GRAPHICAL AIDS FOR THE DESCRIPTION AND ANALYSIS OF VARIATION IN FUSULINE FORAMINIFERA

by J. L. CUTBILL and C. L. FORBES

ABSTRACT. The method of comparing characters of fusuline tests at particular volutions is discussed. A proposed new method uses the growth relation between individual characters and the diameter; spiral form is described separately. The method is illustrated by a study of intraspecific variation in *Schwagerina anderssoni* (Schellwien) from the Lower Permian of Spitsbergen and by an analysis of spiral form in the type species of some genera in the *Schwagerina* and *Paraschwagerina–Pseudoschwagerina* complexes.

FUSULINE tests were formed by addition of elongated chambers in a tight, usually plane, spiral. Thus it is possible to reconstruct the shape of any early growth stage. On suitable sections measurements of the test can be made at different points in ontogeny. The usual practice is to tabulate these measurements for each volution of the spiral. Almost always variation in and between samples has been studied by comparing specimens at the same volution number. This procedure is misleading and in part responsible for the proliferation of taxa at the species level. The difficulty was pointed out quite clearly by Dunbar and Skinner (1937, p. 541), who said: 'In comparing statistical data for a series of specimens, a serious obstacle is presented by the fact that the shells commonly start with unequal proloculi. Truly microspheric forms begin with a small proloculum and pass through several early ontogenetic stages which are completely omitted in the megalospheric shells. The comparison of similarly numbered whorls in the two is, therefore, as indefensible in principle as it is futile in practice; there is no correspondence, even though both represent a single species.'

'A comparable, though far less serious discrepancy, appears to exist among the megalospheric shells of a single species in which the proloculi vary considerably in size.' And again (p. 543): 'It must be emphasized that when specimens of a single species have proloculi differing notably in size, statistical measurements for corresponding whorls will not agree. There should be general systematic correspondence, however, if we begin the comparison with later whorls of similar dimensions.' However, neither Dunbar and Skinner themselves nor any other author known to us has suggested a practical way of making such comparison other than by inspection of large tables of figures.

Roberts (*in* Newell *et al.* 1953) plotted values of half-length and radius for one species as a scatter diagram. This method eliminates the proloculum size from the relation of length to breadth, but is inadequate since information on the growth of individual tests is lost and no method of investigating the spiral was given. However, the procedures described here are a development of Roberts's ideas.

The problem occurs because fusulines seldom show structures indicative of maturity. Nor do they often possess sharply defined juvenile stages; there are no discrete growth stages at which comparisons can be made and no biological or geometrical reasons have been suggested for choosing the termination of particular volutions as datum points.

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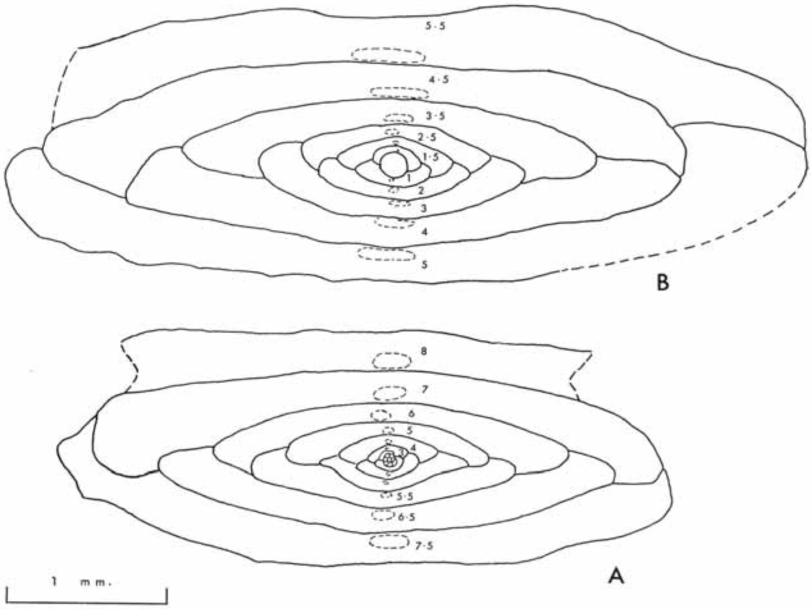
In sections containing the coiling axis there is the added complication that while the measurements can be made at precise intervals of a whole or half volution, the actual volution number from the first chamber can only be specified to the nearest half volution.

