QUANTITATIVE RE-EVALUATION OF ECOLOGY AND DISTRIBUTION OF RECENT FORAMINIFERA AND OSTRACODA OF TODOS SANTOS BAY, BAJA CALIFORNIA, MEXICO

Roger L. Kaesler

Department of Geology, The University of Kansas

ABSTRACT

Environmental and faunal data on Foraminifera (Walton, 1955) and Ostracoda (Benson, 1959) from Todos Santos Bay, Baja California, were used to test applicability of quantitative methods of numerical taxonomy to biofacies analysis. Counts of specimens per species at each station were unreliable indicators of environmental similarity, particularly where total population was considered. Influencing the counts were such factors as mixing, differential productivity, and differential removal and destruction of subfossil forms. Presence-absence data were used. Biotopes were determined by clustering Q-matrices of simple matching coefficients; biofacies were determined by clustering R-matrices of Jaccard coefficients.

The method used requires assumption of the existence of mappable biofacies and biotopes in the study area and adequate sampling, which at any time of year is considered representative of populations for the entire year. If total populations (live and dead forms together) are considered, the method requires that high positive correlation exists between distribution of the live and dead organisms. The method weights occurrence of each species equally for the purpose of delimiting biotopes (Q-technique) and occurrence of each species at each station equally for determining biofacies (R-technique).

When these assumptions are satisfied, use of the numerical taxonomic method of biofacies analysis gives results closely similar to those based on qualitative interpretation. The quantitative method has the advantages that results are objective and repeatable, computation is rapid, results may be expressed graphically, and choice of similarity level is clearly arbitrary and relative.

INTRODUCTION

SCOPE AND PURPOSE OF STUDY

The purpose of this study is to investigate the applicability of the methods developed in numerical taxonomy (Sneath & Sokal, 1962; Sokal & Sneath, 1963) to biofacies analysis. Todos Santos Bay, Baja California (Fig. 1), was chosen as the area of study because the ecology of the Recent Foraminifera (Walton, 1955) and Ostracoda (Benson, 1959) of that area has been thoroughly investigated. In order to succeed in this purpose it was necessary to examine the methods and conclusions of both previous investigators in order to find relationships between their studies and strengths or weaknesses of their methods.

Several terms used throughout this report require definition and discussion.

Biofacies analysis is the study of assemblages of organisms, their areal and chronologic distribution, and environmental factors that affect them. The term *biofacies* has been defined and used in different ways (Glaessner, 1945, p. 183; Imbrie, 1955,27, p. 450; Teichert, 1958, p. 2731-2734). For work on Recent organisms, both living and subfossil, the following definition is applicable: A biofacies is a group of organisms found together and presumably adapted to environmental conditions in their place of occurrence, such group differing from contemporary assemblages found in

different environments. Transportation of sub-fossil material, or less commonly of living material, to environments different from those to which the organisms are adapted may complicate biofacies analysis. An assumption of paleoecology is that effects of transportation and mixing of faunas is

Fig. 1. Location of Todos Santos Bay.

not great enough to obscure biofacies relationships completely.

A *biotic community* (MacGinitie, 1939) is an "assemblage of animals or plants [or both] living in a common locality under similar conditions of environment and with some apparent association of activities and habits." The major difference between a biofacies as defined above and a biotic community is the element of association of activities and habits. One may discuss biofacies without reference to the effects organisms may have on each other, whereas inherent in the community concept is the idea of structure and interaction among the organisms. In addition, the community concept involves organisms of many kinds, in contrast to biofacies which may relate to a single kind of organism (e.g., ostracodal biofacies, foraminiferal biofacies).

The term *biotope* has also been used in different contexts. Discussing the biotic community Hedgpeth (in Hedgpeth *et al.*, 1957, p. 40) considered biotope or environment as the "particular place" occupied by organisms of a community. Thorson (1957, p. 473) equated biotope with substratum in his discussion of sublittoral or shallow-shelf bottom communities. In paleoecologic work on Permian reefs Newell (1957, p. 433) considered biotopes to be ecological zones, but not in a chronologic sense. Hesse, Allee, & Schmidt (1937, p. 135) defined biotope as the "primary topographic unit" of ecology comprising "an area of which the principal habitat conditions and the living forms . . . adapted to them are uniform." In this study biotope is recognized as an area of relatively uniform environmental conditions evidenced by a particular fauna found in the area and presumably adapted to environmental conditions existing there. Thus it is possible to speak of the ostracodal biotopes or foraminiferal biotopes of Todos Santos Bay.

Numerical taxonomy (Sneath & Sokal, 1962, p. 2) is "the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities." In ecologic or paleoecologic studies the "taxonomic units" are ecologic units (stations), and the "taxa" are biotopes. It is believed that these methods will help give the same repeatability and objectivity to paleoecology which they provide for taxonomy.

Tables 1 and 2 are regarded as n by t matrices in which t is the number of columns (stations) and n is the number of rows (species). Such matrices may be studied in two ways (Sokal & Sneath, 1963, p. 123-125), both of which are of value in ecology. First, the stations (columns) may be compared with each other for all species (rows). This comparison may be made by means of any coefficient, such as the *Pearson product-moment correlation coefficient* or, in the case of presence-data, the *simple matching coefficient* or *Jaccard coefficient*. This method, called the *Q-technique*, results in the quantification of relationships among stations. In this study it led to dendrograms showing similarity among stations on the basis of their faunas and to maps showing quantitative biotopes. The other method of studying the data matrices is the *R-technique* in which species (rows) are compared with each other for all stations (columns). This technique quantifies the relationships among species on the basis of the stations at which they occur. The ecologic meaning of the R-technique is discussed more fully in a later section.

The strong emphasis on qualitative techniques in animal ecology during the first half of this century was shown by MacGinitie (1939, p. 48), who wrote: "I know of no way of making any hard or fast rule for determining the limits of a community other than the good judgment of the investigator." The need for quantitative paleoecology of microfossils was expressed by Ellison (1951, p. 221): "A mathematical approach to environmental interpretations by quantitative micropopulation studies, although tedious and slow, promises to be the firmest basis for paleoecological investigations." Difficulties of computation which had not yet been overcome by the advent of high-speed digital computers led Imbrie (27, p. 454), in a discussion of the morphologic aspects of biofacies analysis, to reiterate MacGinitie's position:

> Statistically rigorous methods are available (Leitch, 1940; Burma, 1949) but appear to be excessively laborious. Hence the most nearly complete practicable method of multivariate analysis is embodied in the considered judgment of an experienced taxonomist.

Now, however, the high-speed digital computer is a reality. We need no longer avoid computations that are extremely time-consuming when done with a desk calculator. It is possible to make quantitative interpretations of data from large paleoecologic studies that would have been entirely impractical a few years ago because of the time required.

TABLE 1.—*Number of Specimens of Each Species of Foraminifera Collected at Stations in Todos Santos Bay.*

[Stations yielding barren samples not included. Data from WALTON (1955).]

SPECIES	34	44	73	92	110	111	93	109	108	68	104	86	105	103	64	85	84	83	102	63	80	62	43	42	81	35	79	36	94	71
DEPTH (FATHOMS)	3	25	5	6	8	6	6	10	11	19	13	20	12	19	24	20	22	26	26	22	22	23	40	39	22	8	20	19	10	12
TOTAL NUMBER OF SPECIMENS	64	14	24	3	44	75	60	129	137	42	35	115	64	136	154	71	67	124	60	59	39	55	46	22	40	38	103	63	13	19
NUMBER OF SPECIMENS																														
1. Ammotium planissimum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	1	-	-
2. Proteonina sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
3. Goesella flintii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4. Recurvoides spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5. Labrospira sp. cf. L. advena	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-
6. Reophax curtus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
7. Reophax scorpiurus	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	8	-	-	-
8. Unidentified forms	-	-	-	-	-	-	-	-	1	7	-	-	6	-	2	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9. Bolivina pacifica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
10. Globobulimina spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Bulimina denudata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12. Uvigerina peregrina vars.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
13. Bolivina acuminata	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
14. Reophax gracilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
15. Cancris auricula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-
16. Buccella frigida	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	3	-	-
17. Lagenidae	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
18. Cornuspira sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
19. Planktonic forms	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-
20. Bifarina hancocki	-	-	-	-	-	1	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21. Miliammina fusca	-	-	-	-	-	-	-	-	-	-	-	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
22. Angulogerina angulosa	2	3	-	-	-	-	-	-	-	2	4	3	3	3	3	6	-	5	2	3	3	-	2	1	2	-	-	1	-	-
23. Cibicides fletcheri	19	-	16	1	4	14	19	42	54	-	7	4	11	47	81	17	13	26	21	28	14	6	6	6	10	-	-	7	-	-
24. Rotalia spp.	9	4	3	-	4	12	5	10	19	-	2	2	6	-	14	-	8	3	2	-	1	-	1	-	1	1	8	-	-	-
25. Cassidulina subglobosa	-	-	-	-	-	2	-	-	2	-	-	5	1	16	12	16	6	34	13	4	5	3	2	4	1	-	-	-	-	-
26. Planulina exorna	-	-	3	-	-	-	-	-	-	-	-	-	4	4	1	3	3	8	4	2	1	1	4	3	4	-	-	-	-	-
27. Cassidulina tortuosa	-	-	-	-	-	-	-	-	-	-	1	-	1	16	21	2	11	5	-	6	5	31	14	-	6	-	2	-	-	-
28. Textularia sp. cf. T. schencki	-	-	-	-	-	-	-	-	-	1	-	12	4	17	-	6	2	3	-	7	-	2	-	1	-	-	7	8	-	-
29. Cassidulina limbata	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	6	7	25	5	-	3	3	11	-	-	-	-	-	-	-
30. Cibicidina nitidula	-	-	-	-	-	-	-	-	-	-	1	1	-	2	2	2	1	3	1	-	-	-	-	-	1	-	-	-	-	-
31. Polymorphinidae	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	1	1	1	2	-	-	-	-	-	-	1	1	-	-	-
32. Cibicides gallowayi	1	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	2	-	-	-	1	-	-	1	-	-	-	-	-	-
33. Gaudryina sp. cf. G. subglabrata	-	-	-	-	-	-	-	-	-	-	1	-	5	5	1	1	2	-	1	-	-	-	-	1	-	-	-	-	-	-
34. Trochammina kelletoe	-	-	-	1	-	-	-	2	-	-	-	-	2	-	3	-	1	3	3	-	-	-	-	-	2	-	-	2	-	-
35. Cibicides mckannai	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	-	-	-	-	-	-	-	-	-	-	-
36. Bolivina striatella	-	-	-	-	-	-	-	-	1	1	-	2	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-
37. Nonionella miocenica stella	-	2	-	-	-	-	-	-	2	1	-	6	-	-	-	-	-	-	-	-	-	-	-	-	1	3	5	9	-	-
38. Nonionella basispinata	-	1	-	-	2	-	1	-	2	-	1	19	2	3	2	-	-	-	3	2	2	-	-	-	2	7	25	9	4	-
39. Eggerella advena	1	-	-	1	-	2	1	2	1	1	2	3	-	-	-	-	1	-	-	-	-	-	-	1	-	-	1	2	2
40. Labrospira sp. cf. L. columbiensis	1	-	-	-	-	2	-	2	-	-	-	25	6	1	1	-	1	-	-	-	-	-	-	-	2	1	3	1	5	2
41. Proteonina atlantica	-	-	-	-	-	-	-	1	4	2	2	3	1	1	-	1	3	2	2	-	-	-	-	3	1	3	24	3	4	6
42. Trochammina pacifica	-	-	-	-	-	-	-	5	4	23	8	10	7	1	-	-	-	-	-	2	-	8	2	1	-	2	10	8	2	9
43. Elphidium tumidum	-	-	-	-	-	-	-	40	6	1	3	6	-	-	-	-	-	2	1	-	-	-	-	-	-	-	4	3	-	-
44. Discorbis spp.	9	-	1	-	-	3	3	6	18	5	-	1	-	2	-	-	-	-	-	-	1	-	-	-	-	1	-	4	-	-
45. Elphidium translucens	1	-	1	-	27	26	24	5	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-
46. Miliolidae	-	-	-	-	5	5	2	10	6	-	-	-	-	15	3	1	3	-	-	2	-	-	-	-	-	5	2	-	-	-
47. Triloculina sp. 1	9	1	-	-	1	-	-	-	3	-	-	2	-	-	-	-	-	1	-	1	1	-	-	-	1	-	-	-	-	-
48. Dyocibicides biserialis	2	2	-	-	-	-	1	1	9	-	-	-	3	-	3	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
49. Planorbulina mediterranensis	-	1	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50. Buliminella elegantissima	-	-	-	-	1	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
51. Bolivina vaughani	-	-	-	-	-	-	1	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
52. Elphidium spinatum	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53. Gaudryina arenaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
54. Cassidulina sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55. Pullenia salisburyi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
56. Reophax agglutinatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
57. Quinqueloculina sp.	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
58. Chilostomella ovoidea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
59. Eponides sp. cf. E. repandus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 1.—Continued.

NUMBER OF SPECIMENS

	75	76	91	90	54	51	74	89	88	77	78	95	96	97	87	56	70	55	69	50	67	49	48	65	66	57	38	39	47	61	59	60	45	58	37
	15	16	11	13	11	12	12	15	16	16	17	13	15	15	12	24	17	18	19	20	24	28	30	28	27	31	35	68	108	92	110	110	141	96	25
	17	21	24	37	5	1	18	32	57	8	22	39	44	23	63	13	27	63	33	65	67	44	91	230	105	117	155	103	80	40	88	43	102	144	93
1.	-	-	-	-	-	-	-	2	16	-	-	2	8	4	11	2	-	-	1	-	2	1	14	2	4	11	-	1	-	-	-	-	-	-	1
2.	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	2	1	2	-	-	6	1	1	-	-	-	-	-	1	1
3.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	6	1	6	5	6	3	1	-	-	-	-	-	-	1	2
4.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	2	-	3	2	8	4	1	13	3	-	1	-	-	-	1	2	-
5.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	1	13	4	-	1	-	-	1	3	-	-	-	-	-	-	-	6
6.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	15	1	6	6	5	17	74	6	12	-	-	-	-	-	-	-	-	4
7.	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-	3	1	1	4	6	14	5	33	8	-	10	1	-	-	-	-	-	-	-	4
8.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	11	13	-	-	11	-	7	1	-	-	-	-	1	-	4
9.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	4	4	1	9	4	3	8	32	5	-
10.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	7	33	26	8	8	10	38	25	-
11.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	-	15	-	27	10	13	20	1
12.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-	11	1	3	23	-
13.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	5	3	5	15	11	4	1	16	-
14.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	1	4	2	3	4	1	-	1	1	-	-
15.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	1	-	-	-	-	-	1
16.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	2	2	4	1	-	-	-	-	1	5
17.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	1	-	-	-	-	2	1
18.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	2	8
19.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	8	-	6
20.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	1
21.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
22.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4	-	-	2	-	1	-	-	-	-	-	5
23.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	3	-	-	-	11	2	-	4	-
24.	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	-	1	1	4	6	-	-	20	2	-	-	-	-	-	-	-	-	-	-	1
25.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	1	-	2	4	4	4	-	2	1	5	6	6
26.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	1	-	-	-	-	-	-
27.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1
28.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-
29.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
30.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
31.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
32.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
33.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-
34.	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
36.	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	7	7	2	10	6	-	-	-	-	-	1	11
37.	-	-	1	4	-	-	-	-	-	-	-	-	-	4	-	-	2	-	-	-	3	4	4	36	32	24	77	34	8	5	6	-	7	26	13
38.	-	-	-	-	-	-	-	-	-	2	1	3	2	5	-	-	-	-	-	-	-	1	-	-	10	8	4	-	1	-	-	-	-	-	-
39.	1	1	3	1	1	-	2	-	-	-	-	6	6	2	-	-	1	-	3	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-
40.	3	8	1	11	-	-	-	10	11	1	9	12	7	4	25	2	3	5	1	-	2	-	-	5	1	6	6	1	-	5	-	2	-	3	1
41.	8	11	10	12	-	-	2	17	18	2	9	9	3	2	20	-	5	14	12	4	4	1	2	-	3	-	-	-	1	-	5	2	-	2	-
42.	5	1	7	8	4	1	13	3	12	3	1	2	9	-	3	2	11	25	8	20	8	9	2	8	7	4	-	-	-	-	-	-	-	-	8
43.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
44.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	4	-	-	15	-	-	-	-	-	-	-	1	-	-	-	-
45.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
47.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
48.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
49.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50.	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
51.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-
52.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
54.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	1	-
55.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
56.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	3	-	-
57.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
58.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	2	-	-	-	-
59.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

TABLE 2.—*Number of Specimens of Each Species of Ostracoda Collected at Stations in Todos Santos Bay.*

[Stations yielding barren samples not included. Data from BENSON (1959).]

SPECIES	20	23	21	12	4	85	3	83	80	84	35	104	110	66	45	59	17	97	63	306	5	10	29	37	13	36	105	64	81	1
DEPTH (FATHOMS)	1	0	1	17	19	20	23	26	22	22	8	13	8	27	141	102	00	15	15	30	15	17	18	25	27	19	12	24	22	26
TOTAL NUMBER OF SPECIMENS	6	5	14	10	10	21	5	7	17	36	11	6	23	9	10	5	5	12	7	6	6	84	9	32	10	28	19	30	89	13
1. Xestoleberis aurantia	2	-	9	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2. Bradleya aurita	-	-	2	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Hemicytherura sp. cf. H. clathrata	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	3	-
4. Genus A species A	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5. Brachycythere sp.	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6. Haplocytheridea maia	1	1	68	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-
7. Quadracythere regalia	-	-	2	-	-	-	-	-	-	-	-	-	-	8	-	-	-	4	-	-	-	-	-	-	-	-	3	1	8	-
8. Paracypris pacifica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
9. Bairdia sp. aff. B. verdesensis	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	2	5	8
10. Paracytheridea granti	-	-	-	-	5	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	4	11	2
11. Loxoconcha lenticulata	4	2	3	3	4	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1	1	10	-
12. Brachycythere lincolnensis	5	4	7	10	13	1	-	2	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	37	-
13. Bradleya diegoensis	1	3	-	-	-	-	8	1	-	3	-	2	2	-	-	-	-	-	1	-	-	-	-	-	-	1	-	2	3	2
14. Hemicythere californiensis	-	-	-	55	50	10	-	1	4	14	-	-	-	-	-	-	-	-	18	-	1	71	-	-	-	13	5	11	-	42
15. Hemicythere jolloensis	-	-	-	-	-	2	-	-	1	3	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	3	1	6	2
16. Bradleya sp. cf. B. schencki	-	-	-	-	8	-	-	-	1	3	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	1	1	1	1
17. Cythereis glauca	1	-	-	-	-	6	13	1	5	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	1	8
18. Brachycythere driveri	-	-	-	-	-	-	2	2	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	3
19. Cytherelloidea california	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
20. Caudites fragilis	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
21. Cytherura bajacala	-	-	24	-	-	-	-	-	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	2	1	-
22. Cytherella banda	-	-	-	-	-	-	-	-	-	-	-	-	21	-	1	-	-	-	4	-	2	4	-	-	-	1	-	-	-	-
23. Cytherura sp. cf. C. gibba	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	5	1	-	-	-	-	10	18	6	-	-	-	-
24. Palmanella carida	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	3	2	4	-	2	4	15	1	-	-	-	-
25. Leguminocythereis corrugata	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	2	5	2	8	55	-	-	-	-	-
26. Pterygocythereis semitranslucens	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	3	3	3	-	-	-	-
27. Basslerites delreyensis	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28. Pellucistoma scrippsi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29. Bradleya pennata	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	3
30. Hemicytheridea sp.	-	-	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
31. Brachycythere schumannensis	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	20	-	-	-	-	-	1	-	-	1	-	-	-	-
32. Hemicythere palosensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33. Bythocypris actites	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34. Cytheropteron ensenadum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-
35. Cytheropteron newportense	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
36. Sclerochilus nasus	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
37. Triebelina reticulopunctata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
38. Cytheropteron pacificum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Although not always practical for large studies in precomputer days, quantitative techniques suitable for application to problems in biofacies analysis have been available for many years. Of particular interest are the methods used by plant ecologists because some conditions and methods of study of plant ecology are more closely similar to those of paleoecology of invertebrates than are problems and techniques of animal ecology. This is particularly true where sampling is concerned because both plants and fossils are immobile, and living Foraminifera and Ostracoda may be considered so for sampling purposes. The very extensive literature on quantitative plant ecology has been compiled and summarized by GREIG-SMITH (1964). Some quantitative paleoecologic studies (e.g.,

JOHNSON, 1962; LANE, 1964) have used the methods of COLE (1949) and FAGER (1957) which were also discussed by GREIG-SMITH (p. 96, 108, 198). Analysis of foraminiferal and ostracodal biofacies has remained almost exclusively qualitative or, in some cases semiquantitative, in spite of quantitative ecologic work in other fields.

