, FL U.S.A. See Table 4 for morphological measurements.

Occurrence.—Recent Gulf of Mexico and Panama.

Remarks.—*Cupuladria colonensis* has one of the smaller ratio autozooid vibracula opesia width-autozooid opesia width

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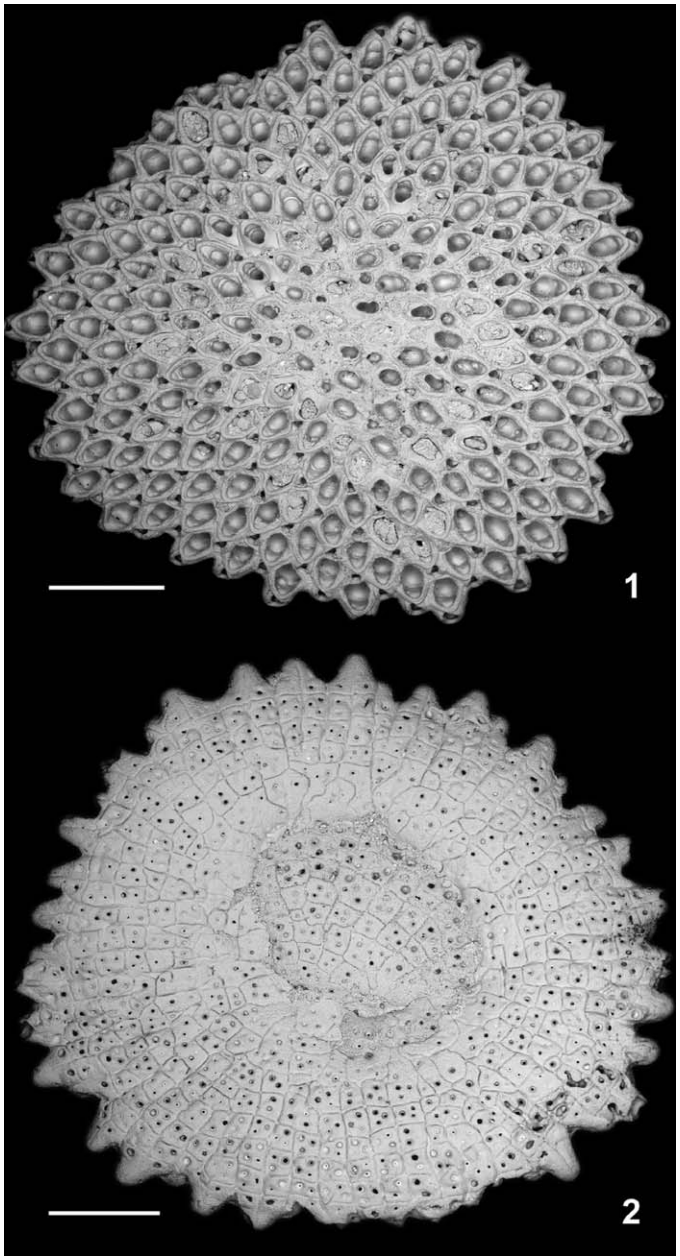

FIGURE *16—Cupuladria exfragminis. 1*, *2*, hypotype, USNM542595, PPP1306, Gatun Formation, late Miocene, Colon, Panama: *1*, colony frontal view; *2*, colony basal view. Scale bar=1 mm.

(RaAwoOw) of 0.62 mm in the C_{V1} clade along with *C. Cheethami* with 0.5 mm, however the ratio vicarious avicularia vibracula opesia length-vicarious avicularia vibracula length (RaVAloVAl) of 0.75 mm in average, are similar to *C. dominicana*.

CUPULADRIA DOMINICANA new species
Figures 26, 27

Diagnosis.—Autozooids have the ratio autozooid vibracula opesia width-autozooid opesia width (RaAwoOw) of 0.68 mm; and vicarious the ratio vicarious avicularia vibracula opesia length-vicarious avicularia vibracula length (RaVAloVAl) of 0.75 mm in average. Colonies are conical with average height diameter ratio of 0.27 mm, and average diameter 9.7 mm.

Description.—Colonies conical with maximum observed diameter 13.4 mm. The central area of the colony is formed mostly by autozooids, cryptocyst descend moderately but septula still visible. Vicarious avicularia are scattered throughout the zone of astogenetic change with gymnocyst well developed, opesia auriform in shape, and VAwo $\geq$0.1 mm (for details see text). Autozooids hexagonal. Basal sectors rectangular or irregular in shape with 3–4 pores per sector.

Etymology.—The name Dominicana refers to "native or inhabitant of the Dominican Republic", where the first specimens were found.

Types.—Holotype USNM542578, northeast coast Sto. Domingo, 19°10′15″ Lat., 69°27′20″ Lon. to 19°10′15″ Lat, 69°28′5″ Lon., Dominican Republic. Paratypes: USNM542579, LCH95–7, 15°59.3′ Lat., 86°30′ Lon., Cayos Cochinos, Honduras; USNM542580, CMN95–9, 14°42′ Lat., 82°54′ Lon., Cayos Miskitos, Nicaragua.

Material.—USNM593772, NMB17830; USNM593773, SB95–20, 9°36.37′ Lat., 78°59.2′ Lon., San Blas, Panama; USNM593774–593776, North East coast Sto. Domingo 19°10′15″ Lat., 69°27′20″ Lon. to 19°10′15″ Lat, 69°28′5″ Lon., Dominican Republic; USNM593777, Caroline Sta. 56, Sto. Domingo 19°10′15″ Lat., 69°27′20″ Lon. to 19°10′15″ Lat., 69°28′5″ Lon., Dominican Republic; USNM593778–593779, LCH95–11, 15°58.62′ Lat., 86°30′ Lon., Cayos Cochinos, Honduras; USNM593780, LCH95–18, 15°58′ Lat., 86°26.46′ Lon., Cayos Cochinos, Honduras; USNM593781, CMN95–9, 14°42′ Lat., 82°54′ Lon., Cayos Miskitos, Nicaragua; USNM593782–593783, CMN95–11, 14°29′ Lat., 82°47.4′ Lon., Cayos Miskitos, Nicaragua.

Other material.—UF50495, Bermont Formation, Belle Glade 01, FL, U.S.A.; MCZ100097, Dry Tortugas, Florida keys, FL, U.S.A.; MHNMC-IB88, 11°19′86″ Lat., 74°5′28″ Lon., Caribe, Colombia.

See Table 4 for morphological measurements.

Occurrence.—Early Pliocene, Cayo Agua Formation, Bocas del Toro, Panama. Pleistocene, Bermont Formation, Belle Glade 01, FL, U.S.A. Recent, from Gulf of Mexico to Colombia.

Remarks.—*Cupuladria dominicana* is similar to *C. floridensis* in several autozooid and vicarious features like RaAwoOw and RaVAloVAl (for details see text), but they differ in the width of vicarious vibracula opesia (VAwo), which is smaller than C. *floridensis* and *C. colonensis*. The cryptocyst of the autozooids of the central area were thickened by secondary calcification in one colony of this species.

CUPULADRIA COLLYRIDA new species
Figures 28, 29

Diagnosis.—Autozooids have a RaAloAl of 0.83 mm, colonies have a circular-dome shape, and determinate growth with vicarious avicularia occupying the central area, average height diameter ratio 0.53 mm, and average diameter 3.4 mm.

Description.—Colonies circular-dome shape, with maximum observed diameter 3.7 mm. Central area of the colony occupied by vicarious avicularia up to the second astogenetic generation with gymnocyst well developed and opesia auriform in shape. Autozooids hexagonal with cryptocyst straight sided and septula not visible. Growth determinate, cessation of growth marked by presence of kenozooids at colony margin, which is formed by almost entirely calcified autozooids leaving a single pore open and vibracula still functional. Basal sectors radial with 2–4 pores per sector.

Etymology.—Collyrida, Latin "roll/cake" with reference to the dinner roll shape of the zooarium.

Types.—Holotype, USNM542561, Pliocene, Bowden Formation, Jamaica.

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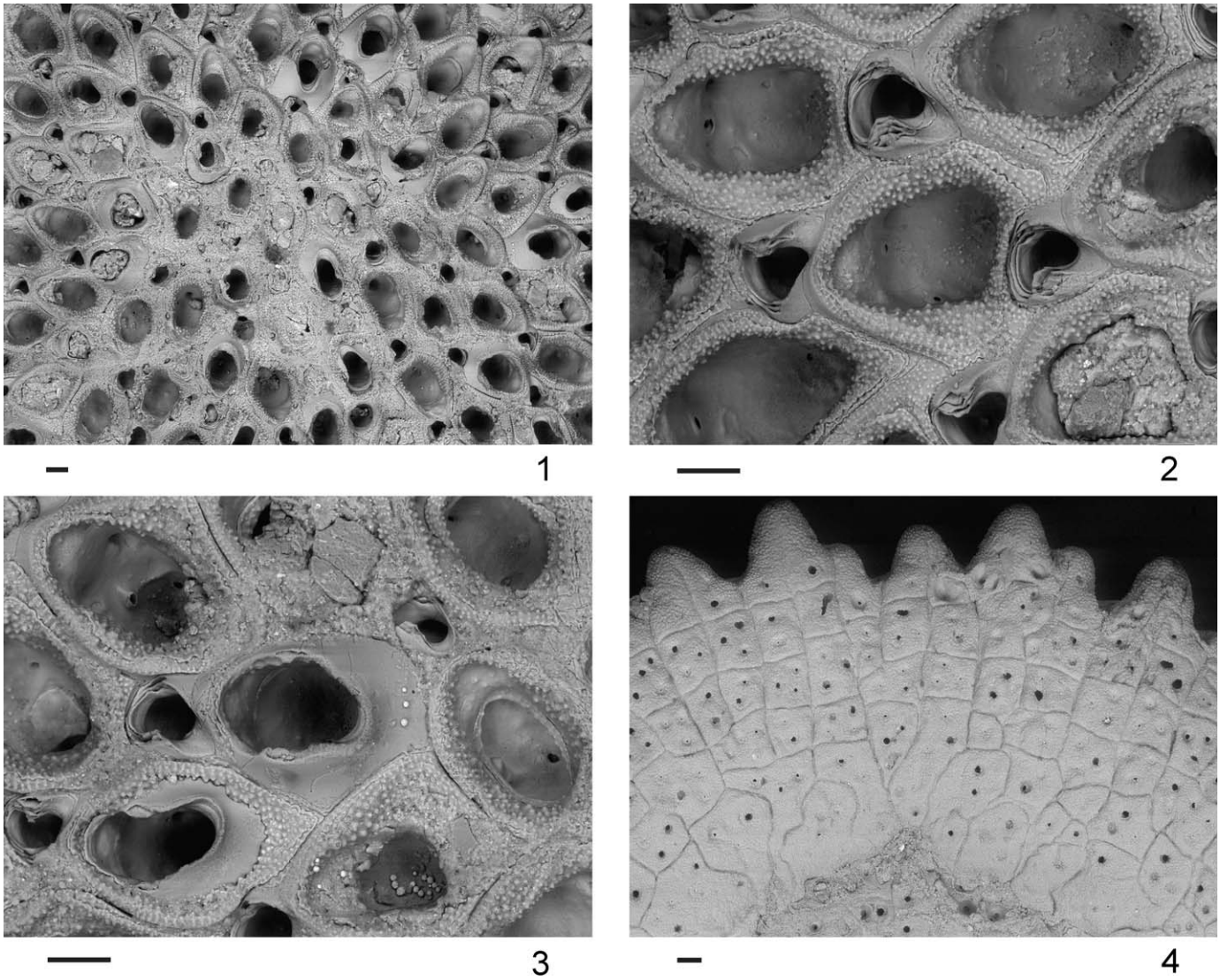

FIGURE 17—*Cupuladria exfragminis*. *1–4*, hypotype, USNM542595, PPP1306, Gatun Formation, late Miocene, Colon, Panama: *1*, colony center showing autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

Material.—BZ3249 Bowden Formation, Jamaica. See Table 4 for morphological measurements.

Occurrence.—Pliocene, Bowden Formation, Jamaica.

Remarks.—*Cupuladria collyrida* has the largest ratio autozooid vibracula opesia length-autozooid vibracula length (RaAloAl) in both C_{V1} and C_{V2} clades; only *C. gigas* in the C_{NV} clade has a similar ratio. The determinate growth observed in this species is a trait that has been more characteristic of extant Discoporella from the Caribbean side of the Isthmus of Panama (Herrera-Cubilla et al., 2008).

CUPULADRIA INCOGNITA Herrera-Cubilla et al., 2006

Description.—Colonies conical with maximum observed diameter of 6.8 mm, living colonies are blue-black. Central area of the colony occupied by vicarious avicularia with gymnocyst well developed and opesia auriform in shape. Autozooids hexagonal, with cryptocyst straight sided and well developed centrally, septula not visible. Basal sectors radial with 7–23 pores.

Types.—Hypotype USNM593785, PPP342.

Material.—USNM593784, 593786, PPP357, 709; USNM593787, NMB17841, USNM593788, PPP368; USNM593789, Bowden Formation, Jamaica; USNM593790, Puerto Limon, Costa Rica; USNM593791, PPP1253; USNM593792–593794, Bastimentos I., Bocas del Toro, Panama; USNM593795–593799, PPP178, 2171, 362, 640, USNM593800, NMB18080; USNM593801, BA98–125, 9°25.3′ Lat., 82°20.4′ Lon., Bahia Almirante, Bocas del Toro, Panama; USNM593802, GM98–74, 9°21.18′ Lat., 80°12′ Lon., Golfo de los Mosquitos, Bocas del Toro, Panama; USNM593803, GM98–90, 8°57.4′ Lat., 80°50′ Lon., Golfo de los Mosquitos, Bocas del Toro, Panama; USNM593804, PB99–225, 9°39.1′ Lat., 79°37.9′ Lon., Costa Arriba, off Islas Farallones, Colon, Panama; USNM523163 designated by Herrera-Cubilla et al., 2006.

Other material.—UF75958, Bowden Formation, St. Thomas Parish, Jamaica; BZ5603, Basal Moin Formation Puerto Limon, Costa Rica.

See Appendix 2 for morphological measurements.

Occurrence.—Early Pliocene Cayo Agua Formation, Punta Piedra Roja, western sequence, Bocas del Toro, Panama; early

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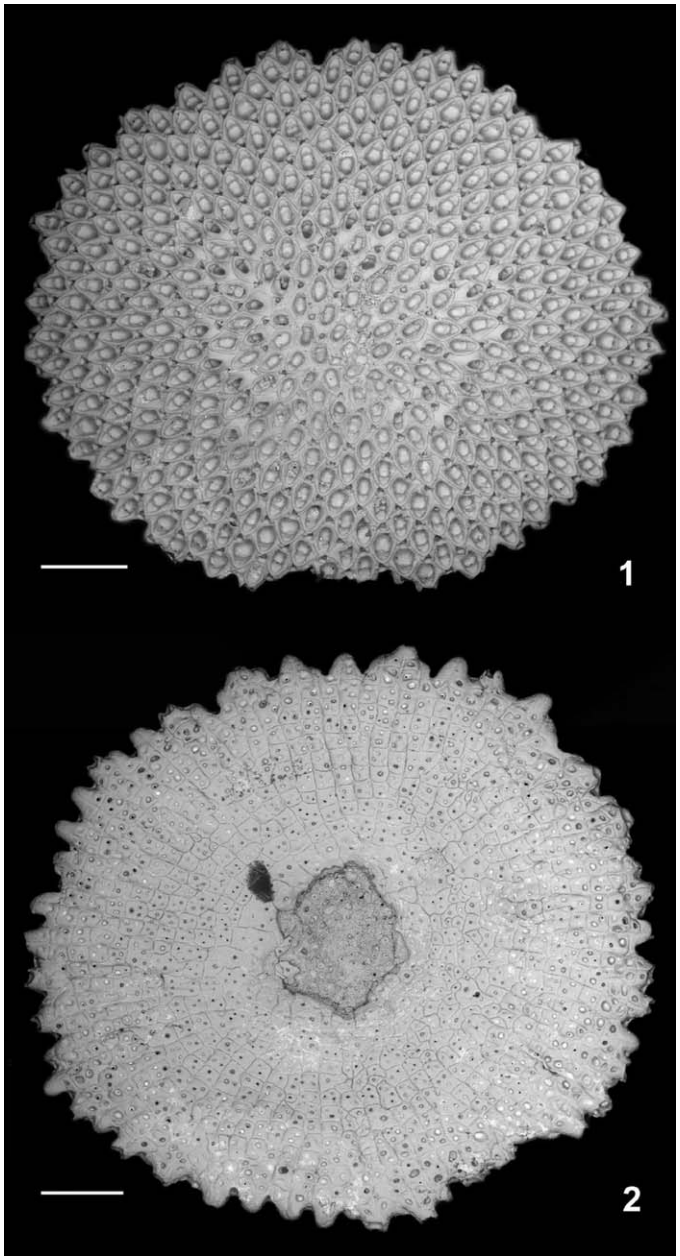

FIGURE 18—*Cupuladria exfragminis*. *1*, *2*, hypotype, USNM542593, PPP65, Cayo Agua Formation, late Pliocene, Bocas del Toro, Panama: *1*, colony frontal view; *2*, colony basal view. Scale bar=1 mm.

Pliocene, Cayo Agua Formation, Punta Norte to Punta Tiburon, Bocas del Toro, Panama; early Pliocene, Bowden Formation, St. Thomas Parish, Jamaica. Late Pliocene, Escudo de Veraguas Formation, northern coast, Bocas del Toro, Panama; late Pliocene, Escudo de Veraguas Formation, Bocas del Toro, Panama; late Pliocene, Bastimentos Island, Fish Hole, western sequence, Bocas del Toro, Panama; late Pliocene, Bastimentos Island, Bocas del Toro, Panama; late Pliocene, Rio Banano Formation, Santa Rita, Limon, Costa Rica; late Pliocene, Moin Formation, Lomas del Mar, eastern sequence, Limon, Costa Rica, late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica; late Pliocene, basal Moin Formation, Puerto Limon, Costa Rica. Pliocene, Puerto Limon, Costa Rica, Pliocene, Bowden Formation, Jamaica. Recent: Bocas del Toro, Colon and San Blas, Panama.

CUPULADRIA MULTESIMA Herrera-Cubilla et al., 2006

Description.—Colonies have a dome shape with maximum observed diameter of 5.6 mm, live colonies are brown. Central area of the colony occupied by vicarious avicularia with gymnocyst well developed and opesia auriform in shape. Autozooids hexagonal, with cryptocyst straight sided and well developed centrally, septula not visible. Basal sectors radial with 4–9 pores.

Types.—Hypotype USNM593805, PPP370.

Material.—USNM593806–593807, PPP2024, 2221; USNM593808, 593811–593812, SB95–18, 9°31.9′ Lat., 78°56.5′ Lon., San Blas, Panama; USNM593809, 593814, BT98–36, 9°13.5′ Lat., 81°53′ Lon., Bocas del Toro, Panama; USNM593810, GM98–69, 9°18.6′ Lat., 80°20′ Lon., Bocas del Toro, Panama; USNM593813, SB95–20, 9°36.9′ Lat., 78°59.2′ Lon., San Blas, Panama; USNM523158, 523160 designated by Herrera-Cubilla et al., 2006.

See Appendix 2 for morphological measurements.

Occurrence.—Late Pliocene, Escudo de Veraguas Formation, northern coast; late Pliocene, Swan Cay Formation, north of Isla Colon, Bocas del Toro, Panama; late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica. Recent: Bocas del Toro to San Blas, Panama.

CUPULADRIA PLANISSIMA new species
Figures 30, 31

Diagnosis.—Vicarious avicularia occupy the central area, and have the vicarious avicularia vibracula width-length ratio (VAwVAl) of 0.82 mm in average, colonies are conical with basal side completely flat and basal sectors radial, average height diameter ratio 0.44 mm, average diameter 3.4 mm.

Description.—Colonies have a dome shape, with maximum observed diameter 5 mm. Central area of colony occupied by vicarious avicularia up to the second astogenetic generation; with gymnocyst well developed and opesia auriform in shape. Autozooids hexagonal with cryptocyst descending moderately and septula still visible. Basal side of colony not concave but completely flat. Basal sectors radial with 4–14 pores per sector.

Etymology.—Planissima Latin "flat, level" with reference to the planar basal side of the colony.

Types.—Holotype USNM542581, Bastimentos I., Bocas del Toro, Panama; Paratypes: USNM542582–542583, PPP2026, 335.

Material.—USNM593815, NMB18105; USNM593816, Bastimentos I., Bocas del Toro, Panama; USNM593817–593818, PPP635, 963; USNM593819, BT98–36, 9°13.5′ Lat., 81°53′ Lon., Bocas del Toro, Panama; USNM593820, GM98–69, 9°18.6′ Lat., 80°20′ Lon., Bocas del Toro, Panama; USNM593821, SB95–18, 9°31.9′ Lat., 78°56.5′ Lon., San Blas, Panama; USNM593822, BT98–5, 9°30.4′ Lat., 82°20′ Lon., Bocas del Toro, Panama.

Other material.—BZ5603, Basal Moin Formation Puerto Limon, Costa Rica. See Table 4 for morphological measurements.

Occurrence.—Early Pliocene, Cayo Agua Formation, Punta Norte to Punta Tiburon, Bocas del Toro, Panama. Late Pliocene, Bastimentos Island., Bocas del Toro, Panama; late Pliocene, Rio Banano Formation, Limon, Costa Rica; late Pliocene, Moin Formation, Lomas del mar eastern sequence, Limon, Costa Rica; late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica; late Pliocene, basal Moin Formation, Puerto Limon, Costa Rica. Recent: Bocas del Toro and San Blas, Panama.

Remarks.—*Cupuladria planissima* has the smaller vicarious avicularia vibracula width-length ratio (VAwVAl) of the C_{V2} clade; and it also differs from *C. multesima* and *C. incognita* in the moderate development of the cryptocyst.

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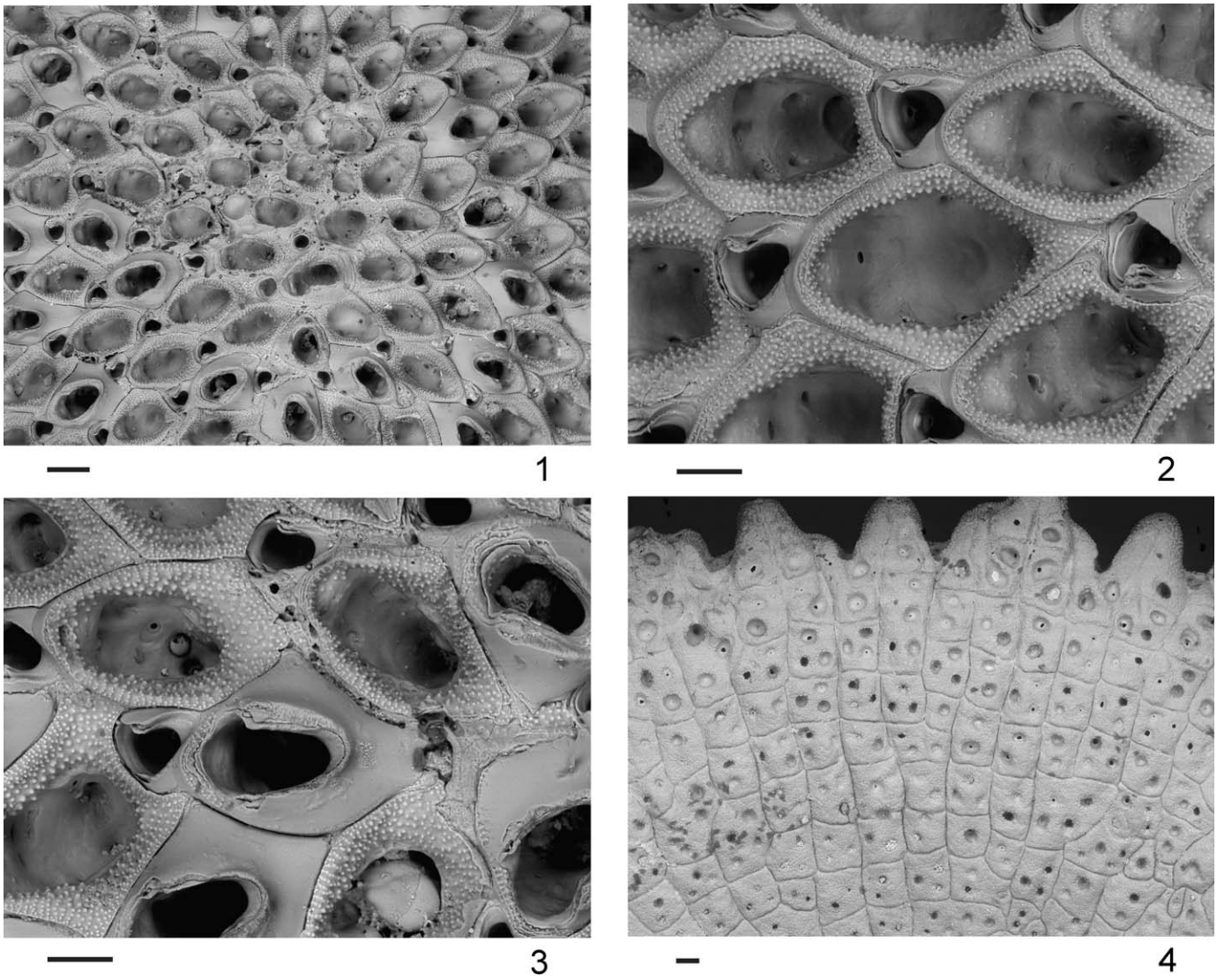

FIGURE 19—*Cupuladria exfragminis*. *1–4*, hypotype, USNM542593, PPP65, Cayo Agua Formation, late Pliocene, Bocas del Toro, Panama: *1*, colony center showing autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

CUPULADRIA VERACRUXIENSIS new species
Figures 32, 33

Diagnosis.—Autozooids have the opesia length (Ol) of 0.27 mm in average; the colonies are conical, with vicarious avicularia occupying the central area, basal sectors rectangular or irregular in shape, average height diameter ratio 0.18 mm, average diameter 4 mm.

Description.—Colonies are conical, with maximum observed diameter 6.1 mm. Central area of colony occupied by vicarious avicularia up to the sixth astogenetic generation; with gymnocyst well developed and opesia auriform in shape. Autozooids hexagonal, with cryptocyst descending moderately and septula still visible. Basal sectors rectangular or irregular in shape with 2–6 pores per sector.

Etymology.—Named for the state of Veracruz (from Latin: Vera Crux), Mexico were the oldest specimen was collected.

Types.—Holotype USNM542562, PPP2171. Paratypes: USNM542563, Fowey lighthouse, Key Biscayne Florida U.S.A.; USNM542564, TU638.

Material.—USNM593823–593827, PPP379, 63, 196; USNM593828–593829, TU638, TU1046; USNM593830, NMB18105; USNM593831–593833, PPP695, 678, 2174; USNM593834, CMN95–5, 14°30′ Lat., 82°29′ Lon., Cayos Miskitos, Nicaragua.

Other material—D34528, Paraje Solo Formation, Veracruz, Mexico; UF53535, Richardson road shell pit, FL, U.S.A.; UF47715, Macasphalt shell pit, FL, U.S.A.; MCZ100096, Marquesas Key, FL, U.S.A.; MHNMC–IB88, 11°19′86″ Lat., 74°5′28″ Lon. Caribbean, Colombia.

See Table 4 for morphological measurements.

Occurrence.—(?)Late Miocene, Paraje Solo Formation, Veracruz, Mexico. Early Pliocene, Shark Hole Point Formation, Valiente peninsula, from Bruno bluff to Plantain cays, Bocas del Toro, Panama; early Pliocene, Cayo Agua Formation, Punta Norte western side, Bocas del Toro, Panama. Late Pliocene, Escudo de Veraguas Formation, northern coast, Bocas del Toro, Panama; late Pliocene, Rio Banano Formation, Limon, Costa Rica. Pliocene Agueguexquite Formation, Coatzacoalcos, Veracruz, Mexico; Pliocene, Richardson road shell pit 01B, Florida,

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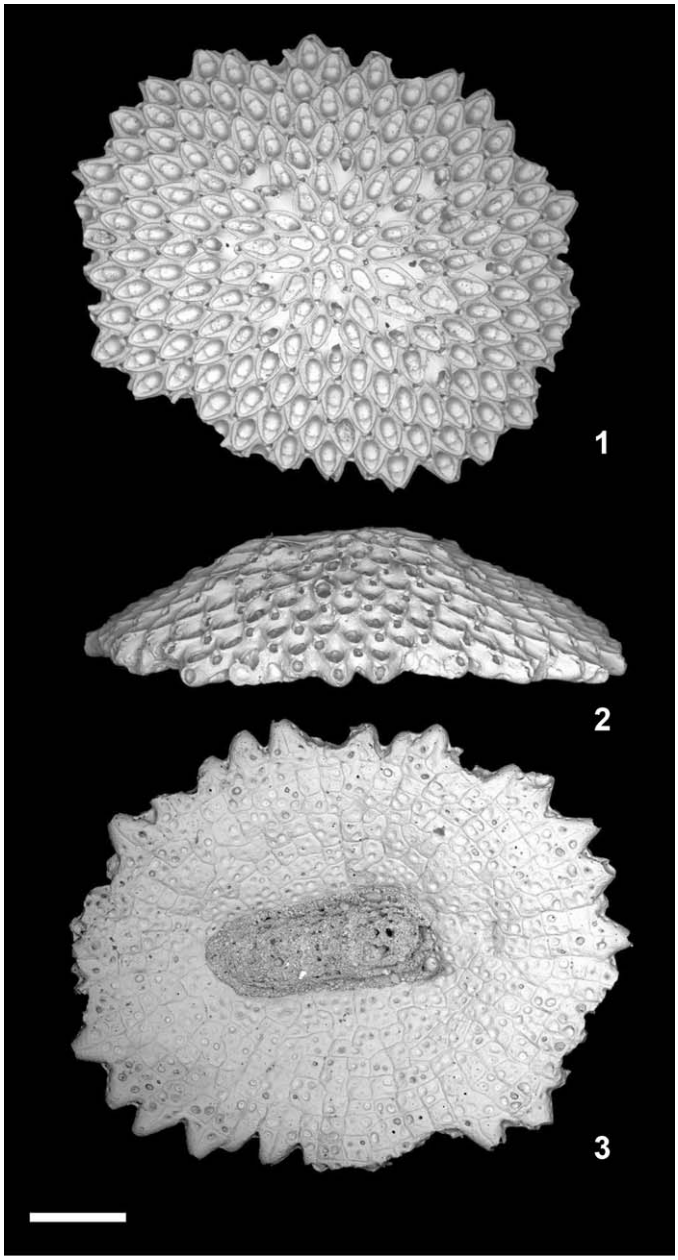

FIGURE 20—*Cupuladria pervagata* n. sp. *1–3*, holotype, USNM542565, BT98–19, Recent, Bocas del Toro, Panama: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

U.S.A.; Pliocene, Macasphalt shell pit, Florida, U.S.A. Recent: Florida, Nicaragua, Caribbean Colombia.

