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NEOGENE CUPULADRIIDAE OF TROPICAL AMERICA. II: TAXONOMY OF RECENT *DISCOPORELLA* FROM OPPOSITE SIDES OF THE ISTHMUS OF PANAMA

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ABSTRACT—We used up to 30 morphological characters to discriminate and describe species of the genus *Discoporella* based on complete colony specimens collected from both coasts of the Isthmus of Panama. The characters included zooidal characters and colony-level characters such as colony size and basal granule density. Species were classified by a series of multivariate cluster and linear discriminant analyses until the majority of specimens were assigned to their putative species with high confidence. In the first phase of the analyses, the colonies were grouped by ocean (Caribbean versus eastern Pacific), discriminated predominantly by colony size and basal granule density, characters that might reflect ecophenotypic responses to different conditions in primary productivity and predation between the two oceans. Further analyses of these two groups separately resulted in the discrimination of seven species. Five new species from the Caribbean (*D. scutella*, *D. peltifera*, *D. bocasdeltoroensis*, *D. terminata* and *D. triangula*), and two from the eastern Pacific (*D. marcusorum* and *D. cookae*). Of these, *D. cookae* had been identified previously as *D. umbellata*, a species once considered cosmopolitan, with a range spanning the Caribbean and eastern Pacific coasts of America. With the exception of one genetically defined clade represented by only two specimens, the correspondence of classification between groups discriminated morphometrically by separate step-wise multivariate analyses and those detected by a previous genetic analysis, ranged from 91% to 100%. In analyses of all specimens combined or separated by ocean, but using the total number of characters, 20% to 30% of the specimens could not be distinguished morphometrically from extremely similar sympatric species or cognate ("geminate") species from the opposite ocean. Diversity was higher in the Caribbean compared to the eastern Pacific, which reflects a similar pattern recently described for the genus *Cupuladria* from the same region.

INTRODUCTION

COLLECTIVELY, SPECIES of free-living bryozoans of the genera *Discoporella* and *Cupuladria* in the family Cupuladriidae are the most common bryozoans found in Recent sediments that have been dredged along the Caribbean and Pacific coasts of the Isthmus of Panama (O'Dea et al., 2004); see Herrera-Cubilla et al. (2006) for an introduction to cupuladriid taxonomy and biology. In addition, these genera are among the most speciose in the Neogene fossil record along the Isthmus, and their record is more nearly complete there than for any other bryozoan clade (Coates et al., 1992; Cheetham et al., 1999; Cheetham and Jackson, 2000). Because of the well-dated timing of final closure of the Isthmus 3.5–3.1 Ma (Coates and Obando, 1996), and the divergence in the marine environments of the Caribbean and tropical eastern Pacific that began prior to final closure and was largely complete by 3 Ma (Vermeij, 1978; Duque-Caro, 1990; Jackson and Budd, 1996; Jackson and D'Croz, 1997), the Isthmus provides an ideal setting for studying how geographical isolation and environmental change affect lineages of marine organisms (Cunningham and Collins, 1994; Lessios, 1998; Dick et al., 2003). Clearly, such studies are facilitated by choosing a taxonomic group with a diverse lineage through time and as complete a fossil record as possible. The cupuladriid bryozoans meet these requirements; however a reliable taxonomy is required to accurately distinguish Recent species from one another and to establish continuity of Recent taxa with fossil lineages. Moreover, to understand patterns and processes of speciation regardless of phylogenetic methodology, it is necessary to know how well morphospecies reflect underlying genetic divergence (Jackson and Cheetham, 1990, 1994). In a previous paper (Dick et al., 2003), we used DNA sequence data to examine species boundaries and phylogenetic relationships among living cupuladriid bryozoans from tropical America. We then conducted a morphometric analysis of the taxonomy of *Cupuladria* using genetically identified (VOUCHER) specimens and a much larger collection of intact (SURVEY) specimens from both sides of the Isthmus of Panama (Herrera-Cubilla et al., 2006). In the present paper, we apply similar morphologically based multivariate analyses to the taxonomy of VOUCHER and SURVEY specimens of *Discoporella* from the same region. The next paper in this series will develop a morphologically based cladistic framework for the entire Recent tropical American cupuladriid fauna. Within this framework, we will be better able to interpret the fossil record in the context of the phylogeny of the abundant Neogene cupuladriids from tropical America.

MATERIAL AND METHODS

Collections.—For this work we used SURVEY and VOUCHERS specimens of *Discoporella* as we did in a previous study of the genus *Cupuladria* (Herrera-Cubilla et al., 2006). Both SURVEY and VOUCHER specimens were obtained by dredging along both coasts of Panama during cruises of the R/V Urraca between 1995 and 1998 (O'Dea et al., 2004; Herrera-Cubilla et al., 2006) and 1999 and 2000 (Dick et al., 2003). The 150 SURVEY specimens came from 30 of the dredge samples, from the Gulf of Panama and Gulf of Chiriqui on the Pacific side and from the Bocas del Toro region westward to central Panama and the San Blas archipelago on the Caribbean side. These specimens were separated from the substrate by sieving with a 2 mm mesh screen and were placed in bags for subsequent washing, drying, and sorting into major taxa in the laboratory.

The 70 VOUCHER specimens of *Discoporella* were identified genetically by sequencing a fragment of the 16S mtrRNA gene (see Dick et al., 2003).

Taxonomic characters.—To identify the 150 SURVEY colonies we first sorted them qualitatively into seven groups morphologically resembling VOUCHER specimens which have been defined as seven Haplotype Groups (HG) by the molecular analysis (Dick et al., 2003). The principal morphological criteria for this preliminary sorting were: autozooid size; number and size of opesiules; opesial morphology (spinous or occluded); number of pores in the frontal shield; basal ornamentation; and mode of colony growth (determinate or semi-determinate). The size and shape of the colony were also used after the appropriate estimation of

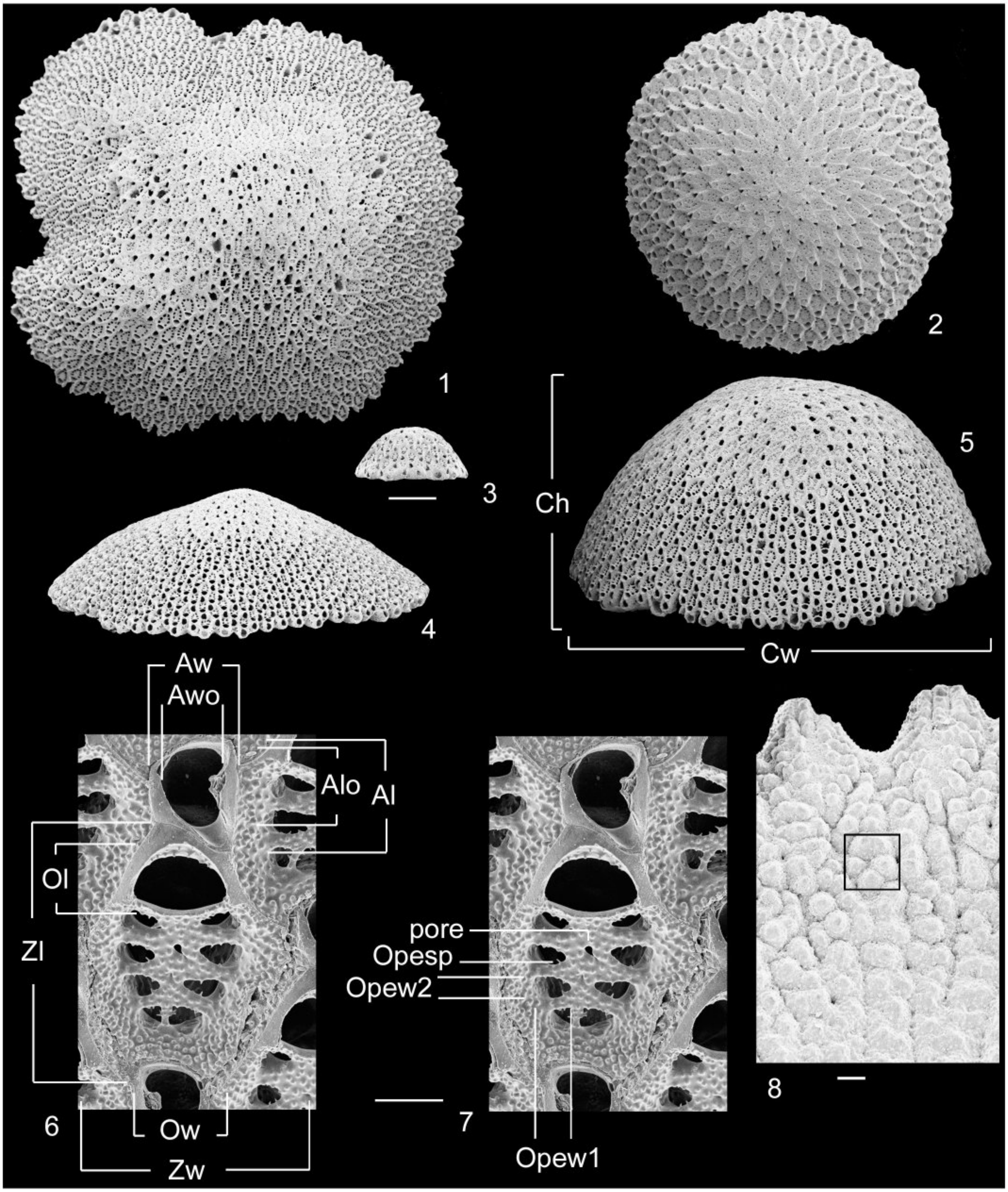

FIGURE *1*—Morphological characters used for discrimination of *Discoporella* morphospecies. *1–5*, Colonies of different shapes and mode of reproduction; *1*, *5*, *D. cookae*, USNM530330, USNM530331; *2, D. scutella*, USNM530297; *3*, *D. triangula*, USNM530315; *4*, *D. bocasdeltoroensis*, USNM530319. *2–4*, Colonies that originated by sexual reproduction; *1*, *5*, colonies regenerated from fragmentation. *5*, *D. cookae*, size of the colony. Bar scale = 1 mm. *6*, *7*, *D. marcusorum*, USNM530326, characters of autozooid and vibracula avicularium; *7*, opesiules, pores and spines; *8, D. marcusorum*, USNM530327, basal granular density (outlined). Bar scale 100 μm. All these characters as well as ratio characters are defined in Table 1.

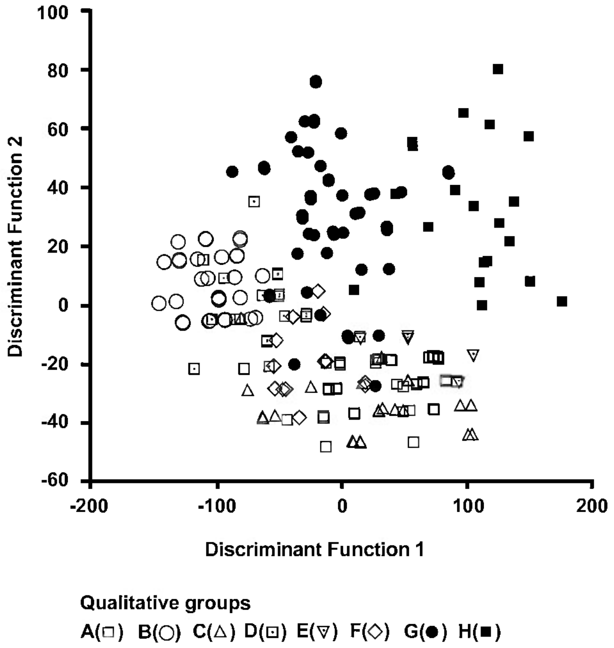

FIGURE 2—The Canonical Discriminant Plot for all 150 SURVEY colonies entered as "groups" based on 30 characters. Each point represents a colony. The groups were identified qualitatively, before quantitative analyses: A–E (open symbols, below), Caribbean specimens; F–G (blackened symbols, above), eastern Pacific specimens.

TABLE 1—The morphological characters used to discriminate *Discoporella* morphospecies.

Cw	Colony diameter
Ch	Colony height
Ra_hw	Colony height-diameter ratio
C_sur	Colony surface area*
C*i*	Calcification index
Zl	Autozooid length
Zw	Autozooid width
ZwZl	Autozooid width-length ratio
Ol	Autozooid opesia length
Ow	Autozooid opesia width
OwOl	Autozooid opesia width-length ratio
Al	Autozooid vibracula length
Aw	Autozooid vibracula width
AwAl	Autozooid vibracula width-length ratio
Alo	Autozooid vibracula opesia length
Awo	Autozooid vibracula opesia width
AwoAlo	Autozooid vibracula opesia width-length ratio
Ra_OlZl	Ratio opesia length-autozooid length
Ra_OwZw	Ratio opesia width-autozooid width
Ra_AlZl	Ratio autozooid vibracula length-autozooid length
Ra_AwZw	Ratio autozooid vibracula width-autozooid width
Ra_AloAl	Ratio autozooid vibracula opesia length-autozooid vibracula length
Ra_AwoAw	Ratio autozooid vibracula opesia width-autozooid vibracula width
Ra_AloOl	Ratio autozooid vibracula opesia length-autozooid opesia length
Ra_AwoOw	Ratio autozooid vibracula opesia width-autozooid opesia width
Nope	Number of opesiules
Opew	Opesiule maximum average diameter (calculated on Opew1 and Opew2 measured on the bigger opesiule found per autozooid)
Opesp	Opesiule median number of spines per autozooid
Npor	Number of pores in autozooid frontal shield
Graden	Granular density near the margin on the basal side of the colony (calculated as the number of granules in an area of 0.1mm^2)

* The calculations of these two characters are explained in O'Dea et al. (2004).