The application of the techniques of numerical taxonomy to ecology and paleoecology, particularly to biofacies analysis of Foraminifera and Ostracoda, has the following aims and advantages:

1) *Repeatable results.* SOKAL & SNEATH (1963, p. 49) have said: "We hope by numerical methods to approach the goal where different scientists working independently will obtain accurate and identical estimates of the resemblance between two

TABLE 2.—*Continued.*

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        68  2 18 34 109   42 108 19  8 149    44 86 65 22 15   111 62 55 11 93    7 14 75 96 49   95 63 73 38  16   60 58
        19 26 65  3  10   39  11 13 15  28    25 20 28  0 39     6 23 18  8  6   15 32 15 15 28   13 19  5 35 137  110 96
        22 16 12 34  46   35  71 14 20 104   162 76 63  1  1     2  2  1  2  2    4  4  3  4  1    4  2  2  2   1    4  2

 1.   - - - - 2 7     3  8  -  - 16     6  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
 2.   - 5 - 8 1       1  4  5 25  9     3  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
 3.   - - - 1 1       -  2  -  1  2     2  2  2  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
 4.   - - - - 1       4  4  1  1  4     3  1  1  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
 5.   - - 2 3 2       2  3  6  4  -    12  1  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -

 6.   - - 1 4 3       1  3  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
 7.   - 2 1 - 4       3 10  - 12  -     -  -  1  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
 8.   - 2 5 2 1       -  2  3  9  9     -  -  4  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
 9.   3 10 15 4 3    11  6  6 51 35    49  -  -  2  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
10.   1 7 - 1 1       4  -  2  1  -     -  6  6  -  1    1  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -

11.   5 5 4 8 13      - 11  6  2  -     9  1  2  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  1  -    1  -
12.   - - 3 - 4       2  3 11 16 10    10  7  2  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
13.   2 2 - - -       2  3  8  7  5     5  9  7  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
14.   - 33 - - 1      -  - 25  6  1    29 35 12  -  -    -  -  -  -  -    -  1  2  -  -    -  -  -  -  -    -  -
15.   6 7 - - 2       -  2  -  6  -     -  1  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  1  -  -    -  -

16.   1 - 2 - -       -  1  2  -  -     -  6 14  -  -    -  1  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
17.   2 2 1 - 1       -  -  6  -  -    15  -  -  -  -    -  -  1  1  1    -  -  -  -  -    -  -  -  -  -    -  -
18.   - 1 - - 1       -  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
19.   1 1 3 - -       -  -  -  3  7     9  -  2  -  -    -  1  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
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21.   - - - - -       -  -  -  -  -     2  1  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
22.   - - - 1 -       -  -  1  5  1     2  -  1  -  -    -  -  -  1  -   10  -  -  2  -    -  -  -  -  -    -  -
23.   - - - - -       -  -  -  -  -     -  1  2  -  -    -  -  -  -  -    1  -  -  -  -    -  -  -  -  -    -  -
24.   - 2 - - -       -  -  -  1  -     1  4  5  -  -    -  -  -  -  -    6  8  -  -  1    -  -  -  -  -    -  -
25.   - - - - -       -  -  -  -  -     1  -  -  -  -    -  -  -  -  -    3  7  4  1  -    4  2  -  -  -    -  -

26.   1 - - - -       -  -  -  -  5     1  1  -  -  -    -  -  -  -  -    -  -  1  1  -    -  -  -  -  -    -  -
27.   - - - - -       -  6  -  -  -     -  -  1  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
28.   - - - - -       -  2  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
29.   - - - - -       -  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
30.   - - - - -       -  1  -  -  -     1  -  1  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -

31.   - 2 - - -       -  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  1  -    -  -
32.   - - - - -       -  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  1  -    -  -
33.   - - - - -       -  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  1  -    2  1
34.   - - - - -       -  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    1  1
35.   - - - - -       -  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -

36.   - - - - -       1  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
37.   - 1 - - -       1  -  -  -  -     -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -  -  -  -    -  -
38.   - - - - -       -  -  -  -  -     -  -  -  -  -    -  1  -  -  -    -  -  -  -  -    -  -  -  -  4    -  -
```

forms of organisms, given the same characters on which to base their judgment." Of course, the same techniques of analysis, that is, the same coefficients of association and the same clustering techniques, must be used for results to be identical. Their statement is part of a discussion of numerical taxonomy, but a similar goal of repeatability is necessary in ecology and paleoecology in order to make interpretations applicable between areas and from one time to another.

2) *Objective conclusions.* In some qualitative approaches to biofacies analysis the conclusions are partially dependent on the original assumptions made about the environment. Some nonquantitative methods of biotope mapping, for example, require that the investigator assume *a priori*, on the basis of physical environment, which stations should be most closely related and then examine species lists until he derives a pattern that is ecologically meaningful. Both WALTON (1955, p. 962-

964) and BENSON (1959, p. 34, 35) arranged their stations in order of increasing depth of water, al-though BENSON modified this order in his study to fit the ostracodal biofacies, which were not as
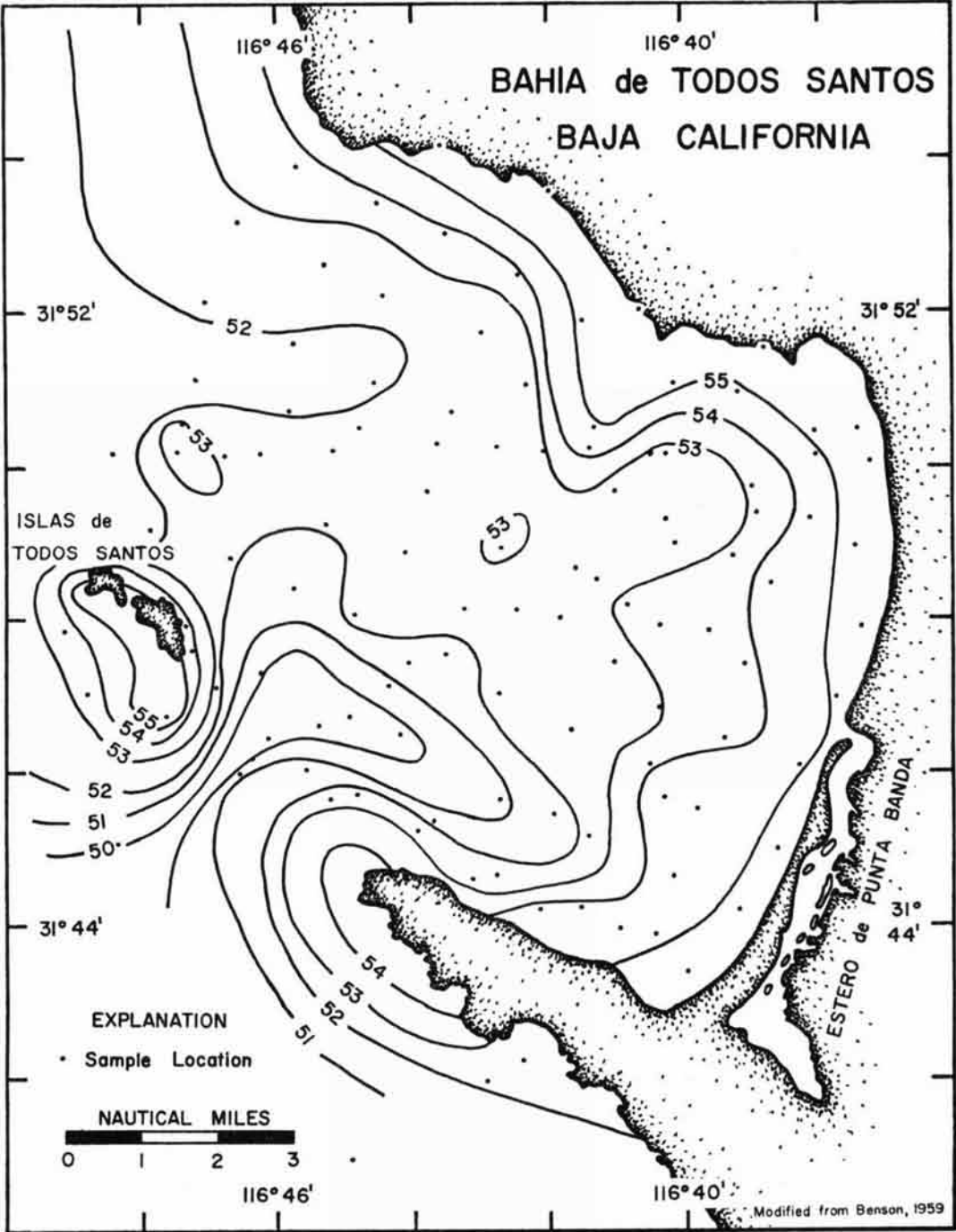
FIG. 2. Mean annual temperature in degrees Fahrenheit of the bottom waters of Todos Santos Bay. (Modified from BENSON, 1959, p. 15.)

strongly controlled by depth as were WALTON's foraminiferal biofacies. Similarly BENSON & KAESLER in their study of the Ostrocoda of the Estero de Tastioto (1963, p. 10-12) initially arranged stations *a priori* on the basis of their increasing distance from (and, hence, supposed dissimilarity to) open Gulf of California stations. In a large or complex study area in which biotope boundaries are not well defined, the final interpretation could depend to a considerable extent on such initial assumptions. If results of Recent ecologic studies are to be applied to study of ancient environments, a method must be found which enables investigators to make interpretive statements about ancient physical environments on the basis of biotope maps, rather than the converse. Numerical taxonomic techniques in ecology eliminate the bias described above and make Recent ecologic interpretations more applicable to studies of ancient environments.

3) *Rapid computations.* The computation of similarity coefficients and clustering of these coefficients into dendrograms was done very rapidly with a digital computer. Once a computer program for the computations was available, the computer time for even a relatively large study (such as 65 stations, 59 species) was almost negligible.

4) *Graphic representation.* Recognition of ecologically meaningful patterns in large matrices of numbers is an extremely difficult or even impossible task for the human mind. Representation of clusters of similarity by dendrograms (SNEATH & SOKAL, 1962, p. 10-11) obviates this difficulty and replaces it was an easily interpreted, graphic portrayal of similarities among ecologic units clustered. The use of a dendrogram, which is a 2-dimensional representation of multidimensional relationships, results in some loss of information (SOKAL & SNEATH, 1963, p. 198-203). The magnitude of the loss of information and an estimate of the closeness of fit of the dendrogram to the matrix may be obtained by the method used by ROHLF (1963). Furthermore, dendrograms express similarities as hierarchies, even though ecologic relationships may not be so structured. I believe that distortion of information in this way is not serious when compared with the shortcomings of alternative methods.

5) *Free choice of similarity level.* Up to this point I have stressed the advantages of a mathematically rigorous method of biofacies analysis. Any method of clustering, whether quantitative or qualitative, has a principal weakness in the neces-

sarily subjective choice of the limiting level of association. Qualitative methods may use "natural breaks" or "best fits" to the physical environment. Statistical methods, such as those of FAGER (1957), JOHNSON (1962), or any of several discussed by GREIG-SMITH (1964), use a statistical level of significance which is chosen arbitrarily. Other quantitative techniques (FAGER & McGOWAN, 1963; LANE, 1964) choose arbitrary levels. The numerical taxonomic dendrograms have the advantage that their "arbitrariness and relativity is obvious" (SNEATH & SOKAL, 1962, p. 12) and unobscured, as in the purely qualitative or statistical methods.

PREVIOUS STUDIES

ECOLOGY OF FORAMINIFERA

WALTON (1955, p. 958) gave a thorough review of studies of the ecology of Foraminifera off the west coast of the United States made before 1955. Many workers (NATLAND, 1933; BUTCHER, 1951; CROUCH, 1952; and BANDY, 1953) considered temperature to be much more important than depth in controlling distribution of benthonic forms. Other studies of the ecology of Foraminifera include work by PHLEGER *(39-44)*, PHLEGER & WALTON *(45)*, PARKER, PHLEGER & PIERSON *(38)*, BANDY *(3)*, BANDY *et al. (4)*, and WALTON *(64)*.

ECOLOGY OF OSTRACODA

An exhaustive list of ecological studies of Ostracoda has been given by BENSON (1959, p. 5-6). Two important papers not included there are studies of Ostracoda and Foraminifera of the Firth of Clyde (ROBERTSON, 1875) and the paleoecology of Pleistocene beds of Scotland (CROSSKEY & ROBERTSON, 1875). Since BENSON completed his work, the ecology and distribution of Recent Ostracoda in North America have been studied by PURI & HULINGS *(47)*, BENDA & PURI *(5)*, BENSON & COLEMAN *(7)*, and BENSON & KAESLER *(8)*. A symposium (PURI, *et al.*, 46) held in Naples in 1963 dealt with the subject "Ostracods as Ecological and Paleoecological Indicators."

FIELD AND LABORATORY TECHNIQUES

STUDY OF FORAMINIFERA

WALTON (1955, p. 958-961) gave a complete discussion of field and laboratory techniques used

by him in studying the Foraminifera of Todos Santos Bay. He took samples on an approximate one-mile grid on February 5, 1952, and additional samples along a traverse from shallow to deep
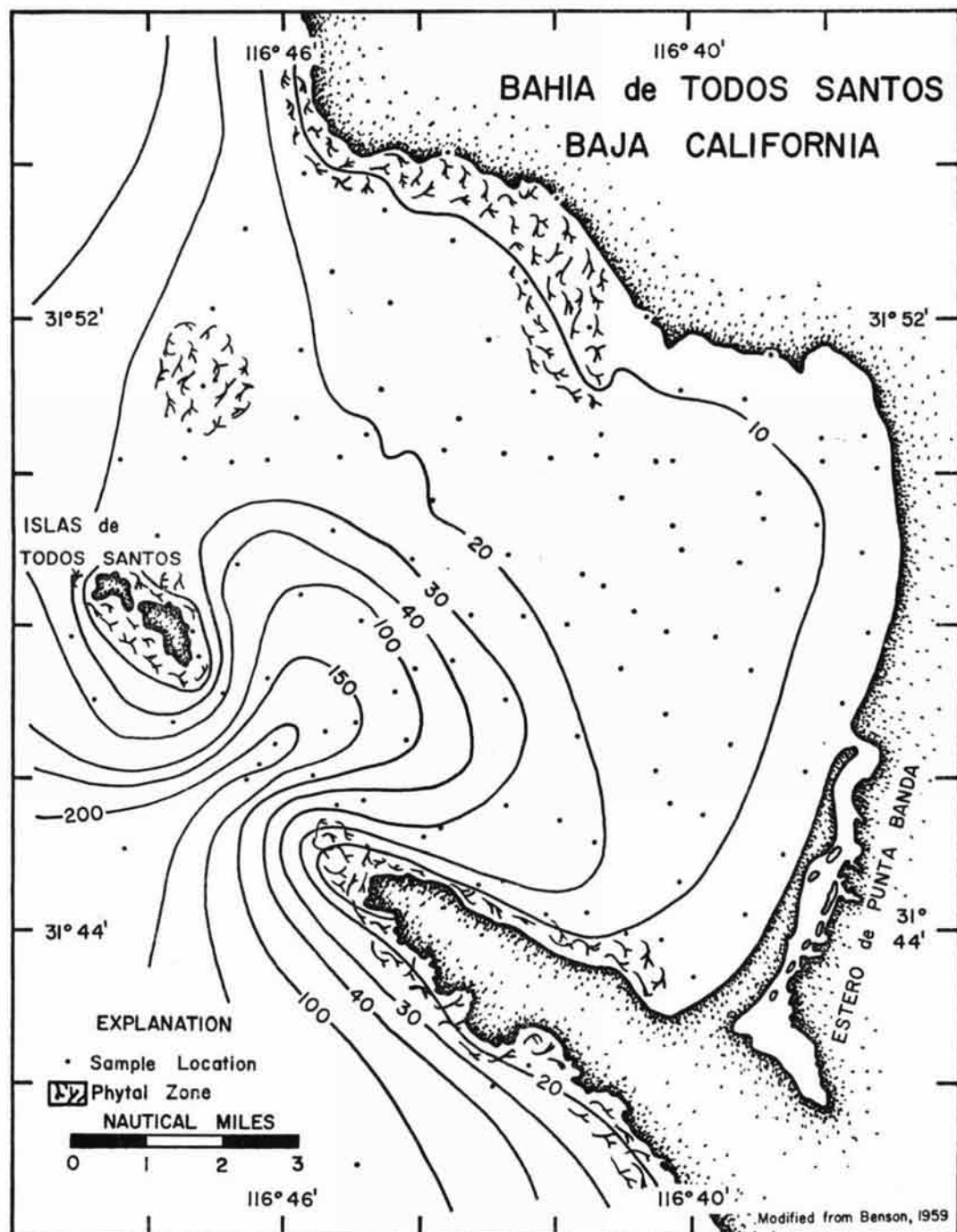
FIG. 3. Bathymetry (in fathoms) of Todos Santos Bay and distribution of attached plant life. (Modified from BENSON, 1959, p. 9.)

water in March, April, June, July, August, October, and November of the same year. The first samples are some that later were used by BENSON and that furnished data for my study. BENSON also collected samples from the Rio San Miguel lagoon and Estero de Punta Banda, both adjacent to Todos Santos Bay, but data from these have not been included in the present paper. Samples were taken with a Phleger coring device (PHLEGER, *40*, p. 3-5) or, in coarse sediment, with an orange-peel dredge and a plastic core liner. Constant volume control was assured by using only the top 1 cm. of a 1⅜-inch diameter core. In coarse sediment the core was taken from the top of the sediment in the orange-peel dredge. As WALTON (*63*, p. 960) pointed out, use of two different methods of sampling as was necessary "introduces a possible source of error in counting or estimating populations of Foraminifera," but "normal variations" in sediment distribution "support the reliability of the samples." Samples were preserved in a 10-percent solution of neutralized formalin. Bottom temperature (Fig. 2) was measured with a bathythermograph on three surveys of Todos Santos Bay in February, June, and October and on two other, more detailed traverses "normal to Punta Banda on both the north and south sides at each season of sampling."

Samples were stained with rose bengal (*62*) to determine which tests contained protoplasm and could, thus, be considered as living (or recently dead) at the time of collection and preservation. Live and dead Foraminifera were counted and sediment was analyzed by standard sieving techniques.

STUDY OF OSTRACODA

BENSON (*6*, p. 17-20) described his field and laboratory techniques and discussed some problems involved with the method of biofacies analysis used by him. Ostracoda are not usually as abundant as Foraminifera; so, in addition to samples collected by WALTON, BENSON gathered 33 large samples (about 50 cc.) on 3-part traverse and in rocky tide pools, as well as a few other scattered large samples. He did not compare the two kinds of samples quantitatively (*6*, p. 18). Rose bengal stain was found to be inadequate for distinguishing live ostracodes from dead ones. Many single valves, which obviously were not living at the time samples were collected, took up stain, apparently because they still contained some original chitin.

QUANTITATIVE RE-EVALUATION

No new samples were collected for my study. WALTON's counts of Foraminifera have been used as he presented them (*63*, p. 962-964), as well as his records of the presence and absence of species at different stations, but those outside of Todos Santos Bay were not included. Also, stations lacking reported Foraminifera were not used in my numerical taxonomic study.

Ostracode counts were treated similarly except in the case of BENSON's large samples. These were divided by 10 for the purpose of reducing them to about the same volume as the original samples. The number of specimens of each species in the large samples was then rounded to the nearest integer, values less than 1 being rounded up in all cases. Presence and absence of ostracode species at stations were also used.

The reliability of counts of numbers of individuals of each species of Foraminifera and Ostracoda was suspect because too many unmeasurable factors affected the number of microorganisms in a grab sample or core. A discussion of some of these factors is given in a later section. Although many of the counts were believed to be without ecologic meaning, both Q- and R-technique correlation coefficient matrices were computed from the raw foraminiferal data and adjusted ostracodal data. Q- and R-technique matrices of simple matching coefficients and Jaccard coefficients were also computed.

Dendrograms were constructed from the matrices by two methods: the unweighted pair-group method with simple arithmetic averages (UPGMA) and the weighted pair-group method with simple arithmetic averages (WPGMA). When clustering by these two methods was compared, only very minor differences were encountered. For a more complete discussion of the methods of numerical taxonomy see SOKAL & SNEATH (1963, p. 290-319).

ACKNOWLEDGMENTS

DESCRIPTION OF STUDY AREA, ENVIRONMENTAL FACTORS, AND SAMPLING

DESCRIPTION OF TODOS SANTOS BAY

Todos Santos Bay is located about 40 nautical miles southeast of the United States-Mexico border on the west coast of Baja California (Fig. 1). Its northern edge is formed by an indentation in the coast and its southern boundary by the peninsula Punta Banda which juts from the coastline at an angle of about N. 45° W. Two islands, the Islas de Todos Santos, lie four or five miles northwest of the seaward extremity of Punta Banda. The bay is nearly square and measures about eight miles on a side.

A complete description of the study area has been given by Walton (63, p. 953-958) and Benson (6, p. 6-12), including observations on the bay margins, surrounding geology, and geomorphology. Following is a summary of Benson's description of the coast of Todos Santos Bay.

The northern margin of the bay consists of narrow beaches, terraces, and sea cliffs with some rocky tide pools. The eastern coast has a wide sand beach, the southern half of which makes up a sand spit separating the Estero de Punta Banda from Todos Santos Bay. The southern coast resembles the northern but is even more rocky, with only isolated crescent beaches.

Mean annual temperature of bottom waters and water depths of Todos Santos Bay are shown in Figures 2 and 3. The temperature data were recorded at each station by Walton (63, p. 960) on February 4, June 4, and October 9, 1952, using a bathythermograph. He also took more detailed temperature data as mentioned above. Mean annual bottom temperatures range from about 55°F. in shallow water to about 50°F. in the deep channel. In shallow water near the shore the annual temperature range is about 10°F., but in the deep-

est part of the channel it ranges only about 2°F. annually.

Figure 3 also shows distribution of attached plant life, principally *Macrocystis* and *Laminaria* (6, p. 9). Depth throughout most of the area ranges from 10 to 20 fathoms. A deep channel between Punta Banda and the south island connects Todos Santos Bay with the open ocean, as does the broad northwest margin of the bay.

The effect of depth on distribution of Foraminifera (Natland, 1933; Butcher, 1951; Crouch, 1952; Bandy, 1953; Walton, 1955) and Ostracoda (Remane, 1933; Elofson, 1941; Benson, 1959; Benson & Coleman, 1963; Ascoli, 1964) is complex. Commonly depth is found to be correlated closely with many other environmental factors such as temperature, nearness to shore, degree of light penetration, wave base, and in some cases sediment size and salinity. Thus temperature, usually strongly correlated with depth, has been considered more important than depth itself as a factor controlling distribution of Foraminifera. Benson & Coleman (1963, p. 11) considered depth as a useful aggregate factor expressing the effects of all the above environmental factors on the ostracode fauna. Relationship of depth to other environmental factors and faunistic characteristics of Todos Santos Bay will be discussed in a later section. Table 3 shows the depth in fathoms at each of Walton's original stations.

Of much less importance to benthonic Ostracoda and Foraminifera is surface temperature which, like the nearshore bottom temperature,

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TABLE 3.—*Depth, Temperature, Grain Size, and Faunal Data from Walton's Todos Santo Bay Station*

[Data from Walton (1955) and Benson (1959).]

EXPLANATION.---A. Station.---B. Depth in fathoms.---C. Temp. in degrees F.---D. Grain size in median phi.---E. Ostracode species.---F. Foraminifer species.---G. Ostracode specimens.---H. Foraminifer specimens.

A	B	C	D	E	F	G	H
34	3	55	2.37	10	12	34	63
35	8	54	1.76	6	16	11	38
36	19	54	3.20	9	18	28	63
37	35	53	2.98	5	27	32	93
38	35	53	3.68	2	26	2	155
39	68	53	3.85	0	17	0	103
40	205	50	—	—	—	—	—
41	39	55	—	—	—	—	—
42	39	54	0.97	12	10	35	22
43	40	54	0.25	0	10	0	46
44	25	55	-0.50	19	7	162	14
45	141	50	5.95	3	11	10	102
46	150	50	5.41	0	6	0	17
47	108	50	5.45	0	17	0	80
48	30	51	4.28	0	13	0	91
49	28	52	3.75	1	12	1	44
50	20	52	3.27	1	8	2	65
51	12	54	2.92	0	1	0	1
52	6	55	3.57	0	0	0	0
53	7	55	3.27	0	0	0	0
54	11	54	3.22	0	2	0	5
55	18	54	3.50	1	7	1	63
56	24	53	4.27	0	7	0	13
57	31	52	4.65	0	19	0	117
58	96	52	5.06	2	19	2	144
59	110	52	5.45	3	13	5	88
60	110	52	5.85	3	11	4	43
61	92	52	5.23	0	8	0	40
62	23	52	1.45	2	8	2	55
63	22	53	2.16	0	12	0	59
64	24	53	2.10	12	18	30	154
65	28	52	3.49	16	22	63	230
66	27	52	4.20	2	21	9	105
