

MORPHOLOGIC VARIABILITY OF THE GENUS *Schwagerina* IN THE LOWER PERMIAN WREFORD LIMESTONE OF KANSAS

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ABSTRACT. Fusulinids referable to the genus *Schwagerina* occur in the basal part of the Threemile Limestone Member of the Permian Wreford Formation in Chase County, Kansas. Three hundred specimens from six collecting localities in four townships in Chase County were used in this study. The restricted stratigraphic range and limited geographic distribution of the fusulinid fauna within the intracratonic, cyclical succession tend to minimize the effects of diachronism, and it is presumed that the collections are approximately contemporaneous.

Considerable morphologic variability is evident within the Threemile fusulinid fauna, and affinities with several previously described species of *Schwagerina* can be demonstrated. Studies of measurable morphologic parameters suggest that all the Wreford schwagerinids sampled are referable to a single population, and thus the validity of several established taxa is open to challenge.

The Permian Wreford Limestone Formation is a cyclical, intracratonic marine unit which is exposed in Kansas along a generally north-south trending outcrop belt (text-fig. 1). Fusulinids referable to the genus *Schwagerina* have been found in the Wreford only in Chase County. The specimens used in this study are from six outcrop localities in four townships within Chase County (text-fig. 1).

Stratigraphically, the Wreford defines the base of the Wolfcampian Chase Group. It is overlain by the Matfield Shale and underlain by the Speiser Shale. The Wreford has three members, which are, in ascending order, the Threemile Limestone, the Havensville Shale, and the Schroyer Limestone (text-fig. 2). In Chase County, the thickness of the Wreford averages approximately 12 m. (Moore *et al.* 1951).

Fusulinids occur abundantly in the Wreford in central Chase County but only in the Threemile Member and only in the lowermost 3-5 cm. of that unit (Hattin 1957). The lower Threemile Member is persistently a grey, porous, cherty limestone in the area of our collections. There are no obvious indications of lithofacies differences among the collections, and we are assuming that a generally similar environment is represented throughout our samples. The geological setting suggests also that the effects of diachronism are minimal. These close stratigraphic, geographic, ecologic and temporal limits which we are able to place upon the Wreford fauna make it particularly well suited to a study of morphologic variability and population distribution.

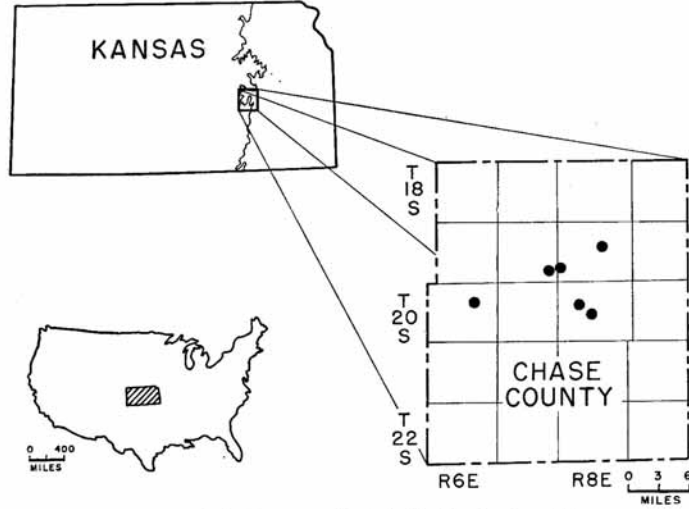
MORPHOLOGY

The Wreford fusulinids exhibit considerable morphologic diversity. Among the specimens illustrated on Plate 35, shape is the most apparent variable (figs. 1, 3, 8, and 11), but closer examination of the fauna shows differences also in other morphologic characters, such as prolocular diameter, wall thickness, tunnel width, and nature of