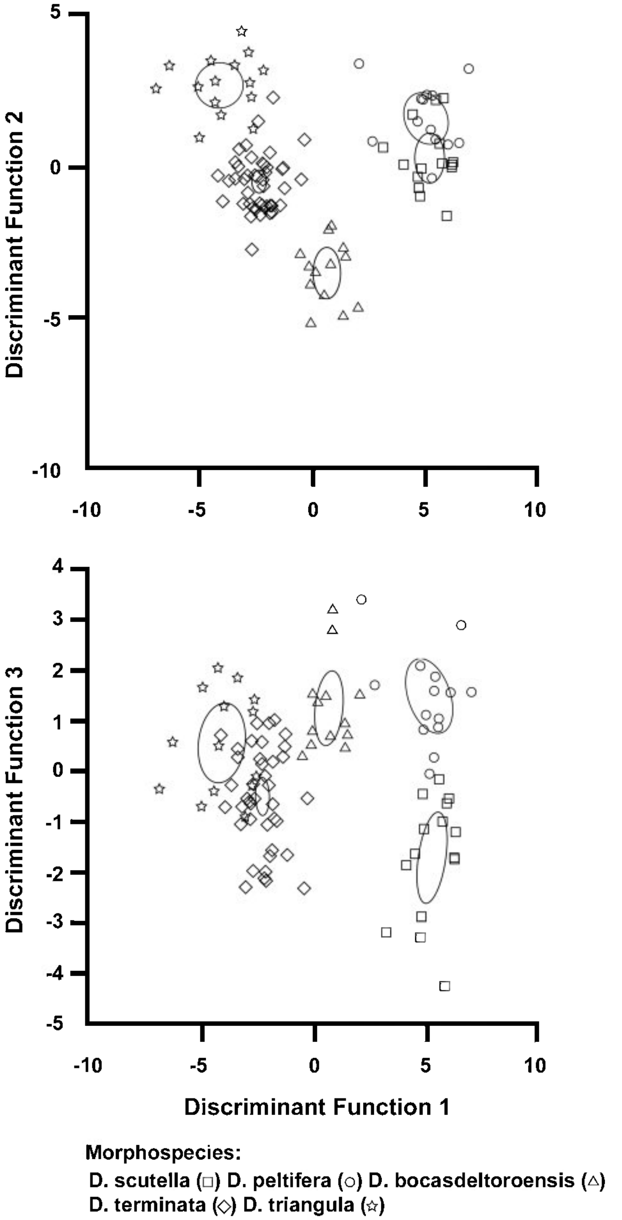

FIGURE 3—Canonical Discriminant Plot based on 30 skeletal morphological characters used for the discrimination of SURVEY *Discoporella* colonies from the Caribbean. Ellipses represent 95% confidence limits of group centroids for the two Discriminant function plots.

TABLE 2—Results for 150 *Discoporella* SURVEY colonies entered as "groups" in a DA based on 30 characters. All characters were transformed like this: $\log_{10}$ (1 + variable), see Methods, and refer to Table 1 for character names. Difference between groups: N = 150, Wilks' Lambda = 0.000, Chi-square = 11,581.12, *P* = 0.0000. Cases correctly classified 99.3%, jackknifed classification 91%.

DF	Eigen value	Cumulative % variance	Characters with largest coefficient
1	8,465.97	0.856	Cw Ra_AloAl Aw
2	1,384.52	0.996	Graden Ra_OlZl Ol

TABLE 3—Results of DA based on 30 characters; for Caribbean SURVEY colonies of *Discoporella*. All characters were transformed like this: $\log_{10}$ (1 + variable), see Methods, and refer to Table 1 for character names. Difference between groups: N = 98, Wilks' Lambda = 0.002, Chi-square = 518.64, P = 0.000. Cases correctly classified 99%, jackknifed classification 91.8%.

DF	Eigen value	Cumulative % variance	Characters with largest coefficient
1	12.18	0.601	C_sur Cw Zl
2	4.89	0.842	ZwZl AwoAlo Awo
3	1.96	0.939	ZwZl Ra_AlZl OwOl

TABLE 4—Results of DA based on 30 characters; for Pacific SURVEY colonies of *Discoporella*. All characters were transformed like this: $\log_{10}$ (1 + variable), see Methods, and refer to Table 1 for character names. Difference between groups: N = 52, Wilks' Lambda = 0.046, Chi-square = 117.20, P = 0.000. Cases correctly classified 100%, jackknifed classification 100%.

DF	Eigen value	Cumulative % variance	Characters with largest coefficient
1	20.85	1.00	Ra_AwZw Ch Aw

these characters for the VOUCHER specimens (see below for details). Specimens that did not resemble any of the VOUCHER clades were sorted into a separate group.

Colony level characters proved useful in high-confidence discrimination of specimens of the genus *Cupuladria* which, like *Discoporella*, exhibits semi-determinate growth (Herrera-Cubilla et al., 2006 and references therein). The use of 15 "shape" characters or ratios calculated between various pairs of the original 15 measured characters (Table 1, Fig. 1), can be considered redundant; however, the results have suggested empirically that new discriminating power has been gained by their addition (see Herrera-Cubilla et al., 2006, and Cheetham et al., 2001). Here we also employed a combination of traditionally used zooidal characters, colony-level characters such as size, shape, dry weight of whole colonies, and the density of the calcified granulate ornamentation on the basal side of the colony (here termed 'basal granule density'; see Table 1, Fig. 1.8).

Colony level characters were measured at a precision of 0.1 mm with a caliper—vernier, and all autozooidal observations and measurements were made with a Leica MZ12 microscope and SigmaScan and SigmaScan Pro image-measurement and automated image analysis software (Jandel Scientific, 1993–1995), at a precision of 0.000001 mm. Weights of colonies for calculation of the calcification index (see O'Dea et al., 2004, p. 151) were measured with a Sartorious Basic Balance (Model B1205-ΦUR) at a precision of 0.001 g. For zooidal measurements we randomly selected three to five autozooids from the zone of astogenetic

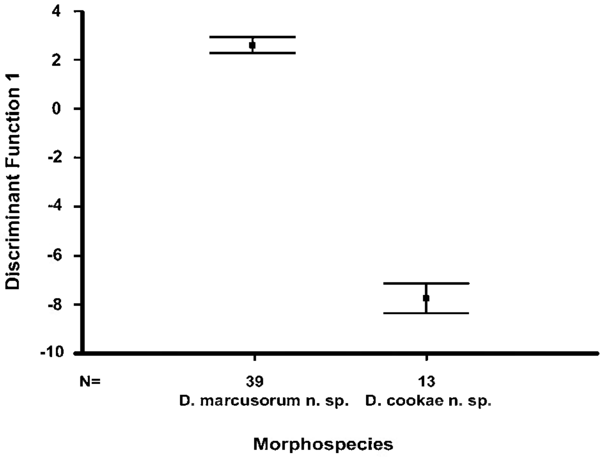

FIGURE 4—Plot of canonical scores from Discriminant Function (1) obtained by a DA based on 30 skeletal morphological characters used for the classification of SURVEY *Discoporella* colonies from the eastern Pacific. Error bars represent 95% confidence limits.

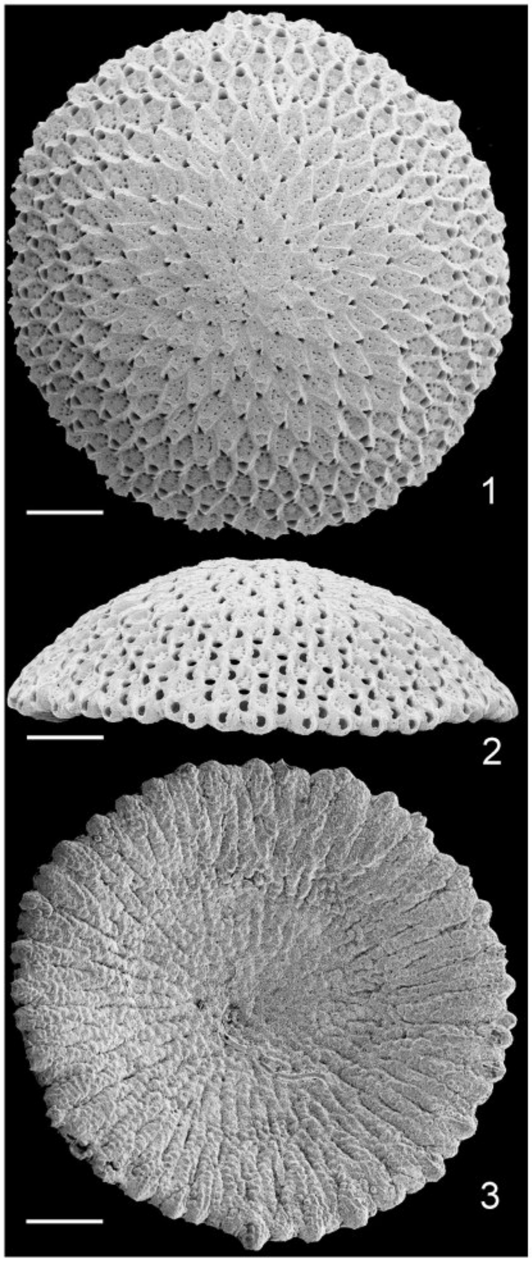

FIGURE 5—*Discoporella scutella* n. sp. *1–3*, USNM530297, San Blas; *1*, colony frontal view; *2*, colony side view; *3*, colony basal view; bar scale = 1 mm.

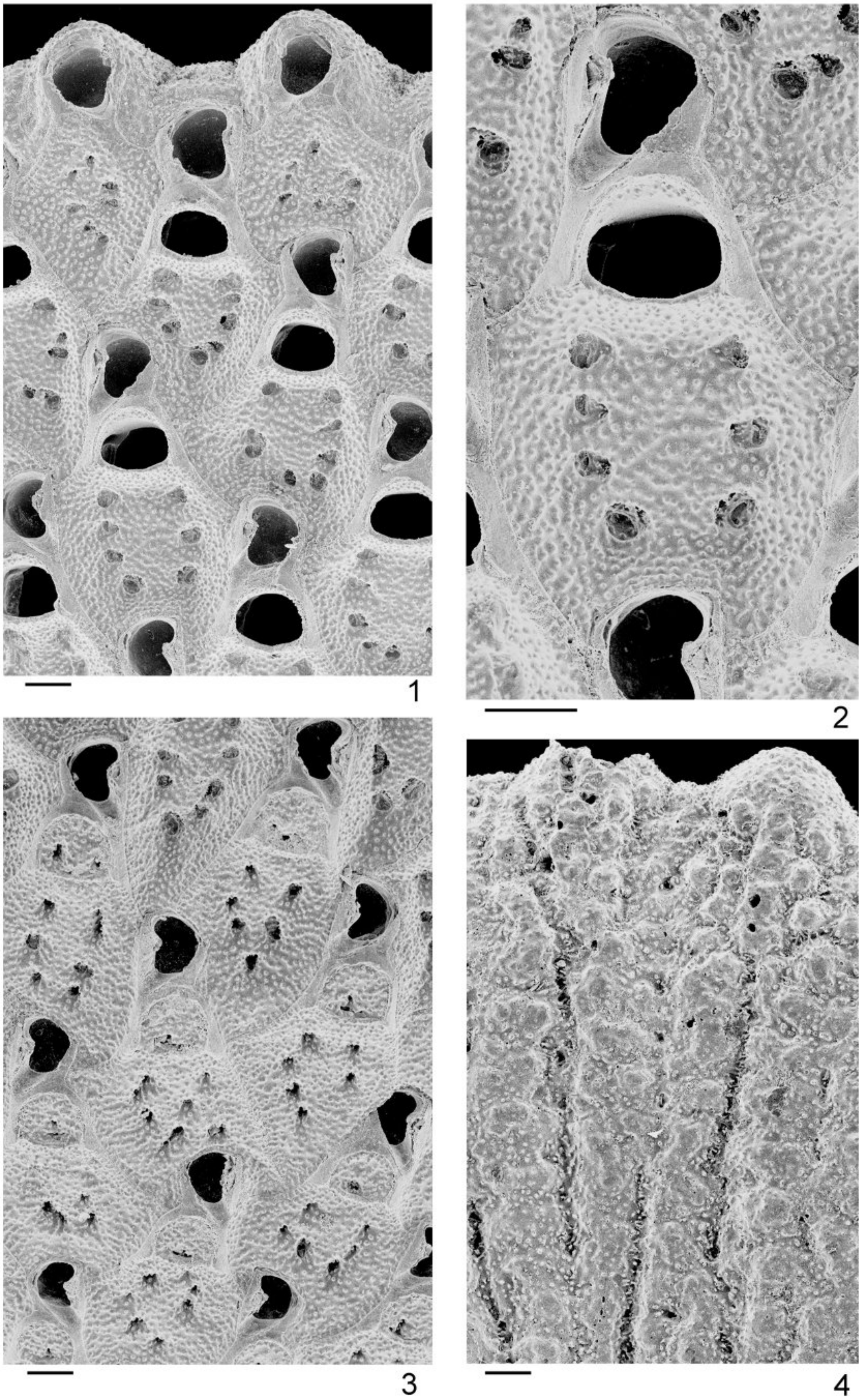

FIGURE 6—*Discoporella scutella* n. sp. *1*, *2*, *4*, USNM530297, San Blas; *3,* USNM530298, Bocas del Toro; *1*, colony border showing autozooids closed by secondary calcification and kenozooids between them; *2*, autozooid and vibraculum; *3*, colony central view; *4*, detail of the basal surface; bar scale = 100 μm.