67	24	52	3.99	0	14	0	67
68	19	53	3.91	9	9	22	42
69	19	53	4.20	0	9	0	33
70	17	53	3.57	0	9	0	27
71	12	54	3.42	0	4	0	19
72	5	55	3.10	0	0	0	0
73	5	55	2.80	2	5	2	24
74	12	54	3.70	0	4	0	18
75	15	54	3.65	3	4	3	17
76	16	53	3.63	0	4	0	21
77	16	53	3.77	0	4	0	8
78	17	53	3.92	0	5	0	22
79	20	53	3.98	0	20	0	103
80	22	52	2.47	9	12	17	39
81	22	52	—	—	—	—	—
82	22	52	—	—	—	—	—
83	26	52	1.92	5	15	7	124
84	22	52	2.40	10	17	36	67
85	20	52	2.40	6	17	21	71
86	20	52	3.51	14	23	76	115
87	12	53	3.93	0	7	0	63
88	16	53	3.73	0	4	0	57
89	15	53	3.70	0	4	0	32
90	13	53	3.61	0	6	0	37
91	11	54	3.62	0	6	0	24
92	6	55	3.20	0	3	0	3
93	6	55	3.48	2	11	2	60
94	10	54	3.65	0	4	0	13
95	13	53	3.72	1	8	4	39
96	15	53	3.91	3	10	4	44
97	15	55	3.93	5	7	12	23
98	16	53	—	—	—	—	—
99	19	53	—	—	—	—	—
100	19	52	—	—	—	—	—
101	21	53	—	—	—	—	—
102	26	53	2.25	0	13	0	60
103	19	54	2.49	0	17	0	136
104	13	54	2.25	3	14	6	35
105	12	54	1.34	10	17	19	64
106	12	54	—	—	—	—	—
107	9	55	—	—	—	—	—
108	11	55	3.65	18	18	71	137
109	10	55	3.44	16	14	46	129
110	8	55	3.87	2	7	23	44
111	6	55	3.47	2	11	2	75

varies seasonally about 10°F. The minimum recorded temperature is 57.0°F. in March; the maximum known is 67.8°F. in August. WALTON (*63*, p. 961) reported that surface temperatures during February, March, and April are quite uniform in Todos Santos Bay.

Average surface temperature in June and July (*63*, p. 966) is 61.8°F., but protected parts of the bay may have temperatures as high as 65°F. A 9° or 10°F. temperature difference between the warm northern and cool southern sides of Punta Banda is common in June, and as great a difference as 21°F. has been recorded. This difference may be ascribed to upwelling along the south side of Punta Banda (*63*, p. 966) which occurs in June and July. In August the 10°F. temperature difference remains, but water both within the bay and on the south side of Punta Banda is considerably warmer. By October and November surface temperature within the bay decreases to about 61°F. and upwelling diminishes so that little temperature differential exists (*63*, p. 966).

Water in the Estero de Punta Banda is very warm in the spring and summer months. Its influence on the temperature of the water in Todos Santos Bay near the mouth of the estuary is increased by the 3.8 foot tidal range (*63*, p. 966).

Salinity in the open ocean off Punta Banda ranges from 33.40‰ in the winter to 33.70‰ in the spring and summer. WALTON (*63*, p. 966) considered this to be a fairly good estimate of salinity in most of the bay, but salinity probably has a wider range of variation near the mouth of the Estero de Punta Banda. If the salinity is as nearly constant as indicated, it seems doubtful that it would have any appreciable effect on faunal distribution.

Sediment distribution in Todos Santos Bay is shown in Figure 4. The distribution patterns on this map were taken from BENSON (*6*, p. 19). WALTON (*63*, p. 966) divided the sediment into three groups on the basis of plots of "phi median against phi deviation and phi skewness." The sediment groups coincide roughly with BENSON's sediment types as follows:

Group I. Medium sand, fine sand, and sediment around the Islas de Todos Santos.
Group II. Very fine sand and coarse silt.
Group III. Medium silt, poorly sorted.

Most size analyses were made with less than 10 grams of sediment. The following discussion of sediment distribution and sediment types in Todos

Santos Bay was taken mainly from WALTON (*63*, p. 966-972) and BENSON (*6*, p. 14-17, 27-29).

The supply of fresh water, and with it detrital sediment, to Todos Santos Bay is not continuous throughout the year. In general, little new sediment is brought into the bay except during occasional floods in winter months. The Estero de Punta Banda acts as a catch basin for all streams entering it and the upper part of the channel within it appears to be filling with silt. WALTON suggested that some of the very fine sand and coarse silt (Group II sediment) may have been carried to Todos Santos Bay during an earlier time when rainfall was more abundant.

Two principal environments of deposition are represented by sediment in Todos Santos Bay. The largest and most easily interpreted of these is the environment occupied by all sediment except fine sand and the coarse sand and gravel around the Islas de Todos Santos (Group 1). Sediment here is apparently in equilibrium with its environment and represents a gradation from nearshore, relatively shallow-water sedimentation to that farther from shore in progressively deeper water.

The other environment of deposition is occupied by fine sand, particularly in the northwest portion of the bay, and coarse sand and gravel around the Islas de Todos Santos. Sediment in this environment is out of adjustment with its environment. WALTON (*63*, p. 970-971) said:

> The depth of water in which they occur, the presence of glauconite, the abundance of organic remains, the presence of pebbles and cobbles encrusted with living organisms, and their geographic position suggest a source or sources other than those supplying sediment to the area at the present time. As with the other boundaries, there is no sharp contact between this group and the adjacent groups. The transition on the bay side is gradual with no apparent change in topography except to the east and south of the south Todos Santos Island, where the narrow insular shelf terminates in the steep walls of the deep channel. The presence of well-rounded pebbles and cobbles over most of this area suggests that it was, at some time in the past, subjected to the rigorous environment of the surf zone. There are no known physical agencies in the area at the present time that could account for such well-rounded pebbles and cobbles at the depth in which they occur. Also, the presence of living encrusting organisms on the pebbles and cobbles indicates that they are not at present undergoing any appreciable transportation or abrasion. The extremely high population of dead Foraminifera and the presence of glauconite over the area suggest slow deposition.

Fine sand of WALTON's Group I at the mouth of the estero is probably the result of scouring by tidal action.

WALTON considered the two environments as indicating 1) the present environment of deposition and 2) an "'unconformable' surface which appears to be the result of a past lowering of sea level." Table 3 shows phi median diameter at each of WALTON's stations.
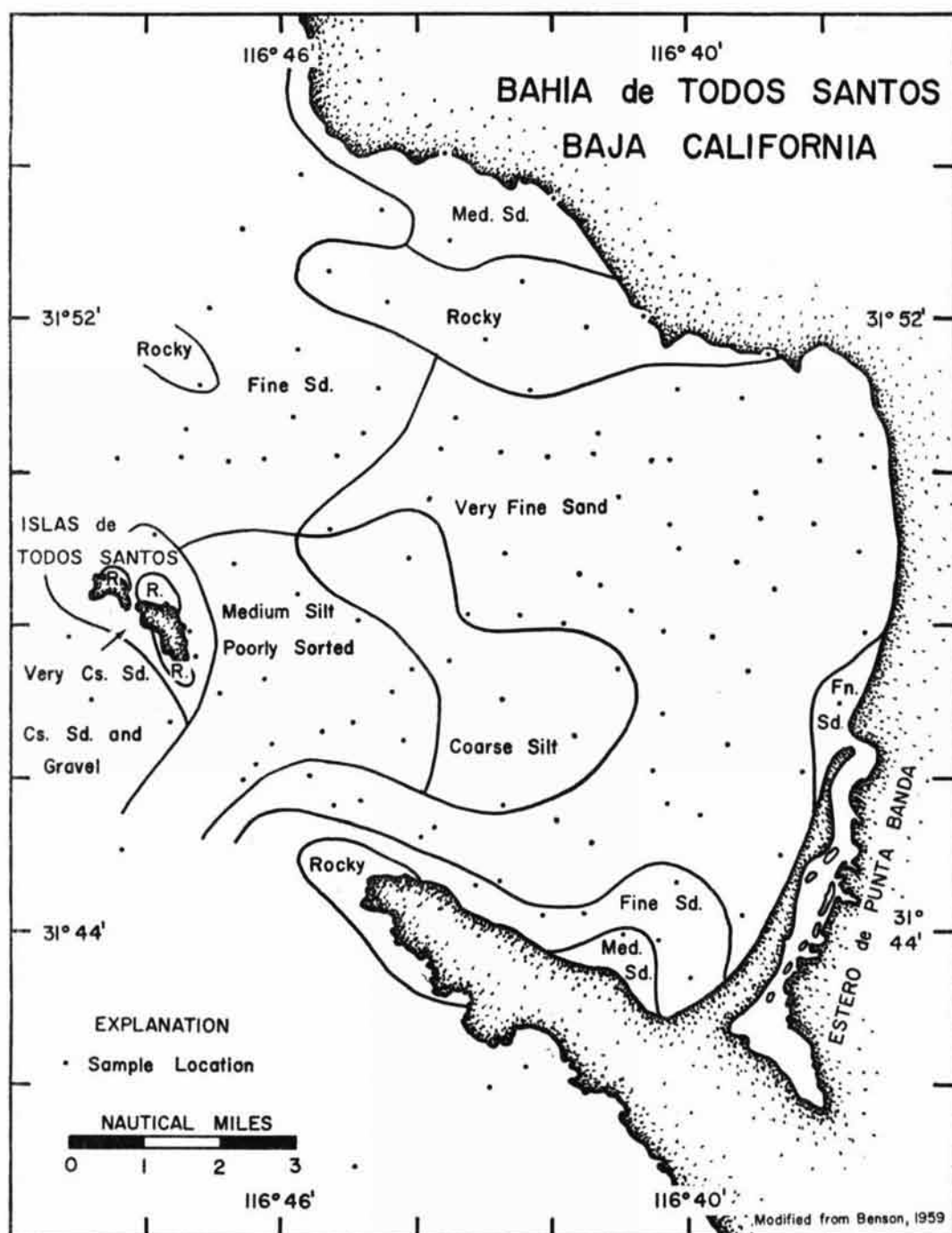
FIG. 4. Sediment distribution in Todos Santos Bay. (Modified from BENSON, 1959, p. 19.)

TABLE 4.—*Correlation Coefficients Computed Between Variables in Table 3.*

[Underlined values are significantly different from zero at 95-percent level.]

	(A)	(B)	(C)	(D)	(E)	(F)	(G)
(A) Depth	---						
(B) Temperature	-0.6648	---					
(C) Grain size	0.0941	-0.0966	---				
(D) Ostracode species	-0.1036	0.1164	-0.0278	---			
(E) Foraminifer species	0.0926	-0.2324	0.4649	0.4083	---		
(F) Ostracode specimens	-0.0852	0.1156	-0.1203	0.8762	0.2483	---	
(G) Foraminifer specimens	0.1144	-0.2394	0.4175	0.4027	0.8529	0.2270	---

QUANTITATIVE RELATIONSHIPS AMONG ENVIRONMENTAL FACTORS

A thorough discussion of the ecology of Foraminifera and Ostracoda was given by WALTON (1955) and BENSON (1959). For details the reader is referred to their studies. Here I consider only some of the gross quantitative aspects of the ecology.

The lower half matrix in Table 4 gives correlation coefficients among depth, temperature, sediment size, and four faunal characteristics of the 78 stations in Todos Santos Bay occupied by WALTON. Values of r significantly different from zero at the 95 percent level are underlined. For discussion of these coefficients the reader is referred to any standard statistical text.

Calculation of correlation coefficients requires the assumption that a linear relationship exists between variables within the population, which is valid when sampling is from a bivariate normal distribution (STEEL & TORRIE, 1960, p. 183). A test of the data of Table 3 for normal distribution using probability paper gave the following results:

1) *Depth.* Slightly skewed right, but probably not significantly so.
2) *Temperature.* Slightly leptokurtic, but probably no significantly so.
3) *Sediment size.* Slightly leptokurtic.
4) *Number of ostracode species.* Not normally distributed, but very much like a Poisson distribution but with considerable contagion. Neither square root nor log transformations improve normality of these data appreciably.

5) *Number of foraminifer species.* Very good fit to normal distribution.
6) *Number of ostracode specimens.* Strongly platykurtic.
7) *Number of foraminifer specimens.* Slightly platykurtic, but probably not significantly different from a normal distribution.

The assumption of normally distributed data, then, is at least roughly met in all cases except number of ostracode species and specimens.

Table 4 shows a negative correlation between depth and temperature. This is what one would expect *a priori* since temperature generally decreases with increased depth. If we ignore the correlation coefficients involving the ostracode data, the only other statistically significant coefficients are between foraminiferal categories and both temperature and sediment size. The negative correlation between temperature and both foraminifer species and foraminifer specimens is only barely significant, but it shows at least a slight increase in number of species and individuals with decrease in temperature.

Of more significance is the correlation between grain size and the two bodies of data on Foraminifera. An increase in median phi size of the sediment correlates with increase in both number of foraminifer species and number of foraminifer specimens. Because phi size is the negative logarithm to the base 2 of the grain size in millimeters, the larger the positive phi value, the smaller the sediment size. Thus, decrease in grain size is accompanied by an increase in both number of fora-

TABLE 5. *Foraminiferal Biofacies of Todos Santos Bay.*

[From WALTON (1955)]

MIDDLE BAY FACIES
Ammotium planissimum
Goesella flintii
Labrospira sp. cf. *L. advena*
Proteonina sp.
Reophax curtus
Reophax scorpiurus
OUTER BAY FACIES
Bolivina acuminata
Bolivina pacifica
Bulimina denudata
Chilostomella ovoidea
Globobulimina spp.
Recurvoides spp.
Reophax gracilis
Uvigerina peregrina subspp.
MARGINAL BAY FACIES
Angulogerina angulosa
Bifarina hancocki
Bolivina striatella
Bolivina vaughani
Cassidulina subglobosa
Cibicides fletcheri
Cibicidina nitidula
Elphidium tumidum
Gaudryina sp. cf. *G. subglabrata*
Planulina exorna
Rotalia spp.
Textularia sp. cf. *T. schencki*
INNER BAY FACIES
Buliminella elegantissima
Discorbis spp.
Eggerella advena
Elphidium translucens
Labrospira sp. cf. *L. columbiensis*
Nonionella basispinata
Nonionella miocenica stella
Proteonina atlantica
Quinqueloculina sp.
Trochammina pacifica

minifer species and number of individuals. As might be expected from the number of other correlations in common, number of foraminifer species is strongly correlated with number of individuals. This correlation indicates that in Todos Santos Bay, at least, few environments are inhabited solely by large numbers of one species of foraminifer as is sometimes found in other areas.

Because of failure of the data to meet the necessary requirement of normality, little faith can be placed in the correlation coefficient computed from the data on Ostracoda. Nevertheless, certain high correlations coefficients in the matrix of Table 5 deserve mention because, as GREIG-SMITH (1964, p. 108) pointed out: "Non-normality of the data does not affect the validity of the use of the correlation coefficient as a test of the *existence* of association" [italics mine]. Ostracode species and specimens correlate nearly as strongly with sediment size as do the Foraminifera, indicating increase in population with decreasing grain size. Also the Ostracoda correlate moderately strongly with the Foraminifera, possibly as result of an underlying productivity factor. As for Foraminifera data, numbers of ostracode species and specimens are strongly correlated with each other.

For ease of computation a value of –4.00 was entered in the median-phi-size data in Table 3 for stations where no sample was collected because of rocky bottom. Although this doubtless introduced some error, it was judged that –4.00 (which corresponds to 16 mm. diameter) represented at least ability of the current at those stations to remove sediment—the "energy level" at the station.

DESCRIPTION OF SAMPLING

Locations of samples collected by WALTON and by BENSON in Todos Santos Bay are shown in Figure 5. Samples numbered 34 to 111 were collected by WALTON; those numbered 1 to 33, 137, 149, 306, and 310-317 were collected by BENSON on a later trip. BENSON collected larger samples (about 50 cc.) than did WALTON "because a 10-cc. sample usually is not large enough for ostracode work." The larger quantities were collected to serve as a "control on the previous samples" (6, p. 18). The longitude and latitude of WALTON's stations and some of BENSON's were reported by BENSON (6, p. 17).

WALTON (63, p. 959) discussed differences in sampling methods used for fine- and coarse-grained sediments. BENSON (6, p. 18) used still other methods of sampling and different sample sizes so that the meaning of numbers of microfossils of each species in a sample is difficult to interpret. Further complications are introduced by the fact that the Foraminifera from BENSON's later samples were not studied, thus making a unified quantitative approach impossible.

Figure 6 shows the gross faunal aspect of the samples collected at each station. Except for nos. 50 and 55, the only stations marked "Ostracoda only" are ones collected by BENSON and not examined for Foraminifera. Nos. 52, 53, and 72 are the only stations of WALTON's which gave barren samples. Stations 9, 137, and 310-17, also marked "barren" were not examined for Foraminifera.

Table 1 shows the number of Foraminifera of each species found in each of WALTON's Todos

Santos Bay samples. Barren samples are not in-cluded in the table. Table 2 gives similar data for Ostracoda from all bay samples—WALTON's and BENSON's. Numbers in Table 2 are actual counts
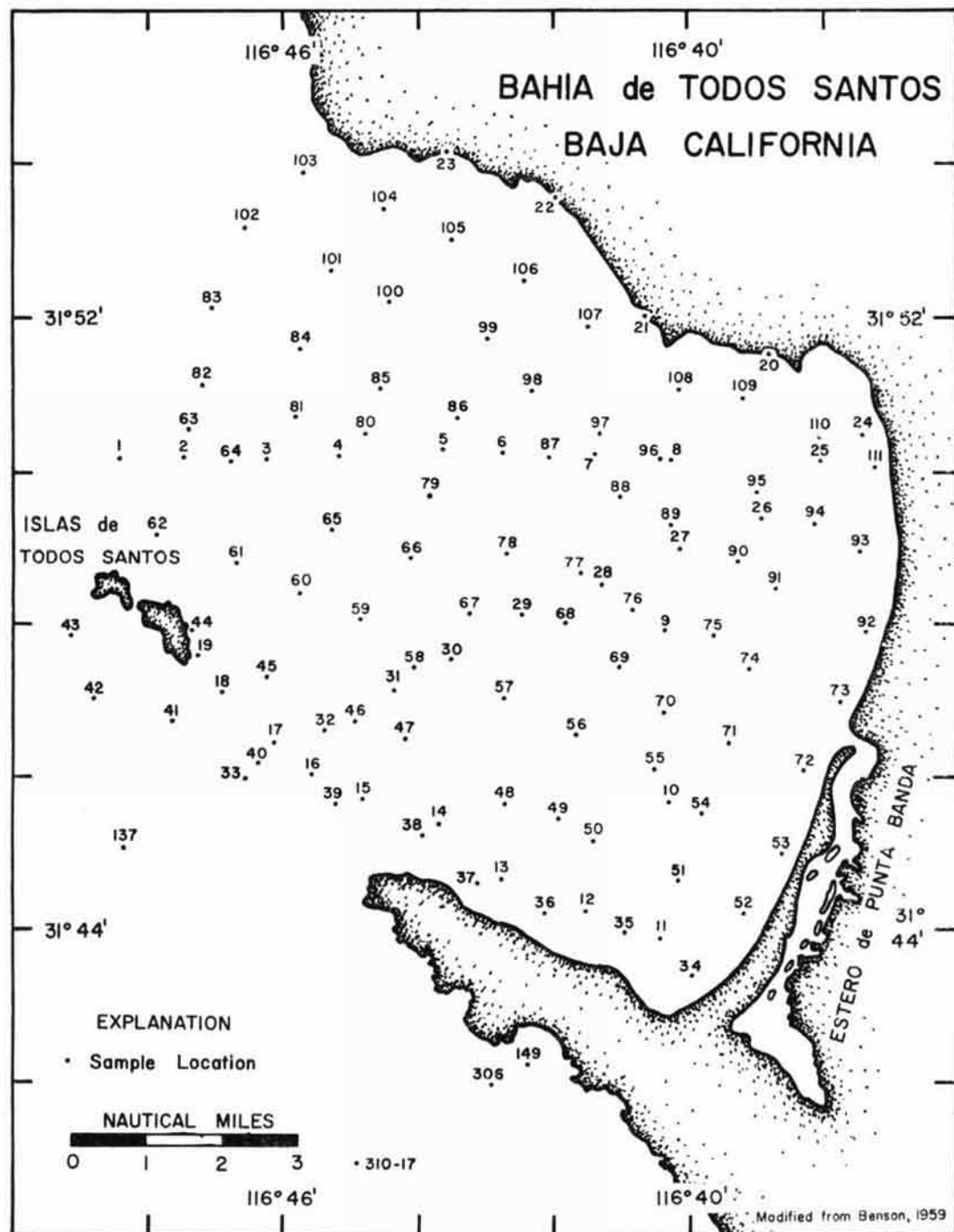
FIG. 5. Location of stations in Todos Santos Bay occupied by WALTON (1955) and BENSON (1959). (Modified from BENSON, 1959, p. 21.)

and are not adjusted for unequal sample sizes. Stations and species are arranged in the tables ac-cording to the order of stations and species in the dendrograms in Figures 10, 14, 20, and 23.
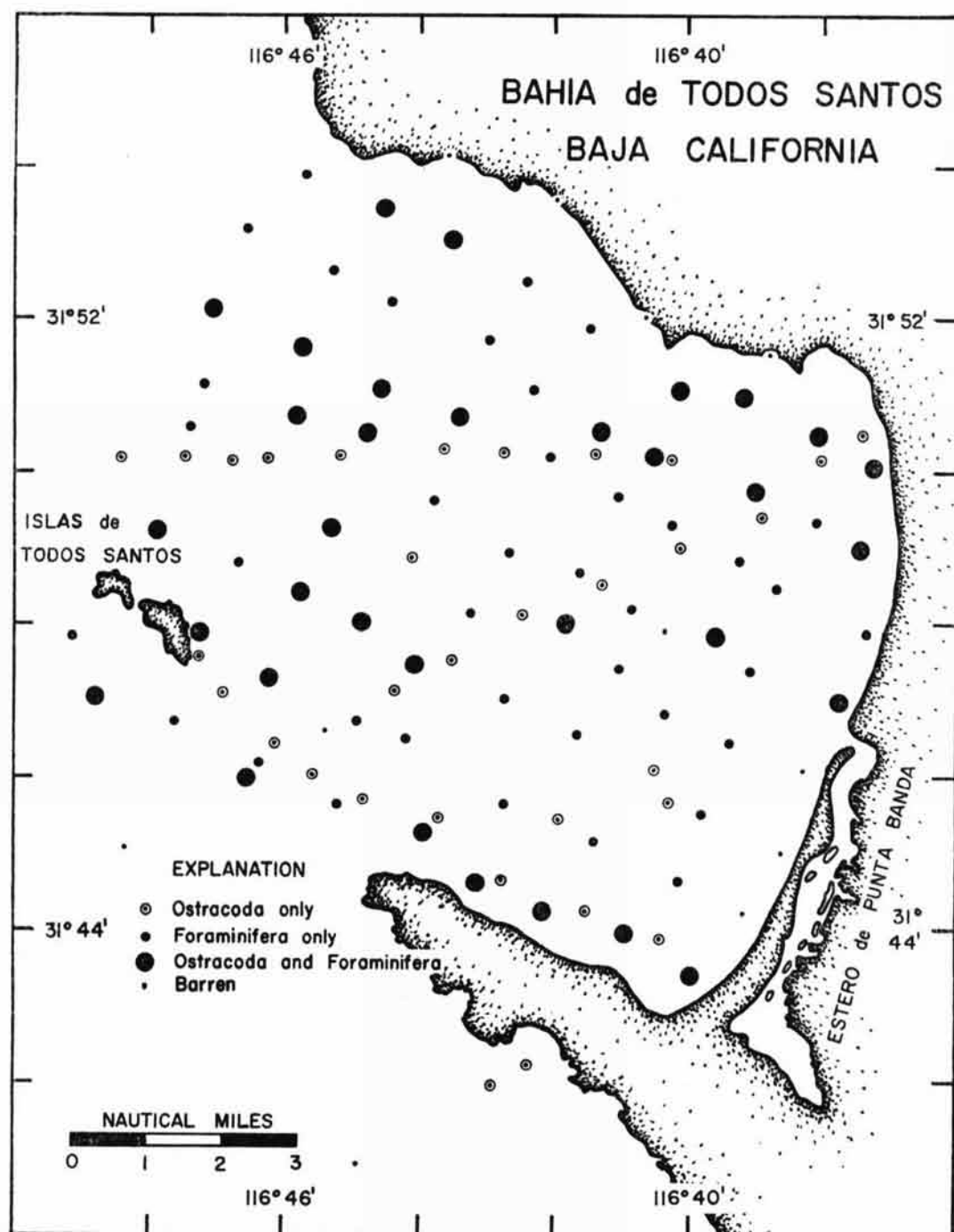
Fig. 6. Gross faunal aspect of the samples collected at each station in Todos Santos Bay. (Data from WALTON, 1955, and BENSON, 1959.)

BIOFACIES ANALYSIS

INTRODUCTION

Determination of foraminiferal and ostracodal biofacies and subdivision of Todos Santos Bay into biotopes constituted a major portion of both WALTON's and BENSON's studies. WALTON (*63*, p. 960) based his biofacies analysis on living or recently dead forms that contained enough protoplasm to be stained by rose bengal. BENSON (*6*, p. 20) worked with both stained forms and empty carapaces and thus established biofacies on the basis of total population, not living population.