Remarks.—*Cupuladria veracruxiensis* has the largest opesia length (Ol) in the C_{V2} clade, and differs also from the rest of their members in the shape of the basal sectors, which are rectangular instead of radial. Some specimens have autozooid and vicarious avicularia with closure plates.

CUPULADRIA SURINAMENSIS Cadée, 1975

Description.—Autozooids have a length (Zl) of 0.53 mm in average; the colonies are conical, with maximum observed diameter of 10 mm. The central area of the colony is formed exclusively by autozooids. Autozooids are hexagonal, their cryptocyst descend steeply and septula are visible. Vicarious avicularia not observed. Basal sectors are radial with 2–17 pores. Few specimens have autozooids with closure plates.

Types.—Hypotypes USNM542586–542588, PPP640, 212, 352.

Material.—USNM593835–593836, PPP326; USNM593837, NMB17830; USNM593838–593844, PPP340, 335, 212, 210, 722, 709, 368; USNM593845, 593847, NMB17841, 18388; USNM593846, 593849, Bastimentos I., Bocas del Toro, Panama; USNM593848, 593850–593853, PPP635, 178, 362, 2024; USNM593854–593856, BT98–46, 9°8′ Lat., 81°33.2′ Lon., Escudo de Veraguas, Bocas del Toro, Panama; USNM593857–593858, SB95–12, 9°32.5′ Lat., 78°57.8′ Lon., San Blas, Panama; USNM593859, GM98–50, 8°57′ Lat., 81°30′ Lon., Escudo de Veraguas, Panama; USNM593860, GM98–73, 9°16.7′ Lat., 80°12′ Lon., Golfo de los Mosquitos, Panama; USNM593861, GM98–74, 9°21.18′ Lat., 80°12′ Lon., Golfo de los Mosquitos, Panama; USNM593862, GM98–89, 8°55′ Lat., 80°50′ Lon., Golfo de los Mosquitos, Panama; USNM593863–593865, BT98–102, 9°20.7′ Lat., 82°7′ Lon., Bocas del Toro, Panama; USNM593866, BT98–125, 9°25.3′ Lat., 82°20.4′ Lon., Bahia de Almirante, Panama; USNM593867, BT98–128, 9°27.78′ Lat., 82°18.37′ Lon., Bahia de Almirante, Panama; USNM593868–593869, LCH95–2, 15°56.4′ Lat., 86°29.9′ Lon., Cayos Cochinos, Honduras; USNM593870, LCH95–11, 15°58.62′ Lat., 86°30′ Lon., Cayos Cochinos, Honduras; USNM593871–593872, CMN95–9, 14°42′ Lat., 82°54′ Lon., Cayos Miskitos, Nicaragua; USNM593873–593875, CMN95–11, 14°29′ Lat., 82°47.4′, Cayos Miskitos, Nicaragua.

Other material.—BZ3249, Basal Moin Formation Puerto Limon, Costa Rica; NHM1975.9.4.2, 6°14.5′ Lat., 53°25′ Lon., Guyana. See Appendix 2 for morphological measurements.

Occurrence.—Early Pliocene, Cayo Agua Formation, Punta Piedra Roja, western sequence, Bocas del Toro, Panama; early Pliocene, Cayo Agua Formation, Punta Norte to Punta Tiburon, Bocas del Toro, Panama; early Pliocene, Cayo Agua Formation, Bocas del Toro, Panama. Late Pliocene, Escudo de Veraguas Formation, northern coast, Bocas del Toro, Panama; late Pliocene, Escudo de Veraguas Formation, Bocas del Toro, Panama; late Pliocene, Solarte Island, western tip, Bocas del Toro, Panama; late Pliocene, Bastimentos Island, Bocas del Toro, Panama; late Pliocene, Rio Banano Formation, Santa Rita, Limon, Costa Rica; late Pliocene, Santa Rita, Limon, Costa Rica; late Pliocene, Moin Formation, Lomas del Mar, eastern sequence, Limon, Costa Rica; late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica. Pliocene, Bowden Formation, Jamaica. Recent, Central America and Guyana.

CUPULADRIA PANAMENSIS Herrera-Cubilla et al., 2006

Description.—Autozooids have a length (Zl) of 0.56 mm in average; the colonies have a dome shape, with maximum observed diameter of 10.3 mm. The central area of the colony is formed exclusively by autozooids. Autozooids are hexagonal; cryptocyst descends moderately but septula still visible. Vicarious avicularia not observed. Basal sectors are radial with 5–24 pores. Few specimens have autozooids with closure plates.

Types.—Hypotypes USNM542589, CMN95–5, 14°30′ Lat., 82°29′ Lon., Cayos Miskitos, Nicaragua; USNM542590, Escudo de Veraguas Formation, Bocas del Toro, Panama; USNM542591, PPP2170.

Material.—USNM593876–593877, PPP350, 212; USNM593878, Escudo de Veraguas formation, Bocas del Toro, Panama; USNM593879, PPP2174; USNM593880–593881, NMB18084; USNM593882–593885, PPP2024, 2038, 942; USNM593886–593887, SB95–4, 9°34′ Lat., 78°35′ Lon., San Blas, Panama; USNM593888–593889, SB95–7, 9°31′ Lat., 78°45′ Lon., San Blas, Panama; USNM593890–593891, SB95–9, 9°31′ Lat., 78°44.3′ Lon., 67 m depth, brown sandy mud, San Blas, Panama; USNM593892, GM98–50, 8°57′ Lat., 81°30′ Lon., Escudo de Veraguas, Panama; USNM593893–593894, GM98–

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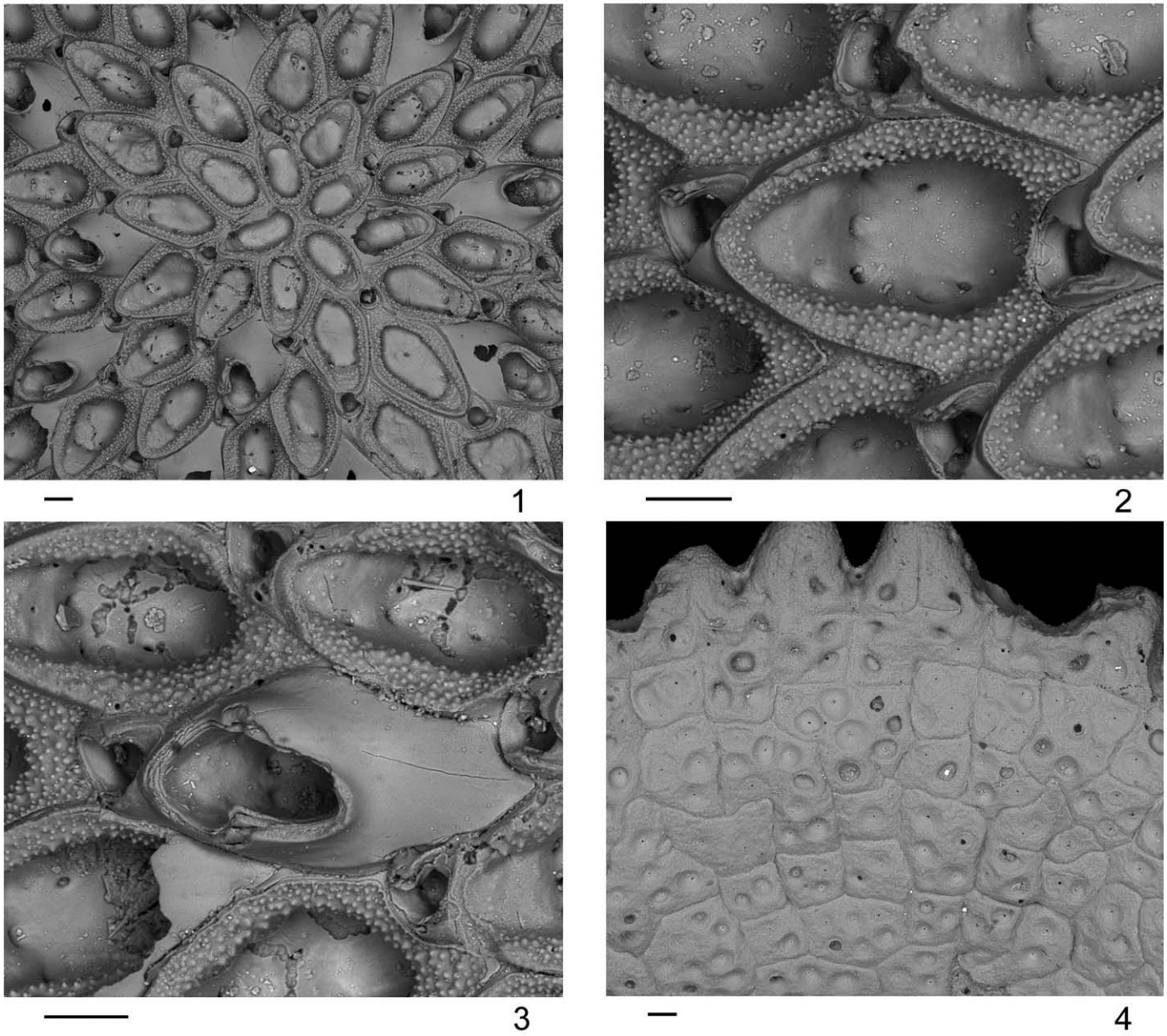

FIGURE 21—*Cupuladria pervagata* n. sp. *1–4*, holotype, USNM542565, BT98–19, Recent, Bocas del Toro, Panama: *1*, colony center showing autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale scale=100 μm.

73, 9°16.7′ Lat., 80°12′ Lon., Golfo de los Mosquitos, Panama; USNM593895–593896, GM98–74, 9°21.18′ Lat., 80°12′ Lon., Golfo de los Mosquitos, Bocas del Toro, Panama; USNM593897–593898, 593910, GM98–90, 8°57.4′ Lat., 80°50′ Lon., Bocas del Toro, Panama; USNM593899 –593901, 593908–593909, GM98–78, 9°28.93′ Lat., 80° Lon., Golfo de los Mosquitos, Bocas del Toro, Panama; USNM593902–593907, SB95–20, 9°36.9′ Lat., 78°59.2′ Lon., San Blas, Panama; USNM593911, LCH95–2, 15°56.4′ Lat., 86°29.9′ Lon., Cayos Cochinos, Honduras; USNM593912–593913, LCH95–11, 15°58.62′ Lat., 86°30′ Lon., Cayos Cochinos, Honduras; USNM593914–593916, CMN95–9, 14°42′ Lat., 82°54′ Lon., Cayos Miskitos, Nicaragua; USNM593917–593919, PB99–225, 9°39.1′ Lat., 79°37.9′ Lon., Colon, Panama; USNM523179, 523182 designated by Herrera-Cubilla et al., 2006.

Other material.—BZ5603, Basal Moin Formation Puerto Limon, Costa Rica. See Appendix 2 for morphological measurements.

Occurrence.—Early Pliocene, Cayo Agua Formation, Punta Piedra Roja, western sequence, Bocas del Toro, Panama. Late Pliocene, Solarte Island, western tip, Bocas del Toro, Panama; late Pliocene, Escudo de Veraguas Formation, northern coast, Bocas del Toro, Panama; late Pliocene, basal Moin Formation, Puerto Limon, Costa Rica; late Pliocene, Moin Formation, Limon, Costa Rica; late Pliocene, Moin Formation, Lomas del Mar, eastern sequence, Limon, Costa Rica; late Pliocene, Lomas del Mar, western reef track sequence, Limon, Costa Rica.

Recent, Central America to Panama.

Remarks.—*Cupuladria panamensis* has the largest zooid size (Zl) in the C_{NV} clade, while *C. surinamensis* is intermediate.

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TABLE 4—Measurements (in mm) of zoarial and zooidal characters for the eight new species described. Refer to Table 1 for character names.

	C. pervagata n. sp					*C. floridensis* n. sp.					*C. colonensis* n. sp.					*C. dominicana* n. sp.				
Characters	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD
Cw	41	5.664	3.500	7.700	0.862	18	13.361	9.550	18.400	2.891	4	16.875	15.650	18.050	1.115	18	9.713	6.275	13.400	1.860
Ch	41	1.111	0.200	1.900	0.467	18	3.672	2.000	5.000	0.939	4	4.500	3.800	5.500	0.770	18	2.647	1.850	4.200	0.708
Rahw	41	0.193	0.040	0.322	0.075	18	0.278	0.187	0.409	0.062	4	0.267	0.222	0.313	0.042	18	0.272	0.201	0.362	0.046
Csur	41	27.925	9.685	49.982	8.294	18	167.248	87.945	298.633	70.030	4	254.739	213.872	285.531	34.064	18	87.563	35.906	157.016	34.242
C*i*	41	0.094	0.047	0.271	0.034	18	0.087	0.057	0.125	0.021	4	0.117	0.073	0.141	0.031	18	0.088	0.055	0.123	0.022
RaZV	41	0.680	0.125	1.000	0.194	18	2.000	2.000	2.000	0.000	4	0.688	0.375	0.875	0.217	18	0.549	0.250	0.875	0.192
Zl	41	0.474	0.399	0.572	0.049	18	0.446	0.382	0.541	0.037	4	0.452	0.403	0.509	0.046	18	0.470	0.395	0.570	0.048
Zw	41	0.329	0.239	0.408	0.039	18	0.308	0.228	0.363	0.038	4	0.324	0.269	0.362	0.044	18	0.310	0.242	0.395	0.045
Ol	41	0.316	0.260	0.381	0.035	18	0.322	0.257	0.405	0.034	4	0.308	0.262	0.363	0.046	18	0.329	0.264	0.391	0.035
Ow	41	0.167	0.133	0.254	0.024	18	0.186	0.141	0.215	0.022	4	0.196	0.171	0.210	0.017	18	0.171	0.134	0.203	0.022
Al	41	0.207	0.173	0.248	0.017	18	0.226	0.164	0.272	0.023	4	0.229	0.205	0.247	0.020	18	0.223	0.192	0.260	0.020
Aw	41	0.167	0.141	0.224	0.016	18	0.180	0.130	0.230	0.022	4	0.181	0.160	0.198	0.016	18	0.164	0.132	0.202	0.018
Alo	41	0.158	0.114	0.198	0.017	18	0.176	0.134	0.202	0.015	4	0.176	0.160	0.188	0.014	18	0.173	0.136	0.209	0.020
Awo	41	0.110	0.091	0.145	0.012	18	0.125	0.099	0.150	0.014	4	0.122	0.110	0.136	0.011	18	0.115	0.099	0.139	0.012
Zcp	41	0.024	0.000	1.000	0.156	18	0.000	0.000	0.000	0.000	4	0.000	0.000	0.000	0.000	18	0.000	0.000	0.000	0.000
Vcp	41	0.024	0.000	1.000	0.156	18	0.000	0.000	0.000	0.000	4	0.000	0.000	0.000	0.000	18	0.000	0.000	0.000	0.000
NV	41	15.780	1.000	49.000	11.385	18	69.778	11.000	141.000	42.379	4	77.000	50.000	131.000	36.670	18	52.056	6.000	134.000	32.310
Vl	41	0.423	0.296	0.517	0.049	18	0.430	0.364	0.506	0.041	4	0.460	0.408	0.511	0.046	18	0.449	0.365	0.515	0.037
Vw	41	0.292	0.190	0.363	0.036	18	0.292	0.258	0.340	0.023	4	0.283	0.258	0.312	0.022	18	0.303	0.266	0.343	0.023
VOl	41	0.229	0.179	0.285	0.023	18	0.277	0.246	0.328	0.022	4	0.284	0.268	0.303	0.017	18	0.260	0.221	0.289	0.021
VOw	41	0.128	0.087	0.182	0.018	18	0.156	0.127	0.199	0.017	4	0.144	0.137	0.161	0.012	18	0.149	0.127	0.177	0.014
VAl	41	0.174	0.112	0.217	0.022	18	0.209	0.146	0.254	0.028	4	0.211	0.179	0.243	0.029	18	0.201	0.170	0.240	0.019
VAw	41	0.138	0.095	0.176	0.019	18	0.164	0.126	0.193	0.016	4	0.156	0.129	0.171	0.020	18	0.153	0.133	0.176	0.012
VAlo	41	0.125	0.077	0.154	0.017	18	0.157	0.123	0.198	0.017	4	0.160	0.127	0.194	0.031	18	0.150	0.124	0.180	0.015
VAwo	41	0.088	0.058	0.108	0.014	18	0.109	0.085	0.129	0.012	4	0.106	0.090	0.124	0.014	18	0.102	0.084	0.121	0.010
Asec	41	0.059	0.026	0.094	0.015	18	0.058	0.044	0.079	0.007	4	0.059	0.048	0.069	0.008	18	0.058	0.047	0.078	0.009
Psec	41	3.240	2.000	5.000	0.712	18	3.863	2.915	5.031	0.579	4	3.542	3.217	4.000	0.356	18	3.934	2.722	4.477	0.434
Ken	41	0.000	0.000	0.000	0.000	18	0.000	0.000	0.000	0.000	4	0.000	0.000	0.000	0.000	18	0.000	0.000	0.000	0.000

CUPULADRIA GIGAS new species
Figures 34, 35

Diagnosis.—Autozooids have a length (Zl) of 0.49 mm in average, colonies large and conical, average height diameter ratio 0.41 mm, average diameter 19.7 mm.

Description.—Colonies conical, with maximum observed diameter 21.5 mm. The central area of the colony is formed exclusively by autozooids. Autozooids are hexagonal, their cryptocyst descend steeply and septula are visible. Vicarious avicularia absent. Basal sectors have a radial shape with 7–20 pores per sector. Autozooids with closure plates not observed.

Etymology.—Gigas, Latin 'a giant' with reference to the large size of the zooarium.

Types.—Holotype USNM542584, Paratype: USNM542585, 9°18.26′ Lat., 82°11.98′ Lon., Bahia de Almirante, Bocas del Toro, Panama.

Material.—USNM593920–593923, Bahia de Almirante, Bocas del Toro, Panama. See Table 4 for morphological measurements.

Occurrence.—Recent Bocas del Toro Panama.

Remarks.—This species has the smallest zooid size (Zl) in the C_{NV} clade, but the largest RaAloAl of 0.83 mm in average (for details see text); and also the largest zooaria observed in members of this clade.

Genus DISCOPORELLA d'Orbigny, 1852

All the Recent species from the Caribbean: *D. scutella*, *D. peltifera*, *D. terminata*, *D. triangula* and *D. bocasdeltoroensis*, and: *D. marcusorum* and *D. cookae*, from the EP coasts of Panama are described in Herrera-Cubilla et al., 2008.

The new species DASP32 was collected in the Gulf of Chiriqui, GC97–65, 7°10.9′ Lat., 81°39.9′ Lon., February 1997, H. Fortunato coll., fine mud, 142 m depth. It corresponds to *Discoporella* sp. nov. P1 in Jagadeeshan and O'Dea, 2012.

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: http://doi.org/10.5061/dryad.49k85.

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TABLE 4—Extended.

C. collyrida n. sp.					*C. veracruxiensis* n. sp.					*C. planissima* n. sp.					*C. gigas* n. sp.				
N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD
4	3.425	3.000	3.700	0.299	21	4.140	3.000	6.050	1.058	12	3.438	1.500	5.000	0.962	6	19.717	17.550	21.450	1.517
4	1.800	1.600	2.000	0.231	21	0.757	0.100	1.600	0.433	12	1.500	0.600	2.350	0.562	6	7.950	7.300	9.200	0.771
4	0.527	0.432	0.571	0.066	21	0.179	0.033	0.355	0.084	12	0.441	0.200	0.629	0.122	6	0.405	0.350	0.490	0.053
4	13.445	10.336	14.612	2.081	21	15.421	7.085	30.593	8.138	12	13.279	2.584	25.148	6.914	6	394.018	338.755	448.634	49.946
4	0.140	0.097	0.168	0.031	21	0.076	0.031	0.107	0.016	12	0.105	0.064	0.153	0.031	6	0.113	0.101	0.122	0.008
4	0.250	0.250	0.250	0.000	21	0.286	0.000	0.750	0.238	12	0.094	0.000	0.625	0.186	6	1.500	1.000	2.000	0.548
4	0.355	0.318	0.387	0.030	21	0.398	0.356	0.462	0.026	12	0.381	0.317	0.423	0.030	6	0.491	0.469	0.523	0.020
4	0.325	0.296	0.362	0.030	21	0.288	0.233	0.348	0.029	12	0.288	0.261	0.322	0.022	6	0.367	0.321	0.404	0.028
4	0.223	0.200	0.241	0.017	21	0.272	0.223	0.321	0.027	12	0.245	0.195	0.280	0.023	6	0.355	0.334	0.381	0.017
4	0.136	0.120	0.161	0.018	21	0.154	0.140	0.186	0.012	12	0.135	0.113	0.162	0.014	6	0.231	0.201	0.246	0.017
4	0.172	0.139	0.183	0.022	21	0.179	0.142	0.222	0.021	12	0.185	0.149	0.222	0.022	6	0.271	0.258	0.284	0.011
4	0.159	0.153	0.166	0.006	21	0.149	0.126	0.171	0.012	12	0.158	0.131	0.177	0.015	6	0.197	0.189	0.205	0.006
4	0.142	0.108	0.161	0.023	21	0.129	0.097	0.170	0.021	12	0.127	0.100	0.162	0.020	6	0.224	0.208	0.232	0.009
4	0.114	0.100	0.121	0.010	21	0.094	0.074	0.110	0.010	12	0.104	0.090	0.121	0.010	6	0.127	0.118	0.138	0.008
4	0.000	0.000	0.000	0.000	21	0.095	0.000	1.000	0.301	12	0.083	0.000	1.000	0.289	6	0.000	0.000	0.000	0.000
4	0.000	0.000	0.000	0.000	21	0.143	0.000	1.000	0.359	12	0.000	0.000	0.000	0.000	6	0.000	0.000	0.000	0.000
4	16.750	16.000	17.000	0.500	21	18.667	4.000	62.000	17.574	12	24.750	3.000	63.000	19.008	6	0.000	0.000	0.000	0.000
4	0.331	0.307	0.353	0.019	21	0.346	0.269	0.429	0.034	12	0.336	0.273	0.388	0.034	6	0.000	0.000	0.000	0.000
4	0.269	0.223	0.290	0.031	21	0.251	0.187	0.314	0.032	12	0.247	0.195	0.302	0.031	6	0.000	0.000	0.000	0.000
4	0.193	0.184	0.204	0.008	21	0.208	0.164	0.256	0.025	12	0.195	0.172	0.230	0.016	6	0.000	0.000	0.000	0.000
4	0.112	0.108	0.117	0.004	21	0.108	0.080	0.139	0.016	12	0.118	0.091	0.135	0.013	6	0.000	0.000	0.000	0.000
4	0.140	0.124	0.149	0.011	21	0.143	0.110	0.189	0.022	12	0.146	0.109	0.187	0.026	6	0.000	0.000	0.000	0.000
4	0.121	0.115	0.134	0.009	21	0.123	0.095	0.154	0.016	12	0.118	0.084	0.153	0.020	6	0.000	0.000	0.000	0.000
4	0.099	0.077	0.111	0.016	21	0.099	0.061	0.145	0.020	12	0.093	0.069	0.132	0.019	6	0.000	0.000	0.000	0.000
4	0.077	0.075	0.080	0.003	21	0.075	0.052	0.097	0.010	12	0.071	0.057	0.094	0.010	6	0.000	0.000	0.000	0.000
4	0.056	0.040	0.070	0.015	21	0.050	0.031	0.083	0.014	12	0.127	0.085	0.160	0.027	6	0.349	0.199	0.435	0.096
4	2.485	2.107	3.481	0.665	21	4.230	2.634	6.114	0.935	12	9.535	4.646	14.275	3.192	6	14.004	7.062	20.195	4.354
4	1.000	1.000	1.000	0.000	21	0.000	0.000	0.000	0.000	12	0.000	0.000	0.000	0.000	6	0.000	0.000	0.000	0.000

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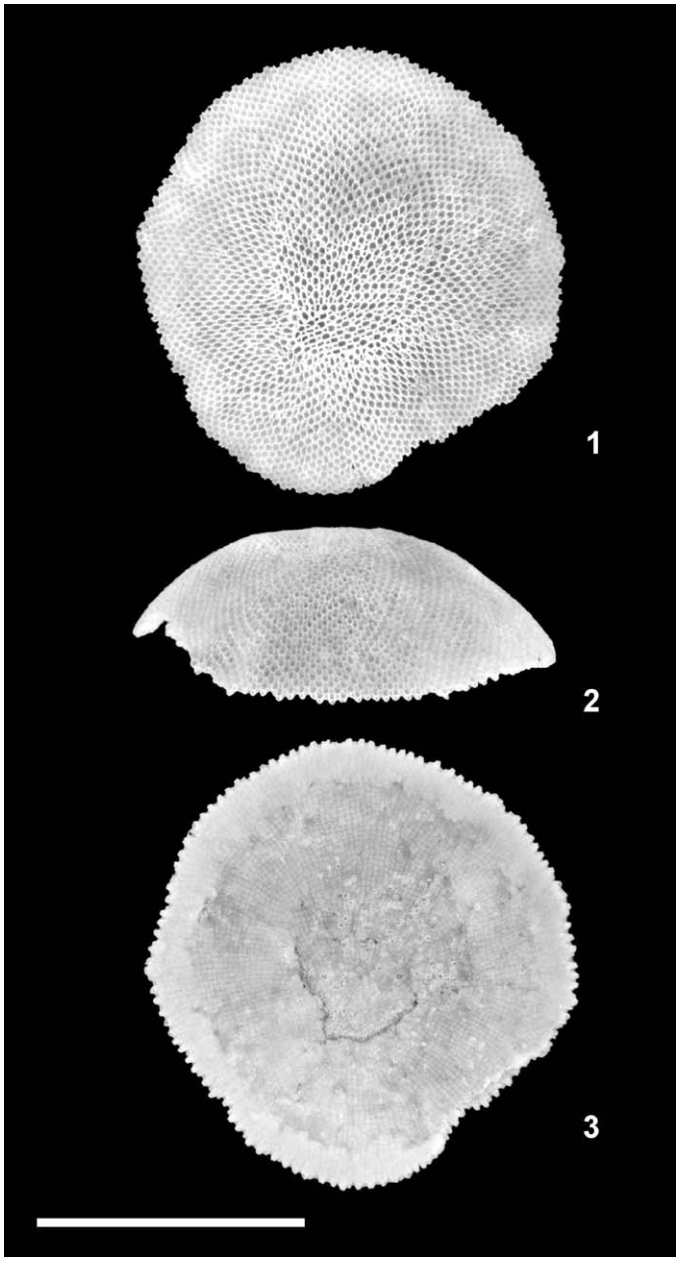

FIGURE *22—Cupuladria floridensis* n. sp. *1–3*, holotype, USNM542571, Recent, New Orleans off coast, Louisiana, U.S.A.: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

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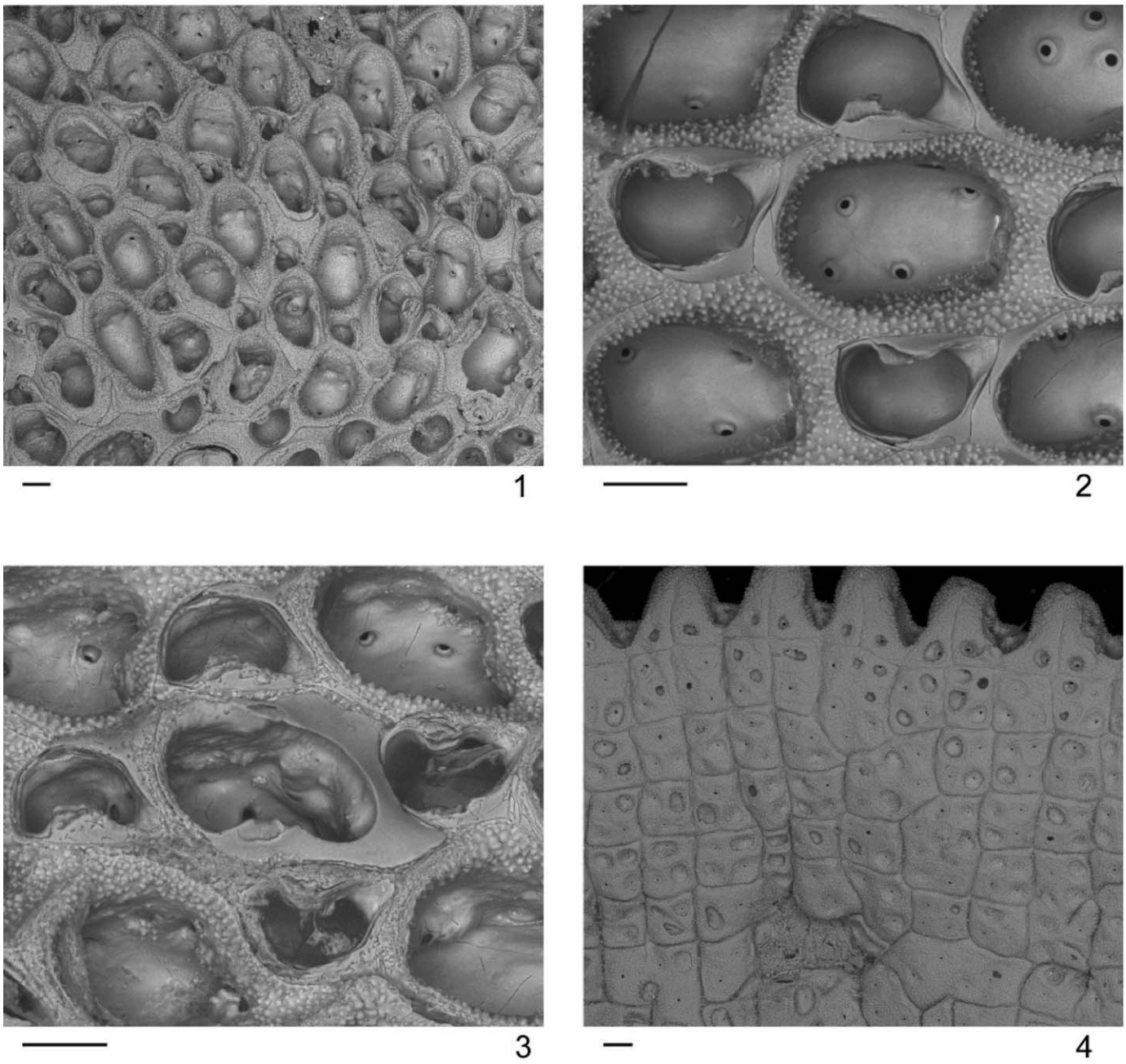