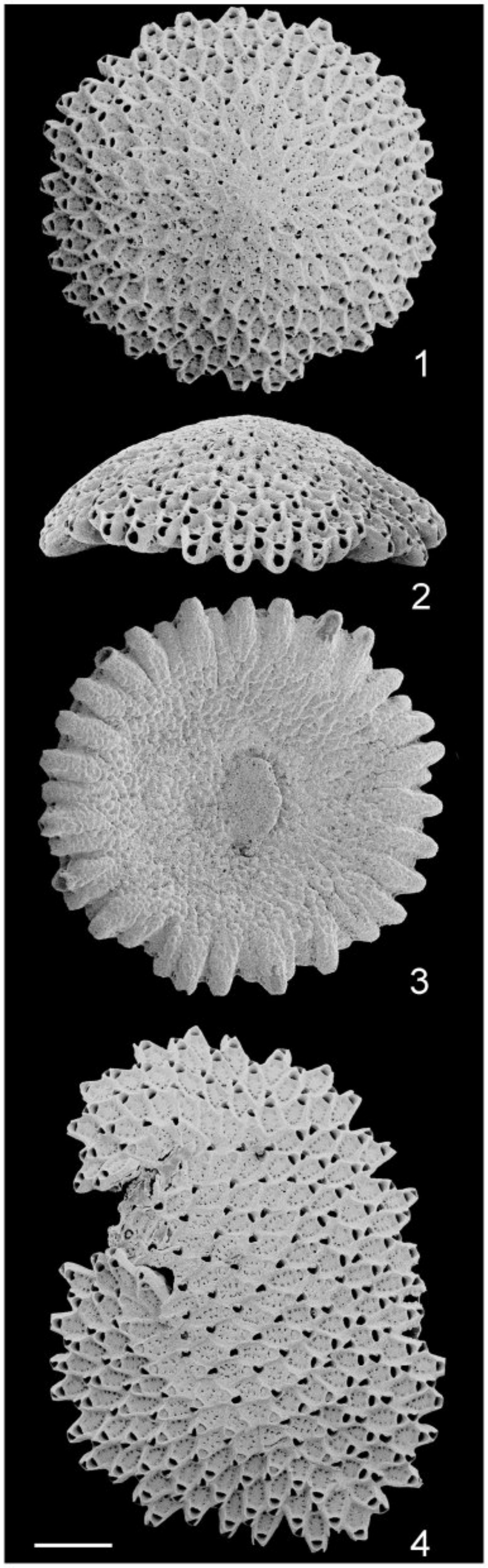

FIGURE 7—*Discoporella peltifera* n. sp. *1–3*, USNM530301, Bocas del Toro; *1*, colony frontal view; *2*, colony side view; *3*, colony basal view; *4*, USNM530302, Bocas del Toro; frontal view of a colony regenerated from fragmentation; bar scale = 1 mm.

repetition to maximize consistency of the results (Boardman et al., 1970; Jackson and Cheetham, 1990, 1994). Measurements of basal granule density were made at an objective magnification of 3.2×, with a Wild 100 mm^2 reticle grid fitted to one 25×/9.5B ocular of a Leica microscope, and calibrated at a precision of approximately 0.1 mm^2. All morphological characters were transformed as $\log_{10}(1 + \text{variable})$, to obtain approximately normal distributions.

Measurements of colony dimensions and weights of whole colonies were not made for the VOUCHER specimens before they were broken apart to homogenize a portion of each for genetic analysis. To estimate these colony-level characters for the vouchers, we employed the same modeling approach utilized in our study of *Cupuladria* (see methods in Herrera-Cubilla et al., 2006). Results of the modeling of *Discoporella* colonies ($n = 30$) showed that measurements of colony-level characters were not significantly different between complete colonies and those reconstructed by modeling (student's t-test: diameter, $t = 0.762$, df $= 58.0$, $P = 0.449$; height, $t = 0.210$, df $= 57.9$, $P = 0.835$; weight, $t = 1.575$, df $= 55.8$, $P = 0.121$).

Discrimination of morphospecies.—We applied to the study of *Discoporella* a methodology used previously to discriminate among other bryozoan taxa, including *Metrarabdotos*, *Stylopoma*, and *Cupuladria* (Cheetham, 1986; Jackson and Cheetham, 1990, 1994; Cheetham et al., 2001; Herrera-Cubilla et al., 2006).

To do the series of multivariable analyses we used SPSS statistical software (SPSS Inc., 2002). The colonies were entered independently or in discrete groups without being pre-assigned to any putative group.

We first entered 150 SURVEY colonies as "groups" into a linear discriminant analysis (DA) based on 30 morphological characters (Table 1, Fig. 1), to test if any pattern emerges from this treatment, as we did in a previous work (see Herrera-Cubilla et al., 2006). A clear pattern emerged of eastern Pacific colonies separated from Caribbean colonies.

To homologize the analyses we then subjected the two groups obtained from the previous analysis, 98 Caribbean and 52 eastern Pacific SURVEY specimens, to separate hierarchical cluster analyses using the nearest-neighbor method based on squared Euclidean distance and employing 30 morphological characters.

The discrete groups of Caribbean and Pacific colonies that emerged from each of the previous cluster analyses were tested for stability in a series of DA (Jackson and Cheetham, 1994), to determine whether the clusters were significantly different from each other and whether each colony was correctly assigned to its cluster (Herrera-Cubilla et al., 2006).

Only 70 VOUCHER specimens were used for morphometric analysis, 13 Caribbean and 57 eastern Pacific, which provided suitable material. They were entered separately in each of the last DA performed by ocean using SURVEY specimens, but left unassigned. We then repeated the DA to determine how the specimens were classified based on the morphological characters.

To improve the classification of Pacific VOUCHER specimens,we performed another series of analyses and entered the 70 VOUCHER colonies as "groups" into a DA based on the 30 morphological characters, as we did for the SURVEY specimens, but also in the same way, in a step-wise DA. No clear pattern emerged from either of these two exploratory analyses.

Therefore we placed the Caribbean and eastern Pacific VOUCHER specimens together in a hierarchical cluster analysis using, as before, the nearest-neighbor method based on squared Euclidean distance and 30 morphological characters. Discrete groups that emerged were then tested for stability in a series of DA, using the same quantity of variables.

Despite that no clear division was obtained in the exploratory

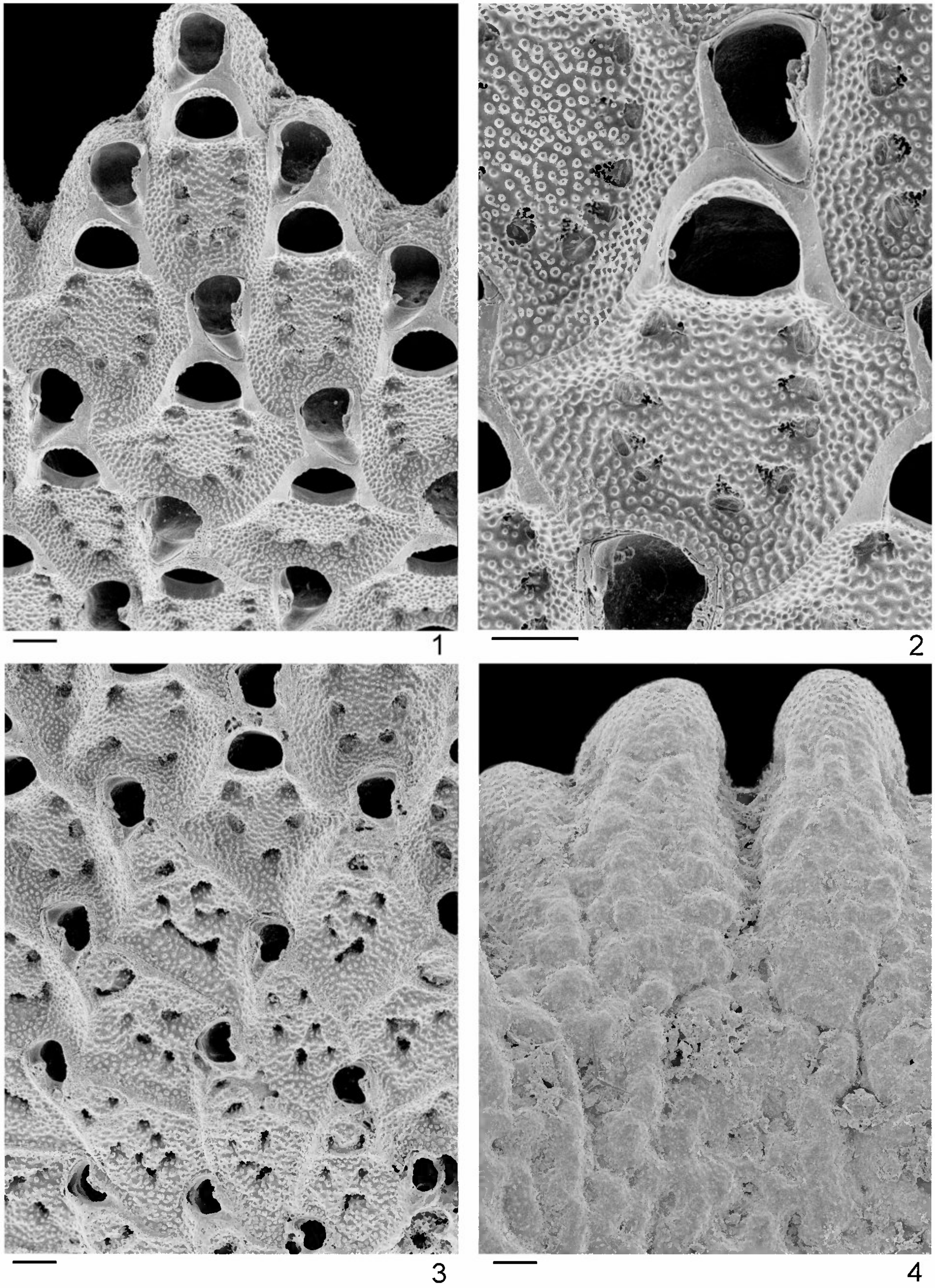

FIGURE 8—*Discoporella peltifera* n. sp. *1*, *2*, USNM530302, Bocas del Toro; *1*, colony border showing autozooids closed by secondary calcification and kenozooids between them; *2*, autozooid and vibraculum; *3*, *4*, USNM530301, Bocas del Toro; *3*, colony central view; *4*, detail of the basal surface; bar scale = 100 μm.

TABLE 5—Measurements in mm of zoarial and zooidal characters for the seven morphospecies described. Refer to Table 1 for character names.

Morphological characters	Caribbean SURVEY morphospecies											
	D. scutella n. sp.				*D. peltifera* n. sp.				*D. terminata* n. sp.			
	N	Mean	Range	SD	N	Mean	Range	SD	N	Mean	Range	SD
Cw	15	6.33	4.78–8.60	1.12	14	5.99	3.43–8.13	1.45	42	3.69	2.43–5.68	0.67
Ch	15	1.98	1.50–3.00	0.41	14	1.51	1.00–2.10	0.38	42	1.12	0.60–2.00	0.32
Ra_hw	15	0.32	0.20–0.46	0.07	14	0.26	0.17–0.43	0.08	42	0.31	0.16–0.52	0.08
C_sur	15	38.15	22.62–70.84	13.15	14	33.24	10.67–58.37	14.00	42	13.00	5.33–28.83	4.69
Zl	15	0.50	0.42–0.60	0.06	14	0.58	0.52–0.67	0.04	42	0.39	0.30–0.50	0.04
Zw	15	0.37	0.32–0.46	0.04	14	0.40	0.32–0.50	0.05	42	0.27	0.23–0.34	0.02
Ol	15	0.12	0.10–0.16	0.02	14	0.13	0.11–0.15	0.01	42	0.10	0.08–0.15	0.01
Ow	15	0.16	0.14–0.17	0.01	14	0.15	0.12–0.16	0.01	42	0.12	0.11–0.15	0.01
Al	15	0.21	0.16–0.24	0.02	14	0.20	0.16–0.23	0.02	42	0.15	0.12–0.19	0.02
Aw	15	0.18	0.12–0.21	0.02	14	0.18	0.14–0.20	0.02	42	0.14	0.11–0.16	0.01
Alo	15	0.14	0.12–0.16	0.01	14	0.13	0.10–0.16	0.02	42	0.09	0.07–0.11	0.01
Awo	15	0.12	0.08–0.15	0.02	14	0.12	0.10–0.14	0.01	42	0.08	0.06–0.10	0.01
Nope	15	5.78	5.00–7.00	0.67	14	6.78	6.00–8.00	0.70	42	6.61	5.00–10.00	1.14
Opew	15	0.05	0.02–0.08	0.02	14	0.04	0.02–0.06	0.01	42	0.04	0.03–0.06	0.01
Opesp	15	0.14	0.00–2.00	0.56	14	0.25	0.00–2.00	0.64	42	2.47	1.00–4.00	0.88
Npor	15	0.03	0.00–1.00	0.13	14	0.00	0.00–0.00	0.00	42	1.00	0.00–4.00	1.08
Graden	15	0.65	0.44–0.88	0.14	14	0.73	0.55–0.88	0.09	42	0.99	0.55–1.65	0.26

analyses between Caribbean and eastern Pacific VOUCHER specimens, we submitted them separately to the same procedure of multivariate analysis. To do this we performed four sets of hierarchical cluster analyses: two separate analyses for Caribbean and Pacific colonies using 30 morphological characters, and two separate analyses as before, but using the characters kept in the stepwise DA done on 70 VOUCHER specimens as "groups." These characters were, in rank order: colony diameter, median number

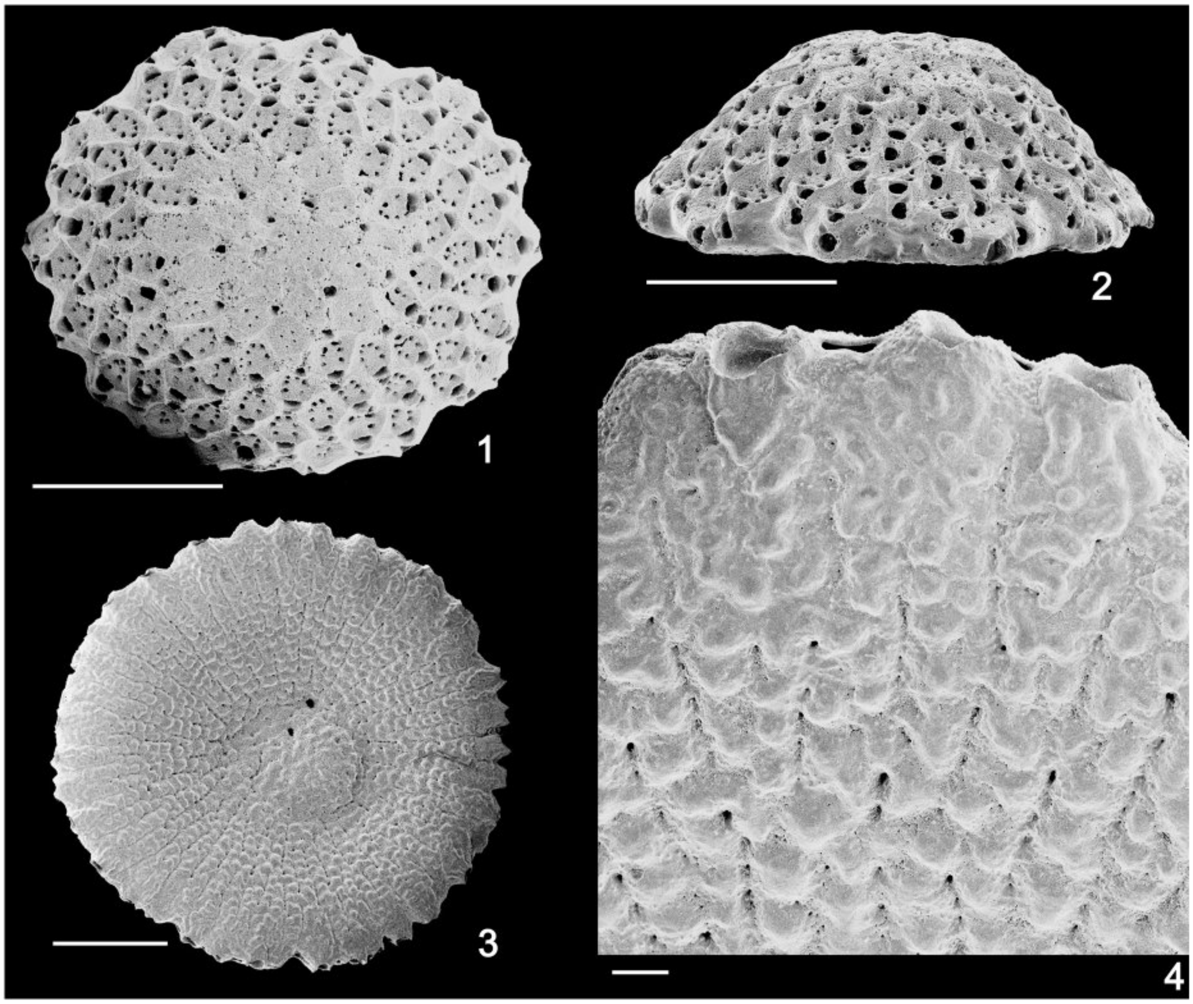

FIGURE 9—*Discoporella terminata* n. sp. *1*, *2*, USNM530306, San Blas; *1*, colony frontal view; *2*, colony side view; *3*, *4*, USNM530307, Bocas del Toro; *3*, colony basal view; bar scale = 1 mm; *4*, detail of the basal surface; bar scale = 100 μm.

TABLE 5—Extended.

Caribbean SURVEY morphospecies								Eastern Pacific SURVEY morphospecies							
D. triangula n. sp.				*D. bocasdeltoroensis* n. sp.				*D. marcusorum* n. sp.				*D. cookae* n. sp.			
N	Mean	Range	SD	N	Mean	Range	SD	N	Mean	Range	SD	N	Mean	Range	SD
14	3.07	2.35–3.85	0.44	13	6.63	4.55–8.50	1.34	39	5.24	3.33–8.45	1.07	13	9.32	6.95–10.78	1.03
14	0.89	0.50–1.30	0.24	13	1.85	1.10–2.50	0.44	39	1.51	0.80–2.30	0.36	13	3.76	2.55–4.85	0.77
14	0.29	0.19–0.42	0.07	13	0.28	0.22–0.44	0.07	39	0.29	0.18–0.40	0.06	13	0.41	0.26–0.54	0.08
14	8.77	4.87–12.73	2.43	13	41.05	18.06–65.84	15.77	39	25.87	10.41–59.97	10.81	13	88.89	47.06–110.16	17.49
14	0.36	0.30–0.50	0.04	13	0.44	0.35–0.54	0.05	39	0.45	0.35–0.57	0.05	13	0.48	0.39–0.52	0.04
14	0.28	0.25–0.30	0.02	13	0.29	0.24–0.33	0.03	39	0.32	0.24–0.38	0.03	13	0.34	0.28–0.38	0.03
14	0.09	0.08–0.11	0.01	13	0.12	0.11–0.13	0.01	39	0.12	0.09–0.14	0.01	13	0.13	0.11–0.14	0.01
14	0.11	0.10–0.12	0.01	13	0.12	0.11–0.15	0.01	39	0.14	0.12–0.16	0.01	13	0.15	0.15–0.17	0.01
14	0.15	0.12–0.18	0.02	13	0.17	0.13–0.21	0.02	39	0.20	0.16–0.23	0.02	13	0.22	0.20–0.25	0.02
14	0.13	0.10–0.15	0.02	13	0.14	0.11–0.16	0.02	39	0.15	0.13–0.19	0.01	13	0.17	0.15–0.20	0.01
14	0.09	0.08–0.12	0.01	13	0.11	0.08–0.14	0.02	39	0.12	0.10–0.16	0.02	13	0.15	0.13–0.16	0.01
14	0.07	0.05–0.08	0.01	13	0.09	0.06–0.12	0.02	39	0.09	0.07–0.12	0.01	13	0.11	0.10–0.13	0.01
14	5.81	5.00–9.00	0.97	13	5.62	3.00–10.00	1.42	39	7.42	6.00–9.00	0.75	13	8.04	7.00–9.00	0.74
14	0.03	0.03–0.04	0.01	13	0.05	0.02–0.07	0.01	39	0.05	0.03–0.07	0.01	13	0.05	0.04–0.06	0.01
14	2.17	0.00–5.00	1.48	13	2.68	1.00–5.00	1.03	39	1.68	1.00–3.00	0.68	13	1.27	1.00–2.00	0.41
14	0.25	0.00–2.00	0.51	13	0.43	0.00–1.00	0.44	39	0.90	0.00–3.00	0.81	13	1.33	0.00–4.00	1.11
14	1.13	0.77–1.43	0.20	13	0.55	0.44–0.70	0.09	39	1.55	0.66–2.53	0.44	13	1.55	0.99–2.53	0.47

of opesiule spines per autozooid, maximum opesiule diameter, autozooidal opesia length, number of pores in autozooidal frontal shield, vibraculum length, number of opesiules, length of vibracular opesia, and length ratio of vibracular to autozooidal opesia. To do these cluster analyses we used the same method and distance mentioned before.

The discrete groups of Caribbean and Pacific voucher colonies that resulted from each of the above cluster analyses were submitted separately, to a series of DA. In two of them we entered all the characters together and in the other two we used step-wise method.

RESULTS

Linear discriminant analysis of 150 SURVEY specimens entered as "groups" clearly separated an eastern Pacific group from a Caribbean group (Fig. 2), distinguished primarily by differences in colony size for discriminant function 1 and basal granule density for discriminant function 2 (Table 2), although many other characters contributed significantly.

Hierarchical cluster analysis of 98 Caribbean SURVEY colonies based on the 30 characters yielded 13 discrete groups at SC ≤ 0.07, with 10 outliers (10.9% of total specimens). In the same manner, 52 Pacific SURVEY specimens clustered as 4 discrete groups at SC ≤ 0.05, with 3 outliers (6% of total specimens).

Nine rounds of DA reduced the 13 clusters of Caribbean SURVEY specimens to five putative morphospecies (Fig. 3, Table 3). Five rounds of DA reduced the four clusters of Pacific SURVEY specimens to two putative morphospecies (Fig. 4, Table 4). Ranks of the canonical discriminant function scores for the first two functions are presented in the Appendix (accessed in the Supplemental Data files at www.journalofpaleontology.org). All of the groups were different at $P = 0.000$, 99% of Caribbean colonies were correctly classified by the classification function of the DA versus 92% by jackknife analysis, while 100% of Pacific colonies were correctly classified versus 100% jackknife analysis. Most colonies were assigned to their cluster at $P > 0.999$. The five new species from the Caribbean include *Discoporella scutella*, *Discoporella peltifera*, *Discoporella terminata*, *Discoporella bocasdeltoroensis* and *Discoporella triangula* (Figs. 5–14). The two new species from the tropical eastern Pacific are *Discoporella marcusorum* and *Discoporella cookae* (Figs. 15–18).

Of the 13 Caribbean VOUCHER specimens left unassigned, two colonies of HG Disc7 (100%) were assigned to *D. scutella*, the five colonies of HG Disc2 (100%) were assigned to *D. bocasdeltoroensis*, but only four of the six colonies of HG Disc8 (67%) were assigned to *D. terminata*. The overall success of these assignments was 89%. Regarding the eastern Pacific VOUCHER specimens also left unassigned, HG Disc3A and Disc3B were indistinguishable from each other. For Disc3A, 17 of 35 colonies (49%) were assigned to *D. marcusorum*, and the other 18 (51%) to *D. cookae*. For Disc3B, two of seven colonies (29%) were assigned to *D. marcusorum* and the other five (71%) to *D. cookae*. Only HG Disc3C could be considered well identified: 13 of the 15 colonies (87%) were assigned to *D. marcusorum* and the other two (13%) to *D. cookae*.

Neither of the two DA done with Caribbean and eastern Pacific VOUCHER colonies entered as "groups" yielded any distinct pattern. However the success of classification was 100% of original cases correctly classified versus 98% jackknifed for the one in which we entered the total number of characters; and 99% of original cases correctly classified versus 99% for the one in which we used the step-wise method.

Therefore hierarchical cluster analysis of the combined VOUCHER specimens from the two oceans yielded eight discrete clusters at SC ≤ 0.03, with 14 outliers (20% of total specimens), including those that fell between clusters. No cluster was obtained for the HG Disc7 clade, which was represented by only two colonies.

Nine rounds of DA reduced the eight clusters to five putative morphospecies. In this analysis 100% of cases were correctly classified vs. only 83% of cross-validated cases. Two of the three monophyletic groups discerned by the molecular analyses in the Caribbean (see Dick et al., 2003) were classified correctly by the discriminant function of the DA, with high confidence ($P > 0.999$). Eighty percent of specimens of HG Disc2, and 83% of specimens of HG Disc8 were clearly classified; however, one of five specimens of HG Disc2 was classified as HG Disc3A, and one of 6 specimens of HG Disc8 was classified as Disc2. The two specimens of HG Disc7 were not classified.

For the *Discoporella* 3A-C clade from the Pacific, only 26 (74%) out of 35 specimens (see Dick et al., 2003), of HG Disc3A were correctly classified by the DA. Of these, 23 were correctly classified at $P \geq 0.99$, two at $P \geq 0.95$ and one at $P = 0.91$. However, HG Disc3B and Disc3C could not be discriminated from one another or from Disc3A.

The hierarchical cluster analysis of 13 Caribbean VOUCHER specimens using 30 characters yielded two discrete groups (SC ≤ 0.07) and five outliers (38% of total specimens). No cluster was obtained for HG Disc7. Analysis of the 57 Pacific VOUCHER specimens yielded four discrete clusters (SC ≤ 0.02) and 15 outliers (26% of total specimens).

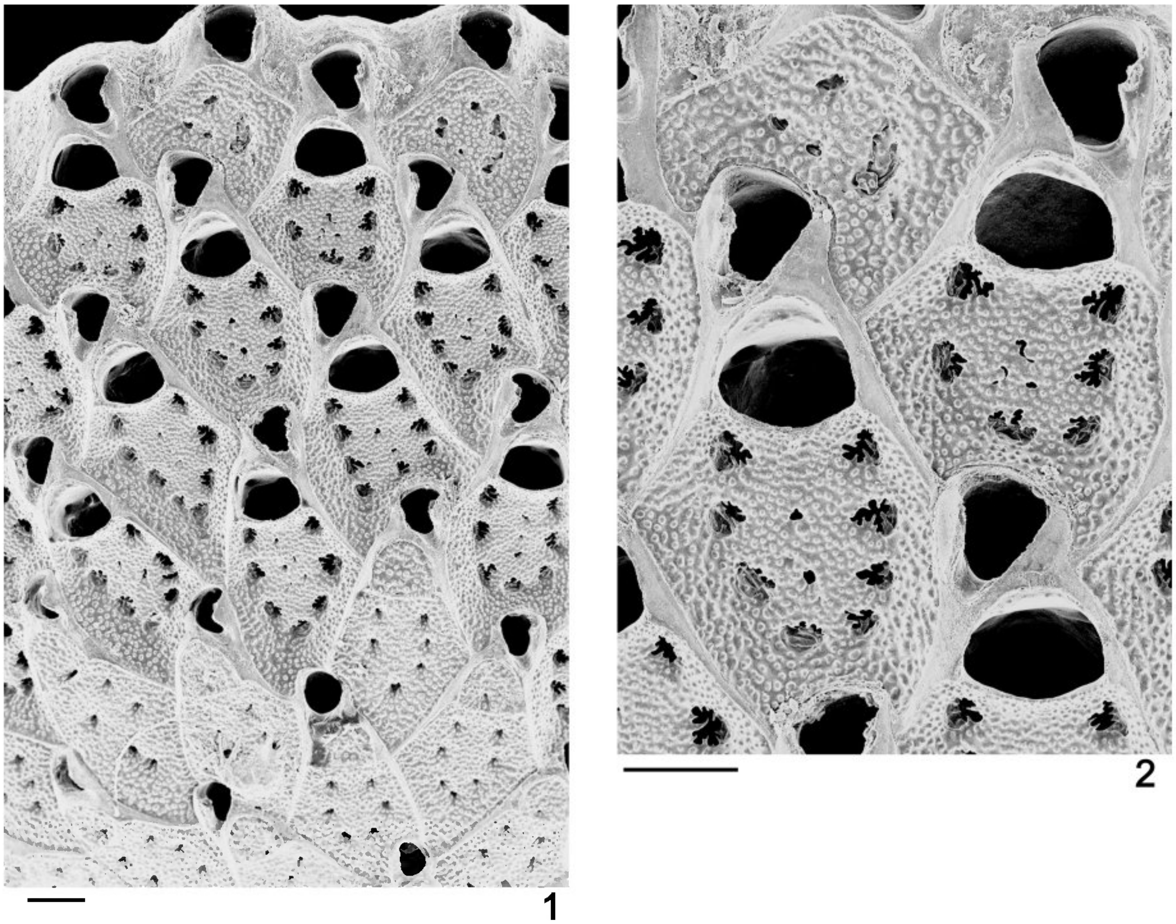

FIGURE *10*—*Discoporella terminata* n. sp. *1*, *2*, USNM530308, Bocas del Toro; *1,* border showing autozooids closed by secondary calcification and kenozooids between them, and central view of the colony; *2*, autozooid and vibraculum; bar scale = 100 μm.

After two rounds of DA of the Caribbean VOUCHER specimens, entering the total number of characters yielded a two species taxonomy in which the HG Disc2 was discriminated correctly (100%), but five out of six colonies (83%) for the HG Disc8. The two specimens of HG Disc7 were discriminated as Disc8. The overall success of classification was 100% of the colonies correctly classified vs. 73% of cross-validated cases, the difference between groups was marginally significant at $P = 0.025$, and DF (1) explained 100% of the variance. The characters with highest coefficients were Zw, ZwZl, and Zl.

For eastern Pacific VOUCHER specimens, seven rounds of DA yielded two groups. The first group, formed of 29 specimens, was composed mostly by HG Disc3A (83%), Disc3C (10%) and Disc3B (3%). The second group, formed of 27 specimens, was composed mostly by HG Disc3C (44%) and Disc3B (22%), but 33% of HG Disc3A. One specimen of Disc3A (3%) was not classified. The success of the discrimination was 100% of cases correctly classified vs. 90% cross-validated cases, the groups were different at $P = 0.000$, and DF (1) had 100% of variance. The characters with highest coefficients were Ra_AwoOw, Alo, and Ow.

The hierarchical cluster analysis of 13 Caribbean VOUCHER specimens using the nine characters kept in step-wise DA (see above), yielded two discrete groups (SC ≤ 0.04) and four outliers (31% of total specimens). Again, no cluster was obtained for HG Disc7. Analysis of the 57 Pacific VOUCHER specimens yielded two discrete clusters (SC ≤ 0.02) and 11 outliers (19% of total specimens).

After two rounds of step-wise DA done in Caribbean VOUCHER specimens, we obtained two taxonomic species in which the HG Disc2 and Disc8 were discriminated correctly. One hundred percent of the colonies were classified correctly vs. 100% of cross-validated cases, the groups were different at $P = 0.000$, and DF (1) explained 100% of the variance. The characters with highest coefficients were Aw, Al, and Ra_OlZl. However, one colony of HG Disc7 was discriminated as HG Disc8 and the other as HG Disc2.

For eastern Pacific VOUCHER specimens, after four rounds of step-wise DA, two species were obtained. The first species corresponds to HG Disc3A, of which 33 out of 35 colonies (91%) were classified correctly, and the second species comprises HG Disc3B and Disc3C, which were discriminated as a single species in 21 out of 22 cases (96%). The success of the discrimination was 100% of cases correctly classified vs. 100% cross-validated cases, the groups were different at $P = 0.000$, and DF (1) had 100% of variance. The characters with highest coefficients were Opew, Al, and C_sur.

DISCUSSION

Extensive new collecting did not greatly increase the number of putative *Discoporella* species from both oceans over those detected in our initial study (Dick et al., 2003). We identified five putative Caribbean *Discoporella* species, compared to three identified by genetic analysis, but only two eastern Pacific species, compared to three identified genetically. All these species are described herein as new. One of them, *Discoporella*

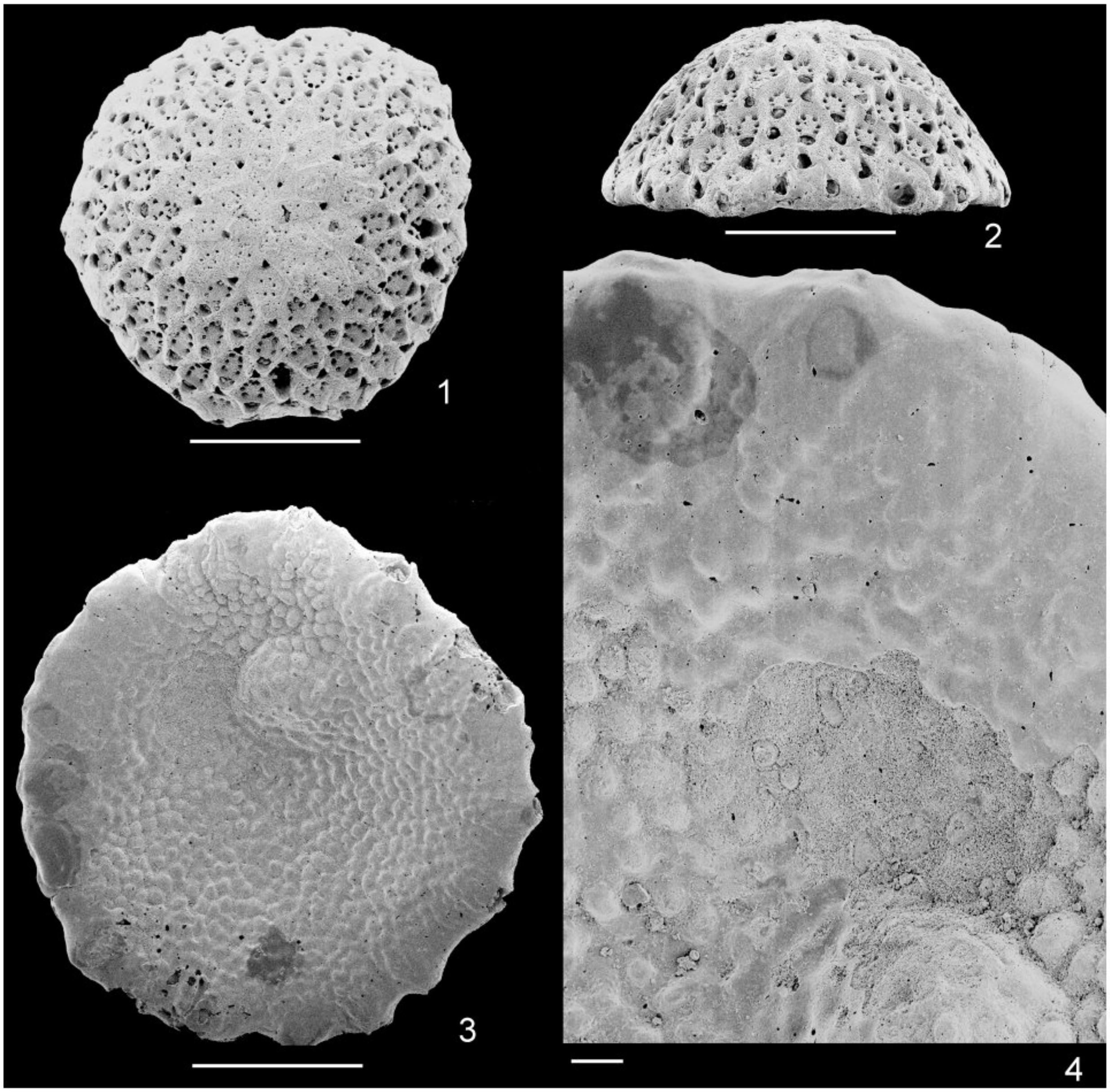

FIGURE *11*—*Discoporella triangula* n. sp. *1, 2,* USNM530315, San Blas; *1,* colony frontal view; *2,* colony side view; *3, 4,* USNM530316, Bocas del Toro; *3,* colony basal view; bar scale = 1 mm; *4,* detail of the basal surface; bar scale = 100 μm.

cookae n. sp., includes Pacific specimens previously identified in the literature as *Discoporella umbellata* (Defrance, 1823). *Discoporella umbellata* had previously been considered to extend from North Carolina to Brazil in the Atlantic and from Hawaii to California and the Galapagos in the eastern Pacific (Cook, 1965a and references therein). However, none of our *Discoporella* specimens has the paired denticles on the proximal edge of the opesia, nor the proximally denticulate vibracular opesia, characteristic of *D. umbellata.* According to Cook (1965, p. 170), "the distribution of [Recent] *D. umbellata* [sensu strictu] is confined to the northern and northwestern coasts of Africa and the neighboring islands."

No clear division was obtained between Caribbean and Pacific VOUCHER specimens in the exploratory analysis (see above), which could be an artifact of the small sample size of specimens from the Caribbean. Despite that, the genetic data strongly support the morphometrically based taxonomy of Caribbean and eastern Pacific VOUCHER specimens obtained separately. The cluster and the step-wise DA identified with high confidence the two monophyletic groups Disc2 and Disc8; the failure to discriminate Disc7 morphometrically was likely due to having only two specimens. Monophyletic groups Disc3A, Disc3B and Disc3C were also identified with high confidence, although Disc3B and Disc3C were discriminated as one morphospecies corresponding to the *Discoporella* 3B+C clade as discussed below. In contrast, analyses done using the total number of characters on Caribbean and eastern Pacific specimens together in the same analysis, discriminated correctly only 74–83% of HG, while the success of discrimination of analyses done on Caribbean and Pacific specimens separately varied greatly. For Caribbean specimens, the discrimination was marginally significant, although 83–100% of

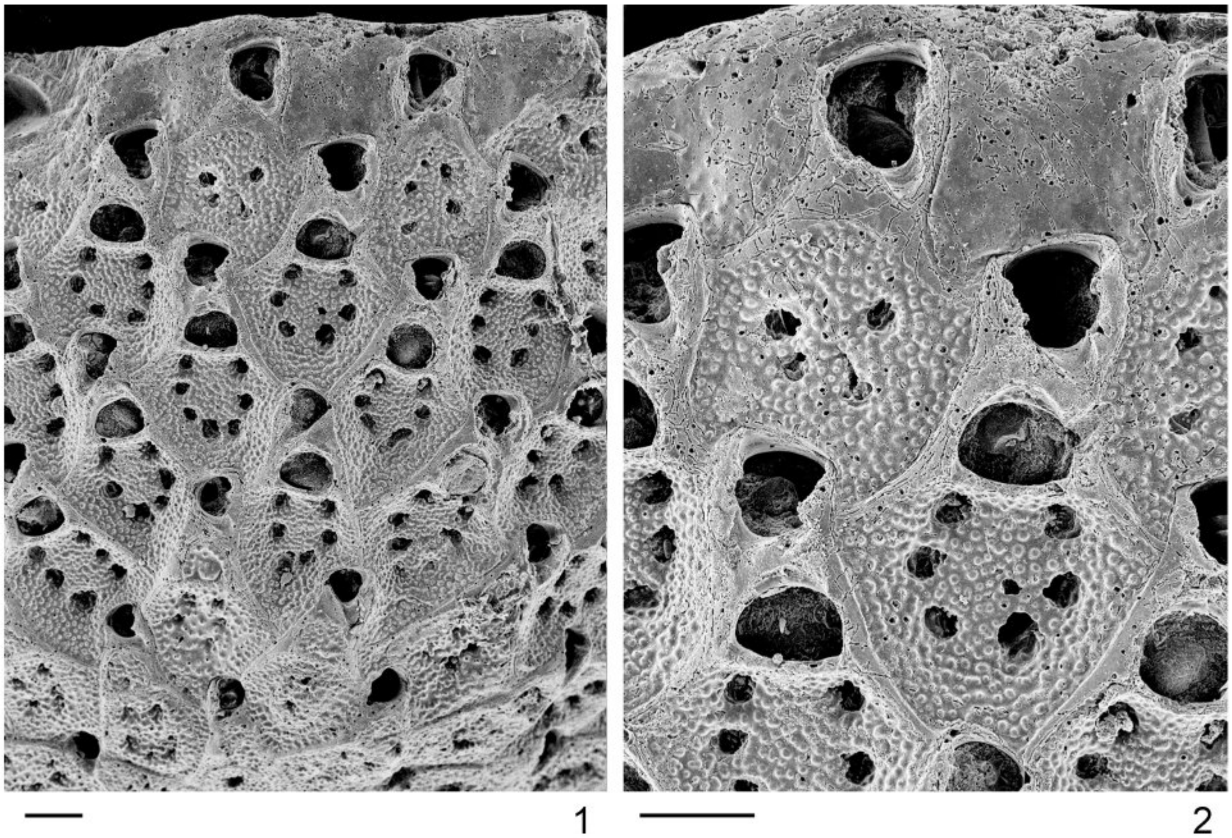

FIGURE *12*—*Discoporella triangula* n. sp. *1, 2,* USNM530315, San Blas; *1,* border showing autozooids closed by secondary calcification and kenozooids between them, and central view of the colony; *2,* autozooid and vibraculum; bar scale = 100 μm.

HG were identified correctly, conversely discrimination was highly significant for Pacific specimens, but 67–87% of HG were discriminated correctly. HG Disc7 could not be classified in any of these analyses. In the analyses in which VOUCHER specimens were left unassigned only 89% of the Caribbean HG and Disc3C from the eastern Pacific were correctly assigned.

The morphometric analysis discriminated Pacific *Discoporella* 3B/C from *Discoporella* 3A. In the genetic analysis (Dick et al., 2003), *Discoporella* 3B and *Discoporella* 3C were both monophyletic groups, as was *Discoporella* 3B+C, whereas *Discoporella* 3A comprised a paraphyletic group, forming a polytomy of slightly diverged branches along with the *Discoporella* 3B+C clade. Interestingly, O'Dea et al. (2004) showed *Discoporella* 3B/C to have a high frequency (88%) of sexual reproduction, whereas *Discoporella* 3A reproduces almost exclusively asexually (98%). This is significant, for it may help explain the discrepancy between the results of the morphometric and genetic analysis, as well as the peculiar topology of the tree based on genetic analysis. It is possible that *Discoporella* 3B and *Discoporella* 3C are indistinguishable morphologically because they represent deep mitochondrial lineages within a panmictic, sexually reproducing population. Both the low intraspecific genetic variation within *Discoporella* 3A, as well as its low divergence from the basal node of the *Discoporella* 3 clade, might be consequences of its asexuality. By the same token, *Discoporella* 3A may be morphologically distinct from *Discoporella* 3B/C because, as a clonal species, it has potentially been reproductively isolated for a long time from the sexually reproducing *Discoporella* B/C lineage.

The clear morphological differentiation between colonies from the Caribbean and eastern Pacific, based on differences in colony size and ornamentation, observed in the first phase of the SURVEY discriminant analyses appears to reflect different oceanographic conditions in productivity and predation. High productivity and consequent increased food availability can ecophenotypically enhance colony growth (Winston, 1976; Jebram, 1977; O'Dea and Okamura, 1999; O'Dea et al., 2004), which in turn is likely related to life-history differences of cupuladriids between the two oceans. A detrended correspondence analysis of cupuladriid colony morphologies and life histories (O'Dea et al., 2004) showed a partitioning of species by ocean similar to that detected by our DA. The eastern Pacific harbors the largest *Discoporella* species found in this study (*Discoporella* 3A = *Discoporella cookae* n. sp.). Moreover, the two species collected on the Pacific side possess a basal surface abundantly ornamented with high-relief granules that might either mimic surrounding granular sediment or strengthen the skeleton. If these are indeed defensive adaptations, they are analogous to similar adaptations documented for marine mollusks in response to higher levels of predation in the eastern Pacific compared to the Caribbean (Vermeij, 1978, 1987). Another interesting feature is that we have observed in a few colonies of *D. marcusorum* from the Gulf of Chiriqui a pattern of zoarial budding similar to that described by Marcus and Marcus (1962). Thus this species could have another form of asexual reproduction besides that of fragmentation.

Among the species studied here, a trend was apparent in the mode of determinate versus semi-determinate growth between the Caribbean and eastern Pacific. Four of the five species of *Discoporella* from the Caribbean exhibit determinate growth, which is easily recognized by cessation of growth at the zoarial border. This is accomplished in several ways. In *Discoporella scutella* n. sp., the autozooids that form this definitive border are closed by

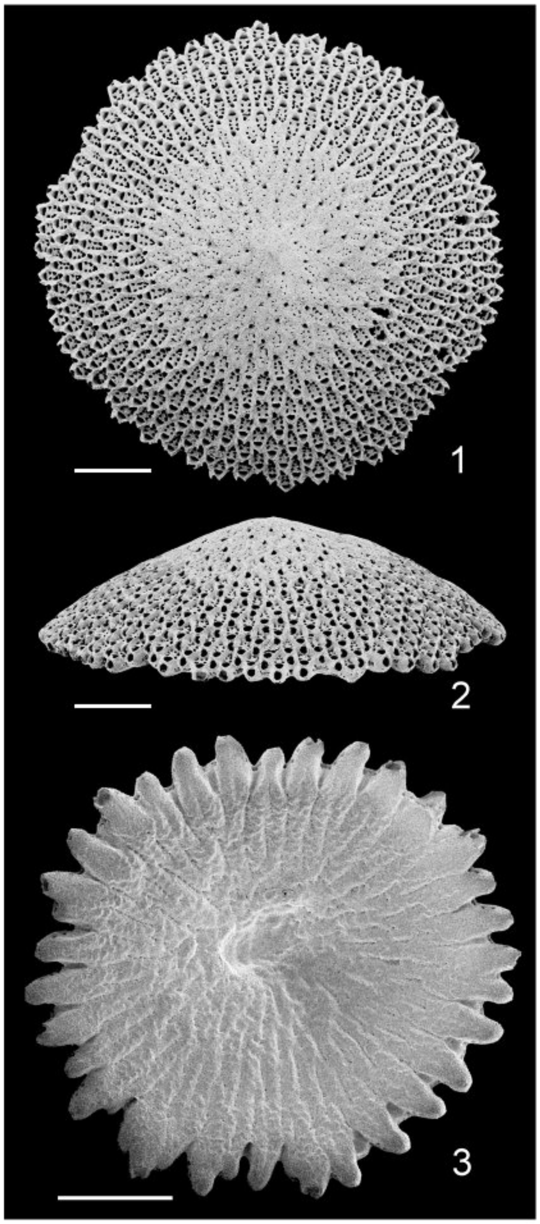

FIGURE *13*—*Discoporella bocasdeltoroensis* n. sp. *1*, *2*, USNM530320, Bocas del Toro; *1*, colony frontal view; *2*, colony side view; *3*, USNM530321, Bocas del Toro; colony basal view; bar scale = 1 mm.

secondary calcification that leaves some pores visible and the vibracula still functioning. In *Discoporella peltifera* n. sp., cessation of growth occasionally occurs and is marked also by development of kenozooids along part of the colony border. In contrast, *Discoporella terminata* n. sp. and *Discoporella triangula* n. sp. form the border by means of closed autozooids, with kenozooids developed between the marginal vibracula. *Discoporella bocasdeltoroensis* n. sp. is the only Caribbean *Discoporella* with semi-determinate growth; both *Discoporella marcusorum* n. sp. and *Discoporella cookae* n. sp. from the eastern Pacific show this growth mode.

Generally, all the species of *Discoporella* studied have basal surfaces with radial grooves and high- to low-relief granulated calcification of variable density. However, these features are better developed in species from the eastern Pacific (Table 5) than in those from the Caribbean. In all species, autozooecial opesiules in the central area of the colony become occluded by secondary calcification that also leaves some pores visible, and the vibracula remain functional (see Figs. 5, 7, 9, 11, 13, 15 and 17). This secondary calcification can extend through several generations of autozooids and is variable among species. In *D. triangula*, for example, only three generations of functioning autozooids remain late in astogeny when the colony has reached determinate size and its central area is occluded by secondary calcification, whereas in *D. terminata* five to seven generations of functioning autozooids remain.

SYSTEMATIC PALEONTOLOGY

Order CHEILOSTOMATIDA Busk, 1852
Suborder FLUSTRINA Smitt, 1867
Superfamily CALLOPOROIDEA Norman, 1903
Family CUPULADRIIDAE Lagaaij, 1952
Genus DISCOPORELLA d'Orbigny, 1852
DISCOPORELLA SCUTELLA new species
Figures 5, 6

Diagnosis.—Colonies flat, discoidal, compact, densely calcified, with a height-diameter ratio of about 0.32, determinate growth, and spines within opesiules coalescing to form a shield.

Description.—Colony discoidal, compact, with maximum observed diameter 8.6 mm. Autozooids in zone of astogenetic repetition have no pores in frontal shield. Those of central area closed by secondary calcification up to 4th–5th generation, leaving some pores open and vibracula avicularia still functioning. Autozooids with 5–7 opesiules, in adult colonies spines within them coalescing to form a shield. Colony growth determinate. Cessation of growth marked by presence of kenozooids between autozooids at colony margin, closed by secondary calcification, but with some pores remaining open and vibracula still functional. Basal surface with radial grooves and basal granule density of 0.65.

Etymology.—*Scutella*, Latin, "of flat dish, saucer" with reference to its zoarium shape.

Types.—Holotype, USNM530297, SB95-20, San Blas (9.23°N, 81.88°W), October 1995, H. Fortunato coll., 50 m depth, coarse sandy mud. Paratype, USNM530298, BT98-19, Bocas del Toro (9.38°N, 82.17°W), October 1998, H. Fortunato coll., 50 m depth, soft black mud.

Measurements.—See Table 5 for morphological measurements.

Occurrence.—Caribbean western San Blas archipelago and Bocas del Toro. Depth range 30–70 m.

Remarks.—*Discoporella scutella* corresponds to Disc7 in the VOUCHER collection and in Dick et al. (2003).

DISCOPORELLA PELTIFERA new species
Figures 7, 8

Diagnosis.—Colonies generally flat and discoidal, but occasionally irregular, smaller than *D. scutella*, with height-diameter ratio about 0.25, but autozooids larger, averaging 0.6 mm in length; growth generally semi-determinate, spines within opesiules coalescing to form a shield.

Description.—Colonies of larval origin flat and discoidal, those regenerated from fragments irregular. Maximum observed colony diameter 8.1 mm. Autozooids in zone of astogenetic repetition have no pores in frontal shield. Those of central area closed by secondary calcification up to 3rd–6th generation, leaving some pores open and vibracula still functioning. Autozooids with 6–8 opesiules, in adult colonies spines within them coalescing to form a shield. Colony growth generally semi-determinate. Cessation of growth marked by occasional kenozooids between autozooids at colony margin, closed by secondary calcification, but with some pores remaining open and vibracula still functional. Basal surface with radial grooves and granular density of 0.73.

Etymology.—*Peltifera*, Latin, "shield bearing" with reference to the armor of spines within opesiules that coalesce, forming a small shield.

Types.—Holotype, USNM530301, GM98-82, Gulf of Mosquitos (9.08°N, 81.68°W), September 1998, H. Fortunato coll., 23 m depth, fine coralline sand. Paratype, USNM530302, BT98-80 Bocas del Toro (8.88°N, 81.5°W), October 1998, H. Fortunato coll., 45 m depth.

Measurements.—See Table 5 for morphological measurements.

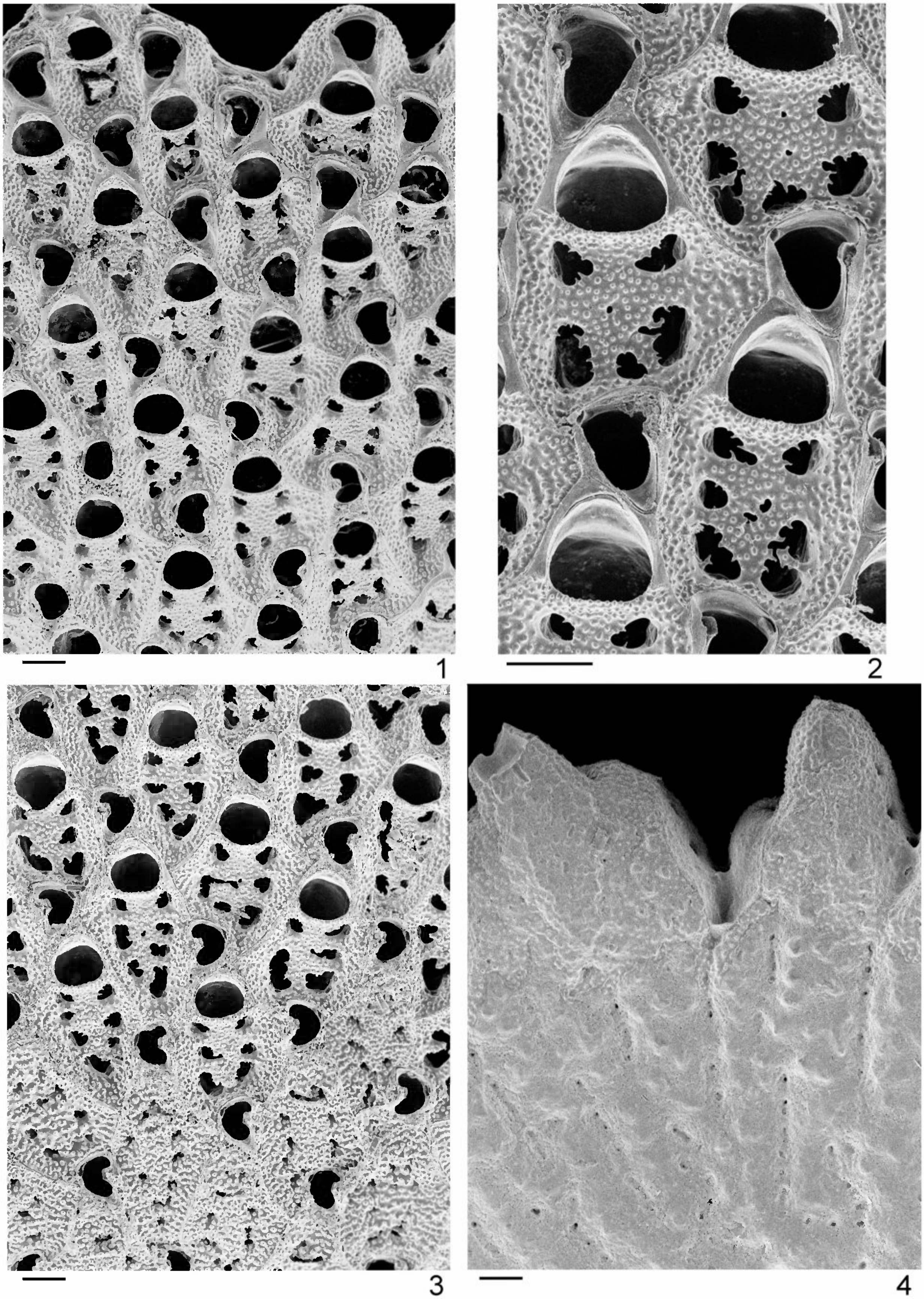

FIGURE 14—*Discoporella bocasdeltoroensis* n. sp. *1*, USNM530320, Bocas del Toro; colony border view; *2*, USNM530319, Bocas del Toro; autozooid and vibraculum; *3*, USNM530322, Bocas del Toro; colony central view; *4*, USNM530321, Bocas del Toro; detail of the basal surface, bar scale = 100 μm.