Any solution must deal adequately with the case shown in text-fig. 1. These two specimens have identical shape except that in A the very small proloculum and first 2·75

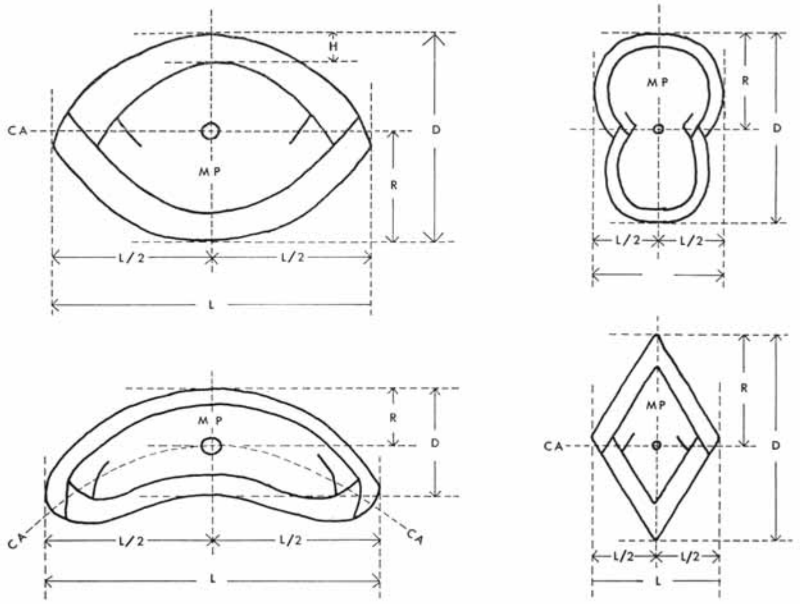


TEXT-FIG. 1. Drawings of microspheric (A) and macrospheric (B) specimens of *Schwagerina anderssoni* from sample G 1152. Only the outer wall and tunnel are shown; septal folds and other structures have been omitted.

volutions occupy the same space as the much larger proloculum of specimen B. If compared at the same volution number they seem to differ markedly in all characters which change during growth. For several specimens compared in this way the observed variation in a character at a particular volution arises from two geometrically, but not necessarily statistically, independent sources. First there is the difference in proloculum size which is equivalent to using an arbitrary origin for the volution scale. Secondly, there is the true variation in the character which may be entirely masked by the effect of the arbitrary origin. However, if one dimension, say diameter, is taken as a measure of size and each character is described by the growth relation between itself and the diameter, the true variation is displayed. The shape of the spiral must be described separately by a method unaffected by the arbitrary origin of the volution scale.

TERMINOLOGY

Operational definitions of the dimensions discussed here are shown in text-fig. 2. The *spiral* is the line connecting points on the outer wall in the plane of symmetry or median plane of each chamber. It is usually but not always a plane figure. The *radius* is the distance from the centre of the proloculum to the spiral. The *diameter* is the distance from the spiral through the centre of the proloculum to a point on the opposite side of the test. This last point will also be on the spiral if it is plane. *Chamber-height* is measured along the radius. *Chamber-length* is the distance between the ends of the chamber measured perpendicular to its plane of symmetry. It is divided into two *half-lengths* measured from a plane through the centre of the proloculum parallel to the plane of symmetry.

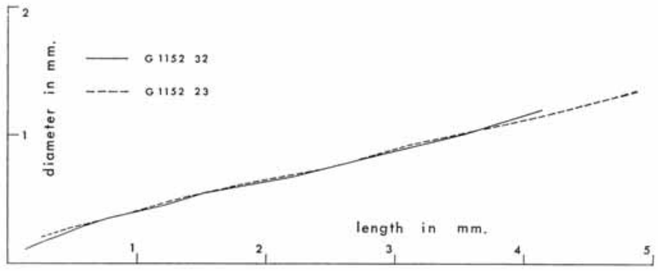


TEXT-FIG. 2. Operational definitions of morphological terms for various shapes of test: diameter (D), radius (R), chamber-height (H), length (L), half-length (L/2), median plane (MP), coiling axis (CA).

Diameter rather than radius is used here as the principal dimension. It may not be easy to locate the reference point for the inner end of the radius vector; the proloculum may not coincide with the geometrical centre of the spiral, and may not even be spherical. However, neither factor introduces significant errors into a measurement of diameter. It has been claimed that radius is easier to measure than diameter, but if data must be compatible with all published usages, measurements of diameter, radius, chamber-height, and length must be taken every half volution.

GROWTH RELATION BETWEEN LENGTH AND DIAMETER

For a single specimen this can be described by plotting values of length and diameter at every half volution and joining the points. Specimens can be compared by superimposing the resulting curves. This is illustrated in text-fig. 3 for the two specimens shown in text-fig. 1. If several curves are superimposed the plot shows both the range of variation and the relation of individual curves to it, as well as providing a good visual aid for assessing sample homogeneity (e.g. text-fig. 10). Different samples can be compared by superimposing their plots and the range of variation finally allowed in a taxon



TEXT-FIG. 3. Length–diameter curves for specimens illustrated in text-fig. 1.

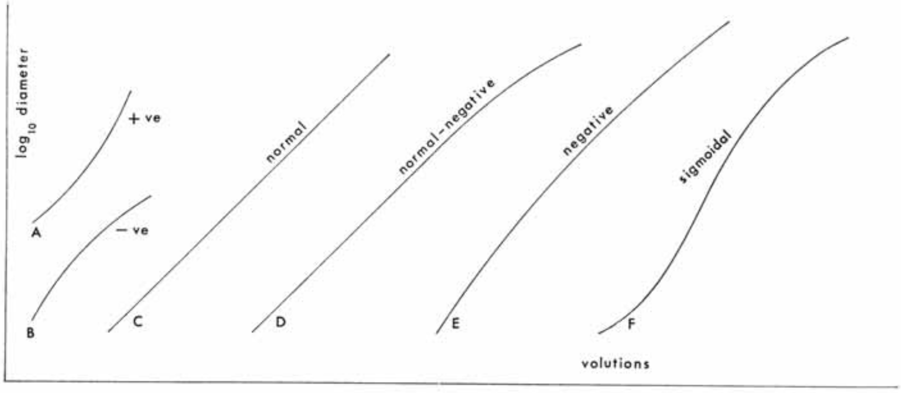
can be shown by an envelope. If too many curves are included in one plot, relationships may be obscured. But the method is adequate for samples with less than twenty-five individuals. It may also be used for characters other than length.

SPIRAL FORM

The data available for describing and comparing spirals are the measurements of diameter, radius, and chamber-height made at half volution intervals starting from an arbitrary origin. Burma (1942) pointed out that as the fusuline spiral is often almost equiangular a simplification is obtained by plotting its dimensions on a logarithmic scale. If the graph of diameter against volution interval is a straight line the rate of increase in diameter per volution is directly proportional to the diameter itself and the spiral is equiangular. But there is no reason to assume that the growth of fusuline spirals will follow one mathematical model rather than another, and it is desirable that descriptive and comparative procedures should not assume a particular model. For this reason mathematical expressions for spirals are not discussed or used here.

The spiral of a single specimen may be described by plotting diameter on a logarithmic scale against volution interval on an arithmetic scale and joining the points. The tightness of coiling or *spiral parameter* at any diameter is defined as the slope of the curve at that diameter. This may vary with growth and its changes form a basis for qualitative description of spiral form. During growth the spiral parameter may remain constant (*normal spiral*), increase (*positive spiral*), or decrease (*negative spiral*) (text-fig. 4A–C). Four spiral types, made up from combinations of these three simple forms, account for most of the variation present in fusulines. These are normal, normal–negative, negative, and sigmoidal (text-fig. 4C–F). Spirals positive throughout growth have not yet been found.

As the shape of these curves does not vary with shifts of origin of the volution scale, spiral parameters of two or more spirals may be compared at a particular diameter by making the curves pass through one point at that diameter. This is illustrated in text-fig. 5A for the two specimens shown in text-fig. 1. In text-fig. 7 the curves from one sample are superimposed at different diameters. These plots may be thought of as showing either the variation in the number of volutions taken for a given increase in diameter, or



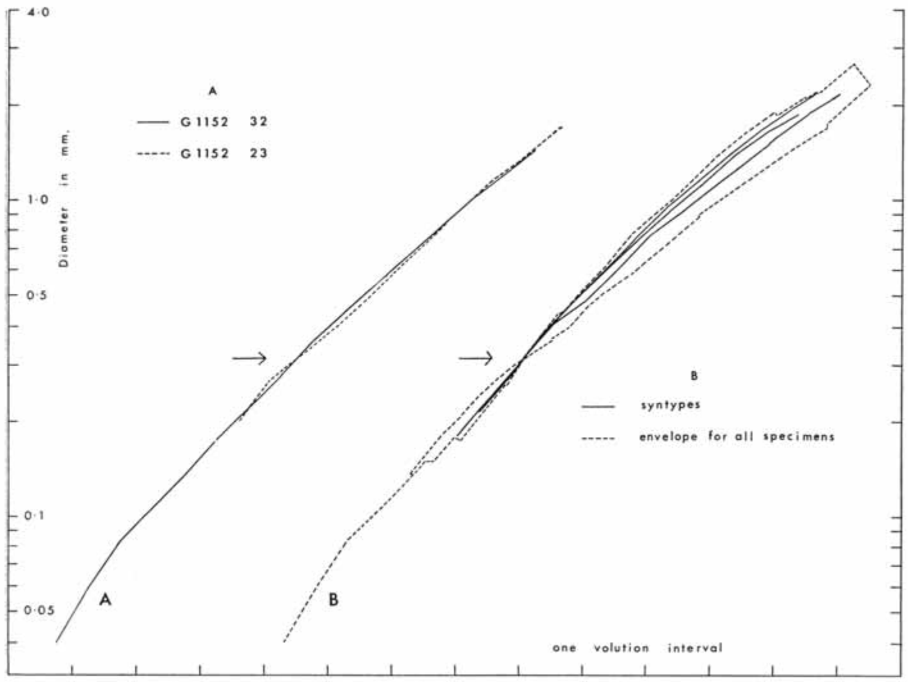
TEXT-FIG. 4. Types of spiral curve.

as the variation in increase of diameter in a given number of volutions. It is usually sufficient to make one plot for each sample, using as a datum the smallest diameter within the range of all specimens involved. It is only meaningful to compare spirals over their common range of diameters.

For non-planar spirals volution interval has no simple meaning and an alternative method is necessary. One way is to plot chamber-height against diameter, both on arithmetic scales. The change in direction of coiling must be described separately but a satisfactory method has yet to be found. Chamber-height curves are also useful for plane spirals and are equivalent to plotting rate of increase in diameter against diameter. A straight line indicates an equiangular spiral. The method tends to emphasize small growth irregularities, but spirals whose chamber-height is constant or decreases in later volutions are explicitly displayed. Both these types appear only as negative spirals in diameter volution plots. Examples of the chamber-height curves are shown in text-fig. 9.

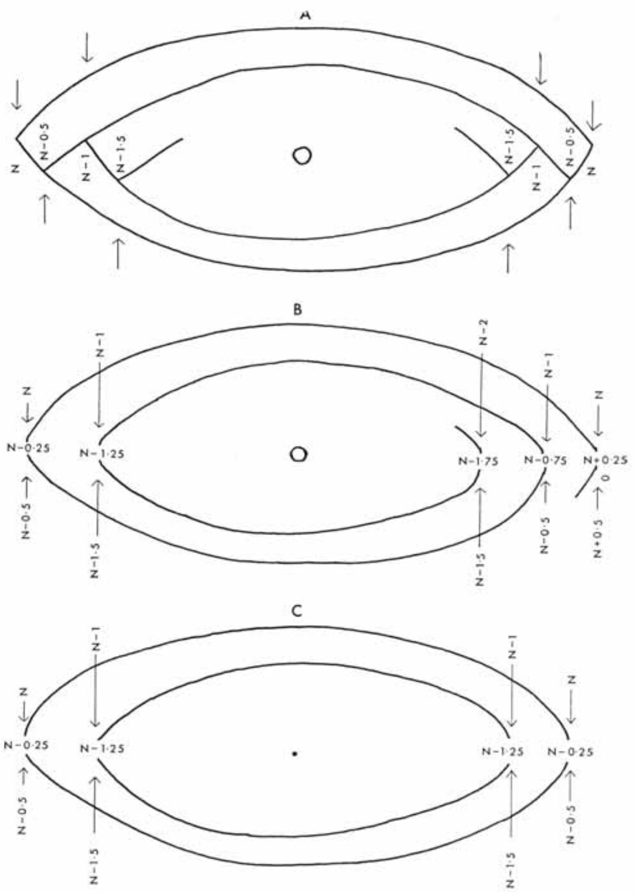
MEASUREMENT ERRORS

Because of slight irregularities in growth and symmetry, sections with all chambers perfectly orientated are rare and the measurement recorded is often not that actually sought. The extent of such errors is difficult to estimate without serial sectioning, but is probably not large. In centred sections measurements on diameter are free from these errors. In a section tangential to the proloculum it is sufficient to reject measurements on the first two volutions, the difference between observed and true diameters being small in subsequent volutions. In sections containing the coiling axis the continuity of the outer wall is broken at the ends of the chambers and thus each half volution appears separated (text-figs. 1 and 6A). If the section is poorly orientated the outer wall appears



TEXT-FIG. 5. Spiral curves of A, specimens illustrated in text-fig. 1 and B, Schellwien's syntypes of *S. anderssoni* from measurements made on photographs in Staff and Wedekind (1910).

either as a series of closed curves or as a spiral (text-fig. 6B and C). It is usual to reject any specimen in which the outer wall does not show at least a slight break at the ends. In the limiting case the points of actual measurement of the length at two succeeding half volutions coincide so that what is actually measured is the length at the intervening quarter volution. From text-fig. 6B it can be seen that in oblique but centred sections errors in length are almost self-cancelling. For sections parallel to the coiling axis but just uncentred the errors are not self-cancelling and values alternately too high and too low will be obtained. However, a smoothed curve from these values will approximate closely the growth relation.

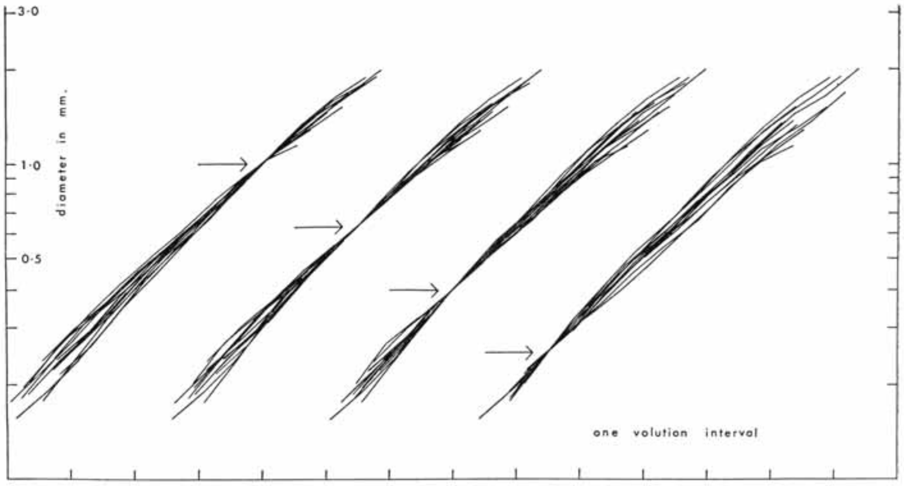


TEXT-FIG. 6. Results of poor orientation on measurements.

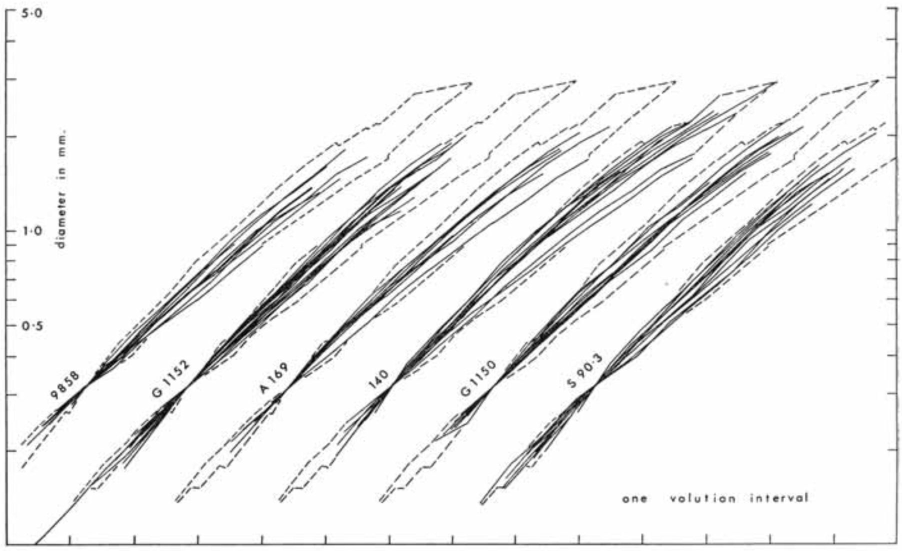
INTRASPECIFIC VARIATION IN *SCHWAGERINA ANDERSSONI* (SCHELLWIEN)

S. anderssoni has an ovate test with regular septal folds, variably developed low cuniculi, and moderate to strong epitheca usually represented by axial deposits. It is common in the lower part of the Permian of Vestspitsbergen (Cutbill and Challinor 1965). Sufficient individuals from six samples are available in Cambridge for analysis:

Sample 140	Brucebyen beds; Teltfjellet, north side.
9858	Brucebyen beds; Tyrrellfjellet, north side.
A 169	Tyrrelfjellet member, 8 m. above top of Brucebyen beds; Trollfuglefjellet, north-east ridge.



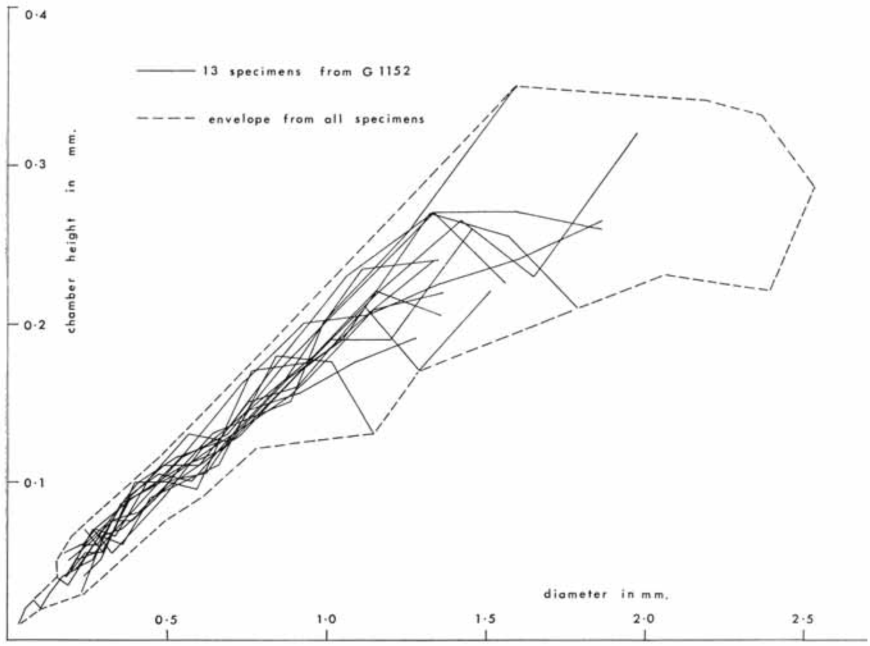
TEXT-FIG. 7. Spiral curves of specimens of *S. anderssoni* from sample G 1152 superimposed at several different diameters (13 specimens).



TEXT-FIG. 8. *S. anderssoni*. Total variation envelope and spiral curves for samples 9858 (8 specimens), G 1152 (13), A 169 (8), 140 (12), G 1150 (8), S 90.3 (12).

G 1150 Brucebyen beds, 1·6 m. below top; Teltfjellet, north side.
G 1152 0·6 m. above G 1150.
S 90.3 Brucebyen beds; Teltfjellet, north side.

One of us (Forbes 1960) described individuals from sample 140 as *S. anderssoni* and from S 90.3 with greater length diameter ratios as *S.* cf. *anderssoni*, a conclusion which is rejected in the light of additional data now available.

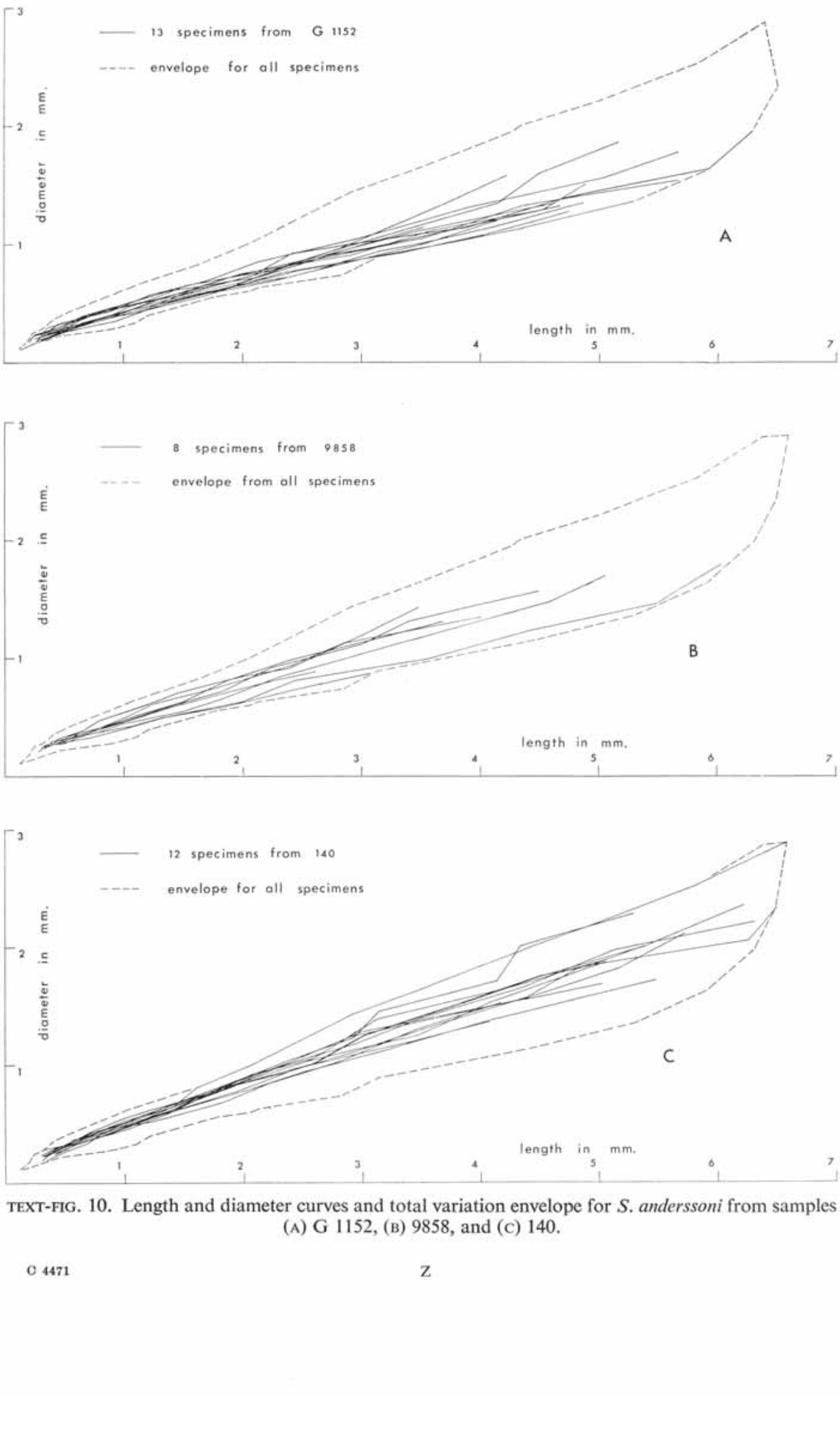


TEXT-FIG. 9. Chamber-height and diameter curves for specimens of *S. anderssoni* from sample G 1152, and envelope of total variation for all six samples.

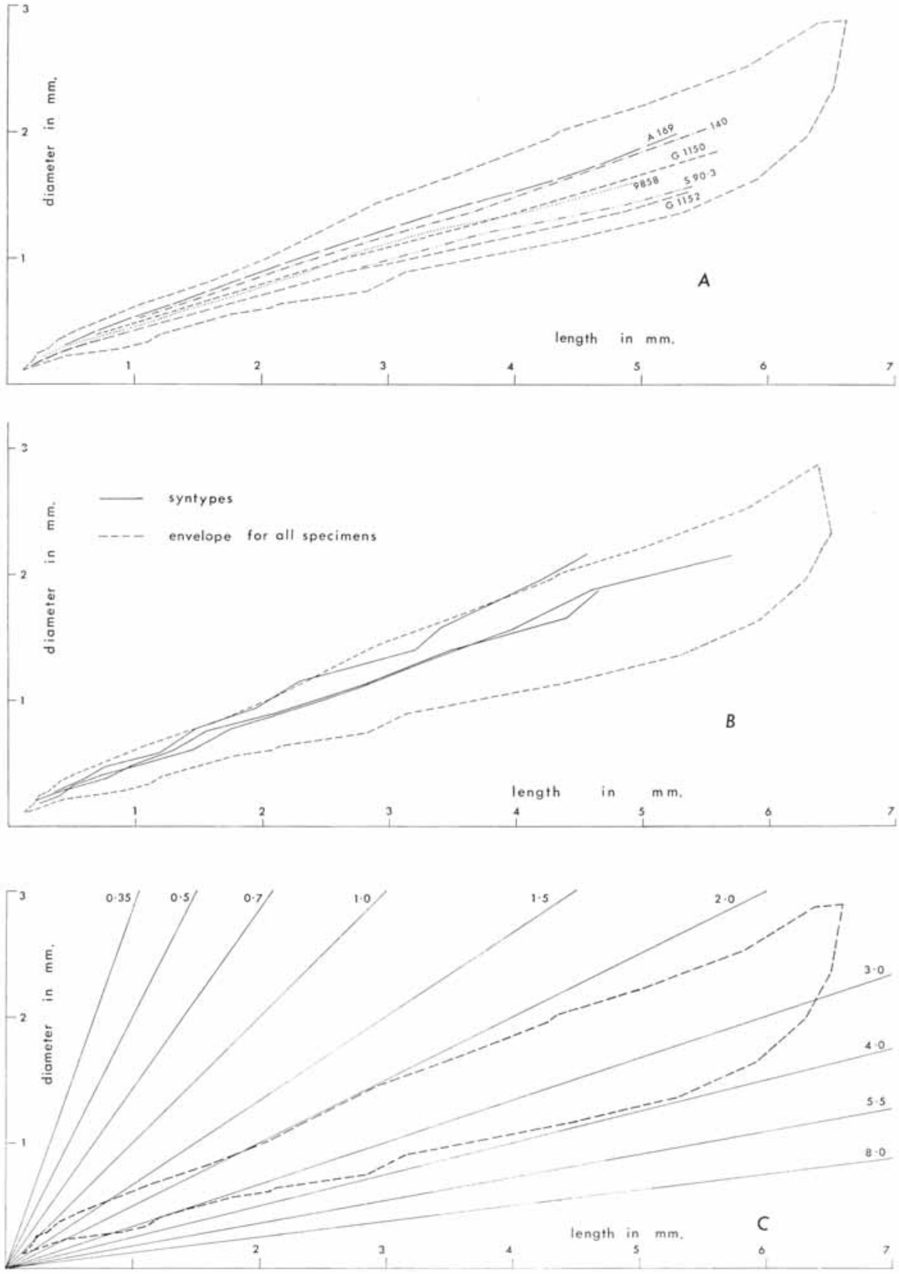
Text-fig. 7 shows the spiral curves from G 1152 superimposed at four different diameters. Text-fig. 8 shows the plots from all six samples and the envelope of total variation. The distributions are slightly skewed towards the upper part of the range and there are slight but not significant differences between samples. It is concluded that the spiral form is the same in each fossil population. Text-fig. 5B shows the curves for Schellwien's syntypes and text-fig. 9 shows a chamber-height and diameter plot for sample G 1152 and total variation envelope for all six samples. These confirm both the similarities of the spirals and the identification.

Text-fig. 10 shows plots of length and diameter for three of the samples, and text-fig. 11A the median for all six. Plots of Schellwien's syntypes are shown in text-fig. 11B and the total variation envelope and lines of equal length–diameter ratio in text-fig. 11C.

Most of the curves fall in the lower three-quarters of the total variation envelope. On



TEXT-FIG. 10. Length and diameter curves and total variation envelope for *S. anderssoni* from samples (A) G 1152, (B) 9858, and (C) 140.



TEXT-FIG. 11. *S. anderssoni*. Total variation envelope and (A) median length–diameter curves for six samples; (B) length–diameter curves for Schellwien's syntypes measured on photographs in Staff and Wedekind (1910); and (C) lines of equal length–diameter ratio.

re-examination those in the upper quarter proved to be poorly orientated. With more critical selection they would have been rejected before measurement, and the true range of variation should not include this upper quarter. However, the specimens have been retained in the plots as they are no worse orientated than the holotypes of many species.

Significant differences between some pairs of samples are present. The plots for G 1152 and 140 show almost no overlap, but the other samples provide a complete range of intermediates between them. Since the samples show no difference in other characters and since there is no evidence that the variation is related to stratigraphical or geographical position, the individuals are retained in one species and the variation is considered as intraspecific.

The high variability of growth relations found in the present study suggests that length–diameter ratios may have been over-emphasized in some taxonomic studies.

SPIRAL FORM IN THE *SCHWAGERINA* AND *PARASCHWAGERINA–PSEUDOSCHWAGERINA* COMPLEXES

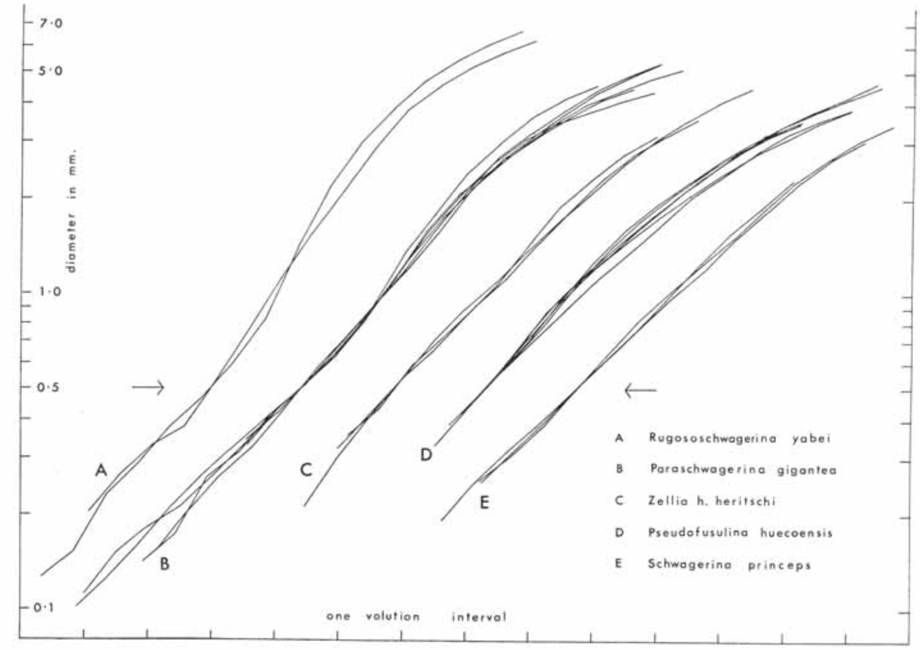
In these groups spiral form plays an important part in the existing classification, which is based on the work of Dunbar and Skinner (1936). They established the true structure of *S. princeps* (Ehrenberg), type species of *Schwagerina* Moeller, and included in that genus forms with uniformly expanding spirals and regular septal folds. They introduced two new genera, *Pseudoschwagerina*, type species *P. uddeni* (Beede and Kniker), and *Paraschwagerina*, type species *P. gigantea* (White). *Pseudoschwagerina* included forms with a tightly coiled spiral in the early stages, rapidly expanding in the middle and becoming tighter in the final stages, and having loose and irregular septal folds. *Paraschwagerina* included forms with a spiral similar to *Pseudoschwagerina* but with regular septal folds as in *Schwagerina*. The genus *Pseudofusulina* Dunbar and Skinner, type species *P. huecoensis* Dunbar and Skinner, was considered a synonym of *Schwagerina*.

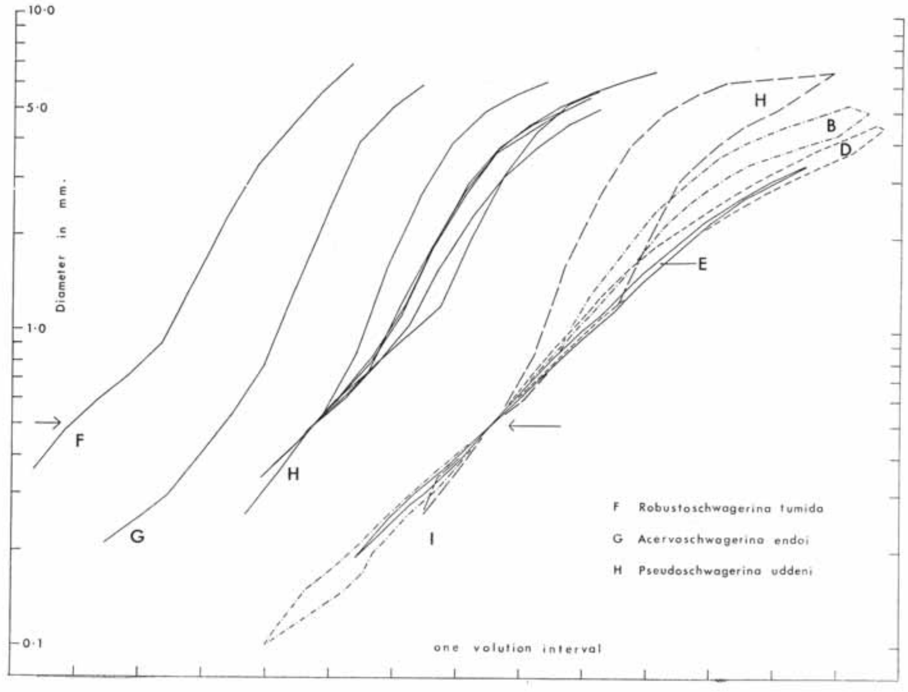
In the 'Treatise on Invertebrate Paleontology' (C) four other genera in the *Pseudoschwagerina–Paraschwagerina* complex are recognized: *Robustoschwagerina* Miklukho-Maklay, type species *O. abichi* Miklukho-Maklay, *Zellia* