

G. Kent Colbath

Department of Earth and Space Science
University of California, Los Angeles
Los Angeles, California 90024*

Abundance fluctuations in Upper Ordovician organic-walled microplankton from Indiana

ABSTRACT

Species of organic-walled microphytoplankton obtained from a well core of the Eden Shale (Upper Ordovician) of Wayne County, Indiana show a reciprocally fluctuating pattern of abundance. Two phytoplankton communities can be identified: the *Baltisphaeridium dasos* Community, consisting of 2 species, and the *Axisphaeridium cylindratum-Dicommopalla macadamii* Community, consisting of 9 species. Three additional species appear to be eurytopic. The 2 communities alternate in dominance according to position in the core, while the abundances of the eurytopic taxa fluctuate independently. A model is proposed in which changing water mass boundaries produce these fluctuations. An alternative model that assumes random sampling of seasonal changes in phytoplankton abundance cannot be excluded with the limited data available. Although speculations about possible causes for the proposed water mass fluctuations are not attempted, it is possible the ancient water masses might be mappable using microphytoplankton, and it is important to biostratigraphic work to recognize such patterns.

INTRODUCTION

The record of the fossilizable microphytoplankton is of considerable importance to an understanding of how the marine biome has developed through time. The position of the phytoplankton at the base of the food chain has led several authors to speculate on possible trophic related causes for major extinction events (Bramlette, 1965; Tappan and Loeblich, 1973; Percival and Fischer, 1977). The present paper focuses on much smaller scale patterns, in the hope that by obtaining detailed information about phytoplankton paleoecology, larger problems will eventually be addressed in a rigorous fashion.

Lower Paleozoic organic-walled microphytoplankton have received relatively little attention compared to other groups. Several authors have suggested facies control over the distribution of these microfossils (Staplin, 1961; Combaz, 1968; Smith and Saunders, 1970; Martin, 1974). Gray and Boucot (1972) proposed a depth stratification model, while Riegel (1974) differentiated what he considered a neritic assemblage from a *Leiosphaeridia*-dominated assemblage found in a more restricted environment. Jacobson (1977b) considered *Leiosphaeridia* a shallow water form. Cramer and Diez have published a series of papers (summarized in Cramer and Diez, 1974) on the paleobiogeography of Silurian microplankton which are difficult to interpret. Vavrdova (1974) has suggested that 2 provinces can be distinguished in Ordovician microfloras of Europe.

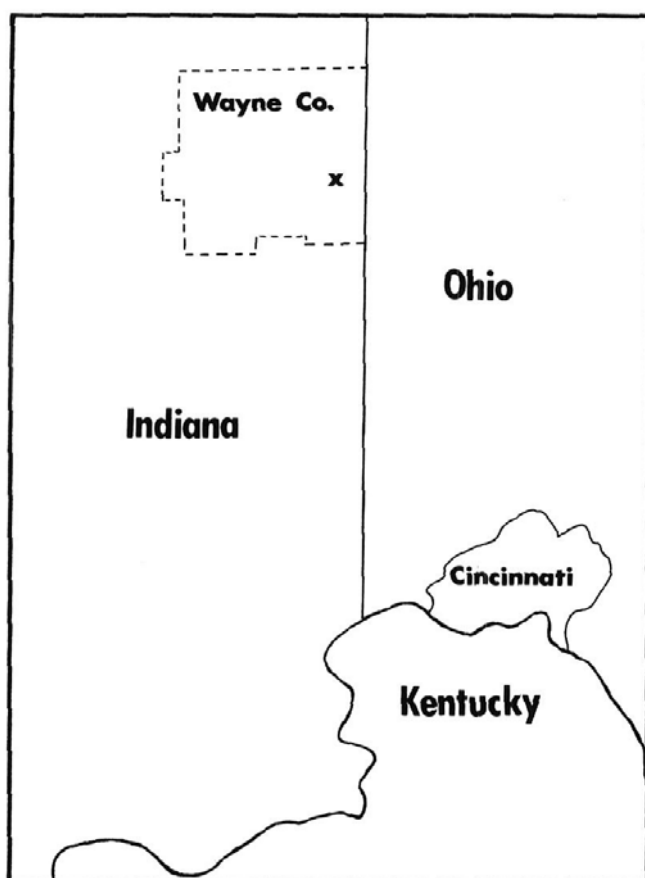
The model proposed here does not directly contradict any of these observations. Instead, I suggest that abundance fluctuations of microphytoplankton from an Upper Ordovician well core (text-fig. 1) might be attributed to a mobile boundary between 2 water masses, each of which was characterized by a different planktonic community.