Both WALTON and BENSON made a qualitative or semiquantitative approach to biofacies analysis of Todos Santos Bay, but their results have somewhat different meaning because their methods of formulating biofacies were slightly different. WALTON (*63*, p. 979) restricted species of Foraminifera to only one biofacies, for he excluded from all biofacies species that occurred abundantly in more than one environment or not abundantly in any environment. As one might expect, few species fit into a biofacies perfectly. For example, *Reophax gracilis* (KIAER), which lives at depths of 10 to 400 fathoms in Todos Santos Bay and adjacent parts of the open Pacific Ocean (*63*, p. 1013), was included in the outer bay facies because it is most common between 50 and 100 fathoms. Similarly *Angulogerina angulosa* (WILLIAMSON) was included in the marginal bay facies because, although it lives at depths of 3 to 360 fathoms in the study area, it is most abundant between 20 and 100 fathoms. Throughout his study WALTON weighted depth very strongly, but it is important to note that distribution of only species of the outer bay facies seems to be controlled dominantly by depth or environmental factors highly correlated with depth. Table 5 gives a list of foraminiferal biofacies as determined by WALTON (*63*, p. 979-981), who wrote the following in explaining his biofacies (p. 979):

> The living representatives of the benthonic foraminiferal species in Todos Santos Bay generally fit into four areal assemblages. The boundaries of these assemblages are generalized but the species associated with each assemblage occur most abundantly within the areas outlined in [his text] Figure 14.

BENSON's (*6*, p. 28, 29) ostracodal biofacies are shown in Table 6. He did not restrict ostracode species to a single biofacies, for both *Hemicythere californiensis* LEROY and *Cytherura bajacala* BEN-

son belong to more than one biofacies, and *H. californiensis* LEROY was considered a "significant facies indicator" (*6*, p. 34). Still other species are found in more than one biofacies if BENSON's entire study is considered rather than the stations

TABLE 6. *Ostracoda Biofacies of Todos Santos Bay.*

[From BENSON (1959)]

ROCKY TIDE POOLS
    Brachycythere lincolnensis
    Caudites fragilis
    Haplocytheridea maia
    Loxoconcha lenticulata
    Xestoleberis aurantia
BIOFACIES I
    Bairdia sp. aff. *B. verdesensis*
    Brachycythere driveri
    Brachycythere lincolnensis
    Bradleya aurita
    Bradleya diegoensis
    Bradleya pennata
    Cythereis glauca
    Cytheurara bajacala
    Hemicythere californiensis
    Hemicythere jollaensis
    Hemicytherura sp. cf. *H. clathrata*
    Paracytheridea granti
    Quadracythere regalia
BIOFACIES II
    Brachycythere sp.
    Cytherella banda
    Cytherura bajacala
    Cytherura sp. cf. *C. gibba*
    Hemicythere californiensis
    Leguminocythereis corrugata
    Palmanella carida
    Paracypris pacifica
    Pterygocythereis semitranslucens
BIOFACIES IV
    Bythocypris actites
    Cytheropteron newportense
    Cytheropteron pacificum

from Todos Santos Bay alone. Furthermore, BENSON (personal communication) grouped stations together on the basis of their similarity of fauna in order to estimate similarity of response to environment.

A map of the foraminiferal biotopes in Todos Santos Bay (*63*, p. 980) is shown in Figure 7 and BENSON's ostracodal biotopes are indicated in Figure 8. The lack of congruence of these two maps is perhaps not as great as first appears. The distributions of Walton's marginal bay facies and part of BENSON's biofacies I agree quite closely. Similarly part of WALTON's outer-bay facies is identical in distribution with BENSON's biofacies IV.

Nevertheless, important differences do exist between the two interpretations, some of which may be explained as follows:

1) BENSON and WALTON had slightly different concepts of the meaning and use of biofacies as discussed above.

2) WALTON worked only with living population, whereas BENSON considered total population.

3) The population of Foraminifera was much greater than that of Ostracoda at almost every station.

4) Ostracoda are vastly more complex than Foraminifera. There is no inherent reason why biotopes based on study of the two groups should be congruent.
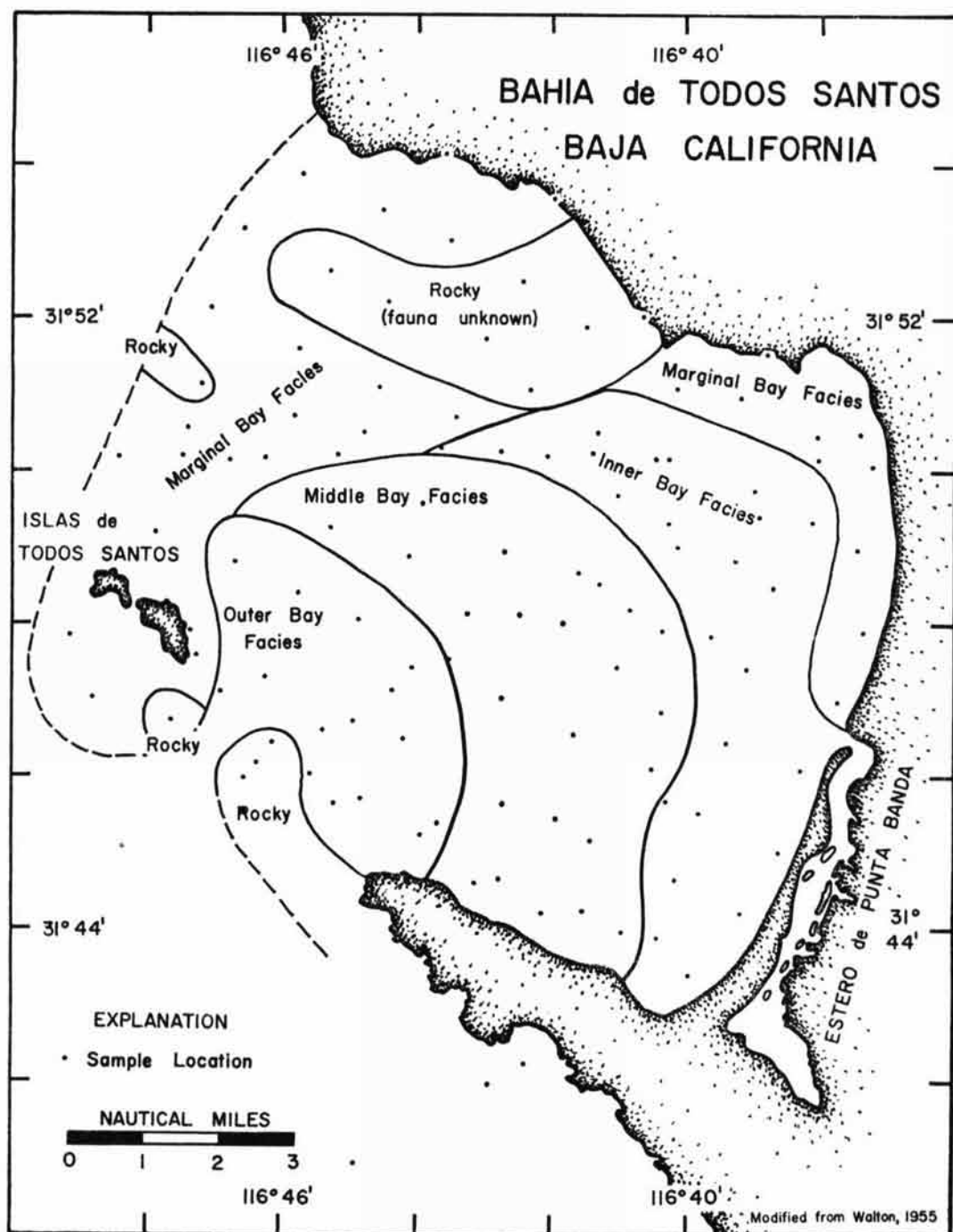
FIG. 7. Foraminiferal biotopes in Todos Santos Bay. (Modified from WALTON, 1955, p. 980.)

They are members of different phyla; their needs are different; their methods of reproduction are different; their modes of life are different. Why, then, should not their responses to their environments be different?

WALTON's marginal-bay biotope on the northwest margin of the bay corresponds with the distribution of sediment group I (63, p. 969), an area
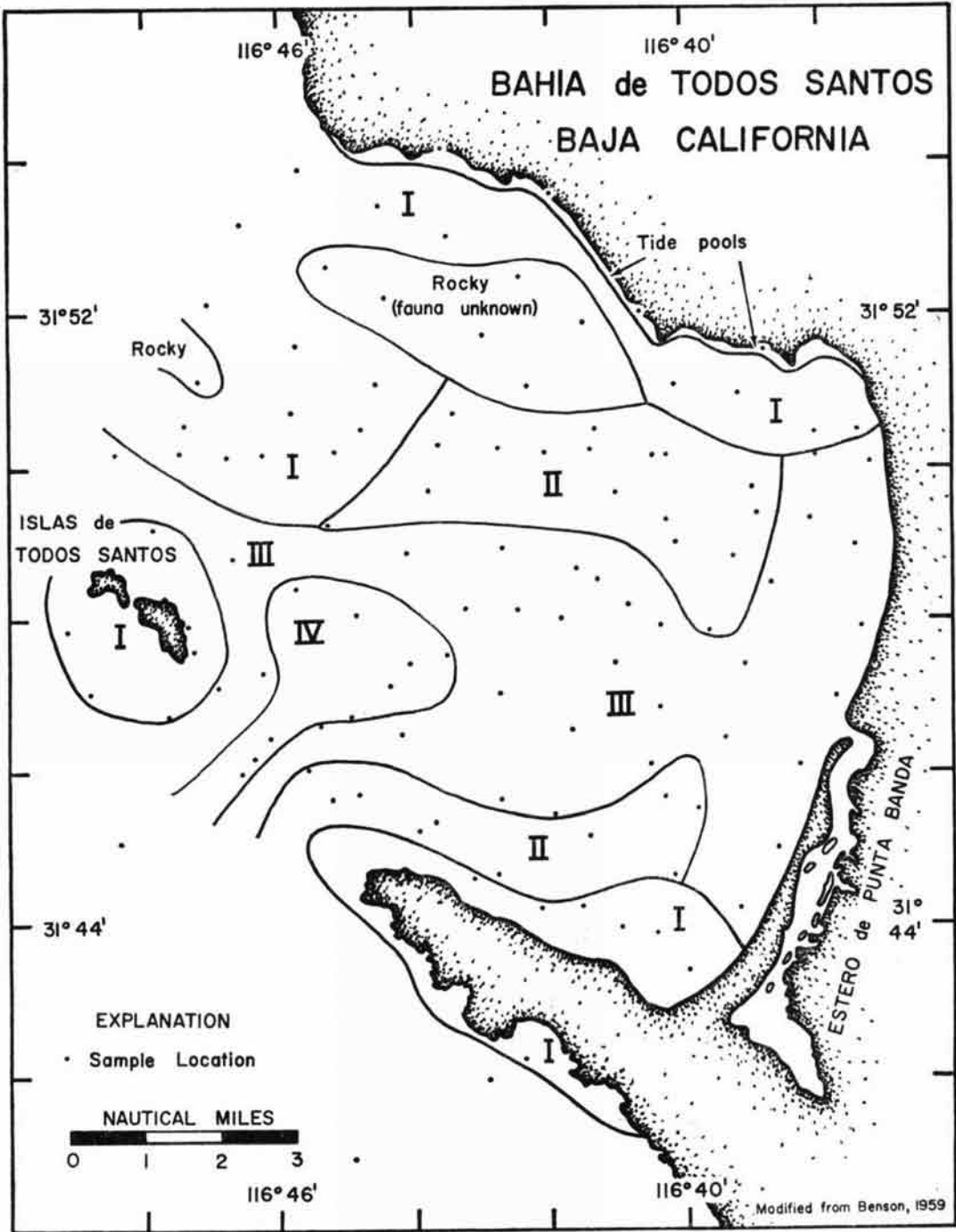
FIG. 8. Ostracodal biotopes in Todos Santos Bay. (Modified from BENSON, 1959, p. 31.)

in which very little sediment is now being deposited. The ostracodal biotopes (Fig. 8) are very closely related to sediment distribution (Fig. 4). The only major deviation from this pattern is the area of biotope III (barren), which transects sediment-type boundaries.

QUANTITATIVE RE-EVALUATION

ASSUMPTIONS

As stated above, the major purpose of this study is to determine applicability of the numerical taxonomic methods of SOKAL & SNEATH (1963) to biofacies analysis. Three assumptions of all biofacies analysis of the type done by WALTON (1955) and BENSON (1959) are: 1) Biofacies and biotopes exist in the study area. 2) A sample adequately represents the population of organisms at a station. 3) Biotopes are mappable.

The first assumption merely requires that we not impose a system on nature where none exists. In an area such as Todos Santos Bay, where environmental factors vary geographically and are mappable, there is little doubt that real biofacies and biotopes exist, although a certain amount of transition from one biofacies or biotope to another is to be expected. GREIG-SMITH (1964, p. 132), in discussing the reality of plant communities, pointed out that the idea of the existence of separate plant communities need not be rejected even if one does not accept the organismal concept of a community (CLEMENTS, 1916). GREIG-SMITH further said (1964, p. 132):

> If species had ranges of tolerances in relation to environmental differences that tended to coincide, so that the total number of species in a region could be arranged in a considerably smaller number of groups, the members of each having approximately the same limits of tolerance, then distinctive communities, with more or less well-defined boundaries, would be expected, each corresponding to, and composed of, one of the groups of species of similar tolerance.

GREIG-SMITH (1964, p. 132, 133) also pointed out that "extensive examination of the limits of tolerance of a geographical group of species in relation to all environmental factors" has not been made and is very likely an impossibility and that "an objective assessment of the reality of plant communities" should be made in an area occupied by more than one community. The preceding discussion applies equally well to biofacies as to plant communities.

If the conditions of the second assumption are not met, that is, if two samples taken from the same locality at the same time have a statistically significant difference in number of specimens or presence-absence patterns, then we can hardly expect to draw conclusions about differences among stations. If sampling is adequate, differences in method of sampling should make no difference except in actual number of specimens found. Adequacy of sampling has not been tested in any study of biofacies analysis of microfossils, but M. A. BUZAS, U.S. National Museum (personal communication), has designed a sampler which will collect multiple samples from one station and which he hopes to use to obtain data for such a test.

If the conditions of the third assumption are not met, that is, if biotopes are not largely continuous geographically, the results of clustering stations into biotopes may appear to be entirely meaningless. If biotopes are real (see assumption 1), they are probably mappable, although sample density may be insufficient to bring out their areal extent. The organisms that make up a biofacies are affected by environmental factors such as depth, temperature, and sediment size, all of which can be mapped. The aggregate effect of these factors should produce a faunal group with a distribution geographically continuous enough to be mapped.

Another assumption must be made when a study includes samples taken at only a few times of the year: 4) An adequate sample (in the sense of assumption 2) taken at any time of the year represents the population for the entire year. This assumption is probably rarely justified if the study considers only living organisms which have a seasonal variation. But in a study like BENSON's (1959) in which total population is considered, dead individuals, which may have accumulated for several years, usually far outweigh living ones. In this kind of study conditions of the assumption are probably met unless some of the species are destroyed or removed much more rapidly than others.

Another assumption that applies only to studies of total population should be stated. 5) A high positive correlation exists between the distribution of live and dead organisms. This assumption is necessary if the biofacies analysis is to be at all applicable to paleoecology. If dissimilarity between
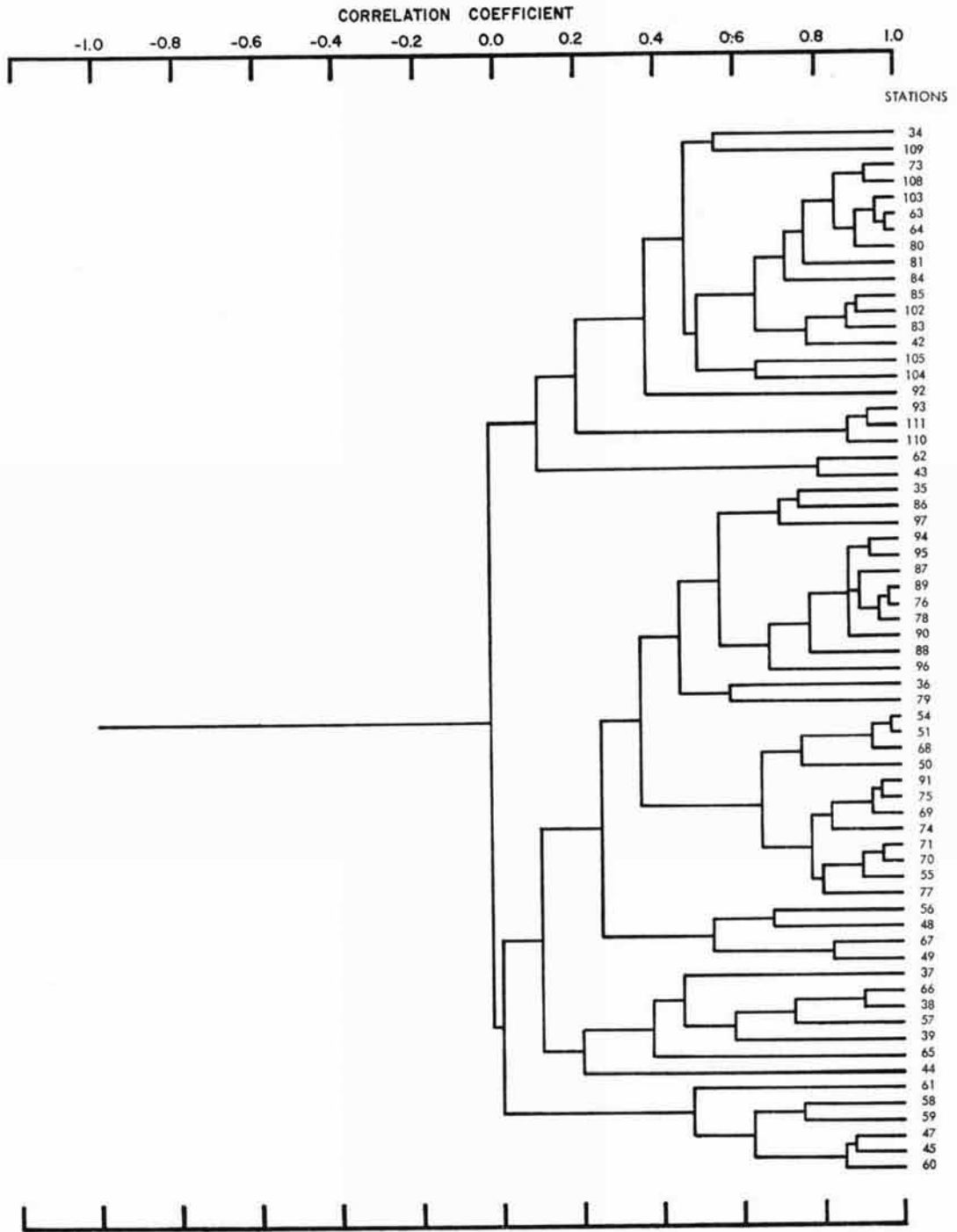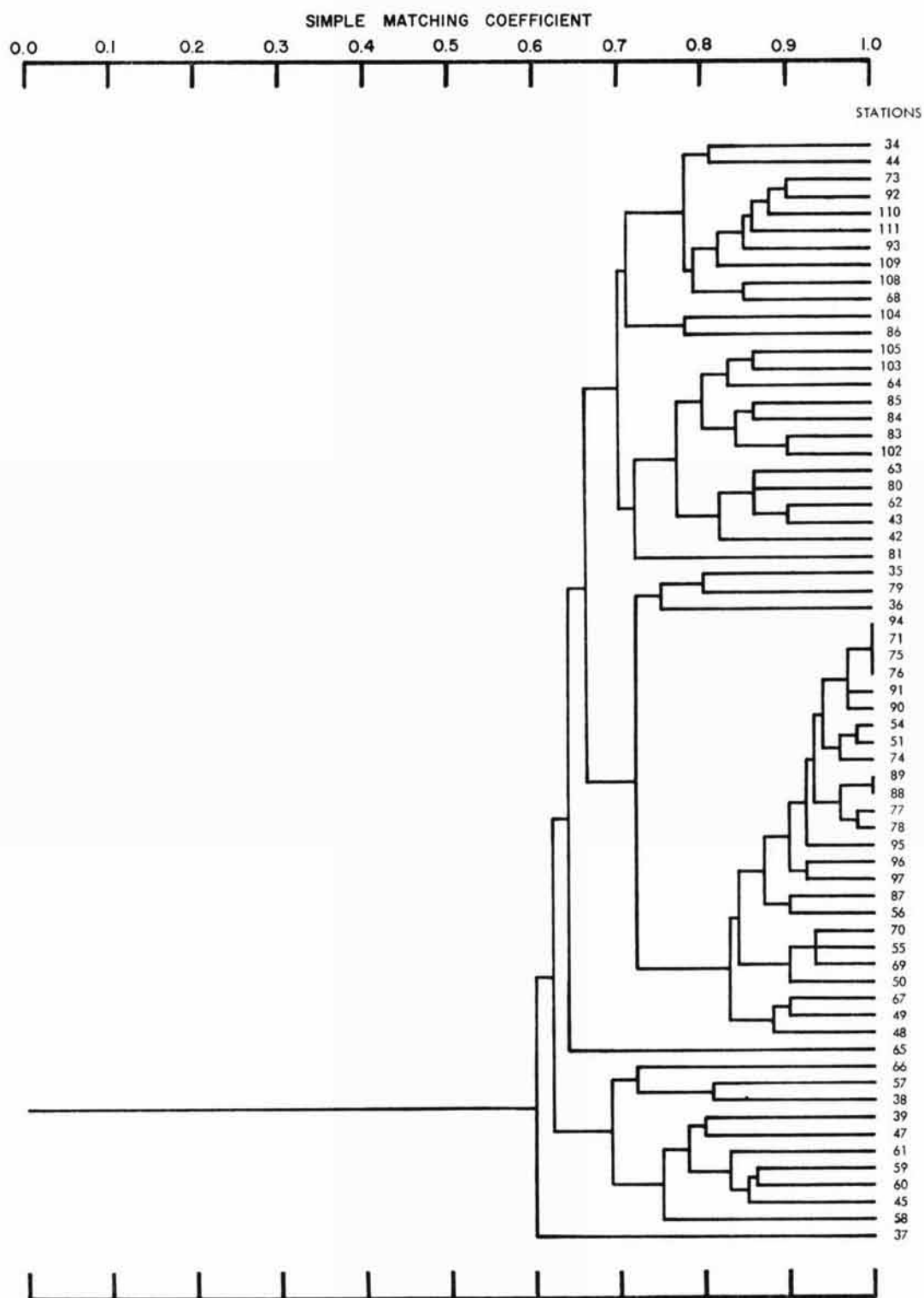
Fɪɢ. 9. Dendrogram (UPGMA) based on Q-matrix of correlation coefficients computed from occurrence data for species of Foraminifera (Table 1).

live and dead populations of organisms is greater than would be expected by chance alone (that is, if the two belong to different statistical populations), no paleoecological interpretations can be made except those that consider transport of the organisms after death *(41)*. Difference of opinion on the validity of total population as an estimate of living population can be found. WALTON *(63,* p. 977) said, "The living populations [of Foraminifera] . . . show different distributions from the dead and total populations." He was concerned primarily with distribution of total numbers of living and dead foraminifers, however, rather than distribution of individual species over the area. ELLISON (1951, p. 218) wrote:

> Marine micro-organisms live and die within community boundaries. When the organisms die the skeletons are potential microfossils and become part of the debris that will eventually be incorporated in sediment. The distribution of dead skeletons is controlled by the original distribution of the living organisms plus the scattering ability of gravity, wave action, currents, mud slides, turbidity currents, and scavengers.

Working deep-water samples BANDY (1964, p. 142) found the following:

> It is important to consider the deeper-water species in faunas as indicators of the proper depositional environment. Less than 10 percent of the species are indigenous deep-water indices in some of the sand samples in core 4486. Most of the remainder are displaced shelf species of which the preponderance are paralic species. Thus, it is fallacious to assume that the major portion of a given fauna is necessarily indicative of the environment of deposition.

Studying both shallow and deep-water forms BANDY *et al.* (1964, p. 422-423) concluded:

> Comparison of different plotting procedures (for Foraminifera) indicate that in the present study live specimens per gram provide better control than live/dead ratios for the determination of the offshore trend and the break in slope, and plots of distribution in percentage are more significant in providing bathymetric control than are plots of specimens per gram.

On the other hand PHLEGER (1955, p. 729-730) in his study of the ecology of Foraminifera from the southeastern Mississippi Delta reported:

> Comparisons of living distributions with distributions of empty tests (total populations, for all practical purposes) show that there is good general correlation for most species. This appears to demonstrate that either there has been little post-mortem transporation of the tests of most species for the area as a whole or the transport which has occurred has moved living and dead populations as a unit. Some of the more abundant marsh forms are an exception to this generalization. . . .

Congruence of distribution between living populations and dead populations of single species has not been tested statistically. JOHNSON (1965, p. 84), working with life and death assemblages of total pelecypod populations of Tomales Bay, California, concluded:

> The death assemblages of Tomales Bay appear to represent with sufficient accuracy, for most paleoecological purposes, the species composition of the life assemblages from which they were derived.

He found the opposite to be true when relative abundances were considered, just as WALTON *(63,* p. 977) found with foraminiferal populations. "The relative abundances of living species are not accurately represented among the dead within most samples" *(32,* p. 84).

Whether requirements of this assumption are met or not depends very largely upon energy conditions in the area of study. If total population counts are to be used, their meaning in terms of the distribution of living organisms should be tested statistically for each species.

SNEATH & SOKAL (1962, p. 4-6) have listed three assumptions of numerical taxonomy and set up four fundamental hypotheses to defend the assumptions based on present knowledge of genetics. When the methods of numerical taxonomy are used in biofacies analysis, these hypotheses take on a different form, and at least one of them does not apply. The assumptions, modified to fit the problems of biofacies analysis, are as follows. 6) All species are equivalent and of equal importance for the purpose of delimiting biotopes (Q-technique study). Similarly data from all stations are equivalent and of equal importance for determining biofacies (R-technique study). 7) The more organisms (or stations) included in a study the more information is gained. 8) An asymptote of information is reached as a large number of characters is accumulated.

Assumption 6) is probably valid only when all organisms included in a study belong to the same taxon or have about the same mass and mode of life. The alternative to the equal-weighing dilemma is not an easy one, however. How much more weight should be given to the presence of one species or one specimen of a species than the corresponding presence of another species or individual? Various criteria for weighting species come to mind (e.g., abundance, ease of identification, fidelity), but each has serious drawbacks. A reliable measure of the abundance of a species, for
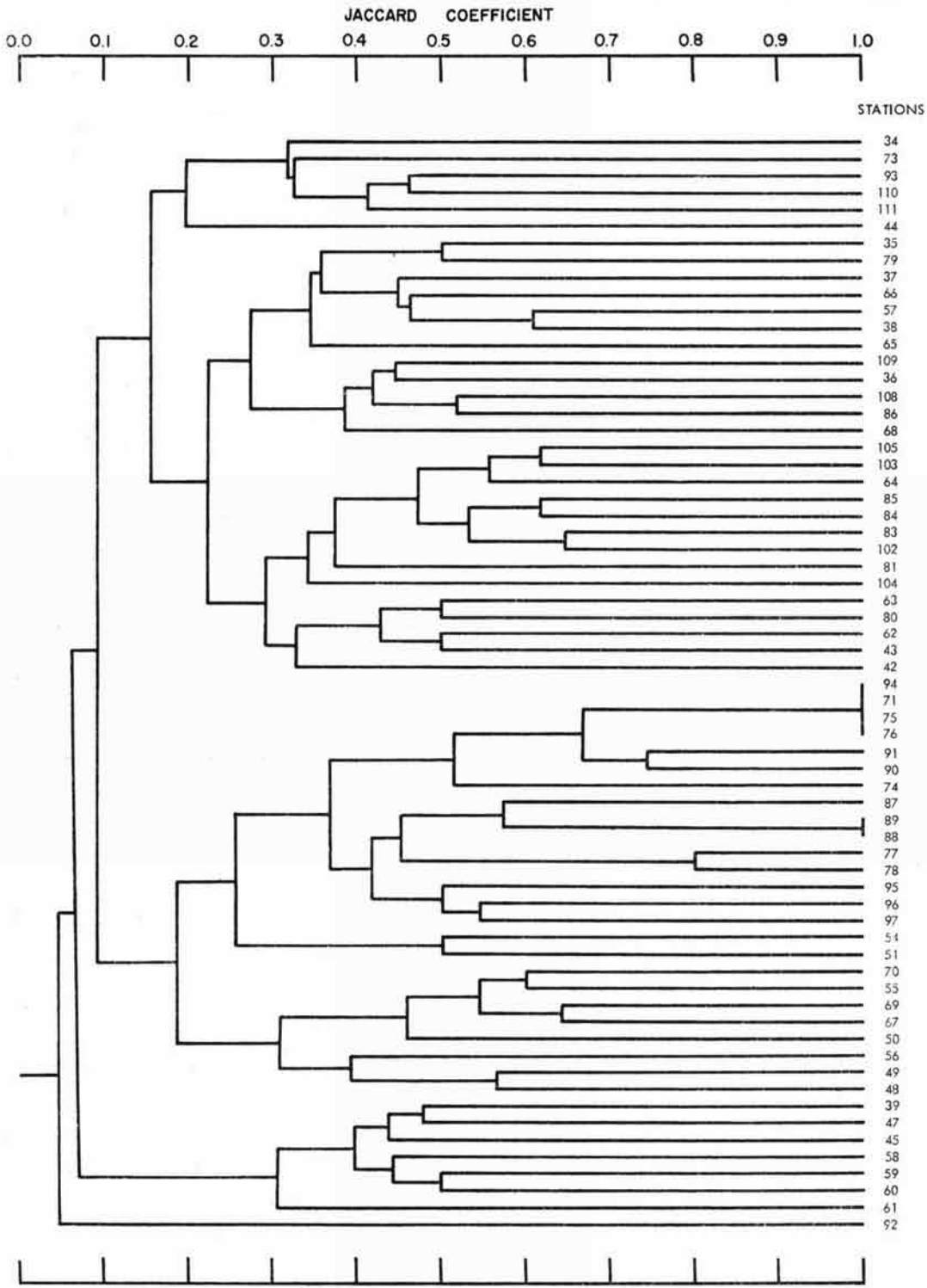