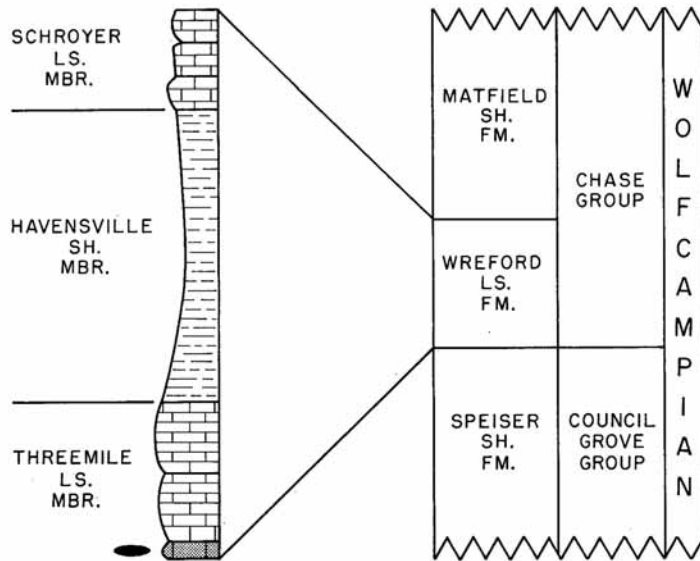
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TEXT-FIG. 1. Index map of Wreford collecting localities.



TEXT-FIG. 2. Stratigraphic chart showing position of fusulinids.

septal folding. Any attempt to evaluate the significance of these differences leads inevitably to consideration of some rather basic questions, such as:

1. How many taxa (populations) are present?
2. How may they be distinguished?
3. What is their geographic distribution?

In an effort to find answers to these questions, a representative sampling was made consisting of 50 randomly selected specimens from each of the 6 collections. Equal numbers of oriented axial and sagittal thin sections were prepared, giving a total of 300 individuals used in this study. This extensive sampling, while statistically adequate and systematically desirable, proved to be disturbing to the traditional method of taxonomic differentiation by visual examination. As might be expected, the morphologic complexity produced by the interaction of multiple variables tends to inhibit consistent differentiation by visual inspection alone.

Only a few specimens of the total Wreford fauna are illustrated on Plate 35, but even here the gradational nature of the morphologic parameters, such as form ratio, for example, is quite evident, and the distinctive individuals labelled as figs. 1, 3, 8, and 11 begin to blend into a morphologic spectrum. The difficulty of separating these forms consistently by visual means is increased progressively as the sample size is increased. Obviously, supplemental quantitative data are required to establish definable limits to the population or populations.

To this end, the following parameters were measured on the appropriate orientations of the 300 sampled specimens: prolocular diameter, length, diameter, radius vector, septal count, volution height, prothecal thickness, half length, and tunnel width. Although they do not quantify every morphologic dimension, these parameters represent the bulk of those commonly employed by fusulinid workers. In all, nearly 24 000 bits of raw quantitative data were accumulated, which subsequently have been manipulated and subjected to statistical treatment.

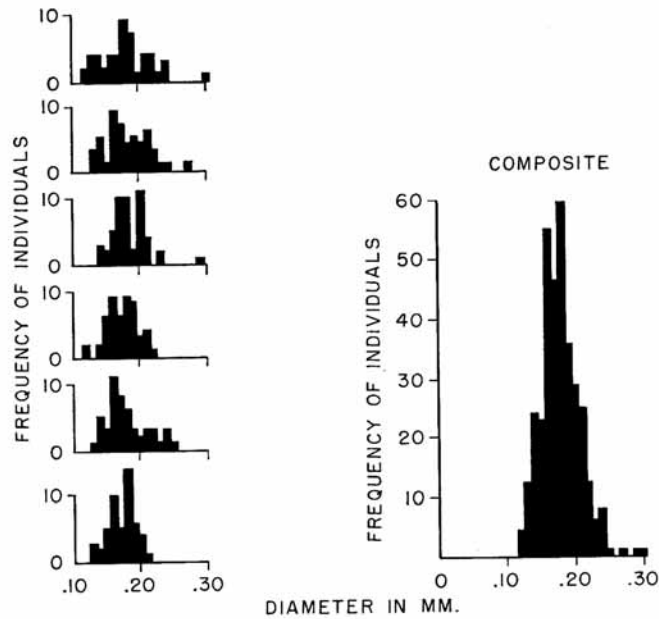
QUANTITATIVE ASPECTS

The quantitative aspects of the Wreford fusulinid fauna were investigated in a three-fold manner: first, by considering the variability of specific parameters within the sampled specimens; second, by examining ontogenetic changes within the population or populations; and, third, by comparing all the individual specimens in the samples with one another statistically. We considered that one or more of these approaches should reveal the existence of a quantitative basis for taxonomic subdivision of the fusulinid fauna.