PROCEDURE

The details of sampling procedures and systematic paleontology are presented by Colbath (in press). Of importance to the present discussion is that the samples were originally prepared to facilitate taxonomic study, and were screened into 4 size fractions. The abundance patterns reported here were first noted well into the course of the taxonomic work, at which time it became apparent that counts of species in different size fractions could not be directly compared. The 36-60 μm fraction was chosen as best illustrating the observed pattern, and only taxa concentrated in that size fraction were counted. Future study may allow inclusion of smaller species in the communities proposed here.

At least 3 strew slides per sample were counted by adjacent traverses under 100X magnification. Only specimens in which more than 1/2 of the vesicle is intact were included. No effort was made to standardize sample sizes; species abundances are thus of relative significance only.

*Present address: Geology Department, University of Oregon, Eugene, Oregon 97403



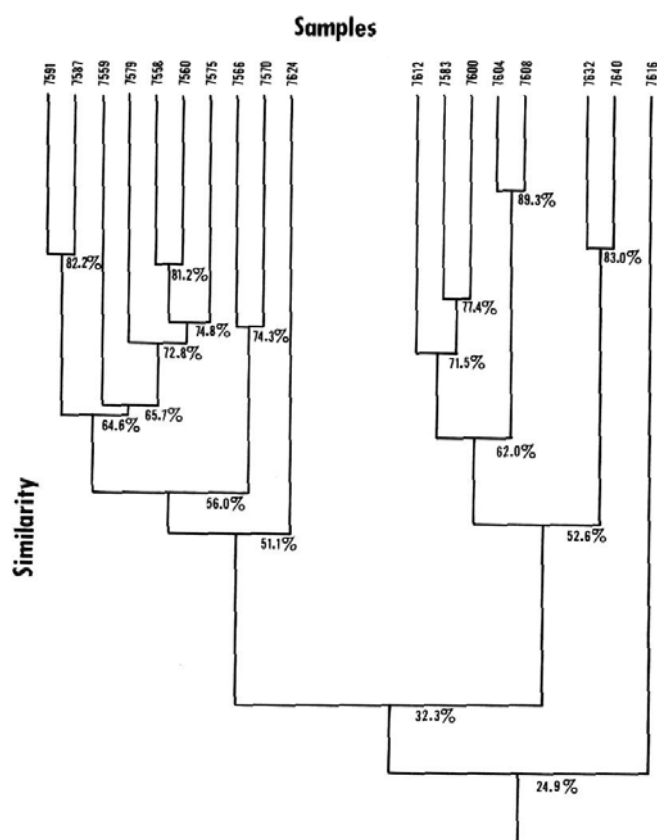
TEXT-FIGURE 1

Index map. Well location indicated by an "x." Wayne County, Indiana, SW 1/4, SW 1/4, NW 1/4, Sec. 12, T14N, R1W.

The taxa included in the present study are of roughly the same size and shape, and presumably had similar hydrodynamic properties. The possibility of differential physical sorting during both deposition and processing was minimal. Restricting study to the 36-60 μm fraction proves advantageous in eliminating the effect of this potentially important variable.

A rather striking reciprocal abundance fluctuation between *Baltisphaeridium dasos* Colbath* and several pylome-bearing taxa (*Axisphaeridium*, *Dicommopalla*, *Peteinosphaeridium*, *Polyancistrodorus*, *Rhopaliophora*, *Tretosohyrtana*) is evident from inspection of table 1. A simple cluster analysis was utilized to present the data graphically. The percentage of individuals in common between 2 samples was used as a similarity measure (Sanders, 1960). This was computed by taking the lesser of the 2 percentages for each species from the samples being compared and adding them up. The resulting matrix was then clustered using arithmetic average linkage clustering, in which similarities for given clusters were averaged after each new link was made. The resulting dendrogram is presented in figure 2.

*All undated species are described by Colbath (in press).



TEXT-FIGURE 2

Dendrogram of arithmetic average linkage cluster analysis performed on data from table 1. The percentage of individuals in common between samples was used as a similarity measure (following Sanders, 1960). Similarities for members of a given cluster were averaged after each new link was made. Note that small differences in levels of clustering are not significant using such crude statistics. Two distinct clusters should be apparent, however, with sample 7616 different from the rest. Note also that omission of eurytopic taxa, as discussed in the text, would tighten both major clusters.

INTERPRETATION

The probable algal origin of Lower Paleozoic "acritarchs" is widely accepted (Loeblich, 1970; Downie, 1973). Although the taxa listed here are of uncertain affinities, they probably represent the acid resistant cysts of prasinophycean green algae, dinoflagellates, or a similar group now extinct (Boalch and Parke, 1971; Dale, 1977).

All samples processed for this study were composed of thinly-bedded, calcareous mudstone (Colbath, in press), indicating that facies changes did not control the reported pattern. Jacobson (1977a) also reported abundance changes that were independent of lithologic facies for rocks of the same age.

Work on the distribution of Holocene dinoflagellate cysts (summarized by Wall et al., 1977) provides a

TABLE 1
Abundances of selected microplankton species.

Sample	Depth (meters)	Species*															Individuals per Sample	Slides per Sample	Diversity**
		A.cyl	A.tom	B.par	B.dan	D.mac	L.kor	N.thy	O.gra	O.ele	Pe.sp	Pe.in	Pa.in	Pg.ce	R.fol	T.imp			
7558	175.3	30.5	1.2	4.2	2.4	12.6	-	13.2	7.8	1.2	12.0	-	1.8	1.8	6.0	5.4	167	5	22
7559	176.1	36.5	0.9	0.9	-	7.8	-	17.4	1.7	-	17.4	-	3.5	2.6	1.7	9.6	115	3	24
7560	176.9	31.5	0.4	12.8	11.0	14.2	-	9.6	5.6	-	7.3	-	-	0.9	4.1	2.7	219	4	20
7566	181.0	15.8	-	8.9	1.0	10.9	-	6.9	3.0	-	32.7	-	14.8	1.0	3.0	2.0	101	3	20
7570	183.9	11.3	-	7.7	3.1	18.0	-	5.2	0.5	0.5	29.9	-	-	-	9.3	14.4	194	3	23
7575	187.5	27.3	-	5.0	5.0	21.5	-	8.3	0.8	0.8	6.6	-	3.3	0.8	17.4	3.3	121	4	27
7579	190.5	20.4	2.6	15.9	1.8	20.4	-	11.5	-	1.8	3.5	-	0.9	7.1	6.2	8.0	113	6	24
7583	193.4	5.5	1.1	2.2	53.0	8.3	0.6	9.4	0.6	0.6	1.6	-	1.1	8.3	4.4	3.3	181	4	22
7587	196.4	27.8	4.6	-	1.8	26.8	-	2.8	-	-	15.7	5.6	-	8.3	1.8	4.6	108	6	23
7591	199.4	35.1	3.0	-	-	20.3	-	1.0	-	-	11.5	15.5	0.5	8.0	1.8	3.2	399	3	27
7600	206.0	4.0	1.1	5.7	44.6	6.3	2.8	5.1	-	3.7	1.7	1.1	0.6	20.0	1.1	-	175	6	21
7604	209.0	4.7	0.8	0.8	77.2	4.7	-	0.8	-	-	1.6	0.8	-	8.7	-	-	127	5	19
7608	212.1	2.3	-	1.2	84.2	5.3	-	-	-	1.8	0.6	1.8	-	2.9	-	-	171	3	20
7612	215.2	4.7	-	21.7	35.6	14.7	1.6	5.5	-	4.7	-	-	0.8	10.8	-	-	129	6	18
7616	218.1	1.6	-	9.0	-	6.3	-	0.5	-	2.1	1.0	0.5	1.0	77.8	-	-	189	3	23
7624	224.2	11.6	0.6	2.2	3.4	21.8	0.3	1.2	-	2.2	11.7	3.4	31.7	9.8	-	-	325	3	22
7632	230.3	6.0	-	2.4	15.7	19.3	-	14.4	-	4.8	3.6	1.2	2.4	30.1	-	-	83	8	19
7640	236.3	4.7	-	0.8	23.4	16.4	0.8	7.8	-	0.8	3.1	1.6	3.1	37.5	-	-	128	5	18
Individuals per species		511	31	156	561	446	10	171	33	42	278	89	144	391	89	93	3,045		

Numbers are percentages each species represents of those counted in a given sample. Only samples having 50 or more specimens are included here.

*Abbreviations are as follows: A.cyl = *Axisphaeridium cylindratum* Colbath; A.tom = *Axisphaeridium tomentum* Colbath; B.par = *Baltisphaeridium parvulisidereum* Colbath; B.dan = *Baltisphaeridium dasos* Colbath; D.mac = *Dicommopalla macadamii* Loeblich 1970; L.kor = *Lophosphaeridium korynum* Colbath; N.thy = *Navifusa thyreosa* Colbath; O.gra = *Ordovicidium gracile* Colbath; O.ele = *Ordovicidium elegantulum* Tappan and Loeblich 1971; Pe.sp = *Peteinosphaeridium spiralicula* Colbath; Pe.in = *Peteinosphaeridium indianaense* Colbath; Pa.in = *Polyancistrodorus intricatus* Colbath; Pg.ce = *Polygonium celestum* (Martin 1969); R.fol = *Rhopaliophora foliatilis* Tappan and Loeblich 1971; T.imp = *Tretosohyrtana impexa* (Tappan and Loeblich 1971).

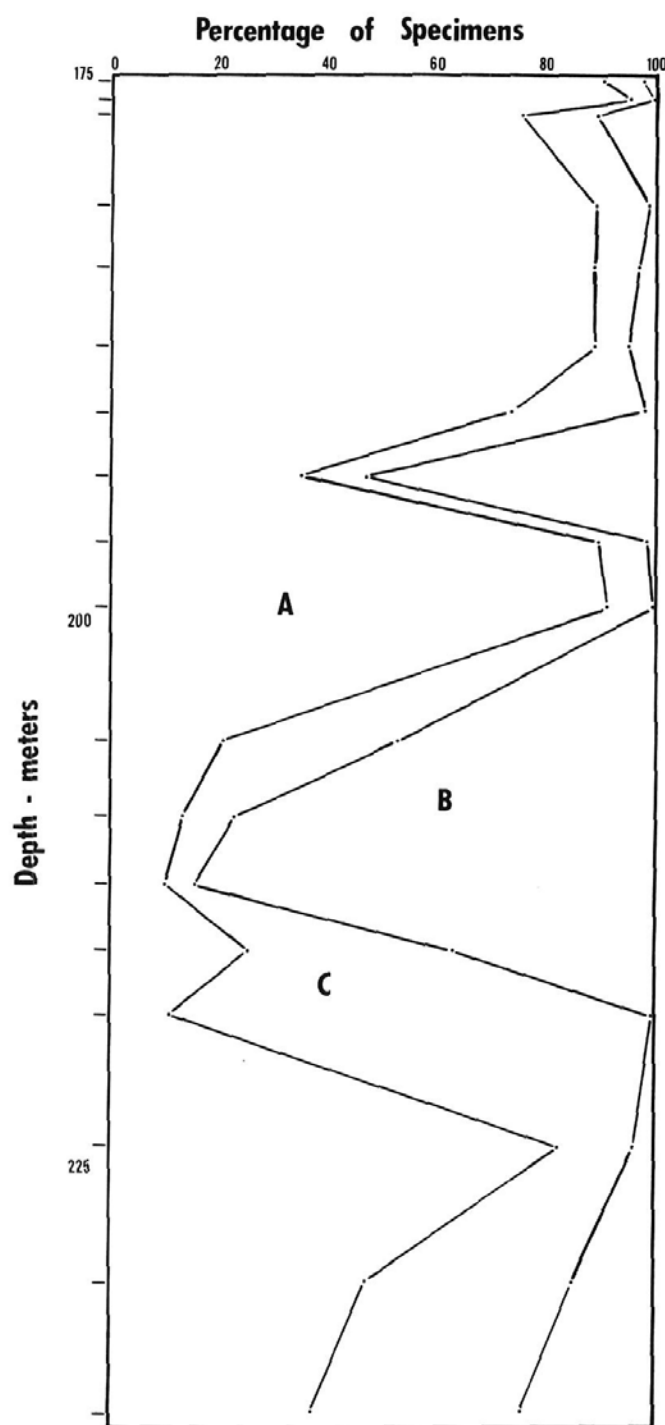
**Total diversity for all size fractions from a given sample. Modified from Colbath (in press).