FIGURE 23—*Cupuladria floridensis* n. sp. *1–4*, holotype, USNM542571, Recent, New Orleans off coast, Louisiana, U.S.A.: *1*, colony center showing its clonal origin, autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

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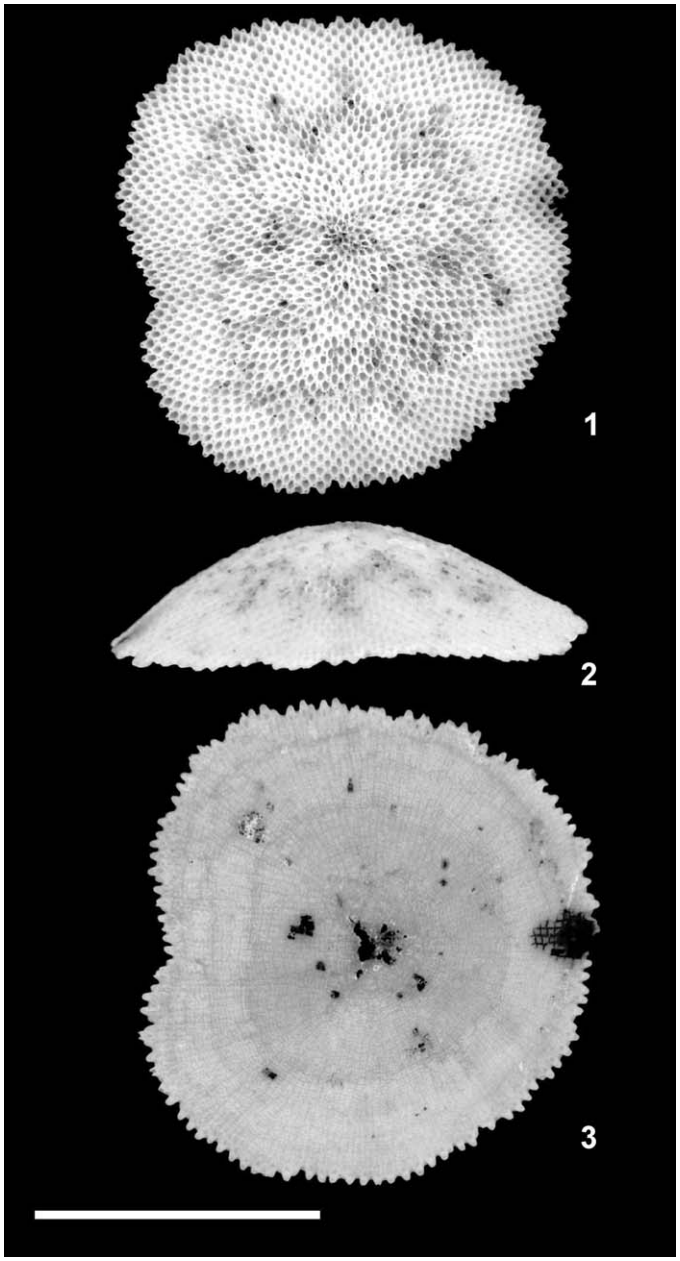

FIGURE *24*—*Cupuladria colonensis* n. sp. *1–3*, holotype, USNM542575, Recent, Colon, Panama: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

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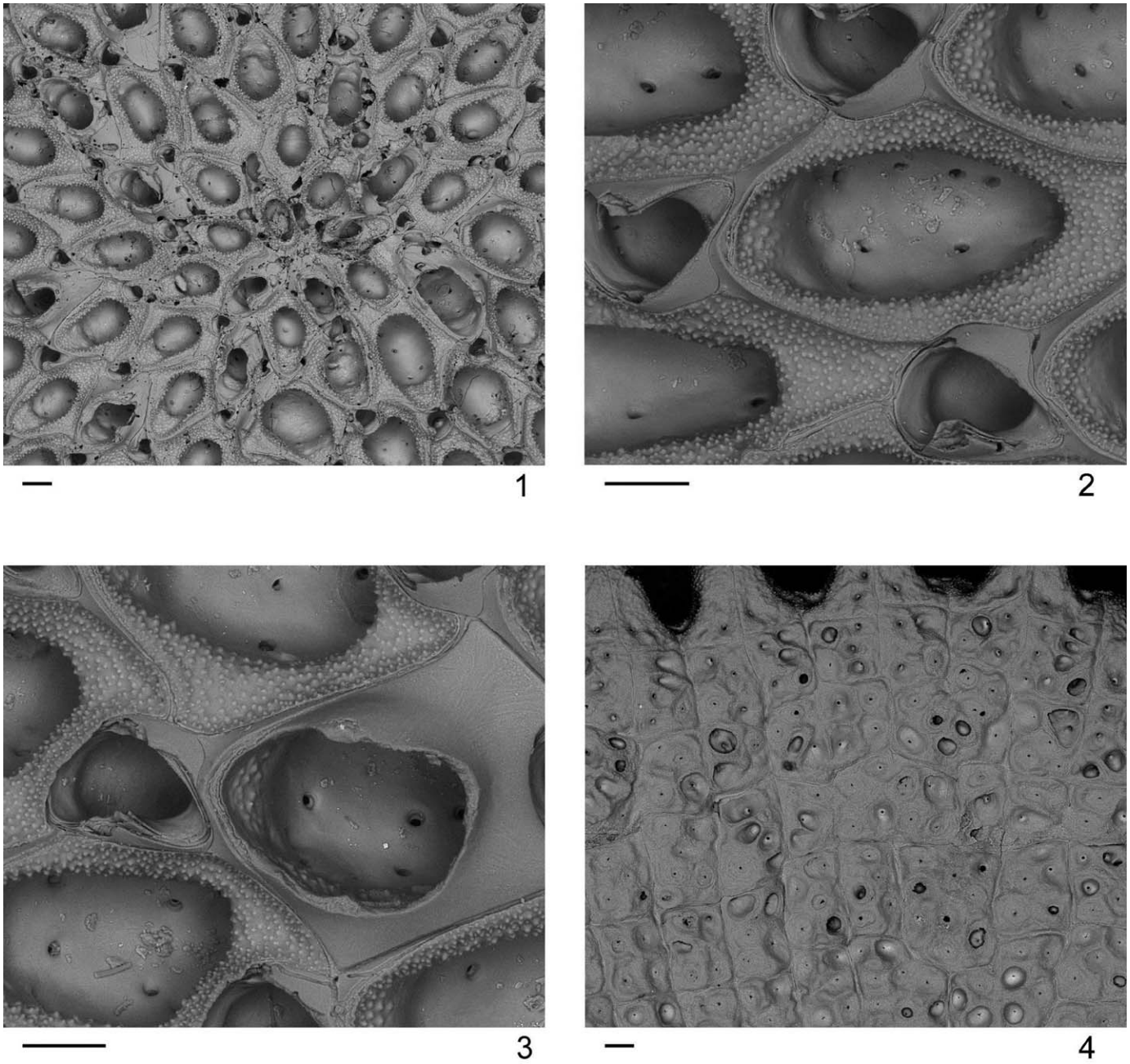

FIGURE 25—*Cupuladria colonensis* n. sp. *1–4*, holotype, USNM542575, Recent, Colon, Panama: *1*, colony center showing autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

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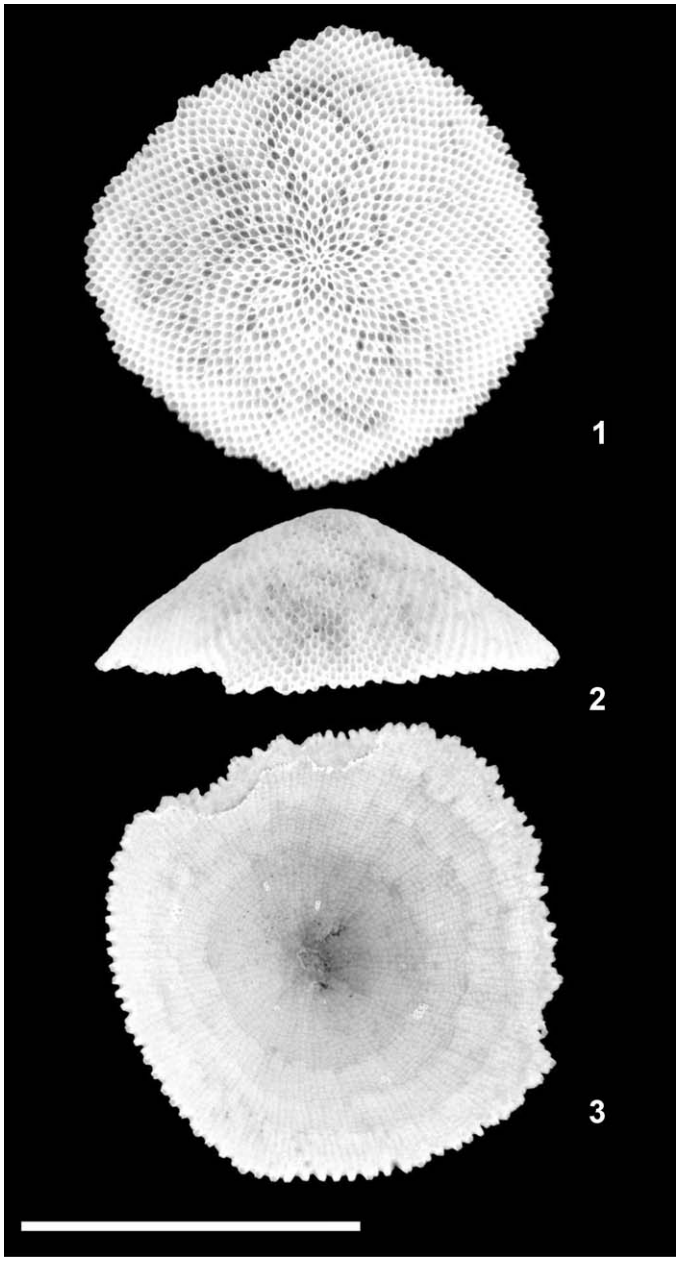

FIGURE *26*—*Cupuladria dominicana* n. sp. *1–3*, holotype USNM542578, Recent, North East coast Santo Domingo, Dominican Republic: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

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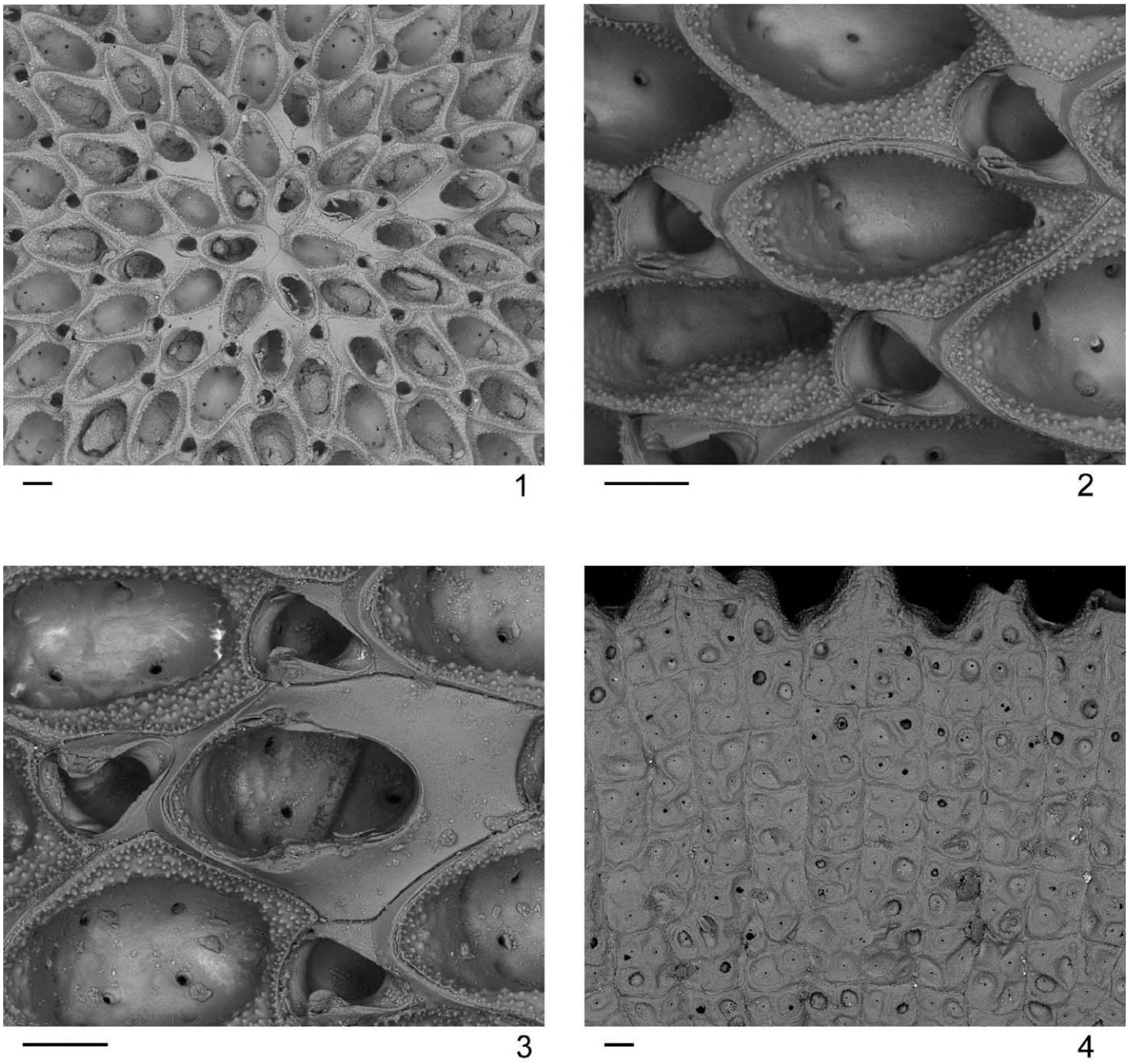

FIGURE 27—*Cupuladria dominicana* n. sp. *1–4*, holotype, USNM542578, Recent, North East coast Santo Domingo, Dominican Republic: *1*, colony center showing autozooids and vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