Parameter variability

Results of the first approach are illustrated in the frequency distribution histograms of several parameters (text-figs. 3-6). Text-fig. 3 shows the number of individuals in each size class of prolocular diameter; on the left are plots for each of the 6 collecting localities, using a common scale on the X-axis and stacked for purposes of comparison. All the histograms suggest a gradation of dimension through a fairly narrow range with a strong clustering tendency about the means, which are virtually identical in all samples. The data in each sample have a high degree of statistical correlation. On the right side

of the same figure is a composite plot of all the data on the left; measurements from all 300 fusulinid specimens are included. In this larger sampling, the distribution is naturally smoother with accentuation of the clustering tendency, but the essential characteristics are similar to those of the separate localities. It closely approaches a continuous, symmetrical distribution about a mean with no indication of bimodality. There would appear to be no reason for any taxonomic separation on the basis of this parameter.



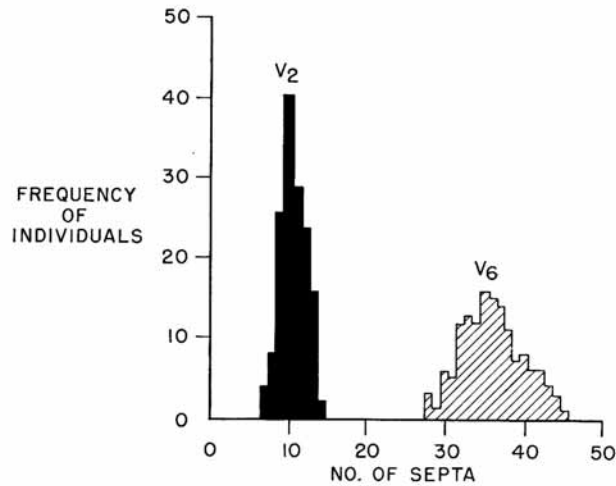
TEXT-FIG. 3. Frequency distribution histograms of prolocular diameter, composite and for individual localities.

A frequency distribution plot of septal count by volution produces similar histograms (text-fig. 4). The same bell-shaped distribution may be observed in all volutions, although the shape changes ontogenetically from more leptokurtic to more platykurtic. Representative distributions are shown for septal counts of all specimens in the second and sixth volutions. These counts are made from sagittal sections only, and the total specimen count is 150. The flattening of the distribution is progressive with growth and suggests a greater range of dimensional variability in the adult test than in the juvenile. None the less the variation seems to be essentially continuous among all the measurements for any given volution.

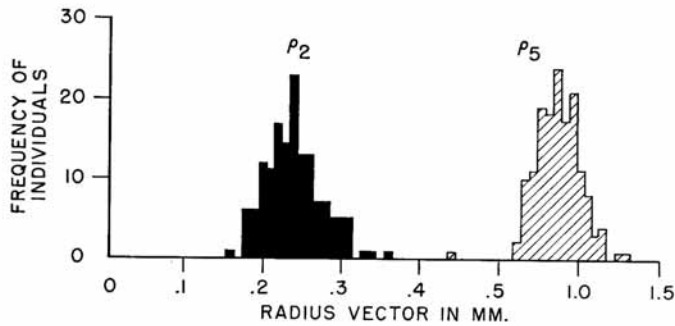
EXPLANATION OF PLATE 35

Morphologic gradation of Wreford schwagerinid fauna, $\times 8$. Figs. 1-11 are specimens 226, 31, 328, 57, 209, 306, 144, 37, 43, 153, and 287, respectively.

It should be noted that these graphic illustrations were plotted from raw measurements made on a volution-by-volution basis before adjustment for position on the growth spiral. The adjusted data have an even smoother frequency distribution. A



TEXT-FIG. 4. Frequency distribution histograms of septal count for volutions 2 and 6.

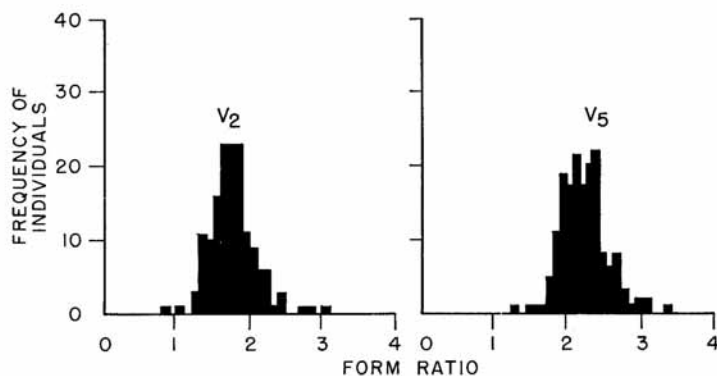


TEXT-FIG. 5. Frequency distribution histograms of radius vector (ρ) for volutions 2 and 5.

statistical evaluation of interpolated values at equal diameters made by Dr. J. L. Cutbill (personal communication) of Cambridge University showed virtually all the distributions to be statistically normal.

An analogous situation may be seen in the radius vector (ρ) distribution. Text-fig. 5 illustrates the values for volutions 2 and 5. Again the frequency histograms are essentially symmetrical and closely clustered about the mean with a tendency toward progressive flattening in outer volutions. In the case illustrated, the flattening is somewhat masked

by the scale change necessitated by size limitations of the graph. The dimensional variability is essentially continuous, and normality of distribution can be demonstrated. Similar plots of other parameters (e.g. text-fig. 6) give the same results; none has yet produced any clear indication of a quantitative basis for taxonomic separation.



TEXT-FIG. 6. Frequency distribution histograms of form ratio for volutions 2 and 5.

Ontogenetic changes

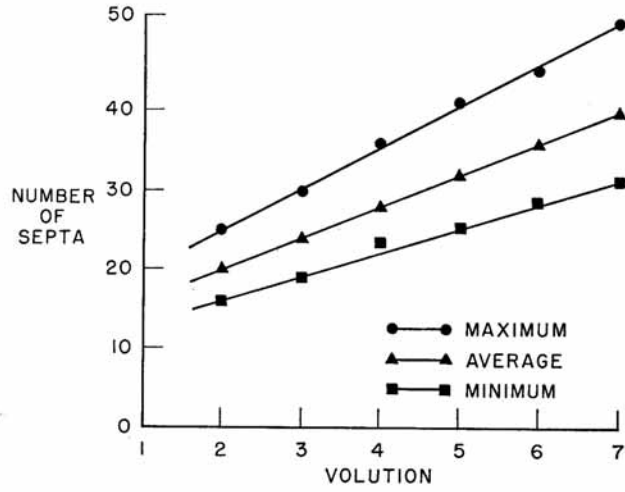
Text-fig. 7 is a plot of increase in septal count with growth. Maximum, minimum, and mean values per volution are given for the entire sampling. With the exception of volution 1, which contains the prolocular aperture and is unique, the septal count in all other volutions increases arithmetically, resulting in the linear relationship shown. Again, there seems to be no compelling reason to attempt taxonomic subdivision of the Wreford fusulinid fauna on the basis of this parameter.

The ontogenetic increase in radius vector is illustrated in text-fig. 8 with the maximum, minimum, and mean values per volution given for all the Wreford specimens. In contrast to the septal count, the growth curve is exponential, but there is still no suggestion that more than one population is present in our samples.

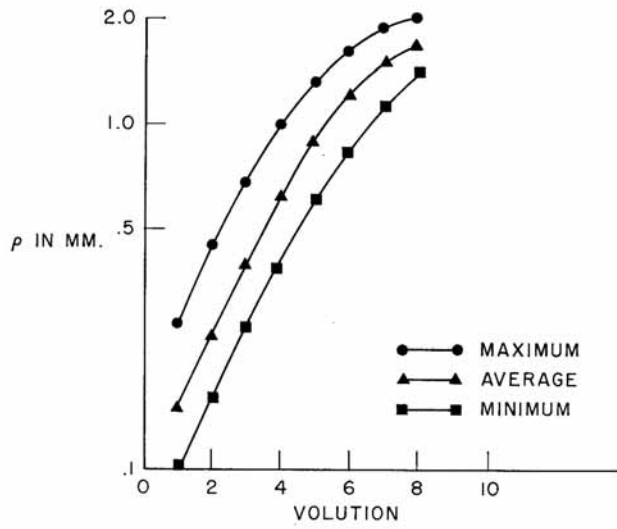
Comparable results appear in other data plots, and the point need not be laboured. All other measured parameters which have not been illustrated correlate closely with those shown or exhibit similar relationships.

Statistical analyses

Various types of multivariate analysis have been used since the study of the Wreford fauna began, and, in fact, the statistical study is continuing as more sophisticated computer hardware and software become available. Our initial studies utilized raw data consisting of measurements made at single volution (e.g. 360°) increments. The volution approach does not, of course, take into account the variability in diameter of the initial chamber and, therefore, comparisons of growth characteristics are only approximate. Although other methods of adjustment have been investigated, the Cutbill data standardization method (unpublished manuscript) of relating measurements to standard reference diameters has been used in most subsequent computer applications.



TEXT-FIG. 7. Plot of maximum, minimum, and mean septal counts per volution for the total Wreford population.



TEXT-FIG. 8. Plot of maximum, minimum, and mean radius vectors per volution for the total Wreford population.

Multivariate analyses run on both the raw data and the adjusted data include R-mode factor analysis, Q-mode factor analysis, and discriminant function analysis. Results of the tests run to date support the premise that the Wreford fusulinids probably belong to a single continuously variable population.

FAUNAL COMPARISONS

Since we have been unable to make taxonomic subdivision of the Wreford fusulinid fauna on the basis of either qualitative or quantitative criteria, our original questions seem to be answered adequately by the simple recognition of a single fusulinid population distributed essentially uniformly throughout our collections. This certainly is not a startling conclusion in view of the geologic evidence, but a disturbing ramification presents itself in the comparisons made on Plate 36, using 6 fusulinid pairs. One member of each pair is a published species, in some cases the holotype, of an age roughly comparable to that of the Wreford; the other is a selected member of the Wreford population from somewhere within the morphologic spectrum. A close degree of similarity is obvious. Perhaps these specimens are not all conspecific, but differentiation certainly would involve extremely subtle differences—of an order well within the range of variability of a single population such as that of the Wreford. Whether or not these particular specimens are conspecific is rather beside the point. What is important is that they are extremely difficult, if not impossible, to differentiate by conventional means—that is, visually or on the basis of limited measurements. In short, there is a reasonable doubt as to their validity, which in turn suggests the need for a reappraisal of commonly accepted taxonomic practices, for there is abundant evidence to indicate that similar studies could be conducted on the majority of published fusulinid faunas with comparable results. Needless to say, our criticism is directed at the present 'state of the art' and not personally at its practitioners among whom we include ourselves.

Unfortunately, there is no easy solution to the problem. Speciation among fusulinid workers is a highly subjective process unfettered by procedural standards or guidelines. Such standards are urgently needed, but it would be naïve, indeed, to assume that they will be forthcoming soon. Nevertheless it should be incumbent upon authors of new taxa to define them in such a manner that they are unequivocally distinguishable. In our view this includes extensive sampling, adequate illustration, and detailed quantitative treatment of the morphologic variability spectrum of the taxon. Cutbill and Forbes (1967) suggest possible procedures for routine taxonomic work which can be used to advantage. Whether graphic representations are used or not, the minimum sampling of twenty specimens suggested by Cutbill and Forbes should be practised whenever possible. A larger sampling would be even better.

Multivariate analysis will undoubtedly play a significant role in population studies in the future, particularly in view of increasing computer availability. Discriminant function analysis can aid in the recognition of morphologic groupings (Harbaugh and

EXPLANATION OF PLATE 36

Faunal comparison, $\times 8$. Figs. 1a–6a are specimens 309, 49, 226, 55, 54, and 43, respectively, of the Wreford schwagerinid population. Figs. 1b–6b are *Schwagerina vervillei* Thompson 1954, *S. colemani* Thompson 1954, *S. emaciata* (Beede) 1916, *S. campensis* Thompson 1954, *S. andresensis* Thompson 1954, and *S. complexa* Thompson 1954, respectively.

Merriam 1968). Factor analysis in the Q-mode and R-mode is applicable to fusulinid studies involving populations of individuals or variable morphologic parameters (Harbaugh and Merriam 1968, Merriam 1966). In fact, study of the spatial and temporal variability of particular morphologic parameters may well turn out to be of greater significance geologically than the characterization of the individual as an aggregate of many variables. In any case, the delimiting of morphologic variability is inherent in realistic taxonomy.

CONCLUSIONS

All available evidence indicates that the Wreford fusulinids studied apparently belong to a single morphologic population distributed more or less uniformly through all six collecting localities. Close similarity is demonstrable between several existing species of *Schwagerina* and specimens within the Wreford population, and it is doubtful whether all of the former represent valid species. Current taxonomic practices are in need of review, and a shift of emphasis from the typological concept to a population-oriented approach seems to be in order. Realistic and objective delineation of species requires consideration of the whole spectrum of morphologic variability, and the erection of any new taxon should entail sufficient quantitative data for adequate characterization.