Fɪɢ. 10. Dendrogram (UPGMA) based on Q-matrix of simple matching coefficients computed from occurrence **data** for species of Foraminifera (Table 1).

example, cannot be attained unless each sample in a study has the same ecologic meaning. This clearly cannot be the case when sampling methods and sample sizes are not the same. Furthermore, if total population is used, even samples of equal size cannot *necessarily* be considered equal in meaning because of transportation, mixing, and differential destruction of the dead population. Other criteria for weighting have equally serious imperfections.

The equal weighting applies more readily to R-technique studies. If sampling is adequate and presence-absence data are used, no problems should arise with the assumption. If abundance of species is to be considered, the investigator should collect samples so that all have as nearly the same meaning as possible. In this study, the samples are not necessarily the same in meaning, and no *a priori* basis exists for weighting. In the absence of a basis for weighting, equal weighting is preferable.

Assumptions 7) and 8) do not apply to biofacies analysis to any great extent because a decision is usually made *a priori* about what taxa to include in a study. Every representative of the chosen taxa is then considered. Biofacies and biotopes established as a result of the study will, of course, depend on what taxa were used, since different groups of organisms need not have the same distributions.

HYPOTHESES

Four hypotheses set up by SNEATH & SOKAL (1962, p. 4-6) to defend the assumptions are modified below to apply to ecologic problems.

NEXUS HYPOTHESIS

The distribution of every species in a study is likely to be affected by more than one environmental factors. Conversely, most environmental factors affect the distribution of more than one species. Few ecologists would have any difficulty accepting this hypothesis. GREIG-SMITH (1964, p. 95) said:

> In any community of more than a few species it is unlikely that an influencing factor will influence one species only, and the concurrent influence on several species will result in association between them.

HYPOTHESIS OF NONSPECIFICITY

No large and distinct classes of environmental factors affect exclusively one species or a restricted

portion of a fauna. This hypothesis does not apply to biofacies analysis. It was proposed for numerical taxonomy at a time when workers in that field were perhaps more concerned with a real or final classification than now. Because the characters (species) in a numerical taxonomic biofacies analysis of the type proposed here are fixed in number and all possible characters are used in the analysis, no difficulties can arise from lack of congruence of classifications.

HYPOTHESIS OF FACTOR ASYMPTOTE

This hypothesis makes three assertions (SNEATH & SOKAL, 1962, p. 5). 1) The more species studied the more information will be accumulated, 2) A random sample of the species should represent a random sample of the environmental factors acting in the area. 3) As more and more species are included, the rate of gain of new information for classificatory purposes will decrease. The hypothesis has only limited applicability to biofacies analysis. As pointed out above, the biofacies analyst is not concerned with how many species to consider; he studies all species of the taxa under consideration which occur in the study area.

HYPOTHESIS OF MATCHES ASYMPTOTE

The similarity between two stations is expressed by the proportion of species in which they agree. SNEATH & SOKAL (1962, p. 6), discussing this hypothesis, wrote:

> If we assume that we are making an estimate of a parametric value of matches of all possible characters by using a sample of characters, we expect that the similarity coefficient would become more stable as the number of characters increases, and would eventually approach that parametric proportion of matches which we would obtain if we were able to include all the characters. Further increase in the number of characters is not warranted by the corresponding mild decrease in the width of the confidence band of the coefficient.

The parametric value in a monotaxic ecologic study is the number of matches if all the organisms belonging to the taxon in the study area have been found. If many samples have been taken from diverse environments within the study area, the actual number of matches should be very close to the parametric value, particularly if total population is used so that seasonal variation is minimized.

FIG. 11. Dendrogram (WPGMA) based on Q-matrix of Jaccard coefficients computed from occurrence data for species of Foraminifera (Table 1).

EVALUATION OF COEFFICIENTS
OF ASSOCIATION

CORRELATION COEFFICIENT

In biofacies analysis the correlation coefficient is computed from counts of specimens of each species at all stations included in the study. Necessary to an evaluation of the usefulness of the coefficient, then, is an evaluation of meaningfulness of the data.

The use of numerical data such as those in Tables 1 and 2, although it seems to give much detailed information, has several fundamental disadvantages in ecologic work. JOHNSON (1960) gave an excellent discussion of the "circumstances leading to the preservation of shallow-water marine organisms." He listed (p. 1084) three characteristics of marine environments which cause death assemblages to differ from life assemblages and which introduce bias into paleoecologic work: 1) Selectivity of destructive processes operating upon death assemblages. 2) Mixing of indigenous and exotic elements in a death assemblage. 3) Physical and chemical alteration of fossils and enclosing sediment.

Limitations of using total number of specimens in a sample for quantitative biofacies analysis were discussed by IMBRIE (*28*, p. 653-654), who listed the following kinds of information represented by the total: specimens of all growth stages, broken material from groups of unequal fragility, and hard parts of organisms bearing various quantitative relations to soft anatomy. Each sample may have an entirely different ecologic meaning, and total number of specimens reflects at least four factors, the first three of which apply even if only the living population is considered in the study. 1) Sample size. 2) Productivity. 3) Rate of sedimentation. 4) Rate of removal of dead material by physical and chemical means.

If total number of organisms is not precisely meaningful, then statistics derived from total number can be of no more value. Specifically, use of number of species per unit weight or per unit volume does not consider variance among samples with respect to the four factors listed.

The correlation coefficient, widely used in numerical taxonomic work presents other problems in addition to those mentioned above when applied to ecologic problems. Discussing the Pearson product-moment correlation coefficient, STEEL & TORRIE (1960, p. 183) said: "It is assumed that, in the population, a linear relation exists between the variables. This is a valid assumption when sampling is from a bivariate normal distribution." COLE (1949, p. 422) stressed the limitations of correlation methods in general because of the distinctly "'non-random' nature of the spatial distributions commonly observed in populations of organisms." This is certainly the case with the data of this study, particularly the Ostracoda (Table 2). JOHNSON (1962, p. 33-34) further questioned the applicability of correlation statistics to delimit faunal associations (R-technique) beyond the failure of the data to fit assumptions of the method:

> A correlation statistic may reflect other sorts of relations . . . , but its use to delimit faunal association is open to question. Two species may occur together frequently and have no constant relationship between their numbers. . . . This circumstance is too common in marine communities to permit the use of a correlation statistic to represent faunal associations. In paleontological samples, the number of individuals of a particular species is difficult to obtain and interpret.

In paleoecological work where the dead population or total population must be used as the best available estimate of the live population, use of numerical data, such as number of specimens per species at a station, should be avoided. In a study in which only the live population is considered for biofacies analysis, actual counts may be used to compute correlation coefficients if the populations are normally distributed and the investigator has some means of ascertaining the ecologic meaning of each sample.

Principal components factor analysis and rotation to simple structure using SOKAL's MTAM rotation (SOKAL, 1958) were done on foraminiferal and ostracodal R-technique correlation coefficients, regardless of the unreliability of the correlation coefficients. The result of the factor analysis were meaningless and are not reported here.

SIMPLE MATCHING COEFFICIENT

The simple matching coefficient was introduced into numerical taxonomy by SOKAL & MICHENER (1958), but it was used earlier by other workers for other purposes (*57*, p. 133). It is calculated by the equation:

$$S_{SM} = \frac{a+d}{n}$$

where *a* is the number of cases in which two compared items are both present, *d* the number of

times both are absent, and *n* the total number of comparisons. This notation is often used to represent a 2 x 2 contingency table and may be found in many biological statistics texts (*51*, p. 187, 315; *57*, p. 220). The simple matching coefficient requires only presence-absence data rather than ac-
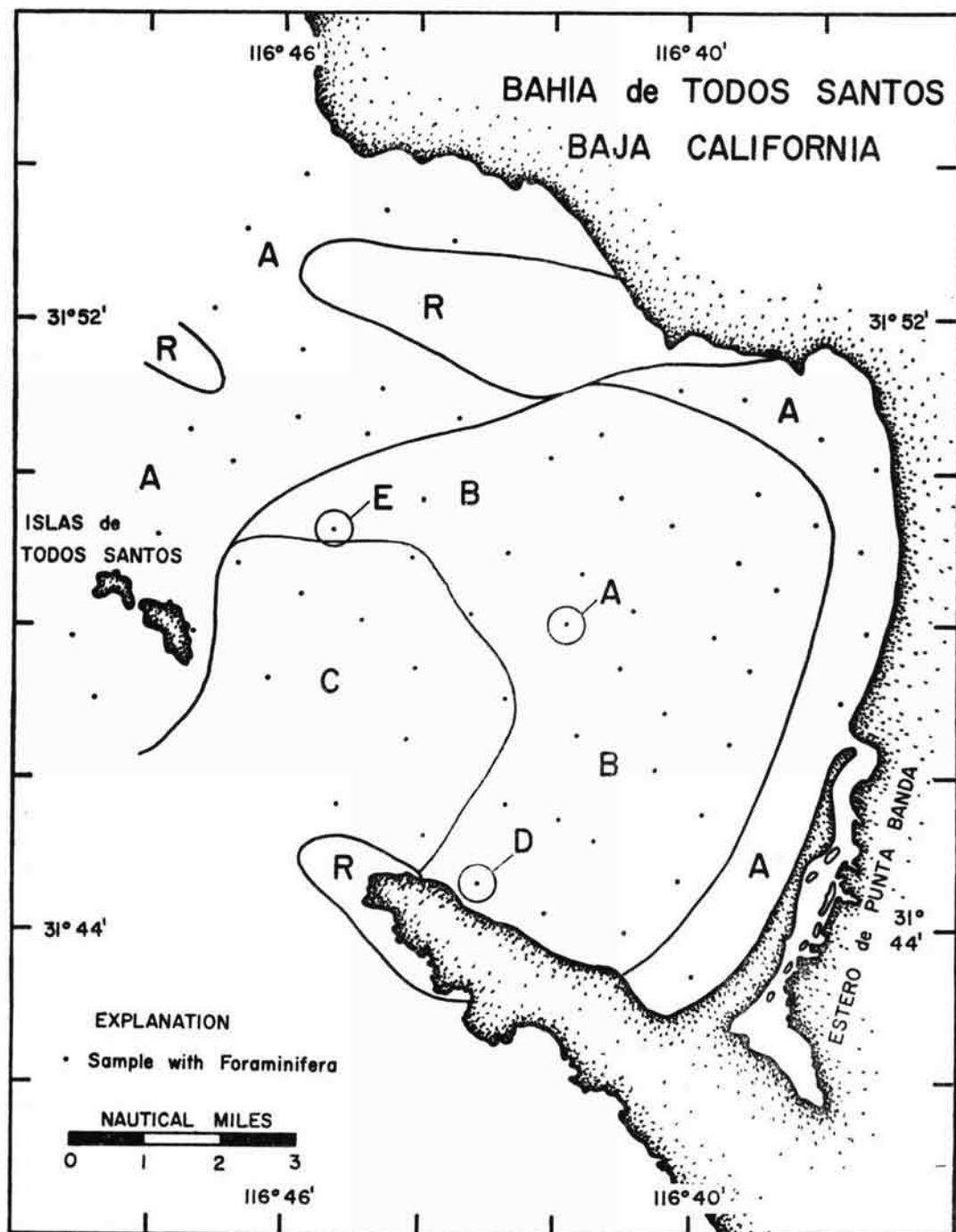

Fig. 12. Quantitative foraminiferal biotopes based on similarity at 0.67 level using dendrogram in Figure 10.

tual counts of organisms, and it gives equal weight to both positive and negative matches.

The importance of negative matches has been widely discussed in ecological literature. The occurrence of an organism in each of two compared samples has obvious meaning to the biofacies analyst. The meaning of its failure to occur in either is not so readily apparent. FORBES (1907) began quantitative study of animal populations by considering the frequency of mutual occurrences of two species in a number of samples. COLE (1949, p. 415) pointed out the failure of FORBES' coefficient if two organisms were very rare and thus had many negative matches. FAGER (1957, p. 558) said, ". . . negative affinity, being based on the failure to find a species, seems potentially subject to too many unavoidable errors." FAGER's objection is an important one, particularly if the organisms used in a study are large (requiring a very large sample for adequate representation) or if the study is purely paleoecological. If sampling is adequate, however, many "unavoidable errors" will not occur.

Evaluation of negative matches and justification for their in the biofacies analysis of Todos Santos Bay are included in a later discussion.

JACCARD COEFFICIENT

The similarity coefficient which SNEATH (1957) introduced into numerical taxonomy was first used by JACCARD in a series of papers on plant distribution and ecology (e.g., JACCARD, 1912). It is calculated according to the equation:

$$S_J = \frac{a}{a+b+c}$$

where *a, b,* and *c* are standard notations for a 2 by 2 contingency table (*51*, p. 187).

Like the simple matching coefficient, the Jaccard coefficient requires only presence-absence data and ranges from 0 to $+1$. It differs from the simple matching coefficient by ignoring negative matches.

Much quantitative ecology concerned with grouping species into communities by statistical tests of presence-absence data has regarded negative matches equally with positive matches and nonmatches through the use of 2 by 2 contingency tables and chi-square tests of significance (*24, 31*). The implication of large, qualitative or semiquantitative biofacies analyses of Foraminifera and Os-

tracoda (*59,63*) on the other hand, is that negative matches have been omitted from consideration. In general, biofacies were determined first and their distributions mapped later. A notable exception is the study by BENSON (1959). He considered negative matches in defining his biofacies III (=biotope, as used in this study), which was a group of stations with very low ostracode populations.

BENSON's use of negative matches in determining groups of stations is noteworthy. If the study area is relatively small (e.g., Todos Santos Bay), or if it comprises an ecologic unit in which many environments and faunas recur, negative matches give important information, as do positive matches on similarity of two stations, although the information is of a different kind. If species A occurs at both stations 1 and 2, a straightforward reason exists for considering the stations similar to the extent $1/n$, where *n* is the total number of species in the study. By similar reasoning, if sampling is adequate, the absence of species B from the two stations is also meaningful. The stations are similar in being ecologically intolerable to species B. Use of the Jaccard coefficient may introduce some error by grouping stations that represent extremes of an environmental condition which are intolerable to many species.

Processing data by the R-technique in order to cluster species into biofacies requires a different approach to negative matches. Whereas the absence of both species A and B at station 1 is of ecologic interest, it provides no useful information for clustering species into biofacies. Because biofacies comprise groups of associated organisms, the occurrence of both species A and species B at station 1 indicates similarity in their distribution to the extent $1/t$, where *t* is the total number of stations. High enough similarity would warrant grouping the two species in the same biofacies. Perfect similarity caused by negative matches alone would not justify grouping the species in the same biofacies, so negative matches must be ignored.

For reasons just presented, negative matches should be ignored in quantitative determination of biofacies, although both positive and negative matches may be appropriate for grouping stations into biotopes by quantitative methods. In this study R-matrices of Jaccard coefficients have been used to define biofacies and Q-matrices of simple matching coefficients have been used to define biotopes.

QUANTITATIVE DETERMINATION
OF BIOTOPES

FORAMINIFERAL BIOTOPES

Figures 9, 10, and 11 are dendrograms showing similarity among Todos Santos Bay stations on the basis of their foraminiferal fauna (see Table 1). The dendrograms were computed from Q-
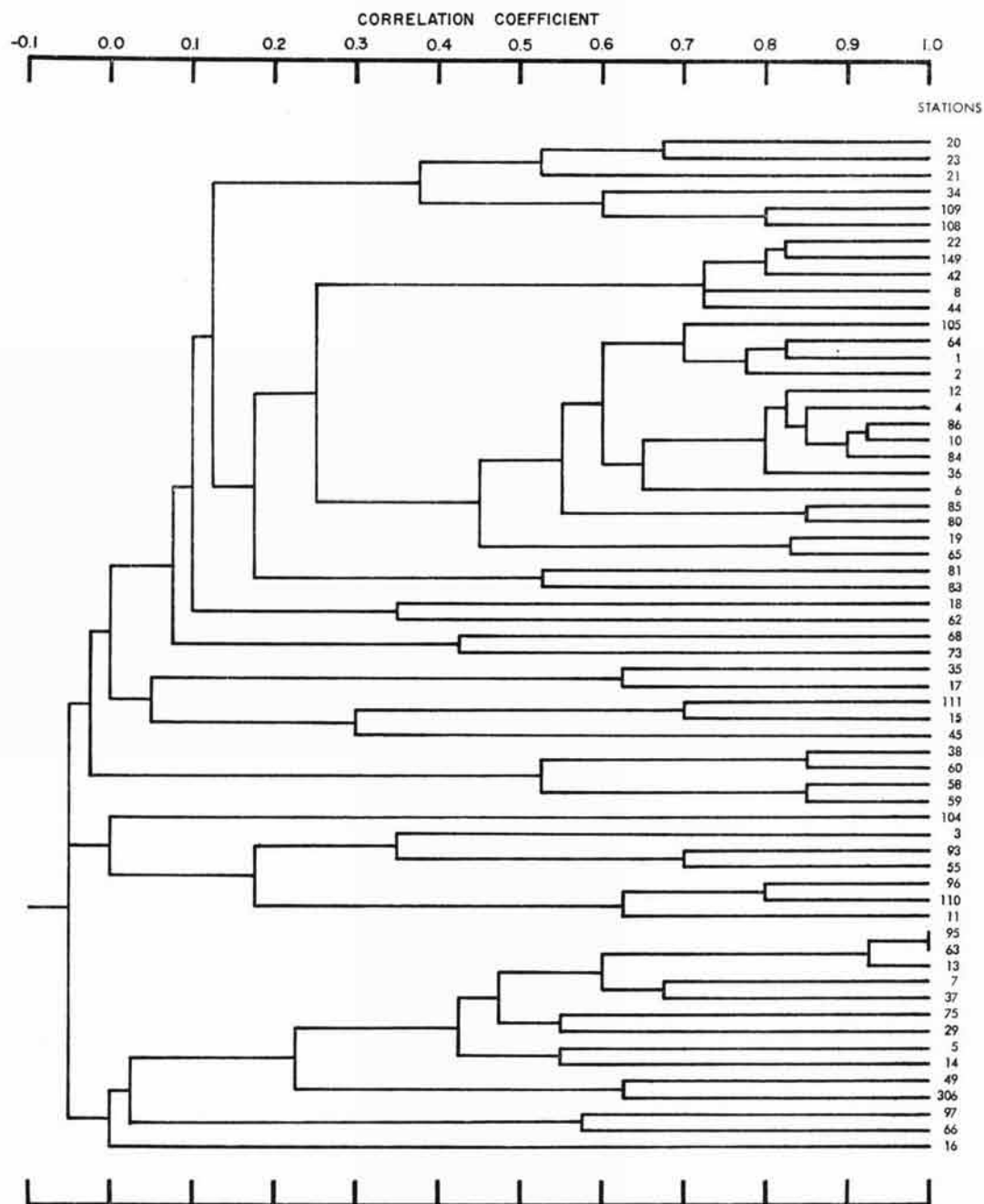

Fig. 13. Dendrogram (UPGMA) based on Q-matrix of correlation coefficients computed from occurrence data for species of Ostracoda. (Table 2 modified for equal sample size.)

TABLE 7.—*Correlation Coefficients Between Half Q-matrices Computed from Occurrence Data for Species of Foraminifera in Todos Santos Bay (Table 1).*

	r	S_{SM}	S_J
r	---		
S_{SM}	0.5433	---	
S_J	0.7483	0.5177	---

matrices of correlation coefficients, simple matching coefficients, and Jaccard coefficients, respectively. According to standard practice in numerical taxonomy *(53, 57)*, a vertical line drawn across the dendrogram divides the stations into groups based on overall similarity. For example, a vertical line drawn through 0.67 on the scale of Figure 10 divides Todos Santos Bay into 5 biotopes, two of which contain only one station each. Similarly, a line through 0.74 distinguishes 11 biotopes. The level chosen depends qualitatively on at least three factors: 1) Natural breaks in the system. 2) Confidence of the investigator in the adequacy of sampling. 3) Desired number of biotopes. The best procedure in biofacies analysis is probably to avoid drawing any lines and to let the dendrograms stand alone as representation of similarity. In this study similarity lines (phenon lines of SNEATH & SOKAL, 1962, p. 11) will be drawn to show similarity of results with those of WALTON (1955) and BENSON (1959).

The three matrices (correlation coefficient, simple matching coefficient, and Jaccard coefficient) from which the dendrograms were prepared may be compared according to the methods of ROHLF (1963, p. 101, 106). If two dendrograms include the same species or stations, it is possible to calculate a correlation coefficient between the original matrices by considering corresponding values in the half matrices as coordinates of points in a scatter diagram. Table 7 is a matrix of correlation coefficients between the three Q-matrices of foraminiferal data.

Fairly high correlations exist between these matrices, for all are significantly different from zero at the 99-percent level. The highest correlation ($r = 0.7483$), between the correlation coefficient and Jaccard coefficient matrices, indicates the similarity between the two. Whereas the Jaccard

coefficient ignores a negative match, the correlation coefficient considers it as a point with zero counts which has very little effect on the coefficient. The lowest correlation coefficient ($r = 0.5177$), between the Jaccard coefficient and simple matching coefficient matrices, is to be expected by the very nature of the coefficients, the first ignoring negative matches and the second counting them as equivalent to positive matches.

It is instructive to compare the dendrograms with WALTON's results. None of the three, of course, gives a map identical to WALTON's biotope map (Fig. 7). On the basis of the evaluation presented above of the three coefficients, we would expect WALTON's results to agree most closely with one of the maps drawn from the simple matching coefficient dendrogram. This is, in fact, the case. Figure 12 is a map drawn from the 0.67 similarity level of the simple matching coefficient dendrogram (Fig. 10); it shows a high degree of similarity with WALTON's biotope map. Areas of generally good agreement are WALTON's marginal-bay biotope with quantitatively determined biotope A and his outer-bay biotope with biotope C. Small circles on Figure 12 indicate anomalous stations. Perhaps station 34, in the extreme southern corner of the bay, should have been circled since it is separated from the rest of biotope A by three barren samples. The quantitative method grouped WALTON's inner-bay biotope and middle-bay biotope together. Choice of a higher similarity level (e.g., 0.86) separates part of the southern middle-bay biotope from the rest, but it does not change the northern part. The 0.86 level does not occur at a clear-cut break in the dendrogram for the area as a whole and should, at best, be considered only as delimiting subbiotopes of biotope B.

It is of consequence that the simple matching coefficient gives the best fit with WALTON's inter-

TABLE 8.—*Correlation Coefficients Between Half Q-matrices Computed from Occurrence Data for Species of Ostracoda in Todos Santos Bay (Table 2).*

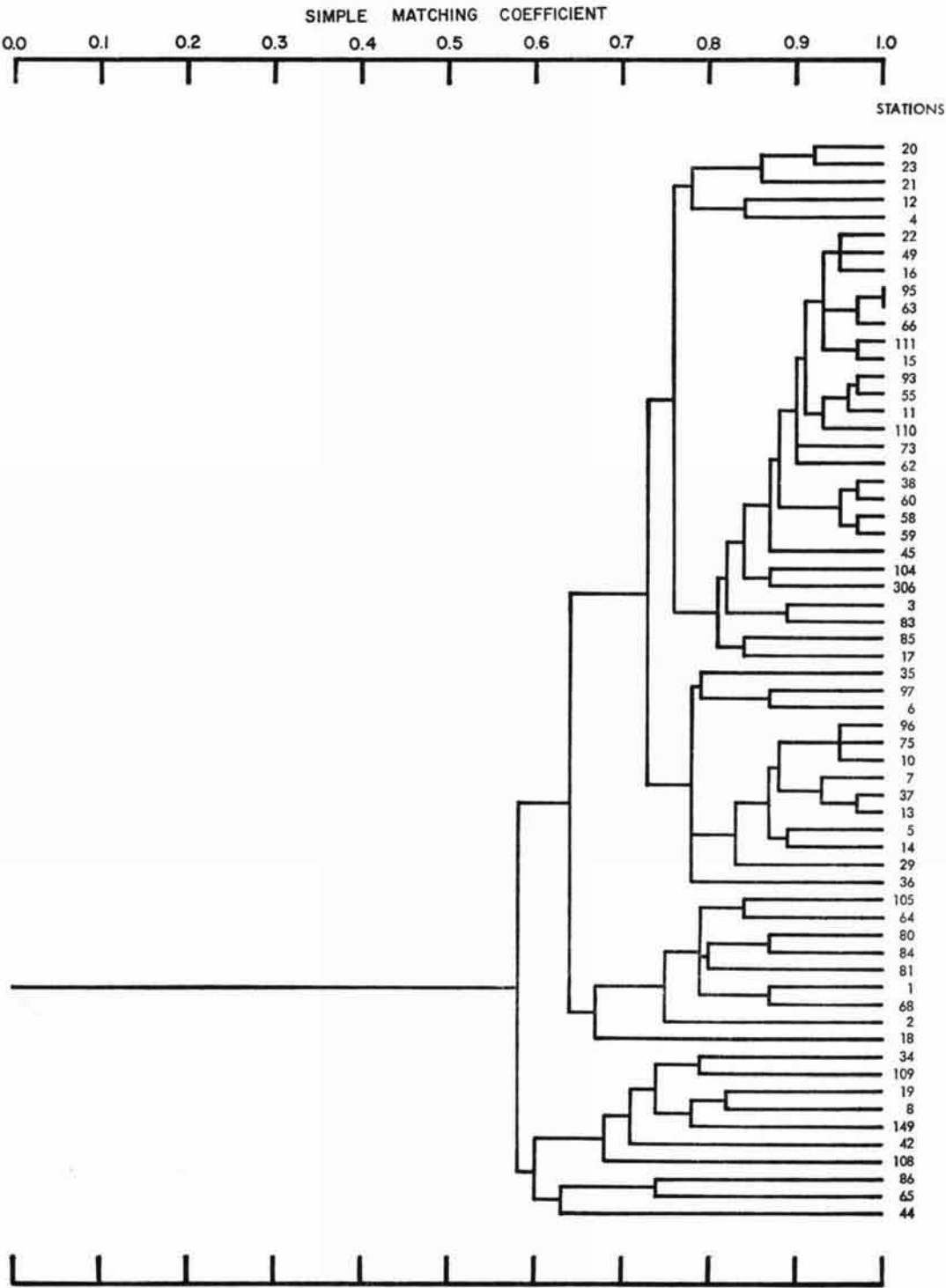|	r	S_{SM}	S_J
r	---		
S_{SM}	0.1464	---	
S_J	0.7072	0.0663	---

FIG. 14. Dendrogram (UPGMA) based on Q-matrix of simple matching coefficients computed from occurrence data for species of Ostracoda (Table 2).

pretation. As suggested above, the absence from two stations of a species found elsewhere in the study area is an *indication* of similarity of environment at the two stations. They are similar in their unsuitability for the species in question, and this similarity contributes to their being clustered into the same biotope. It would appear, then, that although WALTON delimited biofacies first in his study and then mapped their distributions, he, as well as BENSON, may have considered negative matches to be of some importance in clustering stations into biotopes.

OSTRACODAL BIOTOPES

Figures 13, 14, and 15 are dendrograms prepared from Q-matrices of correlation coefficients, simple matching coefficients, and Jaccard coefficients, respectively. The Q-matrices were computed from ostracode distribution data in Table 2. Because of the nature of the distribution of Ostracoda over part of the study area, some assumptions of biofacies analysis are not met, and none of these dendrograms is believed to give a realistic representation of the biotopes in Todos Santos Bay. They are included here only for comparison. Table 8 gives the correlation coefficients between the matrices.

Assumptions not satisfied are: 1) Biofacies and biotopes exist in the study area. 2) Biotopes are mappable. BENSON found much of the central portion of the bay to be nearly barren of Ostracoda, and he grouped the stations in that area together into a "barren biofacies" (=biotope). A so-called biofacies of this sort is a misnomer and does not exist in that area. Furthermore, the barren area is not mappable by quantitative methods because of the nature of the data. Instead it is divided among adjacent biotopes.

In order to meet all assumptions of biofacies analysis and to consider the barren area, all stations with fewer than five ostracodes were temporarily omitted from the study. A Q-technique simple matching coefficient matrix was computed from that modified data matrix, and a dendrogram (Fig. 16) was prepared. A map (Fig. 17) shows the quantitative biotopes at the 0.67 level.

Areas of general agreement with BENSON's results (Fig. 8) are biotope A with parts of BENSON's biotope I and, of course, the barren area B with his biotope III. An area of major disagreement exists between BENSON's biotope IV and the part

of quantitatively determined biotope A that lies in deeper water. Examination of the data in Table 2 reveals that no stations in BENSON's biotope IV were represented by more than a very few species, and only two of them were found at more than one station. Clearly negative matches accounted for the clustering of these stations with each other. All stations in the deep-water portion of biotope A, except the shallowest (station 29), can be separated from most of the rest of A at the 0.83 level on the dendrogram (Fig. 14). The deep-water portion, then, could be considered a subbiotope of quantitative biotope A. Sampling in deep water was probably inadequate; if more Ostracoda had been found at each station, the deep-water stations might have formed a separate biotope.

There are several stations which do not fit well into any pattern. Stations indicated as D and E may be places of uniform environmental conditions that are not continuous. Biotope C nearly everywhere borders areas with a rocky substrate. If samples were collected in the rocky areas, we might find that stations there could be grouped with biotope C to form a rocky bottom biotope.

QUANTITATIVE DETERMINATION OF BIOFACIES

FORAMINIFERAL BIOFACIES

Figures 18, 19, and 20 are dendrograms computed from R-matrices of correlation coefficients, simple matching coefficients, and Jaccard coefficients, respectively, based on Table 1. They show similarity among species of Foraminifera based on their occurrence at stations in the study.

WALTON's biofacies (Table 5) agree most closely with the Jaccard coefficient dendrogram. In particular the 0.20 level gives very close agreement with WALTON's subdivision of the fauna. This result is what we would expect on the basis of the above discussion of negative matches. It is encouraging that field results agree with quantitatively determined biofacies based on a coefficient that excludes negative matches from consideration. Table 9 lists the major quantitatively determined biofacies based on the 0.20 level of the Jaccard coefficient dendrogram. These should be compared with WALTON's biofacies listed in Table 5.

It must be remembered that WALTON's biofacies concept allowed him to exclude some taxa from any biofacies. Thus, not all taxa in the den-
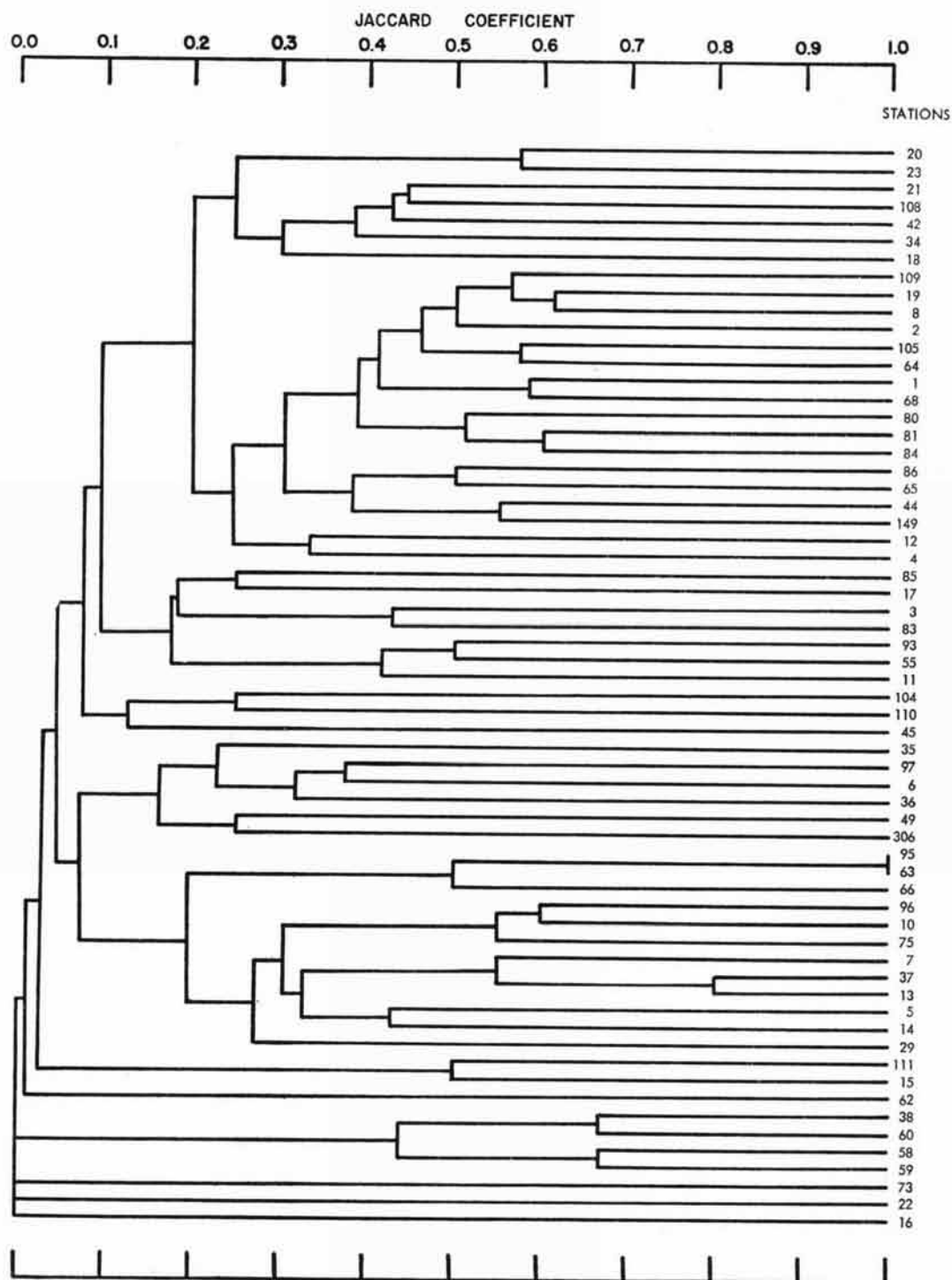
Fig. 15. Dendrogram (WPGMA) based on Q-matrix of Jaccard coefficients computed from occurrence data for species of Ostracoda (Table 2).
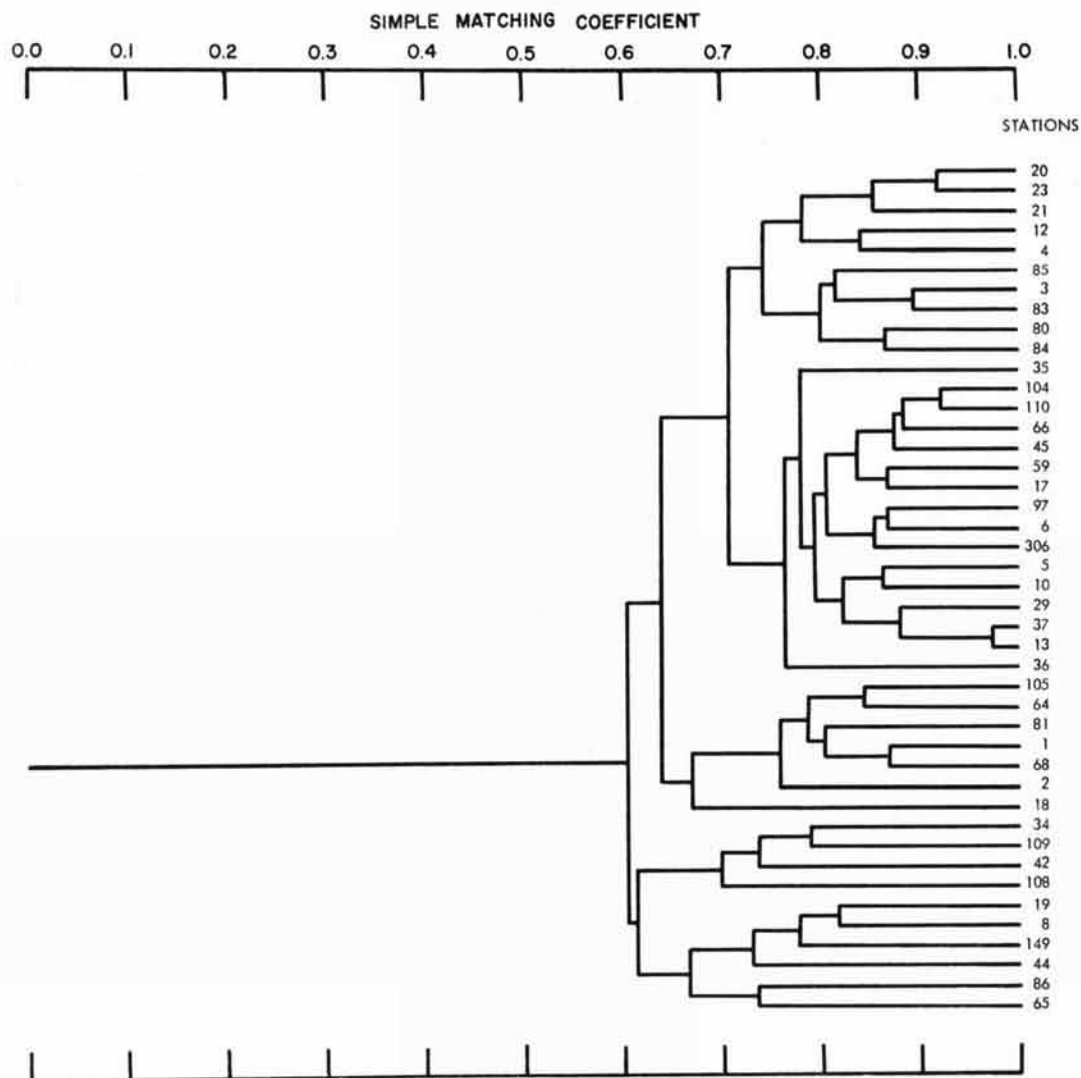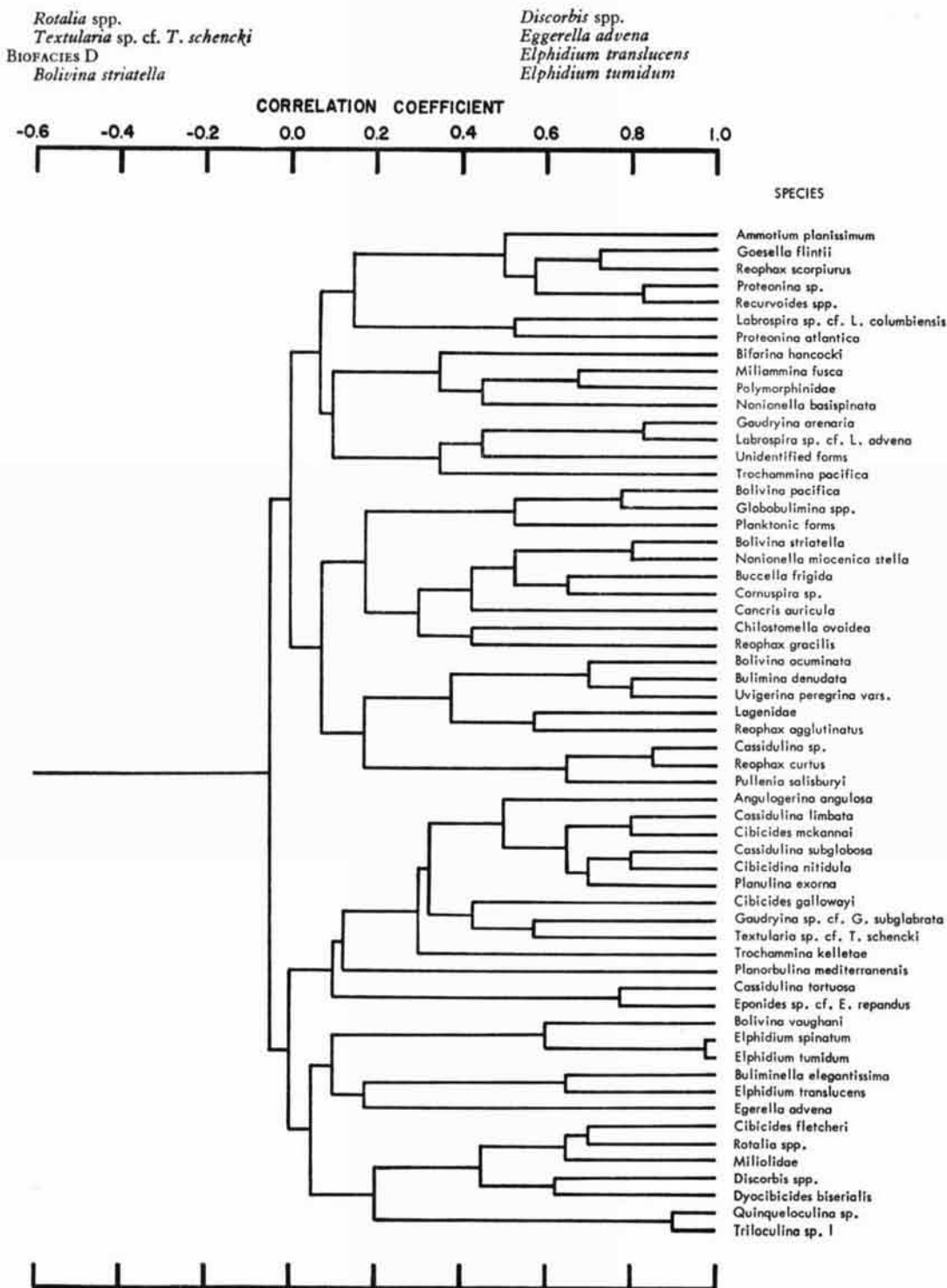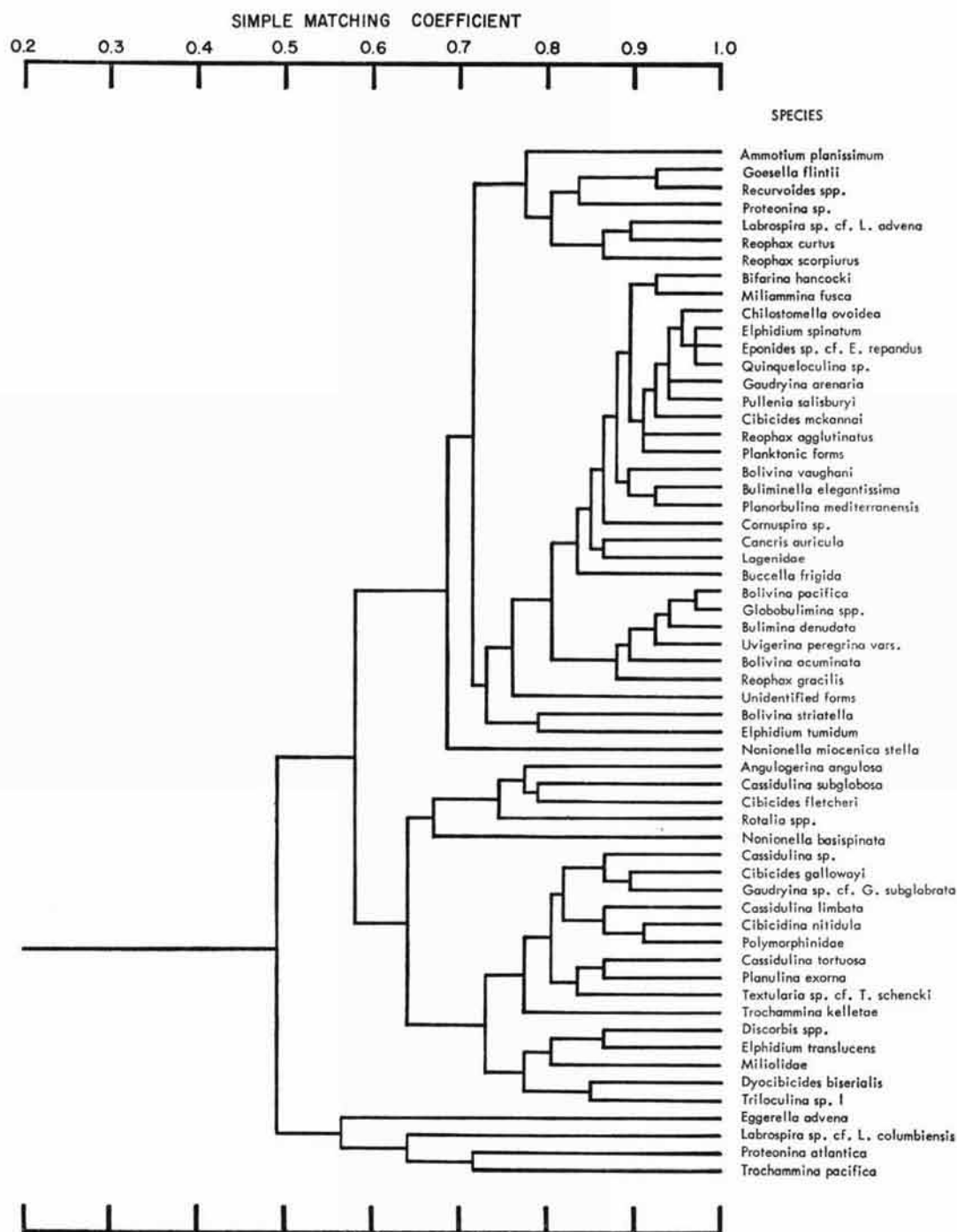
SIMPLE MATCHING COEFFICIENT

FIG. 16. Dendrogram (WPGMA) based on Q-matrix of simple matching coefficients. The matrix was computed using only those stations in Table 2 with five or more ostracodes after modification for equal-sample size.

drogram are included in his biofacies. Excluded taxa fall into three categories: 1) Some larger taxa, such as Lagenidae, or general groupings, such as planktonic forms or unidentified forms.

TABLE 9. *Quantitative Foraminiferal Biofacies Based on 0.20 Level of Jaccard Coefficient Dendrogram (Figure 20).*

BIOFACIES A
  Ammotium planissimum
  Goesella flintii
  Labrospira sp. cf. *L. advena*
  Proteonina sp.
  Recurvoides spp.

  Reophax curtus
  Reophax scorpiurus
  Unidentified forms
BIOFACIES B
  Bolivina acuminata
  Bolivina pacifica
  Buccella frigida
  Bulimina denudata
  Cancris auricula
  Globobulimina spp.
  Lagenidae
  Reophax gracilis
  Uvigerina peregrina subspp.
BIOFACIES C
  Angulogerina angulosa
  Cassidulina limbata

Cassidulina tortuosa
Cibicides fletcheri
Cibicides gallowayi

Cibicidina nitidula
Gaudryina sp. cf. G. subglabrata
Polymorphinidae
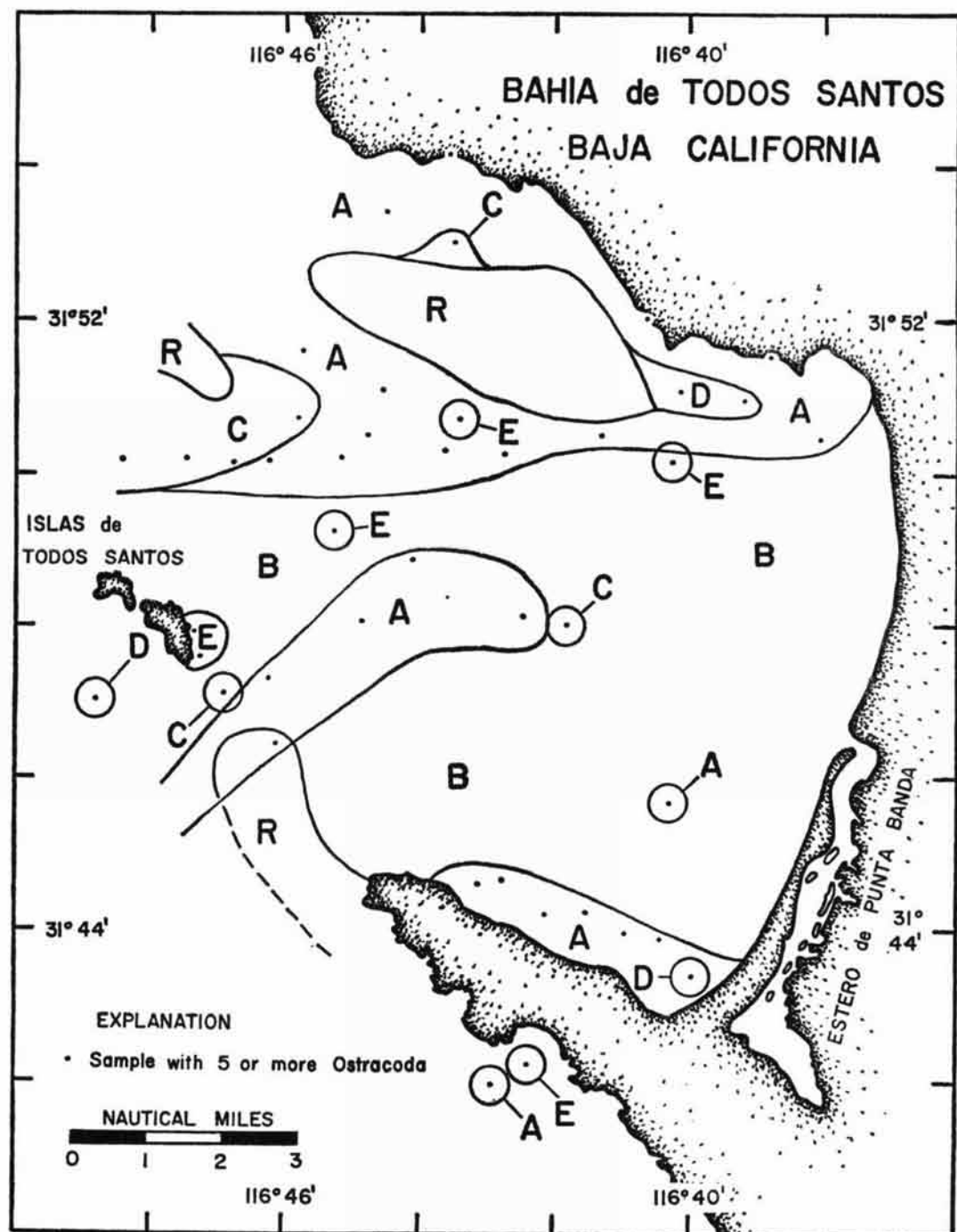
FIG. 17. Quantitative ostracodal biotopes in Todos Santos Bay based on similarity at 0.67 level using dendrogram in Figure 16.

Rotalia spp.
Textularia sp. cf. *T. schencki*
BIOFACIES D
Bolivina striatella

Discorbis spp.
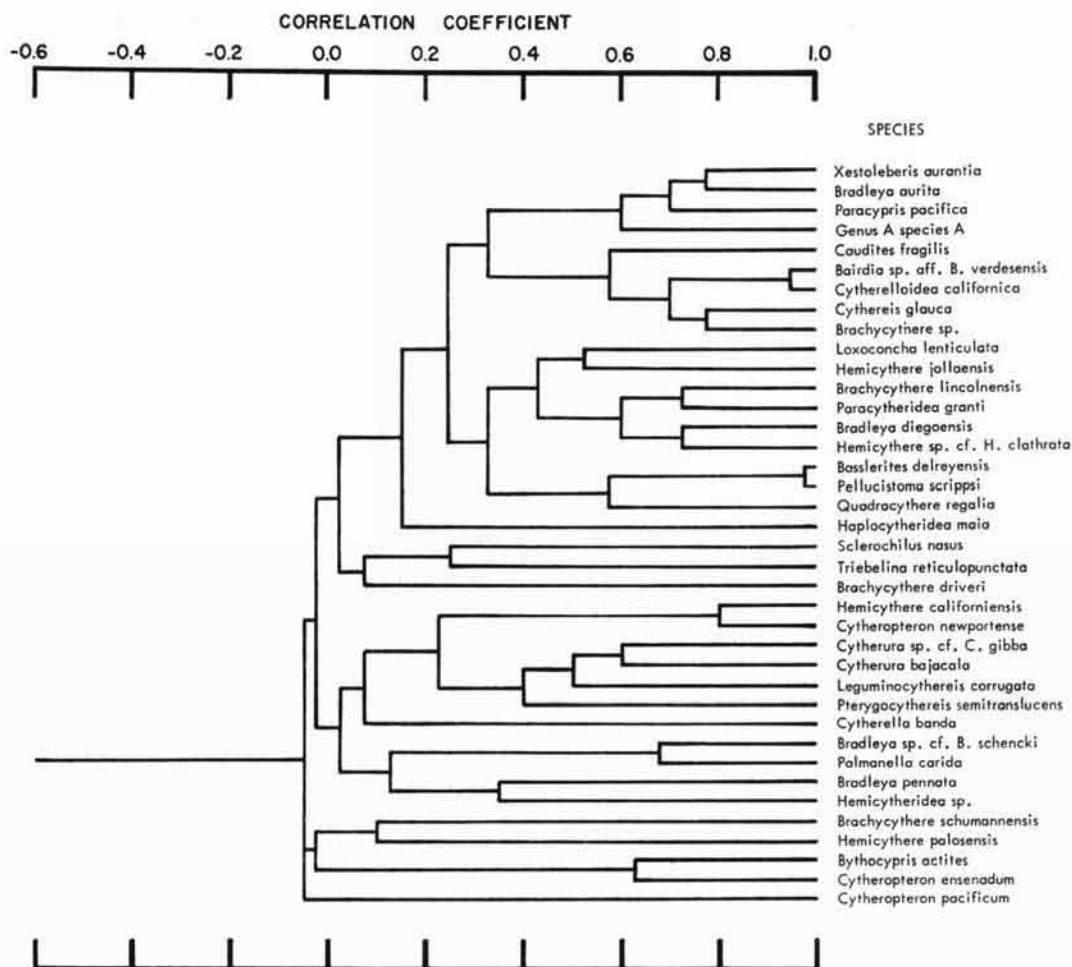*Eggerella advena*
Elphidium translucens
Elphidium tumidum

FIG. 18. Dendrogram (UPGMA) based on R-matrix of correlation coefficients computed from occurrence data for species of Foraminifera (Table 1).

Labrospira sp. cf. *L. columbiensis*
Miliolidae
Nonionella basispinata

Nonionella miocenica stella
Proteonina atlantica
Trochammina pacifica

SIMPLE MATCHING COEFFICIENT

0.2   0.3   0.4   0.5   0.6   0.7   0.8   0.9   1.0

SPECIES

Ammotium planissimum
Goesella flintii
Recurvoides spp.
Proteonina sp.
Labrospira sp. cf. L. advena
Reophax curtus
Reophax scorpiurus
Bifarina hancocki
Miliammina fusca
Chilostomella ovoidea
Elphidium spinatum
Eponides sp. cf. E. repandus
Quinqueloculina sp.
Gaudryina arenaria
Pullenia salisburyi
Cibicides mckannai
Reophax agglutinatus
Planktonic forms
Bolivina vaughani
Buliminella elegantissima
Planorbulina mediterranensis
Cornuspira sp.
Cancris auricula
Lagenidae
Buccella frigida
Bolivina pacifica
Globobulimina spp.
Bulimina denudata
Uvigerina peregrina vars.
Bolivina acuminata
Reophax gracilis
Unidentified forms
Bolivina striatella
Elphidium tumidum
Nonionella miocenica stella
Angulogerina angulosa
Cassidulina subglobosa
Cibicides fletcheri
Rotalia spp.
Nonionella basispinata
Cassidulina sp.
Cibicides gallowayi
Gaudryina sp. cf. G. subglobrata
Cassidulina limbata
Cibicidina nitidula
Polymorphinidae
Cassidulina tortuosa
Planulina exorna
Textularia sp. cf. T. schencki
Trochammina kelletae
Discorbis spp.
Elphidium translucens
Miliolidae
Dyocibicides biserialis
Triloculina sp. I
Eggerella advena
Labrospira sp. cf. L. columbiensis
Proteonina atlantica
Trochammina pacifica
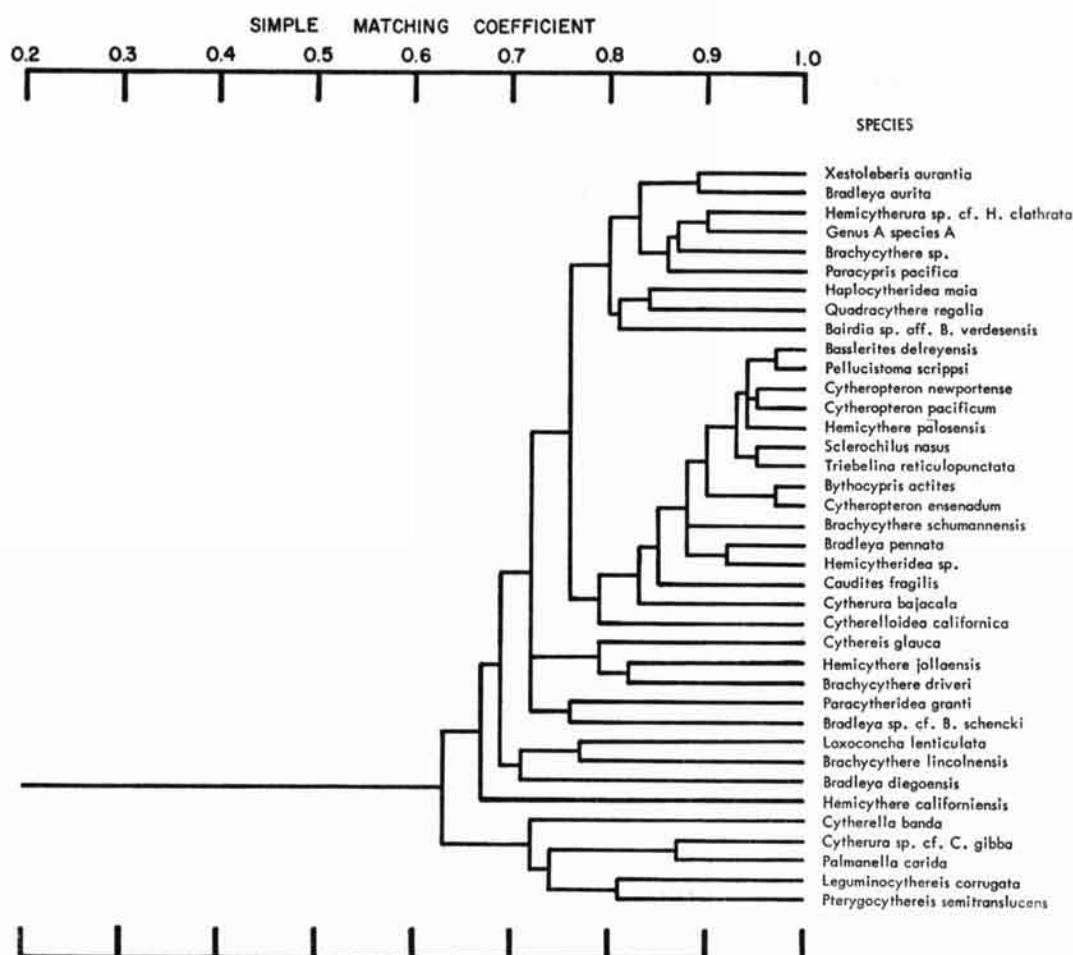
Fig. 19. Dendrogram (UPGMA) based on R-matrix of simple matching coefficients computed from occurrence data for species of Foraminifera (Table 1).

2) Species not restricted to a single biotope, such as *Trochammina kelletae* THALMANN and *Buccella* *frigida* (CUSHMAN). 3) Species too rare in the study area to be included in any biofacies, such as
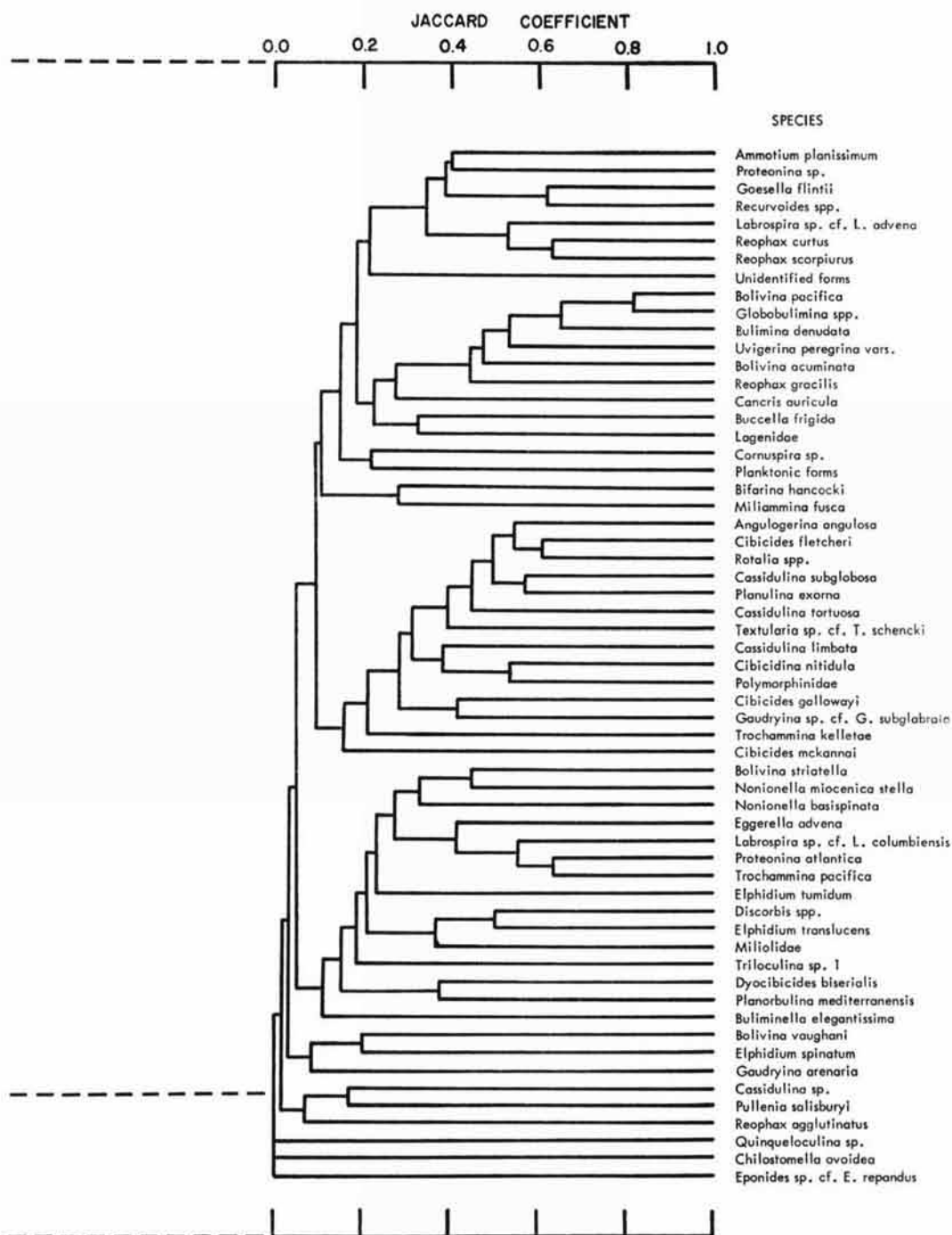
FIG. 20. Dendrogram (WPGMA) based on R-matrix of Jaccard coefficients computed from occurrence data for species of Foraminifera (Table 1).

Fig. 21. Dendrogram (UPGMA) based on R-matrix of correlation coefficients computed from occurrence data for species of Ostracoda (Table 2).

Pullenia salisburyi STEWART & STEWART and *Cibicides mckannai* GALLOWAY & WISSLER.

Some of the species that WALTON included in his various biofacies are excluded or shown in a different one by the dendrogram. In other instances, species indicated as included in a biofacies by the dendrogram were not included by WALTON. These two cases are analogous to Type I and Type II errors of statisticians (*58*, p. 70), although error is not necessarily involved—only difference of opinion. In general, species that the quantitative method places in what seems to be an incorrect biofacies are rare in the study area (low counts) or they occur at very few stations, or both.

Before basing biofacies on dendrograms alone, an investigator should compare the original data

and the dendrogram to look for species that are obvious exceptions to the presumed natural system or that occur so rarely that they are clustered with others only because of blind objectivity of the method. Minor modifications of the quantitative results would be permissible under such circumstances where the sample size is small and some assumptions of the quantitative method obviously are not met.

Table 10 is a matrix of correlation coefficients between the three R-matrices. Correlation between the correlation coefficient matrix and the simple matching coefficient matrix is low but significant. The very low correlation between the Jaccard coefficient matrix and simple matching coefficient matrix results from the diverse nature of the two
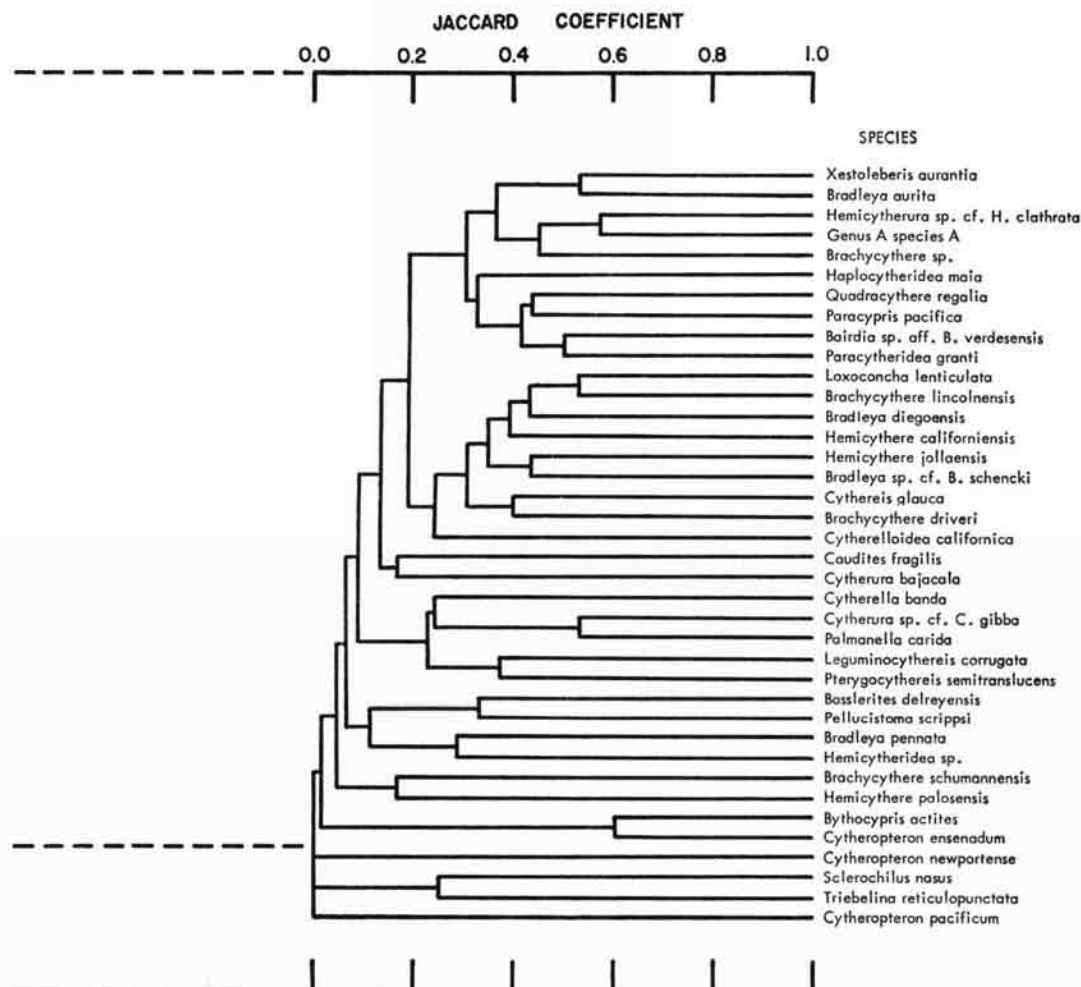
Fɪɢ. 22. Dendrogram (UPGMA) based on R-matrix of simple matching coefficients computed from occurrence data for species of Ostracoda (Table 2).

TABLE 10.—*Correlation Coefficients Between Half R-Matrices Computed from Occurrence Data for Species of Foraminifera in Todos Santos Bay (Table 1).*

	r	S_{SM}	S_J
r	---		
S_{SM}	0.3170	---	
S_J	0.6178	0.0519	---

coefficients. The higher correlation ($r = 0.6178$) between Jaccard and correlation coefficient matrices indicates the similarity between them. Inspection of the dendrograms (Fig. 18-20) shows that goodness of fit with Wᴀʟᴛᴏɴ's biofacies is roughly proportional to the value of the correlation coefficients in row 3 of Table 10 if unity is entered in the principal diagonal. Clearly, the simple matching coefficient dendrogram (Fig. 19) is the poorest fit of the three; correlation coefficients give the second best fit; and Jaccard coefficients give a very close fit.

OSTRACODAL BIOFACIES

