Classification and geographic distribution of *Stylodictya*-type radiolarians

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ABSTRACT: A collection of 485 radiolarian *Stylodictya*-type shells from 17 surface sediment samples from the equatorial to Antarctic western Pacific Ocean was studied. Comparison of conventional taxonomic criteria used for the identification of the closely related taxa *Stylodictya multispina* (= *S. validispina*), *S. aculeata*, *Porodiscus* spp. and *Stylochlamydium asteriscus* with the results of an objective numerical analysis of 11 two-state and quantitative characters suggest that *S. multispina* and *Porodiscus* spp. are members of the same taxonomic unit which decreases in abundance from the equator to the Antarctic. *S. asteriscus* (predominantly warm-water) and *S. aculeata* (predominantly cold-water) are the other two members of this species group. Morphologic differences between these morphotypes are investigated and defined.

INTRODUCTION

A major obstacle for radiolarian studies for stratigraphic, paleoecologic, biogeographic and other applications is the state of disarray of the systematics of the group. Substantial disagreements between authors as to the generic and specific names used and as to the limits between related taxa make comparison of data bases worked out by different researchers extremely difficult or even impossible (see, for example, Empson-Morin 1981; Boltovskoy and Jankilevich 1985). Starting in the late 60's efforts have been made to standardize the nomenclature through revisions of some radiolarian families; however, the improvement achieved has been very limited (Empson-Morin 1981). As a consequence, over 50% of the species are usually ignored in radiolarian-based paleooceanographic, distributional and other surveys because researchers restrict their scope to the 30–50 more or less well-defined taxa. Unfortunately, some of the commonly ignored morphotypes (such as those encompassed by this work) are often dominant components in both plankton and sediment samples from many oceanic areas (e.g. Ling et al. 1971; Sachs 1973; Blueford 1983).

Culturing is probably the most adequate way to address the question of intraspecific and interspecific variability in extant microplanktonic organisms; the systematics of diatoms, for example, has benefited greatly from this approach. Unfortunately, culturing of the polycystines through several generations has not yet been accomplished. Another promising avenue which has not been attempted with Radiolaria is the use of numerical taxonomy. Statistical treatment of large data bases can furnish valuable information on evolutionary trends as a function of time (e.g. Kellogg 1980), as well as on morphologic variability as a function of space or taxonomy (e.g. Bé et al. 1973).

This report constitutes an attempt to critically evaluate the traditional intuitive criteria used for the classification of a group of closely related spongodiscid radiolarians and compare them with the results of some objective numerical techniques. This group was selected because it fulfills the following requirements:

a) It is widespread throughout the World Ocean and it was present in 17 out of the 18 samples available in sufficient numbers for statistical analyses;

b) These radiolarians dwell (and, probably, also have their abundance maxima) in the upper mixed layer (Renz 1976; Kling 1979; Boltovskoy and Jankilevich 1985). Thus, if any consistent morphological differences were found attempts could be made to relate them to ecological changes, whereas deep-living forms are adjusted to a monotonous environment;

c) Within the limits set for this study they could be distinguished easily from other taxa;

d) These specimens have a relatively simple construction and their aspect changes little in fixed preparations because they usually lie flat on one of their sides;

f) Their identification poses problems the solution of which could contribute to the development of more satisfactory approaches toward the classification of Radiolaria.

MATERIAL AND METHODS

The materials used consist of 17 surface sediment samples more or less evenly distributed between the equator and approx. 65°S, in the western Pacific Ocean. In a previous study based on entire radiolarian assemblages (Boltovskoy 1987) the locales in question were consistently grouped into 5 major climatic zones (text-fig. 1).

The radiolarians selected for this study are those included in Nigrini and Moore's (1979) catalogue under the names *Stylodictya validispina* Jorgensen (= *S. multispina* Haeckel), *Porodiscus* sp. A, *Porodiscus* sp. B, *Stylochlamydium asteriscus* Haeckel, and *Stylodictya aculeata* Jorgensen, and all the intergrades between them, and closely related forms. Shells roughly similar to these have been reported in the literature under many different names (e.g. *Circospyris, Lithocyclia, Ommatodiscus, Perichlamydium, Plectodiscus, Porodiscus, Spongopyle, Spongotrochus, Stylodictya, Stylochlamydium, Xiphospira,* etc.). These radiolarians are characterized by discoidal shells composed of more or less conspicuous concentric chambers or growth rings. Thus, in order to define a limit

for the morphotypes encompassed by this study (excluding several often very similar, yet rather well-established taxa such as *Spongotrochus glacialis* Popofsky, *Spongodiscus resurgens* Ehrenberg, etc.), we considered the presence of concentric rings, even if very faint, as the cutoff value for the *Stylodictya*-type specimens included in this study.

In total, 30 specimens from each sample were described and measured, with the exception of samples no. 13 (15 specimens), and no. 14 (20 specimens). The following characters were considered (numbers refer to the corresponding photographs on Plate 1):
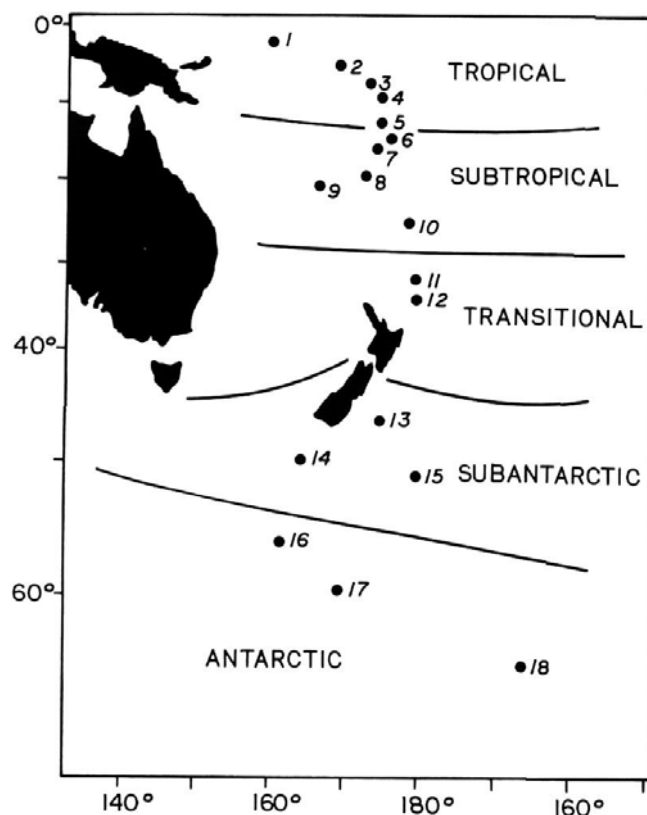
Binary

1) Type of rings: all continuous (1a–c, 2c, 3a, b) vs. some/ all discontinuous or broken (2a, b, d);
2) Shape of rings: all circular (1a–c) vs. some/all wobbly or wavy (2a, d);
3) Shape of central chamber and/or first rings: circular (1a–c, 2a, c) vs. quadrate or rosette-shaped (3a, b);
4) Central part: not thickened (central chamber visible; 1b, 2a, c, 3a, b) vs. thickened (central chamber not visible; 1a, 2b, d);
5) Equatorial porous non-chambered girdle or sieve-plate: presence (2a–d)/absence (1a–c, 3a, b);
6) Relative size of pores at different distances from the center: even throughout (1a–c, 3a, b) vs. larger or smaller in the central part, at the middle, or at the periphery (2a, c);

Quantitative

7) Total diameter of the shell;
8) Ring-width increment toward the periphery, expressed as the slope of the linear regression between ring number (X) and the corresponding ring width (Y); thus, higher values indicate larger ring-width increments toward the edge of the shell;
9) Number of primary spines (arising from the center of the shell);
10) Total number of spines;
11) Diameter of marginal pores with respect to width of last ring.

Two additional measurements were also taken: diameter of the central chamber (when visible, in light-centered individuals only), and diameter of the central, thickened part (when present).

The parameters measured on each individual comprise most of the information that one can routinely extract from a radiolarian *Stylodictya*-type shell, and most of them have been previously used for taxonomic purposes (e.g. Nigrini and Moore 1979, and references therein). Admittedly, it is quite probable that the characters selected do not constitute those which best reflect natural divisions within the group; Kozlova (in Petrushevskaya and Kozlova 1972), for example, attempted a revision of some spongodiscids, including *Stylodictya* and *Porodiscus*; distinctions between these two genera were based mainly on the nature of their central structure, but they required rotation of the shells or even thin-sectioning; given the difficulties involved in the observation of these
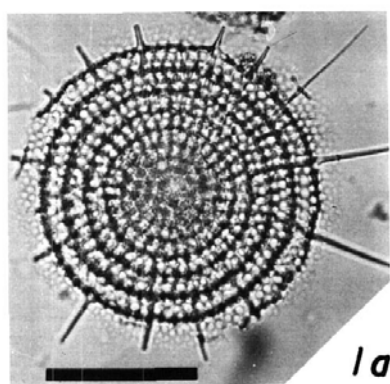

TEXT-FIGURE 1

Geographic location of the samples used and climatic zones established on the basis of their entire radiolarian assemblages; rank correlation and average, weighted linkage (from Boltovskoy 1987).

features, unless very close relationships can be established between them and some readily observable, superficial characters, the divisions thus established are of little practical use for routine surveys.
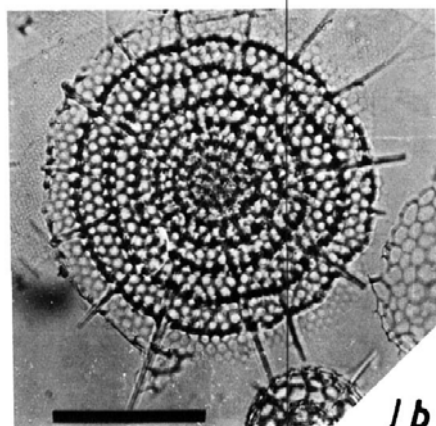
RESULTS