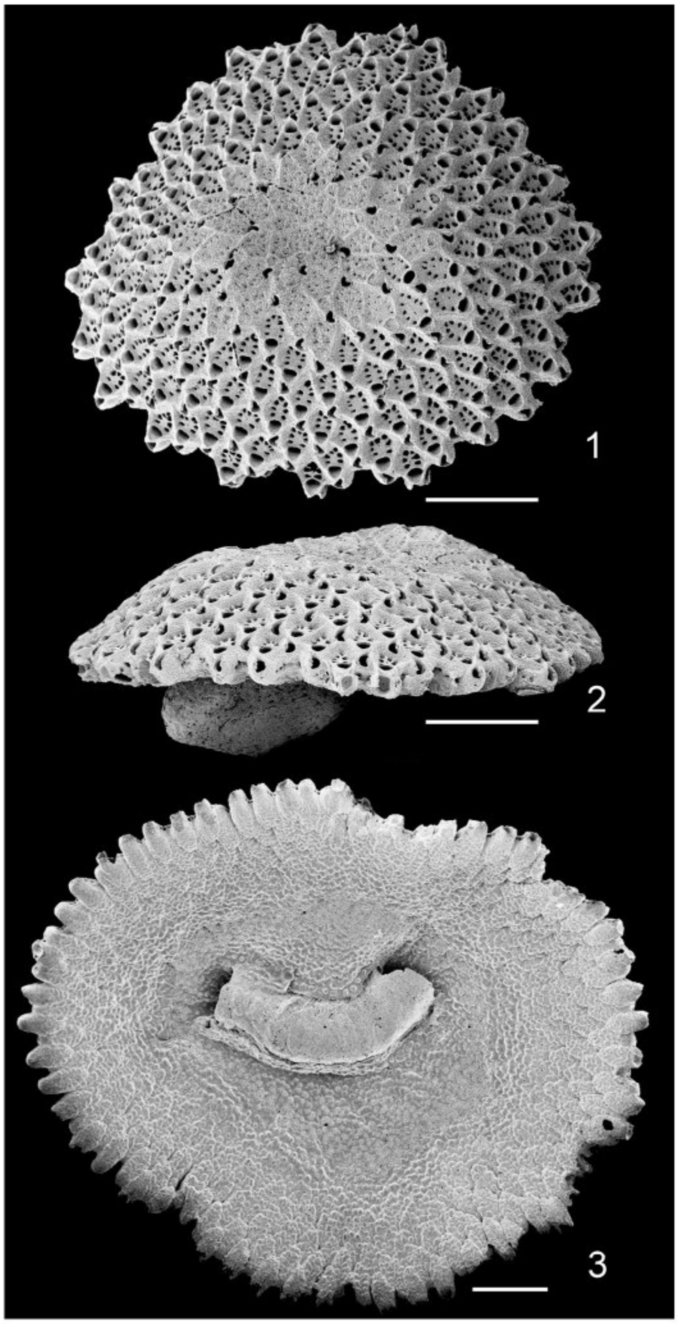

FIGURE *15*—*Discoporella marcusorum* n. sp. *1*, *2*, USNM530328, Gulf of Panama; *1*, colony frontal view; *2*, colony side view; *3*, USNM530329, Gulf of Panama; colony basal view; bar scale = 1 mm.

Occurrence.—Caribbean western San Blas archipelago and Bocas del Toro. Depth range 30–70 m.

Remarks.—*Discoporella peltifera* was more common in the San Blas than in Bocas del Toro. Three quarters of the specimens occurred at depths of 50 m or more, which could explain the absence of *D. peltifera* in the VOUCHER collection that were dredged from a depth less than 40 m.

Discoporella terminata new species
Figures 9, 10

Diagnosis.—Colonies flat, discoidal, with height-diameter ratio about 0.33, average diameter 3.7 mm, growth generally determinate, opesiules armored with spines.

Description.—Colony flat, discoidal, with maximum observed diameter 5.7 mm. Autozooids in zone of astogenetic repetition have pores in frontal shield. Those of central area closed by secondary calcification up to 3rd–4th generation, leaving some pores open and vibracula still functioning. Autozooids with 5–10 opesiules armored with spines. Cessation of growth marked by the presence of kenozooids between autozooids at colony margin, closed by secondary calcification, with some pores remaining open and vibracula still functional. Basal surface with radial grooves and granular density of 0.99.

Etymology.—*Terminata*, Latin, "having a boundary, limit or end" referring to the determinate growth of this species.

Types.—Holotype, USNM530306, SB95-4, San Blas (9.57°N, 78.58°W), October 1995, H. Fortunato coll., 95 m depth, mud. Paratype, USNM530307, BT98-125, Bocas del Toro (9.42°N, 82.34°W), October 1998, H. Fortunato coll., 23 m depth, greenish smelly mud. USNM530308, BT98-29, Bocas del Toro (9.16°N, 81°W), October 1998, H. Fortunato coll., 18 m depth.

Measurements.—See Table 5 for morphological measurements.

Occurrence.—Caribbean western San Blas archipelago to Bocas del Toro. Depth range 20–100 m

Remarks.—*Discoporella terminata* corresponds to Disc8 in the VOUCHER collection and in Dick et al. (2003).

Discoporella triangula new species
Figures 11, 12

Diagnosis.—Colonies conical, with height-diameter ratio 0.25–0.33, average diameter 3.1 mm, determinate growth, opesiules armored with spines.

Description.—Colonys conical, with maximum observed diameter 3.9 mm. Autozooids in zone of astogenetic repetition have pores in frontal shield. Those of central area closed by secondary calcification up to 3rd generation, leaving some pores open and vibracula still functioning. Autozooids with 5–9 opesiules armored with spines. Growth determinate. Cessation of growth marked by the presence of kenozooids between autozooids at colony margin, closed by secondary calcification but leaving some pores open and vibracula still functional. Basal surface with radial grooves and granular density of 1.1.

Etymology.—*Triangula*, Latin, "three-cornered, triangular, of a triangle" with reference to the triangular shape of the zoarium.

Types.—Holotype, USNM530315, SB95-4, San Blas (9.57°N, 78.58°W), October 1995, H. Fortunato coll., 95 m depth, mud. Paratype, USNM530316, BT98-5, Bocas del Toro (9.51°N, 82.33°W), October 1998, H. Fortunato coll., black fine sandy mud, 100 m depth.

Measurements.—See Table 5 for morphological measurements.

Occurrence.—From Caribbean western San Blas archipelago to Bocas del Toro. Depth range 20–100 m.

Remarks.—*Discoporella triangula* is distinguished by the extremely small size of its colony, in average 3 mm in diameter and less than 1 mm in height (Table 5). Its absence from the VOUCHER collection could be an artifact due to loss through the 2 mm mesh screen used to sieve the substrate during collection.

Discoporella bocasdeltoroensis new species
Figures 13, 14

Diagnosis.—Colonies conical, with height-diameter ratio 0.25–0.33, average diameter 6.6 mm, semi-determinate growth, opesiules armored with spines.

Description.—Colony conical, with maximum observed diameter 8.5 mm. Autozooids in zone of astogenetic repetition rarely with pores. Those of central area closed by secondary calcification up to 5th–6th generation leaving some pores open and vibracula still functioning. Autozooids with 3–10 opesiules armored with spines. Colony growth semi-determinate; no kenozooids or closed autozooids by secondary calcification at colony margin. Basal surface with radial grooves and granular density of 0.55.

Etymology.—*Bocasdeltoroensis*, Latin, refers to the Bocas del Toro coasts where this species was found.

Types.—Holotype, USNM530319, BT98-49, Bocas del Toro (8.82°N, 81.5°W), October 1998, H. Fortunato coll., 17.8 m depth. Paratype, USNM530320, BT98-130, Bocas del Toro (9.47°N, 83.33°W), October 1998, H. Fortunato coll., fine black sandy mud, 22 m depth; USNM530321, BT98-80, Bocas del Toro (8.88°N, 81.5°W), October 1998, H. Fortunato coll., 45 m; USNM530322, BT98-49, Bocas del Toro (8.82°N, 81.5°W), October 1998, H. Fortunato coll., 17.8 m.

Measurements.—See Table 5 for morphological measurements.

Occurrence.—From Caribbean west of the Panama Canal to Bocas del Toro. Depth range 20–50 m.

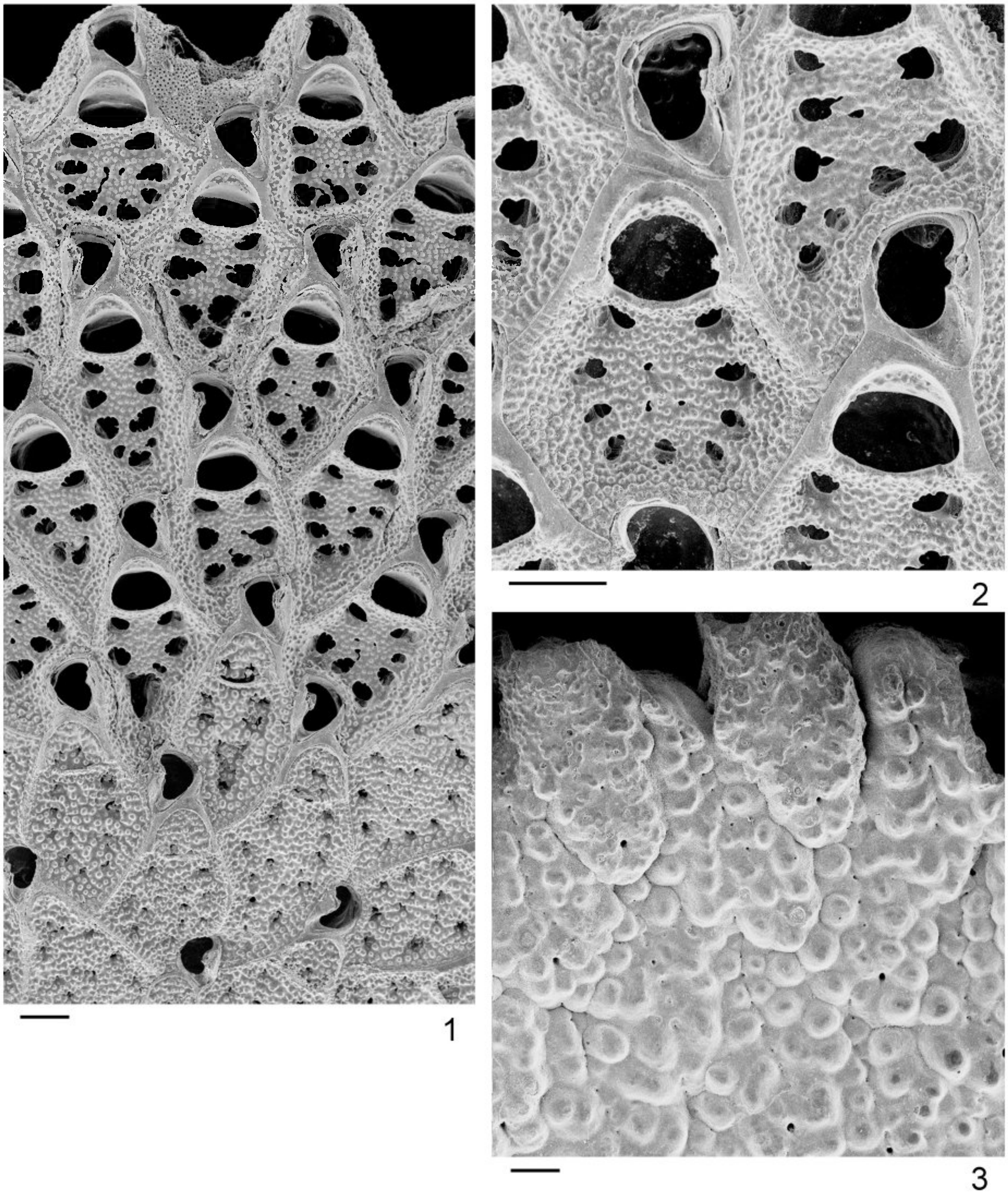

FIGURE *16*—*Discoporella marcusorum* n. sp. *1*, USNM530328, Gulf of Panama; colony border and central view; *2*, *3*, USNM530329, Gulf of Panama; *2*, autozooid and vibraculum; *3*, detail of the basal surface; bar scale = 100 μm.