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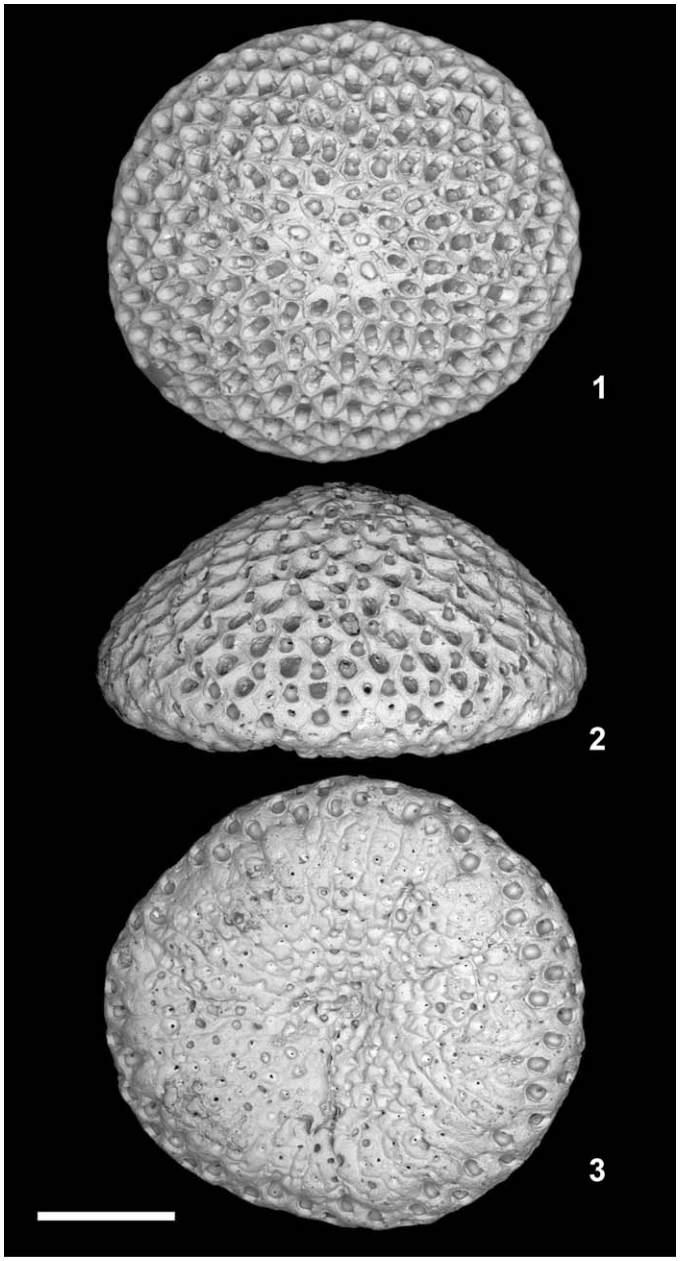

FIGURE *28*—*Cupuladria collyrida* n. sp. *1–3*, holotype, USNM542561, Bowden Formation, Pliocene, Jamaica: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

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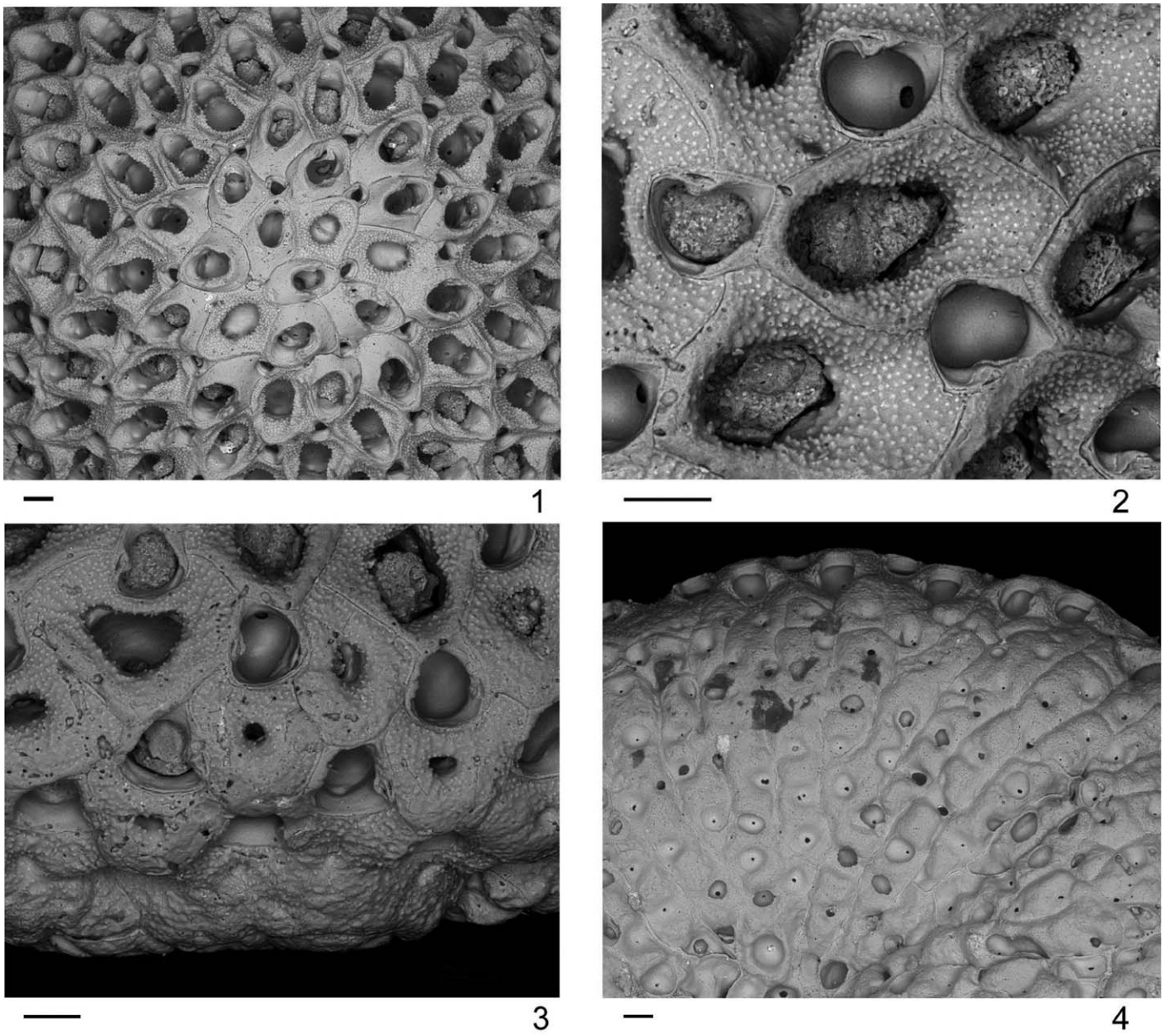

FIGURE 29—*Cupuladria collyrida* n. sp. *1–4*, holotype, USNM542561, Bowden Formation, Pliocene, Jamaica: *1*, colony center showing vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, view of kenozooids at the colony margin; *4*, view of the basal sectors and pores. Scale bar=100 μm.

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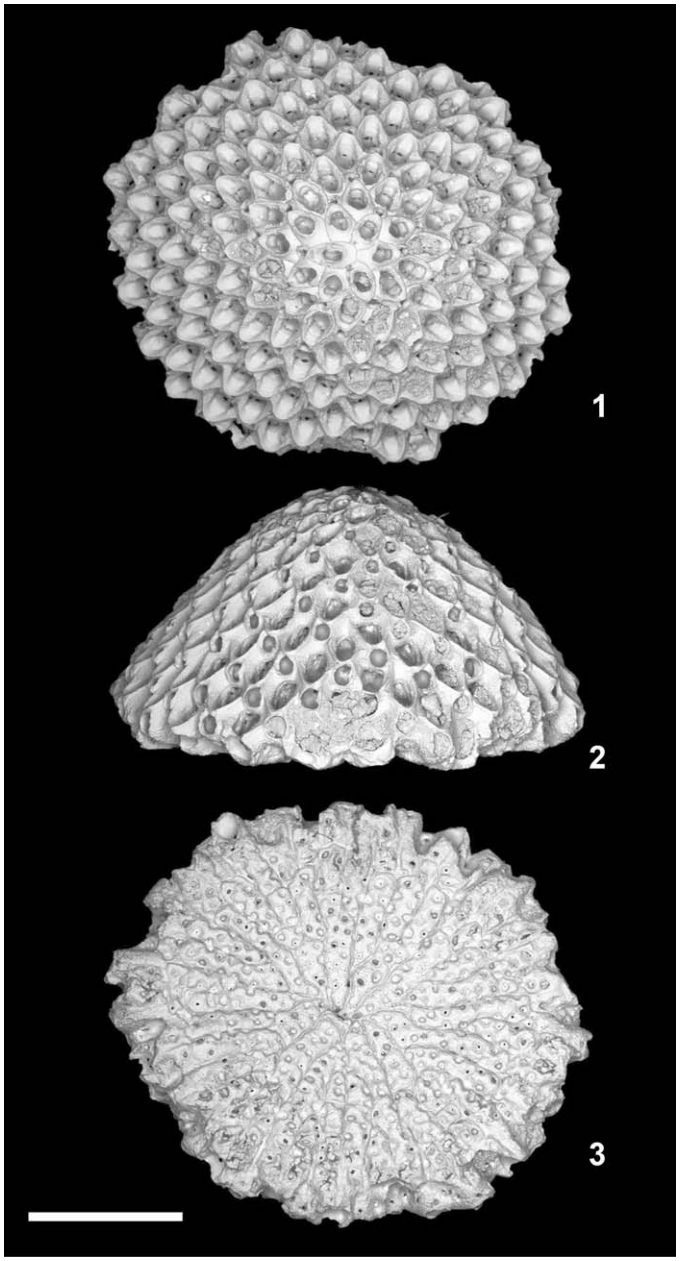

FIGURE *30—Cupuladria planissima* n. sp. *1–3*, holotype, USNM542581, Bastimentos island, late Pliocene, Bocas del Toro, Panama: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

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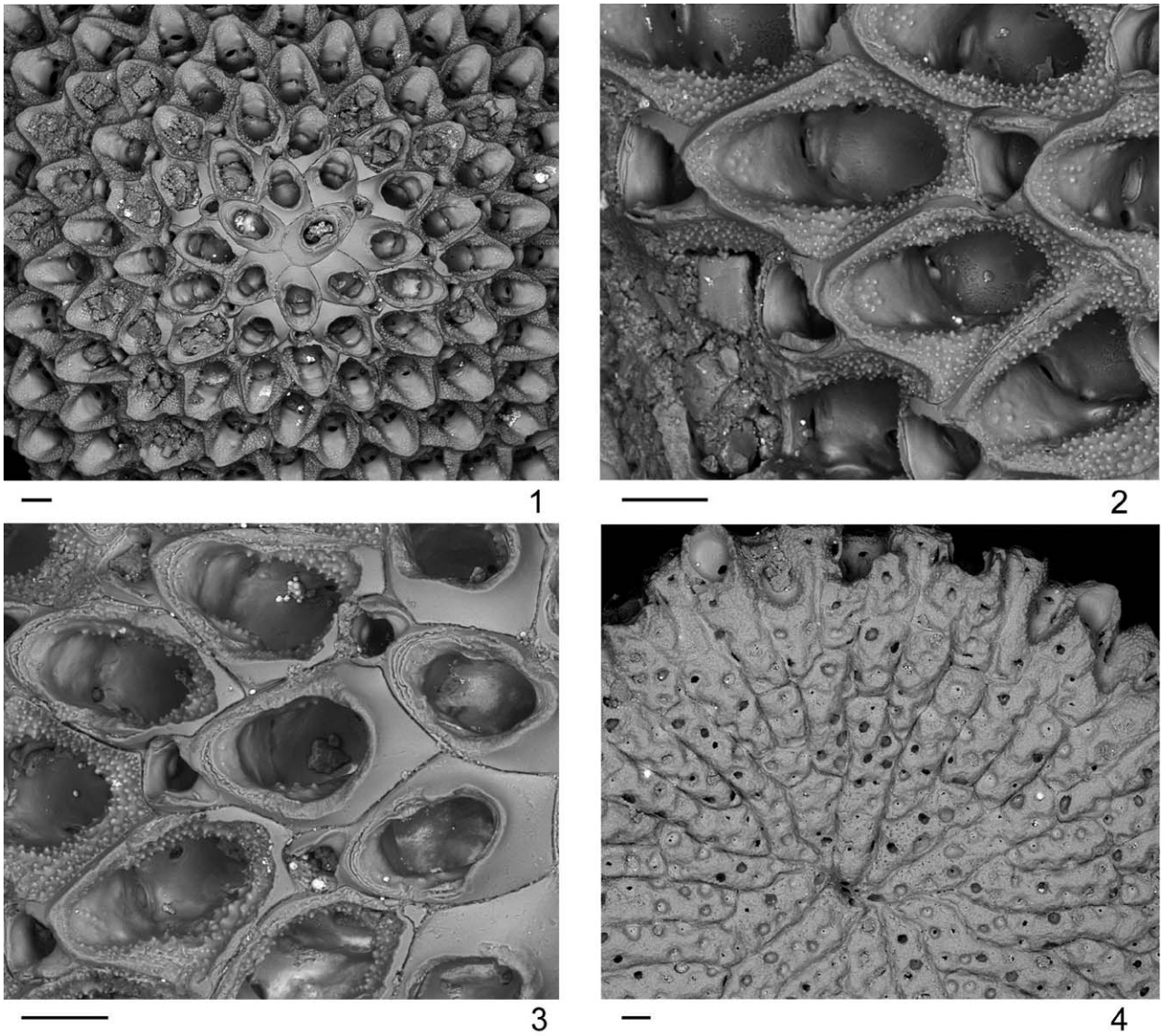

FIGURE 31—*Cupuladria planissima* n. sp. *1–4*, holotype, USNM542581, Bastimentos island, late Pliocene, Bocas del Toro, Panama: *1*, colony center showing vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view of vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

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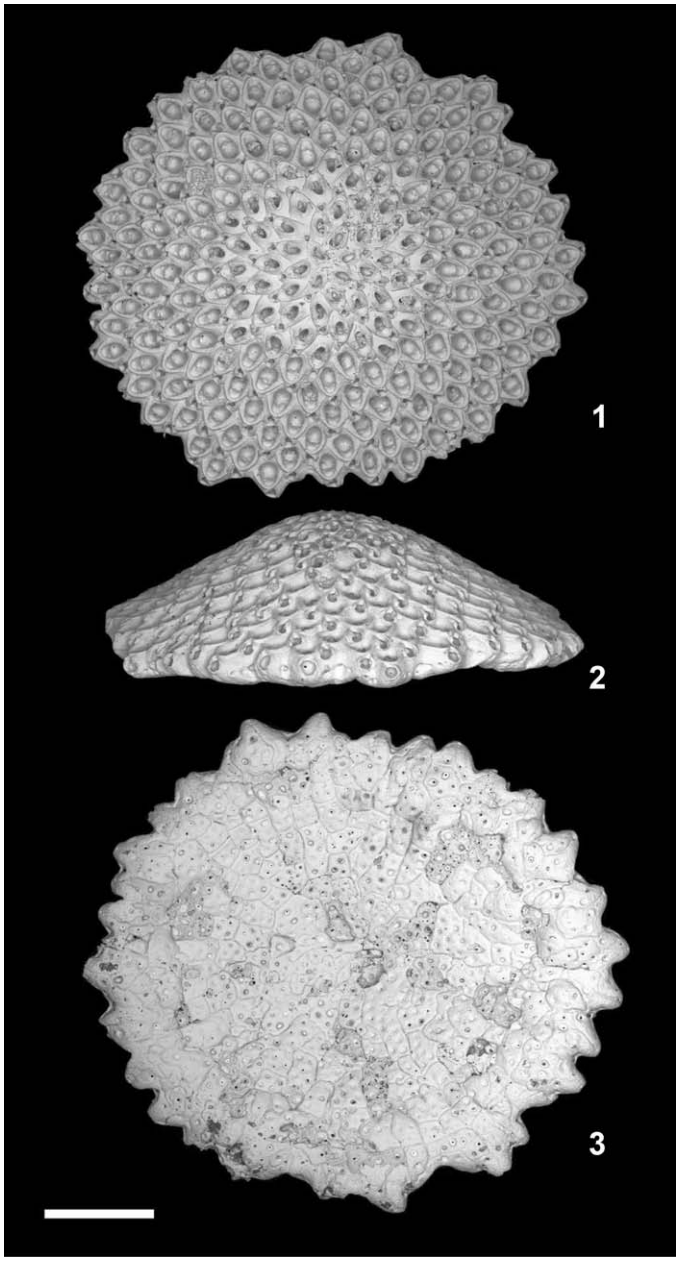

FIGURE 32—*Cupuladria veracruxiensis* n. sp. *1–3*, holotype, USNM542562, PPP2171, Escudo de Veraguas Formation, late Pliocene, Bocas del Toro, Panama: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

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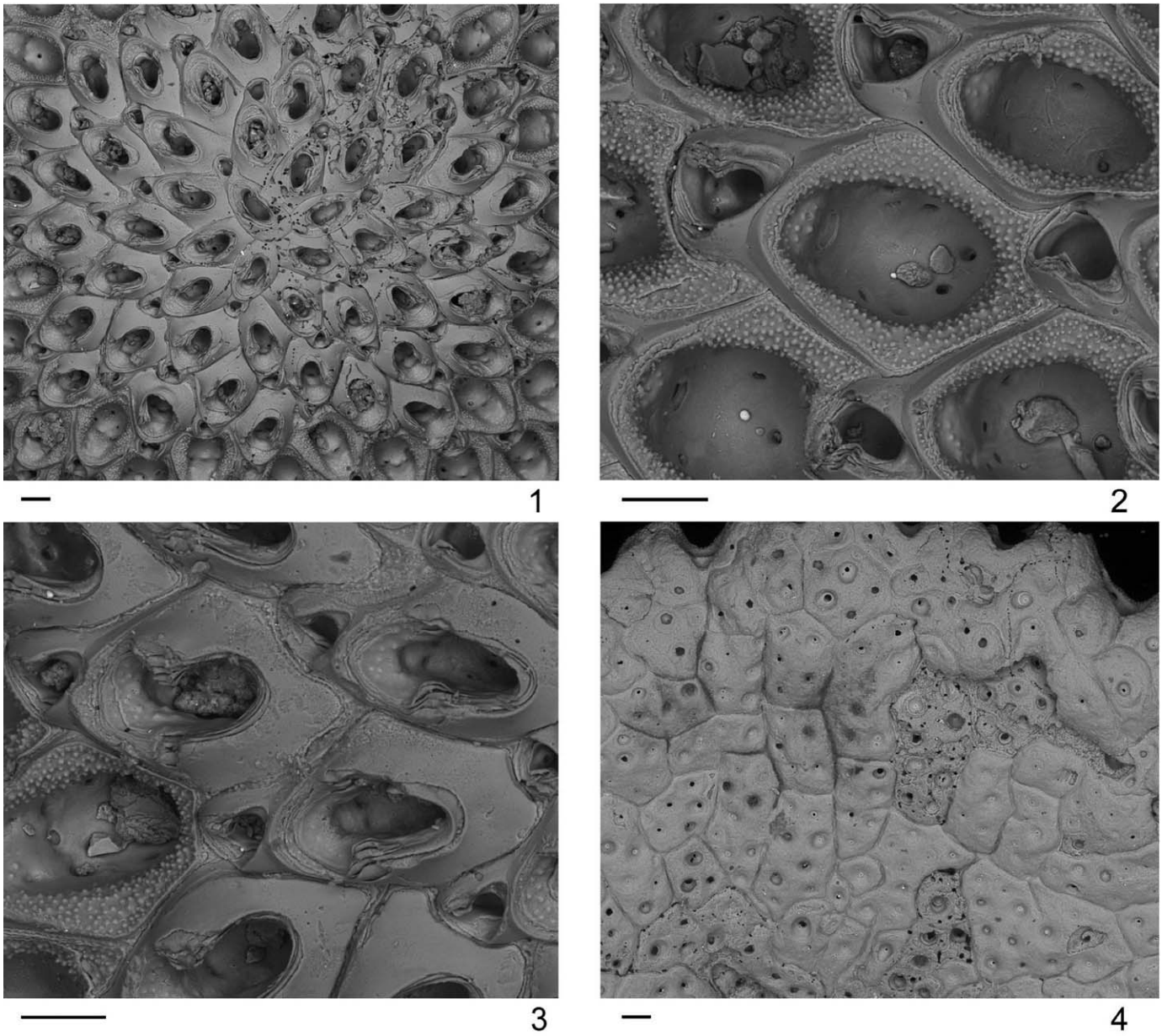

FIGURE 33—*Cupuladria veracruxiensis* n. sp. *1–4*, holotype, USNM542562, PPP2171, Escudo de Veraguas Formation, late Pliocene, Bocas del Toro, Panama: *1*, colony center showing vicarious avicularia; *2*, view of the autozooid and autozooid vibraculum; *3*, closer view vicarious avicularium and vicarious avicularium vibraculum; *4*, view of the basal sectors and pores. Scale bar=100 μm.

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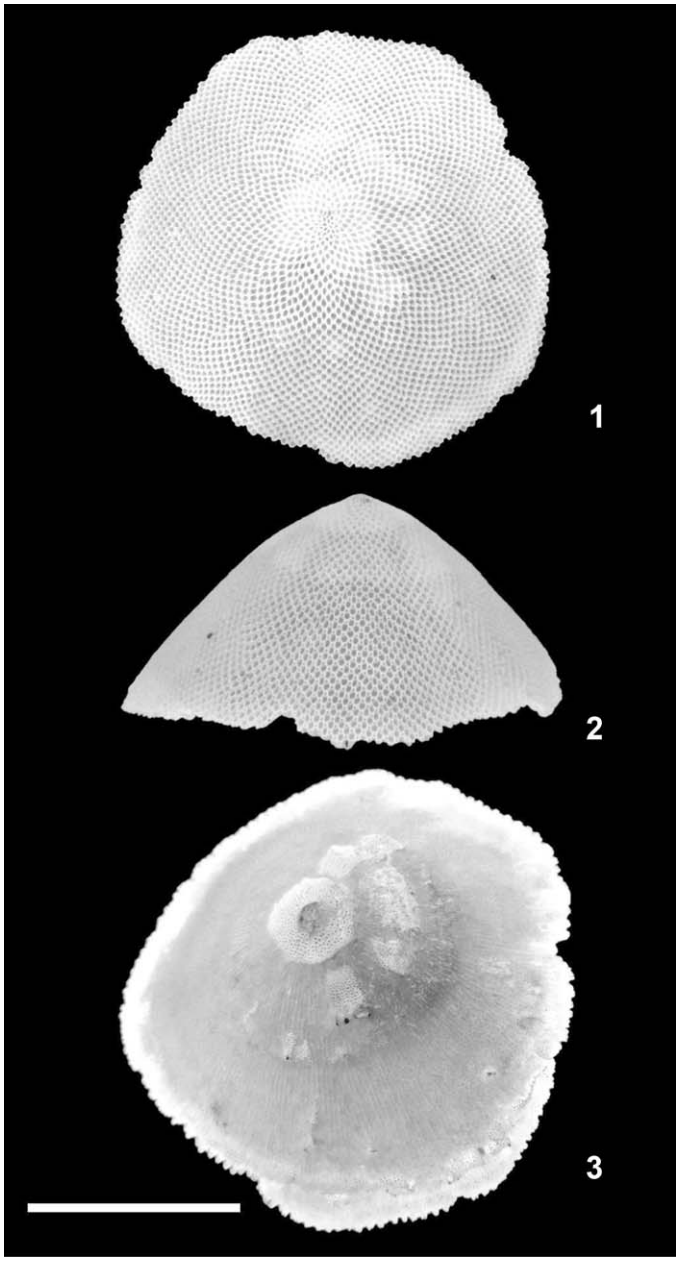

FIGURE *34*—*Cupuladria gigas* n. sp. *1–3*, holotype USNM542584, Recent, Bahia de Almirante, Bocas del Toro, Panama: *1*, colony frontal view; *2*, colony side view; *3*, colony basal view. Scale bar=1 mm.

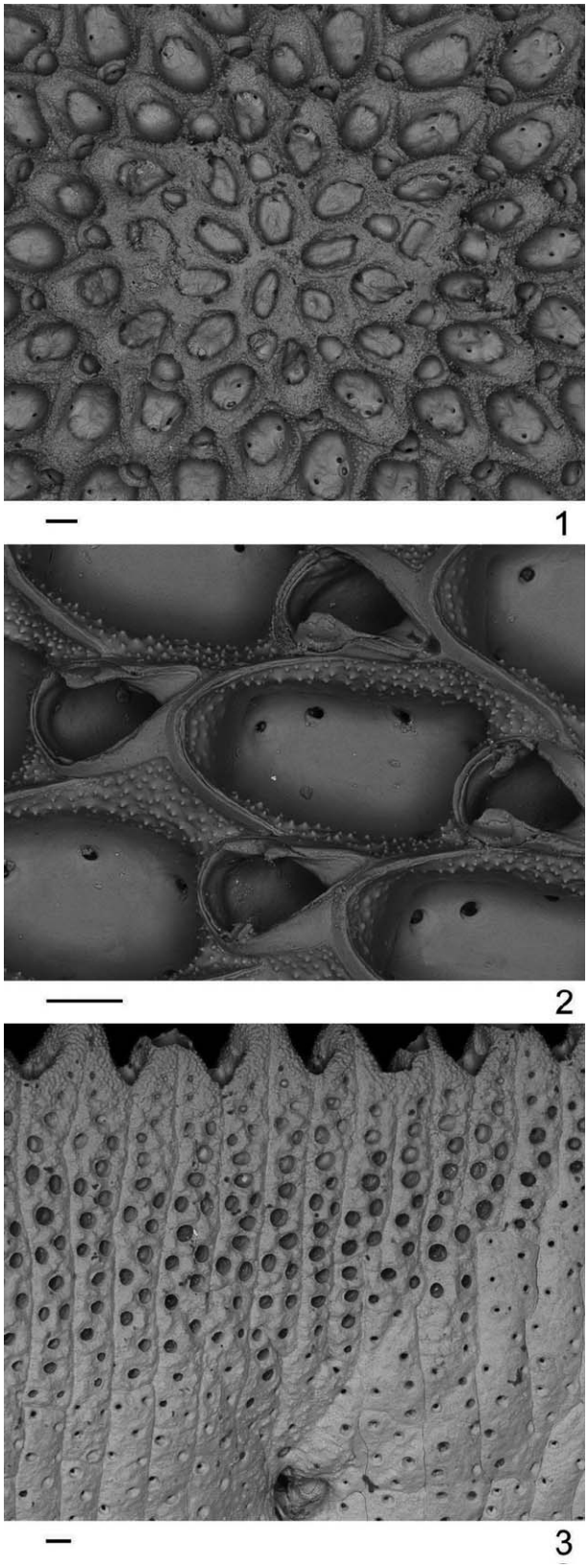

FIGURE *35*—*Cupuladria gigas* n. sp. *1–3*, holotype USNM542584, Recent, Bahia de Almirante, Bocas del Toro, Panama: *1*, colony center showing autozooids; *2*, view of the autozooid and autozooid vibraculum; *3*, view of the basal sectors and pores. Scale bar=100 μm.

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Appendix 1—Characters and character states used in cladistic analysis of extant and fossil vicarious and non–vicarious *Cupuladria* species, plus extant *Discoporella* species. Coding was performed on re–scaled values, see text.

Cw	Coded states: 0=0.606–0.902, 1=0.935, 2=0.985–1.024, 4=1.149, 6=1.252–1.315
Ch	Coded states: 0=0.048, 2=0.233–0.474, 4=0.555–0.566, 5=0.627, 6=0.646–0.737, 8=0.951
Rahw	Coded states: 0=0.006, 2=0.068–0.115, 3=0.122, 4=0.142–0.157, 5=0.174, 6=0.184–0.187, 8=0.219
Csur	Coded states: 0=0.974–1.167, 2=1.346–1.739, 3=1.758, 4=1.918, 5=1.944–1.952, 7=2.191, 9=2.405, b=2.593
C*i*	Coded states: 0=0.000, 2=0.022–0.057, 4=0.081
RaZV	Coded states: 0=0.034–0.041, 1=0.061, 2=0.097–0.102, 4=0.187–0.224, 6=0.301–0.325, 8=0.389–0.423, a=0.477, c=0.602
Zl	Coded states: 0=0.132–0.174, 1=0.184, 2=0.193, 3=0.199–0.203
Zw	Coded states: 0=0.102–0.137, 1=0.144, 2=0.149
ZwZl	Coded states: 0=0.197, 2=0.219–0.283
Ol	Coded states: 0=0.038–0.053, 2=0.087–0.105, 4=0.116–0.123, 5=0.132, 6=0.137, 7=0.142, 9=0.158
Ow	Coded states: 0=0.044–0.074, 1=0.078, 2=0.082, 4=0.090–0.092
OwOl	Coded states: 0=0.169–0.218, 2=0.306, 4=0.334–0.359, 6=0.405
Al	Coded states: 0=0.000, 2=0.060, 3=0.061, 4=0.069–0.090, 6=0.103–0.104
Aw	Coded states: 0=0.000, 2=0.052–0.080
AwAl	Coded states: 0=0.000, 2=0.237–0.287
Alo	Coded states: 0=0.000, 2=0.039, 3=0.043, 4=0.049, 5=0.052–0.070, 7=0.078, 9=0.088
Awo	Coded states: 0=0.000, 2=0.027, 4=0.032, 5=0.037, 6=0.038–0.053
AwoAlo	Coded states: 0=0.000, 2=0.196, 4=0.218–0.278
RaOlZl	Coded states: 0=0.088–0.107, 2=0.212–0.245
RaOwZw	Coded states: 0=0.140–0.168, 1=0.179, 2=0.184–0.216
RaAlZl	Coded states: 0=0.000, 2=0.131–0.198
RaAwZw	Coded states: 0=0.000, 2=0.162–0.202
RaAloAl	Coded states: 0=0.000, 2=0.205–0.262
RaAwoAw	Coded states: 0=0.000, 2=0.179, 4=0.200–0.239
RaAloOl	Coded states: 0=0.000, 2=0.122, 4=0.154–0.214, 6=0.271, 7=0.286, 8=0.303–0.310, 9=0.327, a=0.338, c=0.423
RaAwoOw	Coded states: 0=0.000, 2=0.176–0.268
Zcp	Coded states: 0=0.000–0.030, 2=0.301
Vcp	Coded states: 0=0.000–0.015, 2=0.043
Nope	Coded states: 0=0.000, 2=0.797–0.828, 4=0.874–0.885, 6=0.922, 8=0.953
Opew	Coded states: 0=0.000, 2=0.013, 4=0.016, 6=0.018–0.022
Opesp	Coded states: 0=0.000–0.059, 2=0.350, 3=0.414, 4=0.470–0.471, 5=0.517, 6=0.551
Npor	Coded states: 0=0.000–0.112, 2=0.219–0.283
NV	Coded states: 0=0.000, 2=0.911–1.640, 3=1.742, 4=1.861
Vl	Coded states: 0=0.000, 2=0.124–0.134, 4=0.147–0.155, 5=0.161, 6=0.164, 8=0.190
Vw	Coded states: 0=0.000, 2=0.096, 3=0.097, 4=0.103–0.111, 5=0.115, 6=0.120
VwVl	Coded states: 0=0.000, 2=0.201–0.208, 4=0.222–0.245, 6=0.258
VOl	Coded states: 0=0.000, 2=0.076, 3=0.077, 4=0.082, 5=0.083, 6=0.084, 7=0.089, 8=0.090, 9=0.092, a=0.096, b=0.100, c=0.104, d=0.106–0.109
VOw	Coded states: 0=0.000, 2=0.044–0.063
VOwVOl	Coded states: 0=0.000, 2=0.178–0.181, 3=0.183, 4=0.193, 5=0.195–0.206
VAl	Coded states: 0=0.000, 2=0.057–0.059, 4=0.064–0.069, 5=0.072, 6=0.075, 7=0.078–0.083
VAw	Coded states: 0=0.000, 2=0.048–0.050, 4=0.054–0.066
VAwVAl	Coded states: 0=0.000, 2=0.240–0.280
VAlo	Coded states: 0=0.000, 2=0.039–0.0460, 4=0.051–0.054, 6=0.061–0.064
VAwo	Coded states: 0=0.000, 2=0.030–0.039, 4=0.042–0.045
VAwo VAlo	Coded states: 0=0.000, 2=0.222–0.253
RaVOlVl	Coded states: 0=0.000, 2=0.175, 3=0.183, 4=0.189, 5=0.196–0.205, 6=0.210, 7=0.217
RaVOwVw	Coded states: 0=0.000, 2=0.144, 3=0.153, 4=0.156–0.175, 5=0.179, 6=0.186
RaVAlVl	Coded states: 0=0.000, 2=0.129, 4=0.150–0.173
RaVAwVw	Coded states: 0=0.000, 2=0.163–0.195
RaVAloVAl	Coded states: 0=0.000, 2=0.213–0.244
RaVAwoVAw	Coded states: 0=0.000, 2=0.196–0.226
RaVAloVOl	Coded states: 0=0.000, 2=0.167–0.200
RaVAwoVOw	Coded states: 0=0.000, 2=0.197–0.240, 4=0.261
Asec	Coded states: 0=0.000, 2=0.021–0.030, 4=0.052–0.064, 6=0.085–0.098, 8=0.127–0.129
Psec	Coded states: 0=0.000, 2=0.362, 4=0.537, 6=0.622–0.712, 8=0.900, a=1.003, b=1.050, c=1.112–1.159
Graden	Coded states: 0=0.000, 2=0.190, 4=0.221–0.232, 6=0.296, 8=0.329–0.347, a=0.400
Ken	Coded states: 0=0.000–0.006, 2=0.301

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Appendix 2—Measurements of zoarial and zooidal characters (in mm) for *A. leucocypha*, *C. monotrema* and the eight species described in Herrera Cubilla et al. (2006) including additional fossil and extant specimens. Refer to Table 1 for character names.

Characters	*A. leucocypha*					*C. monotrema*					*C. pacificiensis*				
	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD
Cw	3	8.667	8.000	9.000	0.577	7	5.821	4.200	6.750	0.978	20	5.494	4.225	7.625	0.865
Ch	3	0.116	0.098	0.126	0.016	7	1.486	0.400	2.200	0.540	20	1.365	0.400	2.300	0.420
Rahw	3	0.013	0.012	0.014	0.001	7	0.249	0.095	0.338	0.077	20	0.246	0.089	0.330	0.054
Csur	3	56.972	47.664	69.151	11.028	7	30.856	14.105	40.076	10.070	20	27.167	16.126	53.336	9.499
C*i*	3	0.000	0.000	0.000	0.000	7	0.105	0.087	0.132	0.018	20	0.082	0.037	0.163	0.034
RaZV	3	3.000	3.000	3.000	0.000	7	0.643	0.375	1.000	0.244	20	0.600	0.125	0.875	0.184
Zl	3	0.410	0.323	0.494	0.086	7	0.420	0.386	0.468	0.032	20	0.462	0.381	0.554	0.048
Zw	3	0.287	0.228	0.338	0.056	7	0.303	0.275	0.321	0.016	20	0.321	0.271	0.383	0.032
Ol	3	0.313	0.239	0.378	0.070	7	0.273	0.247	0.331	0.030	20	0.327	0.286	0.378	0.026
Ow	3	0.186	0.135	0.216	0.044	7	0.163	0.131	0.188	0.020	20	0.168	0.143	0.195	0.013
Al	3	0.000	0.000	0.000	0.000	7	0.202	0.174	0.253	0.027	20	0.206	0.171	0.231	0.016
Aw	3	0.000	0.000	0.000	0.000	7	0.178	0.147	0.233	0.029	20	0.159	0.110	0.192	0.016
Alo	3	0.000	0.000	0.000	0.000	7	0.155	0.126	0.185	0.021	20	0.137	0.103	0.159	0.015
Awo	3	0.000	0.000	0.000	0.000	7	0.109	0.091	0.141	0.018	20	0.108	0.090	0.125	0.011
Zcp	3	0.000	0.000	0.000	0.000	7	0.000	0.000	0.000	0.000	20	0.100	0.000	1.000	0.308
Vcp	3	0.000	0.000	0.000	0.000	7	0.000	0.000	0.000	0.000	20	0.050	0.000	1.000	0.224
NV	3	0.000	0.000	0.000	0.000	7	38.286	5.000	81.000	28.129	20	13.908	1.000	32.000	8.540
Vl	3	0.000	0.000	0.000	0.000	7	0.413	0.380	0.525	0.051	20	0.421	0.331	0.536	0.062
Vw	3	0.000	0.000	0.000	0.000	7	0.287	0.248	0.355	0.035	20	0.281	0.212	0.364	0.046
VOl	3	0.000	0.000	0.000	0.000	7	0.216	0.197	0.290	0.033	20	0.237	0.214	0.273	0.017
VOw	3	0.000	0.000	0.000	0.000	7	0.113	0.093	0.151	0.021	20	0.134	0.102	0.160	0.014
VAl	3	0.000	0.000	0.000	0.000	7	0.170	0.153	0.201	0.017	20	0.174	0.145	0.225	0.021
VAw	3	0.000	0.000	0.000	0.000	7	0.153	0.137	0.181	0.014	20	0.137	0.120	0.178	0.014
VAlo	3	0.000	0.000	0.000	0.000	7	0.125	0.094	0.157	0.021	20	0.112	0.076	0.149	0.021
VAwo	3	0.000	0.000	0.000	0.000	7	0.092	0.074	0.123	0.016	20	0.083	0.059	0.120	0.014
Asec	3	0.000	0.000	0.000	0.000	7	0.051	0.040	0.087	0.017	20	0.060	0.033	0.076	0.011
Psec	3	0.000	0.000	0.000	0.000	7	1.352	1.000	2.557	0.581	20	3.884	2.776	5.542	0.746
Ken	3	0.000	0.000	0.000	0.000	7	0.000	0.000	0.000	0.000	20	0.000	0.000	0.000	0.000

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Appendix 2—Extended.

C. cheethami					*C. biporosa*					*C. exfragminis*				
N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD
5	7.655	6.600	9.050	0.912	8	9.429	7.200	11.775	1.938	36	6.066	3.050	9.250	1.506
5	1.600	1.000	2.250	0.486	8	4.138	2.500	6.300	1.623	36	1.061	0.200	2.100	0.512
5	0.206	0.152	0.249	0.041	8	0.425	0.341	0.543	0.082	36	0.171	0.044	0.317	0.065
5	50.671	35.753	71.849	13.560	8	98.019	49.576	157.493	46.805	36	32.711	7.690	69.435	15.691
5	0.053	0.031	0.110	0.032	8	0.098	0.043	0.273	0.074	36	0.080	0.027	0.123	0.027
5	1.125	0.750	2.000	0.500	8	0.641	0.375	0.875	0.170	36	2.000	2.000	2.000	0.000
5	0.597	0.540	0.666	0.045	8	0.436	0.387	0.463	0.026	36	0.444	0.359	0.546	0.045
5	0.340	0.309	0.378	0.031	8	0.319	0.259	0.466	0.066	36	0.314	0.258	0.388	0.033
5	0.438	0.394	0.454	0.025	8	0.309	0.272	0.345	0.026	36	0.311	0.272	0.389	0.025
5	0.208	0.178	0.249	0.027	8	0.181	0.156	0.212	0.022	36	0.168	0.123	0.207	0.019
5	0.215	0.197	0.231	0.012	8	0.230	0.207	0.262	0.019	36	0.205	0.150	0.265	0.023
5	0.165	0.145	0.190	0.019	8	0.176	0.159	0.197	0.012	36	0.168	0.127	0.212	0.018
5	0.142	0.132	0.157	0.009	8	0.158	0.143	0.182	0.012	36	0.150	0.112	0.188	0.018
5	0.103	0.092	0.119	0.011	8	0.118	0.105	0.132	0.010	36	0.109	0.084	0.137	0.014
5	0.000	0.000	0.000	0.000	8	0.093	0.000	0.741	0.262	36	0.000	0.000	0.000	0.000
5	0.000	0.000	0.000	0.000	8	0.000	0.000	0.000	0.000	36	0.000	0.000	0.000	0.000
5	10.200	1.000	23.000	8.701	8	29.500	4.000	75.000	24.071	36	12.500	1.000	50.000	11.421
5	0.548	0.458	0.607	0.062	8	0.411	0.333	0.493	0.049	36	0.404	0.285	0.494	0.055
5	0.318	0.289	0.344	0.024	8	0.290	0.259	0.341	0.026	36	0.287	0.216	0.361	0.036
5	0.272	0.208	0.307	0.038	8	0.246	0.211	0.277	0.019	36	0.231	0.170	0.291	0.028
5	0.153	0.137	0.166	0.011	8	0.140	0.120	0.156	0.013	36	0.133	0.097	0.190	0.021
5	0.189	0.155	0.218	0.024	8	0.198	0.175	0.240	0.024	36	0.181	0.127	0.227	0.022
5	0.144	0.130	0.161	0.012	8	0.152	0.131	0.190	0.019	36	0.146	0.110	0.187	0.019
5	0.134	0.098	0.150	0.021	8	0.128	0.116	0.157	0.014	36	0.130	0.087	0.167	0.018
5	0.089	0.073	0.109	0.013	8	0.093	0.074	0.111	0.012	36	0.091	0.064	0.117	0.013
5	0.071	0.057	0.092	0.015	8	0.051	0.039	0.068	0.009	36	0.057	0.036	0.087	0.011
5	3.311	2.634	4.144	0.709	8	3.439	2.565	5.071	0.950	36	3.498	2.302	5.082	0.819
5	0.000	0.000	0.000	0.000	8	0.000	0.000	0.000	0.000	36	0.000	0.000	0.000	0.000

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Appendix 2—Extended.

C. incognita					*C. multesima*					*C. surinamensis*					*C. panamensis*				
N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD	N	Mean	Min	Max	SD
25	4.685	3.100	6.825	0.920	12	4.181	3.050	5.625	0.929	48	5.324	1.050	9.900	1.953	52	6.347	3.950	10.250	1.633
25	1.816	0.800	2.700	0.532	12	2.732	1.800	3.950	0.616	48	1.477	0.200	2.500	0.574	52	3.290	2.100	4.800	0.670
25	0.391	0.198	0.581	0.108	12	0.658	0.541	0.824	0.093	48	0.287	0.062	0.533	0.084	52	0.544	0.293	0.923	0.151
25	22.547	8.983	43.246	8.474	12	23.650	12.051	42.850	10.093	48	28.826	1.196	83.033	19.531	52	47.744	19.771	108.769	20.222
25	0.115	0.069	0.177	0.033	12	0.104	0.030	0.154	0.034	48	0.070	0.019	0.239	0.041	52	0.083	0.033	0.157	0.033
25	0.200	0.000	2.000	0.439	12	0.115	0.000	0.625	0.203	48	1.062	0.250	2.000	0.307	52	1.017	0.875	2.000	0.140
25	0.392	0.348	0.446	0.027	12	0.385	0.347	0.418	0.021	48	0.529	0.404	0.688	0.058	52	0.561	0.437	0.759	0.064
25	0.321	0.261	0.413	0.044	12	0.327	0.238	0.426	0.043	48	0.365	0.241	0.471	0.051	52	0.410	0.323	0.565	0.053
25	0.249	0.189	0.286	0.024	12	0.256	0.225	0.300	0.021	48	0.373	0.258	0.497	0.051	52	0.389	0.275	0.667	0.064
25	0.144	0.119	0.170	0.012	12	0.149	0.130	0.170	0.011	48	0.207	0.120	0.264	0.032	52	0.236	0.168	0.381	0.033
25	0.209	0.161	0.271	0.027	12	0.222	0.187	0.249	0.021	48	0.230	0.159	0.345	0.039	52	0.269	0.189	0.408	0.037
25	0.181	0.145	0.215	0.022	12	0.185	0.151	0.214	0.017	48	0.171	0.119	0.250	0.027	52	0.202	0.150	0.387	0.035
25	0.156	0.121	0.214	0.023	12	0.146	0.112	0.194	0.020	48	0.175	0.105	0.269	0.037	52	0.197	0.108	0.252	0.028
25	0.120	0.091	0.169	0.018	12	0.112	0.098	0.147	0.014	48	0.113	0.068	0.157	0.019	52	0.129	0.098	0.166	0.016
25	0.040	0.000	1.000	0.200	12	0.000	0.000	0.000	0.000	48	0.083	0.000	1.000	0.279	52	0.019	0.000	1.000	0.139
25	0.000	0.000	0.000	0.000	12	0.000	0.000	0.000	0.000	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	48.960	5.000	102.000	31.085	12	39.250	7.000	139.000	36.849	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.363	0.279	0.440	0.040	12	0.361	0.305	0.403	0.029	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.274	0.206	0.336	0.030	12	0.270	0.210	0.327	0.030	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.210	0.157	0.257	0.024	12	0.211	0.183	0.238	0.017	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.119	0.095	0.149	0.015	12	0.123	0.093	0.152	0.018	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.159	0.134	0.193	0.017	12	0.161	0.125	0.210	0.022	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.132	0.095	0.164	0.015	12	0.140	0.118	0.183	0.019	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.110	0.074	0.137	0.018	12	0.103	0.081	0.124	0.012	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.080	0.058	0.098	0.011	12	0.079	0.070	0.101	0.011	48	0.000	0.000	0.000	0.000	52	0.000	0.000	0.000	0.000
25	0.216	0.159	0.347	0.048	12	0.161	0.055	0.234	0.054	48	0.255	0.026	0.456	0.078	52	0.344	0.167	0.599	0.101
25	12.428	7.082	22.538	3.839	12	7.066	4.518	9.459	1.596	48	10.837	2.915	16.660	3.549	52	12.763	5.082	23.450	4.374
25	0.000	0.000	0.000	0.000	12	0.000	0.000	0.000	0.000	48	0.021	0.000	1.000	0.144	52	0.000	0.000	0.000	0.000

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