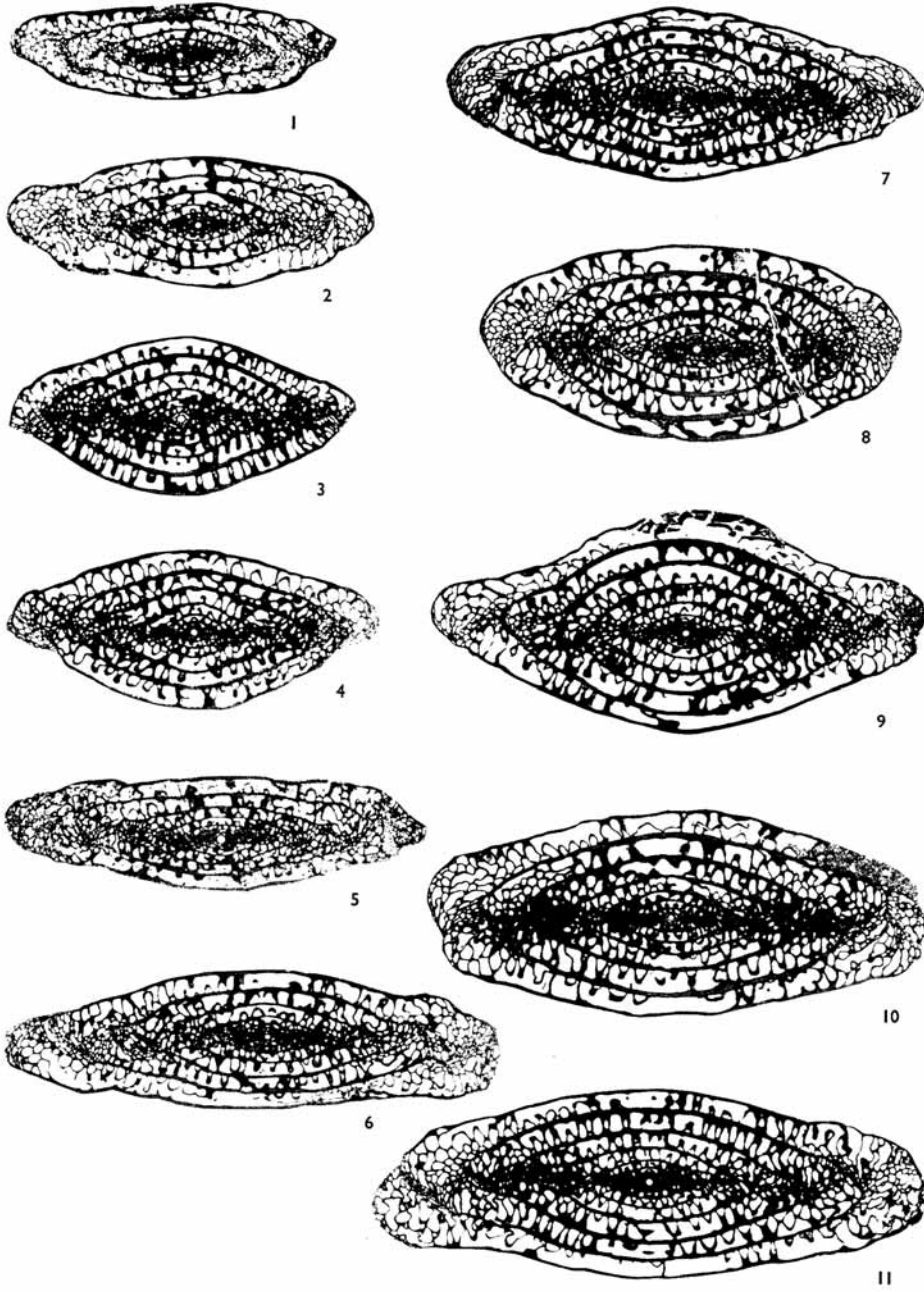
Acknowledgements. We are particularly grateful to Dr. J. L. Cutbill who made the first statistical test of our data with his data standardization routine and who has also permitted us access to unpublished manuscript material. His counsel and encouragement are appreciated. Pan American Petroleum Corporation provided computer and other facilities utilized in this study and granted permission for publication. Among the Pan American colleagues who have aided materially this study, we wish to acknowledge the efforts of Messrs. L. V. Brown, N. Di Vittorio, and K. Wignall in statistical aspects of the project. We also wish to thank Dr. Alan B. Shaw with whom several fruitful discussions were held.

Repository. All specimens are filed by specimen number under Localities 2795-2800 inclusive at the Research Center of the Pan American Petroleum Corporation (address below).

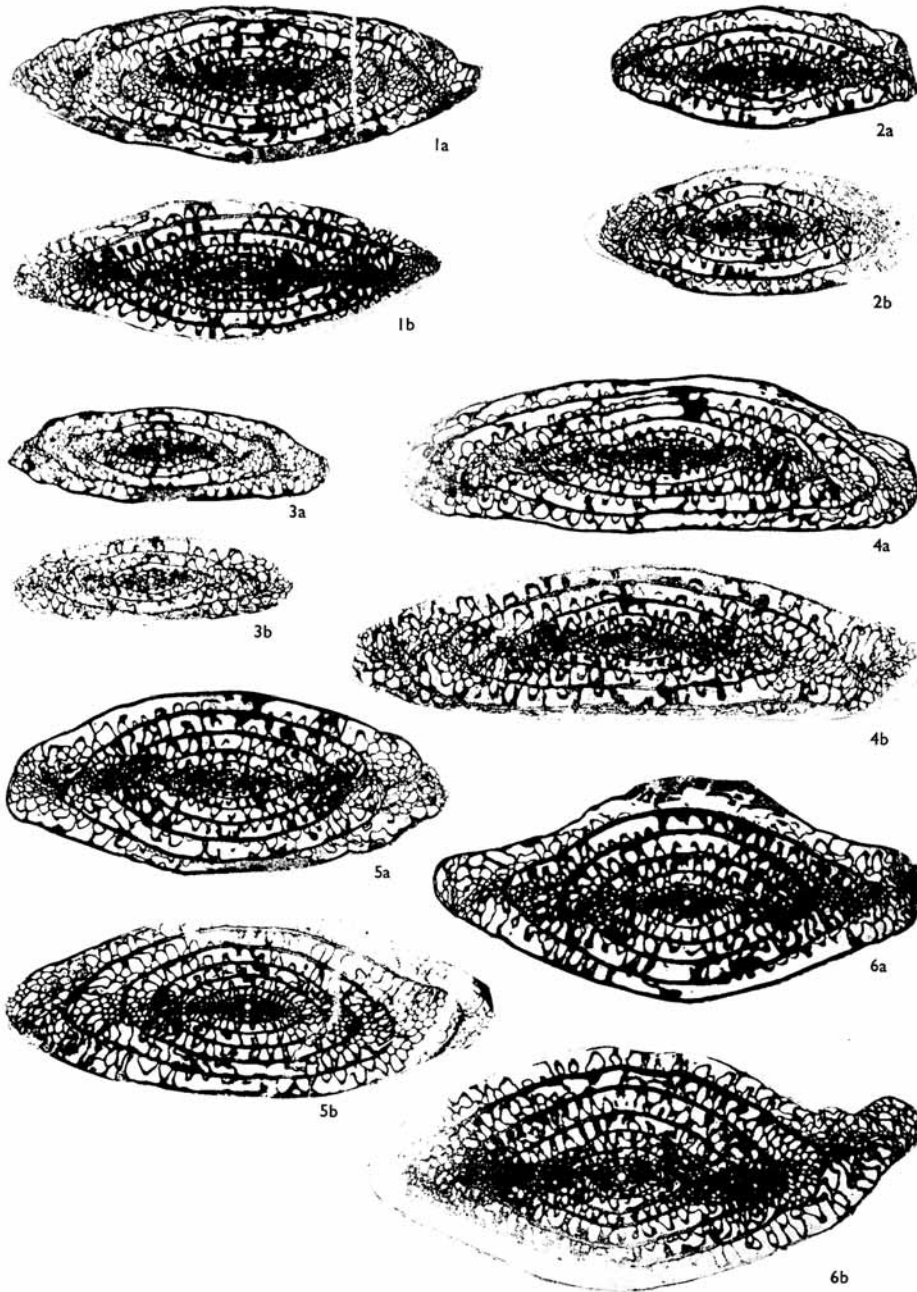
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