Remarks.—*Discoporella bocasdeltoroensis* corresponds to Disc2 in the VOUCHER collection and in Dick et al. (2003).

DISCOPORELLA MARCUSORUM new species
Figures 15, 16

Diagnosis.—Colonies conical, with height-diameter ratio 0.25–0.33, average diameter 5.2 mm, semi-determinate growth, basal surface densely granulated.

Description.—Colony conical, with maximum observed diameter 8.5 mm. Autozooids in zone of astogenetic repetition have pores in frontal shield. Those of central area closed by secondary calcification up to 2nd–3rd generation, leaving some pores open and vibracula still functional. Autozooids with 6–9 opesiules armored with spines. Colony growth semi-determinate; no kenozooids or closed autozooids by secondary calcification, at colony margin. Basal surface with radial grooves and high granular density of 1.5.

Etymology.—*Marcusorum*, Latin, is in honor of Ernst and Evelyn Marcus.

Types.—Holotype, USNM530328, GP97-56, Gulf of Panama (7.48°N, 81.03°W), February 1997, H. Fortunato coll., fine black mud, 32 m depth. Paratype, USNM530329, GP97-9, Gulf of Panama (7.55°N, 78.18°W), February 1997, H. Fortunato coll., fine black muddy sand, 19 m.

Measurements.—See Table 5 for morphological measurements.

Occurrence.—Pacific Gulf of Panama and Gulf of Chiriqui. Depth range 10–200 m.

Remarks.—*Discoporella marcusorum* corresponds to Disc. 3B+C in the VOUCHER collection and in Dick et al. (2003).

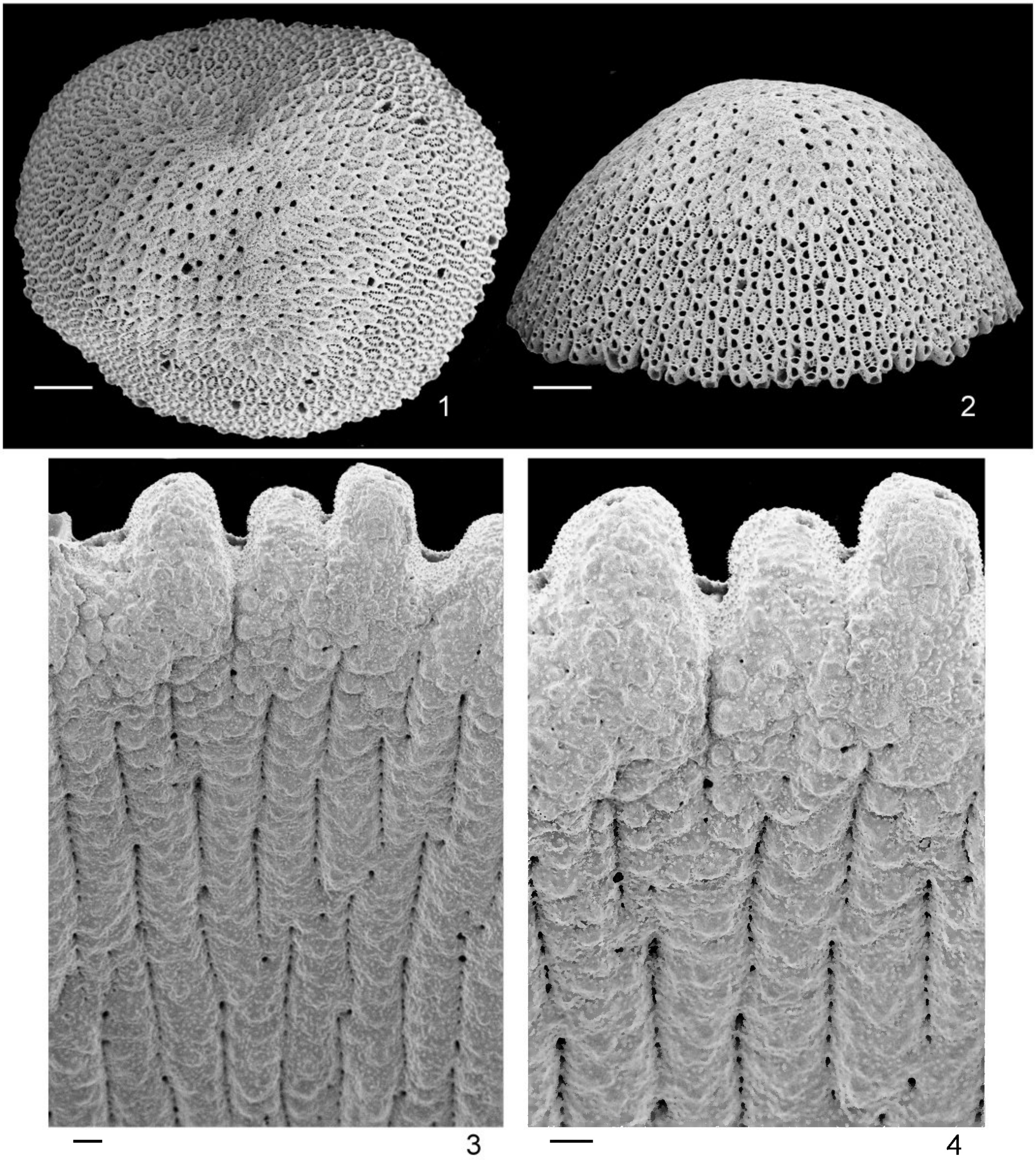

FIGURE 17—*Discoporella cookae* n. sp. *1*, *2*, USNM530331, Gulf of Panama; *1*, colony frontal view; *2*, colony side view; bar scale = 1 mm; *3*, *4*, USNM530332, Gulf of Panama; detail of the basal surface; bar scale = 100 μm.

DISCOPORELLA COOKAE new species
Figures 17, 18

Discoporella umbellata (Defrance, 1823). Hastings, 1929, p. 718, pl. 2, fig. 54 (in part?).

Discoporella umbellata subsp. *depressa* (Conrad, 1841). Cook, 1965a, p. 180, pl. 3, figs. 2, 4 (in part?).

Diagnosis.—Colonies dome shaped, sometimes irregular in shape, with height-diameter ratio 0.26–0.54, average diameter 9.3 mm, semi-determinate growth, basal surface densely granulated.

Description.—Colony dome shaped, but occasionally very irregular in shape, with maximum observed diameter 10.8 mm. Autozooids in the zone of astogenetic repetition have fewer pores in frontal shield than *D. marcusorum*. Those central are closed by secondary calcification up to 6th–12th generation, leaving some pores open and vibracula still functional. Autozooids with 7–9 opesiules armored with spines. Colony growth semi-determinate; no

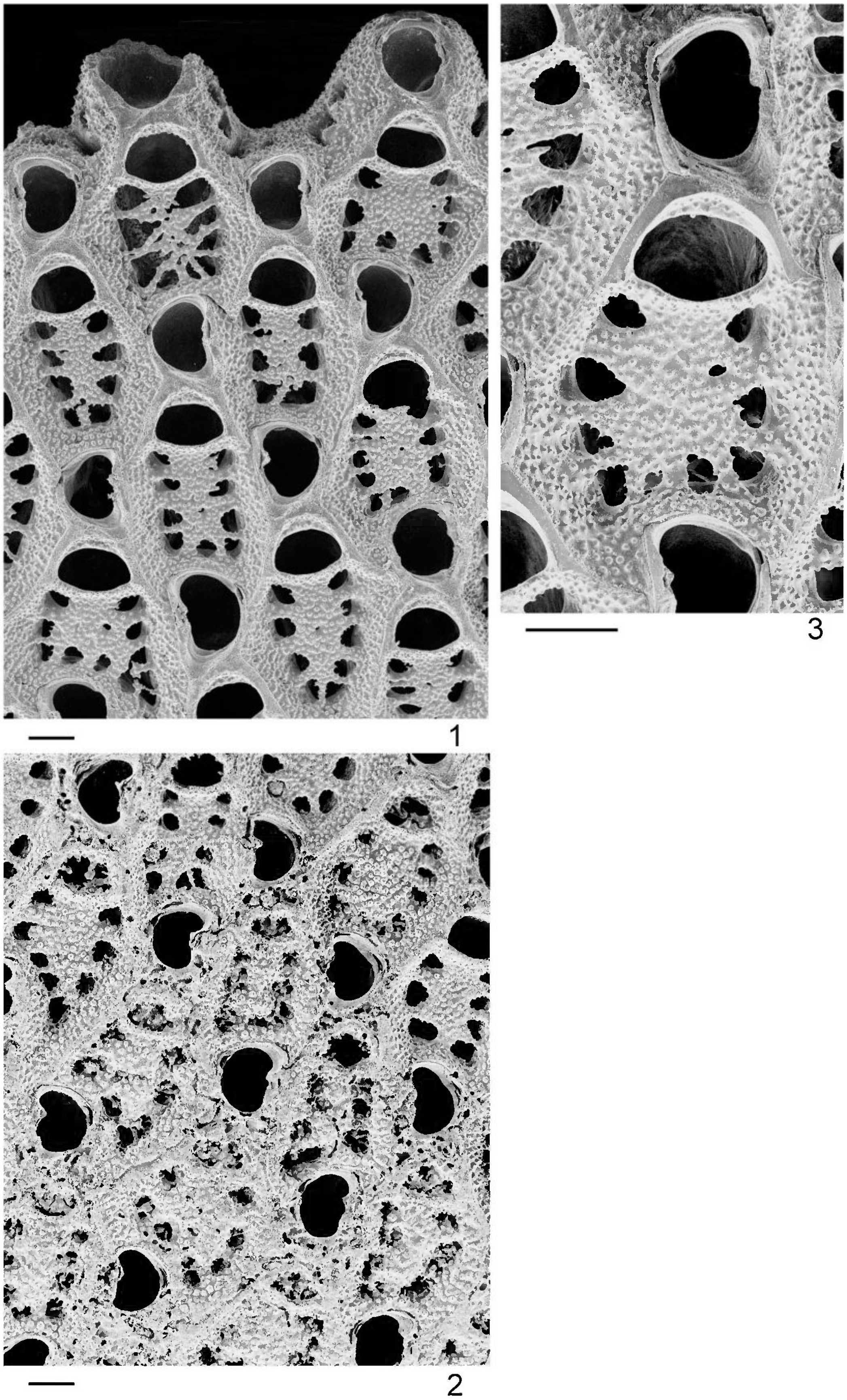

FIGURE *18*—*Discoporella cookae* n. sp. *1*, USNM530331, Gulf of Panama; colony border; *2*, USNM530333, Gulf of Panama; central view of the colony; *3*, USNM530332, Gulf of Panama; autozooid and vibraculum; bar scale = 100 μm.

kenozooids or closed autozooids by secondary calcification, at colony margin. Basal surface with radial grooves and high granular density of 1.5.

Etymology.—*Cookae*, Latin, is in honor of Patricia Cook for her outstanding contributions to understand the biology of Cupuladriidae.

Types.—Holotype, USNM530331, GP97-21, Gulf of Panama (7.83°N, 79.75°W), February 1997, H. Fortunato coll., coarse sand, terrigenous, 76 m depth. Paratype, USNM530332, USNM530333, GP97-21, Gulf of Panama (7.8°N, 79.8°W), February 1997, H. Fortunato coll., black/brownish coarse sand, terrigenous, 76 m depth.

Measurements.—See Table 5 for morphological measurements.

Occurrence.—Pacific Gulf of Panama and Gulf of Chiriqui. Depth range 10–80 m.

Remarks.—*Discoporella cookae* corresponds to Disc3A in the VOUCHER collection and in Dick et al. (2003).

KEY TO SPECIES

1) Basal surface of the colonies densely granulated with an average density of 1.5. 2
– Basal surface of the colonies not densely granulated with an average density of 1 or less. 3
2) Average colony surface of about 90 mm^2; average colony diameter 9 mm; average height/diameter ratio 0.4 (range 0.3–0.5). . . . . *D. cookae* n. sp.
– Average colony surface of about 25 mm^2; average colony diameter 5 mm; average height/diameter ratio 0.3 (range 0.2–0.4). . . . . *D. marcusorum* n. sp.
3) Opesiules armored by spines that coalesce forming small shields. . . 4
– Opesiules armored by spines. 5
4) Colony flat discoidal; average autozooid length of about 0.5 mm; autozooid width–length ratio range 0.6–1.0. . . . . *D. scutella* n. sp
– Colony generally flat disc shaped; average autozooid length of about 0.6 mm; autozooid width–length ratio range 0.5–0.7. . . . . *D. peltifera* n. sp.
5) Colony growth semi-determinate; autozooids of the border of the colony not closed by secondary calcification; average colony diameter of 7 mm. . . . . *D. bocasdeltoroensis* n. sp.
– Colony growth generally determinate; autozooids at colony margin generally closed by secondary calcification; kenozooids present, average colony diameter of 4 mm. . . . . *D. terminata* n. sp.
– Colony growth determinate; autozooids at colony margin closed by secondary calcification; kenozooids present; average colony diameter of 3 mm. . . . . *D. triangula* n. sp.

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