Classification of Stylodictya-type Radiolarians on the Basis of Conventional Taxonomic Criteria
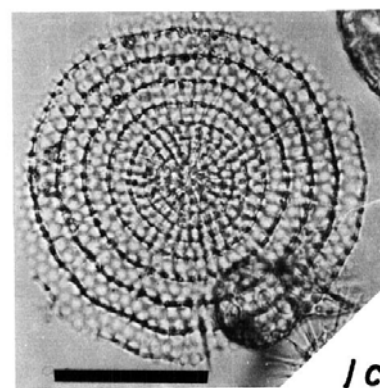
Nigrini and Moore (1979) summarized some previously published criteria (chiefly by Petrushevskaya 1967; Kozlova, in Petrushevskaya and Kozlova 1972) for the classification of this group. This system was subsequently adopted in many of the reports which included *Stylodictya*-type radiolarians (Lombari and Boden 1985; Weinheimer et al. 1986; etc.). We therefore used the criteria summarized by Nigrini and Moore (1979) for the classification of our 485 specimens. However, a shortcoming of these descriptions (that the authors themselves recognized) is that they are preliminary and inconclusive: for several of the characters the degree of overlap between taxa is considerable (e.g. diameter, number of spines), while for others only the maxima (rather than average values or ranges) were given. Thus, we selected only four characters, the combination of which is unique for each of the morphotypes recognized, and which were defined reliably in our data base (table 1). Out of the total of 485 radiolarians,
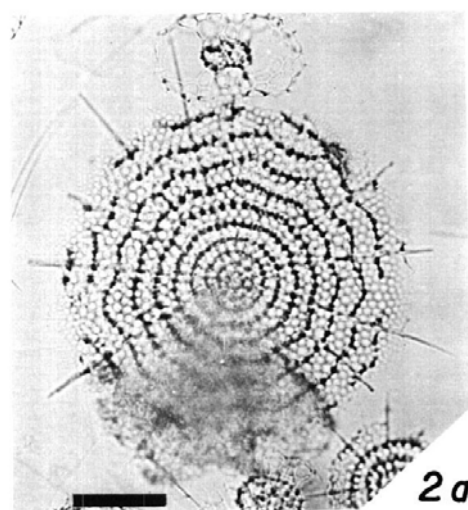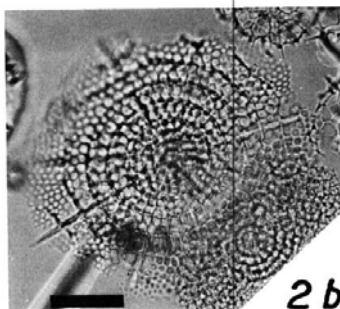
PLATE 1

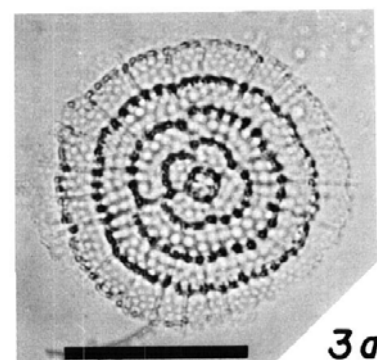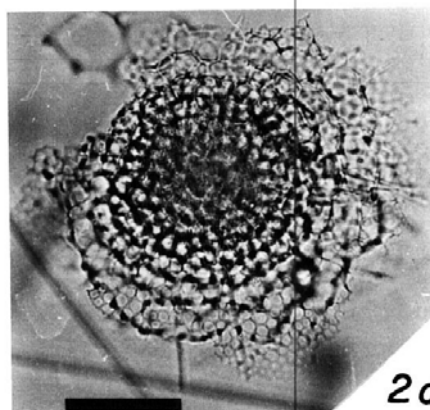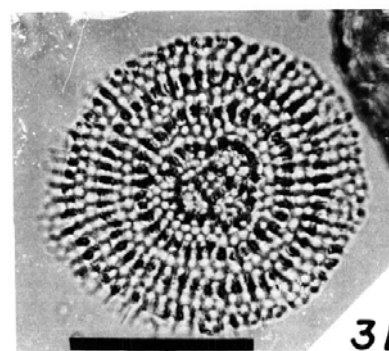Morphotypes belonging to specimen groups I+II (*Stylodictya multispina/Porodiscus* spp.; 1), III (*Stylochlamydium asteriscus*; 2) and VI (*Stylodictya aculeata*; 3). The provenance of the individuals illustrated is as follows: from sample no. 1: 1a; sample no. 3: 1c; sample no. 4: 1b, 2a, c; sample no. 5: 2b; sample no. 6: 3b; sample no. 10: 3a; sample no. 15: 2d. Scale bars represent 50 micrometers.

TABLE 1

Characters used for grouping the *Stylodictya*-type specimens into the four most commonly accepted taxa (based on the criteria summarized by Nigrini and Moore 1979; *S. multispina* = *S. validispina*).

	Stylodictya multispina	*Porodiscus* spp. a, b	*Stylo-chlamydium asteriscus*	*Stylodictya aculeata*
Shape of rings	Circular	Wobbly or circular	Wobbly or circular	Wobbly
Shape of central rings	Quadrate or circular	Circular	Quadrate or circular	Quadrate
Central part	Not thick.	Thickened	Thick. or not thick.	Not thick.
Equatorial sieve-plate	Without	Without	With	Without

432 (89%) were included into one of the four morphotypes established by this procedure.

Table 2 shows the percent occurrence and the average values for the qualitative and quantitative (respectively) characters within each of these four morphotypes. Some of these values are in fair agreement with the descriptions supplied by Nigrini and Moore (1979), e.g. highest ring-increment (for *S. asteriscus* and *S. aculeata*), highest number of total spines (for *Porodiscus* spp.). On the other hand, our ranges are considerably greater than those reported in the literature; for example, the number of total spines in *S. multispina* (= *S. validispina*), according to Nigrini and Moore (1979) (on the basis of Petrushevskaya 1967) varies between 12 and 16, while according to our results the variation ranges between 0 and 59. Table 2 shows that the averages for most quantitative characters differ between morphotypes; the statistical significance of these differences is illustrated in table 3. Some features, like total diameter, are significantly different for all the comparisons performed, while others (e.g. ring increment, relative size of marginal pores) differ significantly in only two (out of six) cases. Sharpest separations involve the pairs *S. multispina/S. aculeata*, *Porodiscus* spp./*S. aculeata*, and *Porodiscus* spp./*S. asteriscus*; while *S. multispina/Porodiscus* spp. differ significantly in only one quantitative feature.

Text-figure 2 illustrates the relative distribution of the above-discussed four morphotypes along the transect studied. *S. aculeata* shows a clear tendency to increase in abundance toward the pole, while *S. multispina* is characterized by an increase toward the equatorial zone. *S. asteriscus* peaks in the subtropics decreasing both toward the equator and, especially, toward the Antarctic. The relative distribution of *Porodiscus* spp. does not seem to follow any regular pattern.

Classification of Stylodictya-type Radiolarians by Means of Objective Numerical Techniques

In order to allow using both qualitative and quantitative attributes for the classification the former were coded numerically and the entire data base was standardized. The 11 figures for each possible pair of specimens (i.e. one for each character considered, see Material and Methods section of

this paper) were then correlated and the resulting resemblance matrix used for a cluster analysis. The latter divided the entire collection (485 specimens) into 8 groups. Table 4 provides information on the prevailing aspect of the radiolarians included in each one of these subsets.

Cluster analysis is a powerful tool for partitioning a collection of objects characterized by several attributes into more or less homogeneous subgroups, yet the information it provides on the sharpness of separation of the subgroups is subject to discussion. An independent technique is thus desirable in order to check the classification derived by clustering. Discriminant function analysis (DFA) is especially useful for this purpose: it transforms an original set of measurements on an item (e.g. a radiolarian specimen) into a single discriminant score which represents the item's position along a line defined by the linear discriminant function (see, for example, Davis 1973). Thus, pairwise comparisons of the specimen groups defined by cluster analysis allows investigation of the degree of overlap between the groups along the discriminant function; highest overlaps (i.e. highest percentages of specimens originally clustered within group A and placed on the

TABLE 2

Percentage distribution of qualitative attributes and averages for quantitative characters for the four morphotypes defined in our materials according to conventional taxonomic criteria. Values marked by an asterisk denote characters used for the classification (cf. table 1; *S. multispina* = *S. validispina*).

			S. multispina	*Porodiscus* spp.	*S. asteriscus*	*S. aculeata*
Qualitative characters (% of totals within each group)	Type of rings	Continuous	100	96	66	94
		Discontinuous	0	4	34	6
	Shape of rings	Circular	100*	88	56	0*
		Wobbly	0*	12	54	100*
	Shape central rings	Circular	85	100*	72	0*
		Quadrate	15	0*	28	100*
	Central part	Not thick.	10*	0*	62	100*
		Thickened	0*	100*	38	0*
	Equat. sieve-plate	With	0*	0*	100*	0*
		Without	100*	100*	0*	100*
	Relative size of pores	Even	91	96	82	97
		Uneven	9	4	18	3
Quantitative characters (average values)	Total diameter (mm)		0.112	0.122	0.139	0.090
	Ring-width increment		0.32	0.28	0.45	0.36
	No. of prim. spines		10.3	14.0	7.5	3.6
	Total no. of spines		13.2	15.7	10.6	9.5
	Diam. marginal pores		0.5	0.5	0.4	0.3
Total specimens			63	169	121	79

TABLE 3
Statistical significance of the differences between the mean values of five quantitative attributes for the groups indicated in table 2 (t-tests; **, $P < 0.01$; ***, $P < 0.001$; *S. multispina = S. validispina*).

	S. multispina vs. Porodiscus spp.	S. multispina vs. S. asteriscus	S. multispina vs. S. aculeata	Porodiscus spp. vs. S. asteriscus	Porodiscus spp. vs. S. aculeata	S. asteriscus vs. S. aculeata
Total diameter (log)	**	***	***	***	***	***
Ring-width increment	—	**	—	***	—	—
No. of prim. spines (log)	—	—	***	***	***	***
Total no. spines (log)	—	—	**	**	**	—
Diameter marginal pores	—	—	***	—	***	—

B-side of the discriminant function line, and vice versa) are indicative of lowest overall morphological dissimilarity between the specimen-groups compared, while low percentages of misclassified individuals point to consistent differences between the radiolarians encompassed by the groups under comparison.

Table 5 summarizes the results of the 28 DFA's carried out on the pairs of groups derived by clustering. With only one exception, maximum percentages of misclassified individuals (over the totals discriminated) did not exceed 9%, which suggests that most divisions inferred from the results of the cluster analysis reflect adequately the data base used. The exception in question involved groups I and II, in which case almost half of the specimens (47%) of both groups could not be properly identified on the basis of the attributes used.

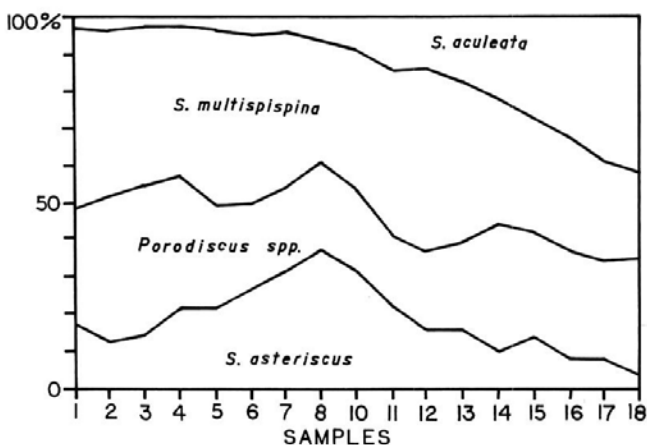Text-figure 3 illustrates the relative distribution of these groups along the transect studied.

Comparison of Conventional and Numerical Classifications

Table 6 illustrates the overlap between the specimen groups defined with the aid of numerical techniques with those established on the basis of conventional taxonomic criteria. There is fairly good coincidence between *S. asteriscus* and group III (57% of all the specimens encompassed by these categories are common to both of them), and especially between *S. aculeata* and group VI (73%). *Porodiscus* spp. is scattered among 7 of the 8 groups defined numerically with highest loading on group I, while *S. multispina* loads highest on groups II and I, and has lower numbers of individuals in groups VIII, VI and III. This poorly defined difference between *S. multispina* and *Porodiscus* spp. is in good agreement with the results illustrated in table 3, which show that only one out of the five quantitative characters considered differed significantly between these two morphotypes. On the other hand, the DFA's discussed above were unable to separate

adequately the radiolarians included in groups I and II (see table 5).

Comparison of the geographic distribution of the radiolarian categories established by the two methods is also in agreement with the results presented in table 6. *S. aculeata* and group VI peak at the southern extreme of the transect, while *S. multispina* + *Porodiscus* spp. and groups I+II decrease in abundance toward the pole. *S. asteriscus* and group III are, in general terms, more abundant at the equatorial end of the transect than south of the transition zone (compare text-figs. 2 and 3).

DFA treatments allow not only checking a classification based on multivariate data, but also assessing the relative contribution of each variable (e.g. each measurement made on the radiolarian shells) to the separation between the two groups compared; this furnishes evidence of the usefulness of each of the characters for identifying the morphotypes in question. The results so far described suggest that groups I and II are very similar both morphologically and in their geographic distribution; we therefore carried out additional DFA's merging these two groups into one. Table 7 presents the results of these calculations showing that in all cases only two to three features are almost entirely responsible for the classifications obtained. Groups I+II (*S. multispina* + *Porodiscus* spp.) and III (*S. asteriscus*) differ from group VI (*S. aculeata*) mainly by the shapes of the rings and the central rings (see also table 4); these features are easy to observe in most specimens (compare figs. 1a–c with figs. 3a, b on pl. 1) and they depend little on overall size and state of preservation. On the other hand, the major differences between groups I+II and III are the equatorial sieve-plate and the relative size of the pores at different distances from the center (the latter is dependent largely on the former, since the equatorial sieve-plate has smaller pores than the main body of the shell); these features are often hard or even impossible to define (in young or broken specimens), which makes separation of these two categories much less reliable.

TEXT-FIGURE 2
Relative abundances of the four morphotypes defined on the basis of conventional taxonomic criteria along the transect studied. (*S. multispina = S. validispina*; percentages are smoothed by a running mean.)

TABLE 4
Percentage distribution of qualitative characters and averages for quantitative characters for the 8 groups of specimens defined by cluster analysis in the collection studied.

| | | | | | | | Specimen groups | | | |
			I	II	III	IV	V	VI	VII	VIII
Binary characters (% of totals within each group)	Type of rings	Continuous	100	100	64	96	98	100	100	100
		Discontinuous	0	0	36	4	2	0	0	0
	Shape of rings	Circular	100	100	53	0	80	1	74	100
		Wobbly	0	0	47	100	20	99	26	0
	Shape of central rings	Circular	95	100	80	96	92	0	84	57
		Quadrate	5	0	20	4	8	100	16	43
	Central part	Not thick.	47	88	60	65	47	100	5	70
		Thickened	53	12	40	35	53	0	95	30
	Equat. sieve-plate	With	1	0	67	4	0	3	0	0
		Without	99	100	33	96	100	97	100	100
	Relative size of pores	Even	100	100	61	100	100	100	100	100
		Uneven	0	0	39	0	0	0	0	0
Quantitative characters (average values)	Total diameter (mm)		0.101	0.116	0.135	0.142	0.104	0.096	0.101	0.148
	Ring-width increment		3.4	3.4	3.4	3.5	3.2	3.4	2.7	3.3
	No. of prim. spines		7.4	9.1	7.5	8.8	30.1	4.3	6.0	8.7
	Total no. of spines		8.8	13.6	9.6	11.3	30.6	10.4	8.2	10.5
	Diam. marginal pores		0.6	0.4	0.4	0.4	0.5	0.3	0.5	0.4
Percentage of total specimens in the collection			17	18	21	5	10	15	4	9

Table 8 illustrates some additional morphometric differences between the radiolarians encompassed by these groups. Group VI shows the lowest number of rings per specimen, and the highest separation between rings; this conforms with the differences between *S. multispina* (our groups I+II) and *S. aculeata* (group VI) noticed by Petrushevskaya (1967).

In total, 345 individuals were comprised by groups I, II, III and VI (71% of all the shells included in the analyses; 80% of those encompassed by the four morphotypes defined by conventional means). Most of the remaining 140 specimens are probably intergrades between these major morphotypes.
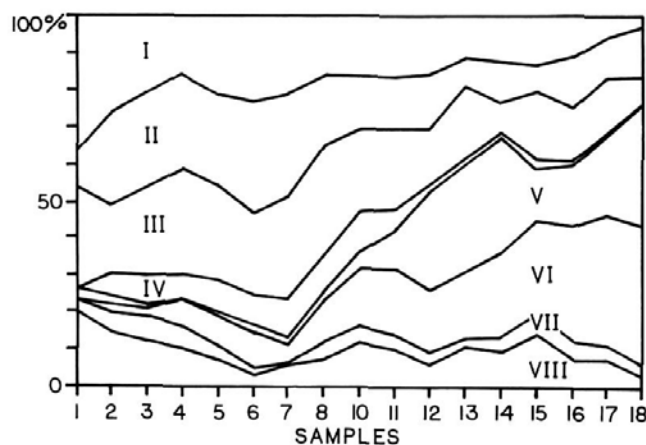
DISCUSSION AND CONCLUSIONS

Consistent identifications of biological species are important per se, but when these species are used as indicators of past

TABLE 5
Results of discriminant function analyses for the specimen groups defined by clustering (cf. table 4), as shown by the percentages of radiolarians misclassified by the discriminant function (100% = total in both groups compared; see text for detailed explanation).

	II	III	IV	V	VI	VII	VIII
I	47	3	0	0	1	9	8
II		3	0	0	0	3	4
III			6	1	5	5	2
IV				7	0	2	0
V					3	0	2
VI						0	1
VII							0

or present oceanographic settings consistent identifications are a sine qua non condition. A species referred to as *Ommatodiscus* sp., *Stylodictya validispina* or *Stylodictya multispina,* and illustrated and/or referenced with figures very similar to our *S. multispina* (pl. 1, figs. 1a–c), has been reported to characterize and/or peak both in equatorial to subtropical latitudes (Renz 1976; Molina Cruz 1977; Boltovskoy 1987) and in subpolar areas (Dow 1978). The morphotypes *Porodiscus* spp. and *S. aculeata* (cf. Petrushevskaya 1967; Nigrini and Moore 1979), in turn, have not been commonly referred to in recent radiolarian literature. Our results show

TEXT-FIGURE 3
Relative abundances of the 8 radiolarian groups defined by clustering along the transect studied. (Percentages are smoothed by a running mean.)

TABLE 6
Overlap between the specimen groups defined by conventional taxonomic criteria (cf. table 1) with those derived numerically (cf. table 4), as expressed by the percentages of individuals shared by each pair. Most likely correspondences (*S. multispina* = *S. validispina*) are noted by an asterisk.

	S. multispina (63 indiv.)	*Porodiscus* spp. (169)	*S. asteriscus* (121)	*S. aculeata* (79)
I (83)	18*	25*	1	0
II (88)	40*	6*	0	0
III (100)	5	4	57*	3
IV (26)	0	6	1	0
V (49)	7	17	0	0
VI (74)	0	0	9	73*
VII (19)	0	11	0	0
VIII (46)	16	9	0	0

that morphologic differences between the types usually classified as *S. multispina* and *Porodiscus* spp. are very poorly defined; objective groupings based on 11 characters give ample support to this conclusion suggesting that the two entities are members of the same taxonomic unit. Most of these specimens are characterized by circular, continuous rings, circular central rings, absence of an equatorial sieve-plate and evenly sized pores throughout the entire shell; the central part of the shell can be thickened or non-thickened. Some previous references to this taxon are:

Ommatodiscus sp., SACHS 1967, p. 149, pl. 2.3, fig. f.— DOW 1978, pl. 1, fig. 8.
Stylodictya sp., PETRUSHEVSKAYA 1967, p. 35, figs. 18: I–IV.
Stylodictya validispina (Jörgensen). ?MOLINA CRUZ 1977, p. 335, pl. 4, fig. 7.—MCMILLEN and CASEY 1978, pl. 2, fig. 17.

TABLE 7
Results of discriminant function analyses for the cluster-defined groups I+II, III and VI.

	I+II vs. III	I+II vs. VI	III vs. VI
Percentages of misclassified specimens	0.7	0.4	5.0
Percentage contribution of each variable (= character) to the separation between groups			
Type of rings	2.9	1.1	13.2
Shape of rings	15.2	76.0	7.5
Shape central rings	0.5	21.2	50.1
Central part	0.3	0.2	4.2
Equat. sieve-plate	51.8	1.2	7.0
Relat. size pores	27.2	0.0	14.4
Total diameter	0.0	0.0	2.0
Ring-width increm.	0.0	0.1	0.1
No. primary spines	0.2	0.0	0.1
Total no. spines	0.0	0.0	0.4
Diam. marginal pores	2.0	0.3	0.0

Stylodictya multispina Haeckel. RENZ 1976, p. 111, pl. 3, fig. 13.—BOLTOVSKOY and RIEDEL 1980, p. 118, pl. 4, figs. 4A, B.—TAKAHASHI 1981, p. 195, pl. 20, fig. 10 (only). BOLTOVSKOY and JANKILEVICH 1985, p. 121, pl. 3, fig. 13.

This morphotype is most abundant in the tropical and subtropical sediments where it comprises up to around 7% of total polycystine assemblages, decreasing more or less evenly toward the pole (text-fig. 4).
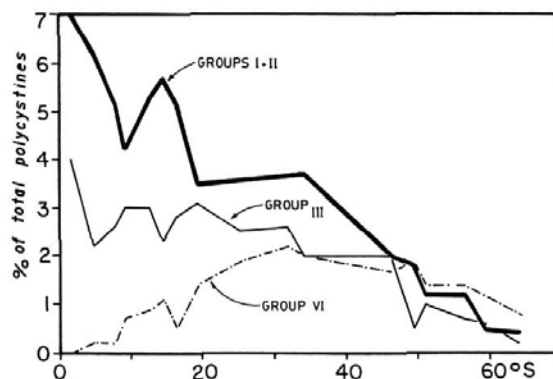
S. aculeata is morphologically closely related to the former; it probably has often been counted together with or even misidentified as *S. multispina*/*Porodiscus* spp. (with a few notable exceptions, e.g. Petrushevskaya 1967; Sachs 1973). Typical specimens of *S. aculeata* are best distinguished from the other two morphotypes by their continuous but wobbly rings, and their quadrate or rosette-shaped central rings, which are always clearly visible because their central part is not thickened. Previous references and illustrations of this taxon include the following:

Staurodictya sp., MCMILLEN and CASEY 1978, pl. 2, fig. 18.
Stylodictya validispina Jörgensen. PETRUSHEVSKAYA 1967, p. 33, figs. 17:IV–V.—SACHS 1967, p. 150, pl. 2.3, fig. g.
Stylodictya aculeata Jörgensen. PETRUSHEVSKAYA 1967, p. 35, figs. 17:I–III.

As opposed to the preceding taxon, *S. aculeata* is most abundant in the transitional to Subantarctic sediments comprising up to 2% of the entire radiolarian assemblages (text-fig. 4).

Stylochlamydium asteriscus is characterized by the presence of an equatorial sieve-plate; this feature, however, is only present in full grown and well preserved individuals. From *S. multispina*/*Porodiscus* spp. it can also be distinguished by some other traits, such as the presence, in many specimens, of wobbly and discontinuous rings (especially the outermost ones). This taxon has been previously mentioned—among others—under the following names:

Stylochlamydium sp. PETRUSHEVSKAYA 1967, p. 37, figs. 19:I, III, IV, VI.

TEXT-FIGURE 4
Approximate percentage contributions of groups I+II, III and VI (cf. table 4) to the entire radiolarian assemblages along the transect studied. (Percentages are smoothed by a running mean.)

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TABLE 8
Average diameter of the central chamber and average width of consecutive growth rings for thin-centered specimens of groups I+II, III and VI. (Values are in micrometers.)

	I+II		III		VI	
	n	Aver.	n	Aver.	n	Aver.
Diameter central chamber	115	10.7	60	11.1	74	11.3
Ring no. 1	115	7.0	60	7.7	74	8.6
2	119	8.3	60	10.0	74	10.8
3	118	9.4	58	10.1	72	11.6
4	104	10.1	49	11.8	41	11.8
5	76	12.4	36	12.4	11	12.3
6	37	12.4	23	12.4	1	14.4
7	11	12.7	12	14.1	1	10.3
8	4	12.3	5	16.8	1	12.3
9			2	12.3		
Average no. of rings	4.9		5.1		3.7	

Stylochlamydium venustum (Bailey). ?LING et al. 1971, p. 711, pl. 1, figs. 7, 8.—TAKAHASHI 1981, p. 196, pl. 20, fig. 11; ?BLUEFORD 1983, figs. 5a, b.
Stylochlamydium asteriscus Haeckel. RENZ 1976, p. 109, pl. 3, fig. 12.—MOLINA CRUZ 1977, pl. 335, p. 4, fig. 6.—MCMILLEN and CASEY 1978, pl. 2, fig. 20.—BOLTOVSKOY and RIEDEL 1980, p. 118, pl. 4, fig. 2.—?BOLTOVSKOY and JANKILEVICH 1985, p. 121, pl. 3, fig. 12.

S. asteriscus was found, sometimes in high numbers, at the tropics/subtropics (Renz 1976; Molina Cruz 1977; McMillen and Casey 1978; Moore 1978; Pisias 1978; Takahashi 1981; Boltovskoy and Jankilevich 1985). A species morphologically indistinguishable from it, but usually referred to as *Stylochlamydium venustum,* was reported as very common to dominant in Arctic and Subarctic latitudes (Ling et al. 1971; Sachs 1973; Blueford 1983). In the southern hemisphere polar and subpolar assemblages either lack this radiolarian altogether (e.g. Riedel 1958; Morley and Stepien 1985), or it is very scarce (Petrushevskaya 1967). Its geographic distribution is characterized by more or less even abundances in the tropical and subtropical zones (approx. 2 to 4% of the entire radiolarian sedimentary assemblages), and a sharp decline south of the subtropical convergence (text-fig. 4). Analysis of additional materials from the north Pacific is needed in order to define whether *S. asteriscus* is a synonym of *S. venustum.* Our results suggest that, as far as the southern Pacific is concerned, *S. asteriscus* is predominantly a warmwater radiolarian.

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REFERENCES

BÉ, A. W. H., HARRISON, S. M., and LOTT, L., 1973. *Orbulina universa* d'Orbigny in the Indian Ocean. Micropaleontology, 19(2): 150–192.

BLUEFORD, J. R., 1983. Distribution of Quaternary Radiolaria in the Navarin Basin geologic province, Bering Sea. Deep-Sea Research, 30:761–781.

BOLTOVSKOY, D., 1987. Sedimentary record of radiolarian biogeography in the equatorial to Antarctic western Pacific Ocean. Micropaleontology, 33:230–245.

BOLTOVSKOY, D., and JANKILEVICH, S. S., 1985. Radiolarian distribution in east equatorial Pacific plankton. Oceanologica Acta, 8:101–123.

BOLTOVSKOY, D., and RIEDEL, W. R., 1980. Polycystine Radiolaria from the Southwestern Atlantic Ocean plankton. Revista Española de Micropaleontología, 12:99–146.

DAVIS, J. C., 1973. Statistics and data analysis in geology. New York: John Wiley & Sons, 550 pp.

DOW, R. L., 1978. Radiolarian distribution and the late Pleistocene history of the southeast Indian Ocean. Marine Micropaleontology, 3:203–227.

EMPSON-MORIN, K. M., 1981. Campanian Radiolaria from DSDP Site 313, Mid Pacific Mountains. Micropaleontology, 27(3):249–292.

KELLOGG, D. E., 1980. Character displacement and phyletic change in the evolution of the radiolarian subfamily Artiscinae. Micropaleontology, 26(2):196–210.

KLING, S. A., 1979. Vertical distribution of polycystine radiolarians in the central north Pacific. Marine Micropaleontology, 4:295–318.

LING, H.-Y., STADUM, C. J., and WELCH, M. L., 1971. Polycystine Radiolaria from Bering Sea surface sediments. In: Farinacci, A., Ed., Proceedings of the Second Planktonic Conference, Roma, 1970. Tecnoscienza, Roma, pp. 705–729.

LOMBARI, G., and BODEN, G., 1985. Modern radiolarian distributions. Cushman Foundation of Foraminiferal Research, Special Publication 16A, pp. 1–24 + charts.

MCMILLEN, K. J., and CASEY, R. E., 1978. Distribution of living polycystine radiolarians in the Gulf of Mexico and Caribbean Sea, and comparison with the sedimentary record. Marine Micropaleontology, 3:121–145.

MOLINA CRUZ, A., 1977. Radiolarian assemblages and their relationship to the oceanography of the subtropical southeastern Pacific. Marine Micropaleontology, 2:315–352.

MOORE, T. C., 1978. The distribution of radiolarian assemblages in the modern and ice-age Pacific. Marine Micropaleontology, 3: 229–266.

MORLEY, J. J., and STEPIEN, J. C., 1985. Antarctic Radiolaria in late winter/early spring Weddell Sea waters. Micropaleontology, 31(4):365–371.

NIGRINI, C. A., and MOORE, T. C., 1979. A guide to modern