useful base for ecological interpretations of fossil abundance patterns. On a large scale, the world's oceans can be divided into water masses possessing distinctive chemical and physical characteristics, each inhabited by distinctive assemblages of planktonic organisms. Wall et al. (1977) reported a strong correlation between the geographical extent of water masses and characteristic cyst assemblages in underlying sediments. These authors were also able to identify the influence of mixing during sedimentation, and in a few cases, the admixture of relict Pleistocene assemblages.

The possibility that ancient water masses might have produced similar distinctive cyst assemblages is an intriguing one. I would like to suggest, tentatively, that the 2 assemblages of Ordovician microplankton reported here actually represent cysts of the inhabitants of 2 separate water masses, with the boundary between the 2 moving across the sample locality at least 4 times during the interval in which the rocks studied were deposited. These 2 assemblages or "communities" (used here as a consistently recurring association of taxa) are defined as follows: the *Baltisphaeridium dasos* Community includes *B. dasos* as the dominant member, and the rare species *Lophosphaeridium korynum* Colbath. In the *Axisphaeridium cylindratum*-*Dicommopalla macadamii* Community the named species are both the largest and most consistent contributors. Other included taxa are *Axisphaeridium tomentum* Colbath, *Navifusa thyreosa* Colbath, *Ordovicidium gracile* Colbath, *Peteinosphaeridium spira-*

licula Colbath, *P. indianaense* Colbath, *Polyancistrodorus intricatus* Colbath, *Rhopaliophora foliatilis* Tappan and Loeblich 1971, and *Tretosohyrtana impexa* (Tappan and Loeblich, 1971). The remaining 3 species counted do not clearly correlate with either of the above communities, and are considered to be cysts of eurytopic phytoplankters. Text-figure 3 illustrates changing abundances of these 3 sets of taxa within the core.

Polygonium celestum (F. Martin, 1969) is the most abundant of the 3 species that here are considered eurytopic. A good modern analogue might be the cyst species *Spiniferites bulloideus* (Deflandre and Cookson) Sarjeant, 1970 as described by Wall et al. (1977, p. 147). *Spiniferites bulloideus* occurred in all samples studied by those authors, with its highest abundance in areas of brackish, non-stratified water. This agrees with the generalization that eurytopic species tend to be cosmopolitan, and are able to exploit stressed environments where less tolerant taxa are reduced or excluded. *Polygonium celestum* (and species considered synonymous) has been described from strata in Belgium, East Germany, Algeria, and possibly Poland (see Colbath, in press). Further study may reveal an even wider geographic distribution. Drawing even further on the modern analogue, perhaps the predominance of individuals of *P. celestum* in sample 7616 represents a temporary change in salinity conditions (i.e., an influx of fresh water, etc.). Such an interpretation is highly speculative, but fits well with the model proposed here.



TEXT-FIGURE 3

A graphical presentation of abundance fluctuations among the 3 groups of taxa defined in the text. Marks at left are sample points. Depth is in meters below ground surface. The width of a given field is proportional to the percentage represented by a group within a particular sample. A, *Axisphaeridium cylindratum*-*Dicommopalla macadamii* Community; B, *Baltisphaeridium dasos* Community; C, eurytopic taxa.

Of the 2 remaining species that are considered eurytopic, *Baltisphaeridium parvulisidereum* Colbath is similar to *B. hirsutoides* (Eisenack) Eisenack, 1959, a

species commonly reported from Europe, whereas *Ordovicidium elegantulum* Tappan and Loeblich, 1971 was described from the Middle Ordovician of Oklahoma. These species may prove to be good cosmopolitan taxa with more detailed study of additional regions.

Cysts of pylome-bearing taxa were generally poorly preserved in samples dominated by *B. dasos*, suggesting possible reworking or long-distance transport in the water column. Any bioturbation by benthonic invertebrates would also tend to smear out changing abundance patterns. Such effects may explain why samples 7632 and 7640 do not fit neatly into either community.

Wicander (1975) noted an inverse relationship between abundances of *Leiosphaeridia* and *Gorgonisphaeridium* in the Upper Devonian of Ohio. Perhaps this might also be explained in terms of water mass fluctuations.

An alternative hypothesis calling on seasonal changes in the phytoplankton cannot be excluded with the data at hand. Using such a model, the observed abundance pattern could be explained as the result of random sampling of differences in the spring and fall plankton. Laufeld (1974, p. 121) has argued for seasonal controls over the distribution and abundance of Silurian chitinozoans in Sweden. Abundance changes were observed to correlate with alternating lithologies in a rhythmically bedded sequence, while seasonal inferences were based on growth banding in associated corals. No rhythmic bedding was observed in samples processed for the present study, nor were samples restricted to single laminae.

These 2 alternative hypotheses should be testable with further sampling. The water mass model predicts that there should be geographic areas within rocks of the same age which contain only one community or the other. The seasonality model predicts that abundance patterns like those reported here should occur without regard to geographic changes.

Many tempting speculations are possible concerning causes for the water mass fluctuations called upon by the model presented here. The limited data base available does not warrant such speculations at the present time. Nonetheless, the possibility that microphytoplankton might be used for mapping Paleozoic water masses is intriguing (see also Sarjeant 1967, p. 259).

BIOSTRATIGRAPHIC IMPLICATIONS

The importance to biostratigraphy of recognizing paleoecologic controls over fossil distribution patterns is obvious. Floral changes of a purely local nature

might otherwise be mistakenly assigned a time significance.

The detailed counting reported here supports the suggestion (Colbath, in press) that the first appearances of *Ordoviciidium gracile*, *Tretosohyrtana impexa*, and *Rhopaliophora foliatilis* might be usable in a zonation scheme. The taxa were first found at various levels above 216 m within the core, even though sample 7624 (224.2 m) was dominated by the *Axisphaeridium cylindratum-Dicommopalla macadamii* community, to which these species belong. The first appearances of these taxa thus probably represent evolutionary or migrational events, and should be useful for biostratigraphy, at least within the Cincinnati region.

CONCLUSIONS

1) Striking vertical abundance changes are observable for selected species of Upper Ordovician microphytoplankton. 2) These abundance changes are not correlative with facies changes. 3) Two "communities" can be recognized: the *Baltisphaeridium dasos* Community and the *Axisphaeridium cylindratum-Dicommopalla macadamii* Community. 4) Three species that did not correlate in abundance with either community are probably eurytopic. 5) A water mass model may explain the observed pattern. If the two communities are considered characteristic of different water masses, the boundary between these water masses moved across the sample location at least 4 times during deposition of the interval sampled. 6) An alternative model calling upon random sampling of seasonal fluctuations within a single phytoplankton assemblage cannot be excluded with the data available. 7) It may be possible that ancient water masses might be mappable on a fine scale using microphytoplankton. 8) The first appearances of *Ordoviciidium gracile*, *Tretosohyrtana impexa*, and *Rhopaliophora foliatilis* within the Eden appear to have significance for biostratigraphic work.

ACKNOWLEDGMENTS

Special thanks are due A. R. Loeblich, Jr., who initiated this research, provided much technical assistance, and critically read the manuscript. Helen Tappan, Arthur J. Boucot, Sarah Pierce Damassa, and E. Reed Wicander also read the manuscript, and made numerous helpful comments. The core samples were made available by Dr. R. H. Shaver of the Indiana Geologic Survey. Sharon Larson helped draft the figures. Julie Knaack typed table 1.

This research was partially supported by National Science Foundation Grant GA 42977 to A. R. Loeblich, Jr.

REFERENCES

- BOALCH, G. T., and PARKE, M., 1971. The prasinophycean genera (Chlorophyta) possibly related to fossil genera, in particular the genus *Tasmanites*. In: Farinacci, A., Ed., *Proceedings II Planktonic Conference*, Roma 1970, 1: 99-107.
- BRAMLETTE, M. N., 1965. Massive extinctions in biota at the end of Mesozoic time. *Science*, 148: 1696-1699.
- COLBATH, G. K., In press. Organic-walled microphytoplankton from the Eden Shale (Upper Ordovician), Indiana, U. S. A. *Palaeontographica*, Abt. B.
- COMBAZ, A., 1968. Un microbios du Trémadocien dans un sondage d'Hassi-Messaoud. *Actes Soc. Linné Bordeaux*, 104 (29) sér. B: 1-26.
- CRAMER, F. H., and DÍEZ, M. C. R., 1974. Silurian acritarchs: distribution and trends. *Rev. Palaeobot. Palynol.*, 18: 137-154.
- DALE, B., 1977. New observations on *Peridinium faeroense* Paulsen (1905), and classification of small orthoperidinioid dinoflagellates. *Brit. Phycol. Jour.*, 12: 241-253.
- DOWNIE, C., 1973. Observations on the nature of the acritarchs. *Palaeontology*, 16: 239-259.
- GRAY, J., and BOUCOT, A. J., 1972. Palynological evidence bearing on the Ordovician-Silurian paraconformity in Ohio. *Geol. Soc. Amer. Bull.*, 83: 1299-1314.
- JACOBSON, S. R., 1977a. Biostratigraphy and paleoecology of acritarchs from middle and upper Ordovician rocks in the Cincinnati region (abstr.). *Geol. Soc. Amer. Abstr. Prog.*, 9: 609-610.
- , 1977b. Middle and upper Ordovician acritarchs, eastern midcontinent, U. S. A. (abstr.). *Prog. Abstr., Colloquio Int. Palinol., Inst. Invest. Palinol., Leon, España*: 21.
- LAUFELD, S., 1974. Silurian chitinozoa from Gotland. *Fossils and Strata*, no. 5: 1-130.
- LOEBLICH, A. R., JR., 1970. Morphology, ultrastructure and distribution of Paleozoic acritarchs. *Proc. North Amer. Pal. Conv.*, pt. G: 705-788.
- MARTIN, F., 1974. Ordovicien Supérieur et Silurien Inférieur à Deerlijk (Belgique). *Palynofacies et microfacies*. *Mém. Inst. Roy. Sci. Nat. Belgique*, no. 174: 1-71.
- PERCIVAL, S. F., and FISCHER, A. G., 1977. Changes in calcareous nannoplankton in the Cretaceous-Tertiary biotic crisis at Zumaya, Spain. *Evolutionary Theory*, 2: 1-35.
- RIEGEL, W., 1974. Phytoplankton from the upper Emsian and Eifelian of the Rhineland, Germany—a preliminary report. *Rev. Palaeobot. Palynol.*, 18: 29-40.
- SANDERS, H. L., 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. *Limnol. Oceanogr.*, 5: 138-153.
- SARJEANT, W. A. S., 1967. The Xanthidia—the solving of a palaeontological problem. *Mercian Geol.*, 2: 245-266.
- SMITH, N. D., and SAUNDERS, R. S., 1970. *Paleoenvironments and their control of acritarch distribution in the Silurian of east-central Pennsylvania*. *Jour. Sed. Petrol.*, 40: 324-333.
- STAPLIN, F. L., 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology*, 4: 392-424.
- TAPPAN, H., and LOEBLICH, A. R., JR., 1973. Evolution of the oceanic plankton. *Earth-Sci. Rev.*, 9: 207-240.