Dendrograms based on occurrence data for ostracode species (Table 2) are shown in Figures 21, 22, and 23. The dendrograms were computed from R-matrices of correlation coefficients, simple matching coefficients, and Jaccard coefficients, re-

FIG. 23. Dendrogram (WPGMA) based on R-matrix of Jaccard coefficients computed from occurrence data for species of Ostracoda (Table 2).

TABLE 11. *Quantitative Ostracodal Biofacies Based on 0.20 Level of Jaccard Coefficient Dendrogram (Figure 23).*

BIOFACIES A
Bairdia sp. aff. *B. verdesensis*
Brachycythere sp.
Bradleya aurita
Haplocytheridea maia
Hemicytherura sp. cf. *H. clathrata*
Paracypris pacifica
Paracytheridea granti
Quadracythere regalia
Xestoleberis aurantia
Genus A species A
BIOFACIES B
Brachycythere driveri
Brachycythere lincolnensis
Bradleya diegoensis
Bradleya sp. cf. .B. schencki
Cythereis glauca

Cytherelloidea californica
Hemicythere californiensis
Hemicythere jollaensis
Loxoconcha lenticulata
BIOFACIES C
Cytherella banda
Cytherura sp. cf. *C. gibba*
Leguminocythereis corrugata
Palmanella carida
Pterygocythereis semitranslucens

spectively. Table 11 shows quantitatively determined biofacies taken from the 0.20 similarity level on Figure 23. Although BENSON's biofacies (Table 6) agree roughly with quantitatively determined biofacies at this level, the fit is not as good as for WALTON's biofacies. Two reasons for lack of good fit are: 1) Sampling for Ostracoda

TABLE 12.—*Correlation Coefficients Between Half R-matrices Computed from Occurrence Data for Species of Ostracoda in Todos Santos Bay (Table 2).*

	r	S_{SM}	S_J
r	---		
S_{SM}	0.1340	---	
S_J	0.6844	0.0369	---

was not completely adequate over the entire bay (6, p. 18). 2) Table 2 gives total population and thus introduces the effects of mixing faunas and differential removal and destruction of some species.

No method of analysis can evaluate such introduced effects adequately. Each investigator making a nonquantitative approach to the problem would evaluate them differently. The quantitative method used here assumes a high positive correlation between the distribution of live and dead faunas and partly compensates for differential removal and dstruction by using presence-absence data instead of counts.

Correlation coefficients between the three similarity matrices are shown in Table 12. As previously, Jaccard coefficients are poorly correlated with simple matching coefficients and more strongly correlated with correlation coefficients.

EVALUATION OF QUANTITATIVE METHODS

As discussed above, the numerical taxonomic method of biofacies analysis has the characteristic that categories erected by it are hierarchic and, hence, mutually exclusive. SOKAL & SNEATH (1963, p. 171-174) have discussed the kinds of distributions that may appropriately be given nested classifications. Further discussion of pattern as applied to ecology may be found in GREIG-SMITH (1964, p. 54-93).

In general, one would not expect ecologic units (stations, species) to be related in a strictly hierarchic manner, for such arrangement is inappropriate unless the ecologic distribution of points is "clumped at each level at which it is desired to make a hierarchical division" (57, p. 173). Nevertheless, only limited use is made of these properties of the dendrogram so little practical difficulty is encountered. In biofacies analysis, unless subbiotopes or subbiofacies are recognized, only a single division of the dendrogram is needed. A Q-type study requires that stations in an area be grouped at one level only. Grouping, of course, is on the basis of the fauna contained in the samples, not on geographic position. Similarly, an R-type study requires that species plotted on presence-absence basis in an *n*-dimensional space (where *n* is the number of stations) be clustered at one level at least.

It is too much to expect perfect clustering of ecologic data, and GOODALL *(22)* believed intergrading groups to be more likely than discrete groups. Examination of Tables 1 and 2 shows good clustering of some stations and species, although this representation is only two-dimensional. Furthermore, stations often cluster into clearcut biotopes that are similar in areal extent to what would be expected *a priori* after an examination of only the physical features of the environment. The foraminiferal and ostracodal biotopes in the area of relict sedimentation in the northern part of Todos Santos Bay are the best examples of this, but others exist, such as the "barren ostracodal biotope" where it coincides with the area of very fine sand substrate. Finally, even though occasionally it may be somewhat unrealistic, "the advantages of hierarchies are so great that we will generally employ them, even when this means we must distort the system of affinities to some extent *(57, p. 171).*

Some difficulties are encountered in interpreting R-technique results. First, not all investigators (e.g., 6, 59) accept mutually exclusive biofacies. Second, the meaning of large, low-similarity clusters on dendrograms is open to question.

If a worker demands biofacies that are not mutually exclusive, some method other than the one suggested here must be used. He may, for example, organize data as in Tables 1 and 2 in which stations are arranged in the order given on appropriate dendrograms. Biofacies may then be determined easily as indicated by the list of all species found within a given biotope. Alternatively, some proportion of the total number of stations in the biotope at which a species occurs may be used as a limiting level. This alternative leads to difficulties in the general case where biotopes contain different numbers of stations.

GOODALL *(23)* (see also *24*, p. 204-205) proposed an index to express the degree of fidelity of

TABLE 13.—*Species of Foraminifera in Todos Santos Bay with Fidelity Significant at 70-Percent Level, Chi-Square Value, Significance Level, and Fidelity Index.*

EXPLANATION.---A. Biotope.---B. Species.---C. Chi-square. ---D. Probability.---E. Fidelity index.

A	B	C	D	E
C	Goesella flintii	1.5884	P .30	1.1778
C	Recurvoides spp.	3.4455	P .10	1.3692
C	Bolivina pacifica	26.2533	P .001	14.8333
C	Globobulimina spp.	25.7610	P .001	41.5000
C	Bulimina denudata	21.5874	P .001	36.5000
C	Uvigerina peregrina vars.	10.7188	P .01	8.1667
C	Bolivina acuminata	12.3329	P .01	4.3571
C	Reophax gracilis	16.5886	P .001	7.4000
C	Cancris auricula	1.3125	P .30	1.5000
C	Buccella frigida	8.2031	P .01	4.5000
C	Lagenidae	1.3125	P .30	1.5000
A	Cornuspira	1.6656	P .20	1.8000
A	Cibicides fletcheri	8.2031	P .01	1.0000
A	Rotalia spp.	8.3055	P .01	1.3059
C	Cassidulina subglobosa	1.2635	P .30	0.2879
A	Planulina exorna	2.4205	P .20	1.1600
A	Cassidulina tortuosa	5.3293	P .05	8.2000
A	Cassidulina limbata	1.2635	P .30	1.2667
A	Cibicidina nitidula	3.1448	P .10	5.8000
A	Gaudryina sp. cf. G. subglobosa	2.5318	P .20	5.0000
A	Trochammina kelletae	2.4593	P .20	1.4000
C	Bolivina striatella	1.8515	P .20	1.0455
C	Nonionella miocenica stella	6.6500	P .01	1.2667
C	Proteonina atlantica	7.3045	P .01	0.6204
B	Trochammina pacifica	15.4006	P .001	1.0575
A	Elphidium tumidum	1.5724	P .30	1.0800
A	Discorbis spp.	3.2674	P .10	1.3644
A	Elphidium translucens	2.4593	P .20	1.4000
A	Miliolidae	6.3730	P .02	3.2560
A	Triloculina sp. 1	1.2635	P .30	1.2667
A	Dyocibicides biserialis	2.5318	P .20	5.0000
C	Chilostomella ovoidea	2.2405	P .20	6.5000

plant species. The concept of fidelity as faithfulness of a species to a certain community was suggested by BRAUN-BLANQUET (1951). Faithfulness to a *biotope* may be expressed by the same index:

$$\text{FIDELITY INDEX} = \frac{(a - \frac{1}{2})(b+d)}{(b+\frac{1}{2})(a+c)} - 1$$

where *a*, *b*, *c*, and *d* are notation for a 2 x 2 contingency table, *a* is the number of occurrences in the biotope where the species in question is most frequent, *b* its number of occurrences in the biotope in which it occurs next most commonly, and *c* and *d* are respective absences. At the same time fidelity-to-biotope may be tested for significance with a chi-square test. Table 13 lists species of Foraminifera having a significant fidelity at the 70-percent level with their corresponding fidelity indices and Table 14 gives similar information for Ostracoda. Many other methods for grouping species into biofacies can be found. In each the

investigator must decide what criteria biofacies recognized by him must meet before he selects the method. If mutual exclusiveness is desired, or not objected to, the method presented in this study is suggested. (It is interesting to note that the species in Table 13 with highest fidelity are deep-water forms, suggesting transportation of shallow-water species into environments in which they are not indigenous.)

The meaning of a cluster of two species having a mutually highest Jaccard coefficient is that the two species tend to occur together to the extent indicated by the coefficient. Similarly, species which never join larger clusters or which do so at a similarity level too low to be meaningful are most commonly species which occur at a very few stations in the study area. Species which join larger clusters late but still at a meaningful level are generally species that occur at a wider range of stations than others of the cluster (e.g., *Trochammina kelletae, Cibicides mckannai*, Fig. 20) and that could be regarded as transitional in range. As new species are added to a cluster at increasingly low levels of similarity, the overall range of stations occupied by the cluster as a whole, and thus, presumably, the range of tolerance to environmental conditions, is increased. It is unfortunate that this method must place transitional forms with one biofacies or another. I believe, however, that this characteristic is not a serious drawback to the method if one keeps in mind the necessarily hierarchic nature of dendrograms. R-technique studies in ecology using the methods of numerical taxonomy will be much more meaningful if roughly the same quantitative biofacies are obtained from future studies of areas with similar species of Foraminifera and Ostracoda or other organic assemblages.

TABLE 14.—*Species of Ostracoda in Todos Santos Bay with Fidelity Significant at 70-Percent Level, Chi-Square Value, Significance Level, and Fidelity Index.*

EXPLANATION.---A. Biotope.---B. Species.---C. Chi-square.---D. Probability.---E. Fidelity index.

A	B	C	D	E
D	Xestoleberis aurantia	3.3750	P .10	1.8000
D	Haplocytheridea maia	1.5469	P .30	0.7500
E	Hemicythere californiensis	1.3645	P .30	0.4259
C	Cythereis glauca	5.7117	P .02	1.7238
E	Cytherella banda	5.4026	P .05	0.0000
A	Bythocypris actites	1.2036	P .30	0.0000
A	Cytheropteron newportense	1.2036	P .30	0.0000

CONCLUSIONS

Todos Santos Bay and ecologic studies of Foraminifera and Ostracoda in this area provide excellent means of testing the applicability of methods of numerical taxonomy to biofacies analysis. On the basis of preceding discussions, the following conclusions are warranted.

1) For studies in which basic assumptions are met and in which the study area behaves as an environmental unit with frequently recurring environmental conditions and associations of organisms, the methods of numerical taxonomy are conveniently applicable to problems of biofacies analysis.

2) Negative matches should be given equal weight with positive matches in forming biotopes if sampling is adequate and the study area behaves as an environmental unit (see conclusion 1). Dendrograms computed from Q-matrices of simple matching coefficients are suitable for defining quantitative biotopes.

3) Negative matches should be omitted from consideration in delimiting quantitative biofacies. Biofacies from dendrograms based on R-matrices of Jaccard coefficients are mutually exclusive. If one does not object to exclusivity in biofacies, dendrograms computed from R-matrices of Jaccard coefficients are appropriate for biofacies.

4) Actual counts of organisms and use of correlation coefficients give moderately good results if only living populations are being studied and if samples are of nearly uniform size or ecologic meaning. In studies involving total populations, unequal sizes of samples, or both, counts may be almost entirely meaningless, as are statistics derived from the counts.

5) If populations are very small in part of the study area, nearly barren stations may be clustered into a barren area by temporarily omitting them from the study and proceeding with the reduced raw data matrix.

6) Different investigators use biofacies (and to a lesser extent, biotope) to express different concepts. The meaning adopted by WALTON (1955) and BENSON (1959) is fairly clear, but this is certainly not true in work published by others. Effort should be made to determine what various paleoecologists mean by these terms to see by what criteria, quantitative or otherwise, and at what similarity level they cluster species into biofacies and stations into biotopes.

7) Biofacies determined by the quantitative method of this study do not necessarily occupy biotopes defined quantitatively. This does not mean that these biofacies and biotopes are inherently different from biofacies and biotopes determined by nonquantitative means. Indeed, the distinction should be avoided. Rather, one should recognize lack of congruence of biofacies and biotopes as inherent in the use of hierarchical classification, particularly where no obvious natural breaks occur in the classification.

The use of methods of numerical taxonomy in biofacies analysis is not without disadvantages. Four disadvantages the user should remember are:

1) The dendrogram is a two-dimensional representation of a multidimensional relationship. Some information is lost, particularly as one looks at larger clusters in a hierarchy, which are based on lower similarity.

2) The simple matching coefficient indicates high similarity between stations at which only a few species are found, even if no species occurs at both stations.

3) The numerical taxonomic method requires a large study to reduce the effects of random error. It would be dangerous to place too much trust in a small study in which this method of analysis was used. This objection applies particularly to R-technique studies.

4) This method of biofacies analysis forms mutually exclusive biotopes and biofacies; that is, it groups transitional species and stations into one biofacies or another. One can, however, detect transitional species from the dendrogram and raw data matrix, so that the disadvantage of exclusivity is not a serious one.

No doubt other disadvantages will become apparent as the method is used in other areas and on other groups of organisms. To compensate for disadvantages of the method and for cases in which assumptions are not met, the investigator may make minor adjustments in his interpretations. This procedure is not new to science, and certainly not to geology. I believe disadvantages of the method are outweighed by the advantages, which, restated, are: 1) Results are repeatable. 2) Results are objective. 3) Computation of dendrograms is rapid. 4) Representation of results is graphic. 5) Arbitrariness and relativity of the similarity level is not obscured.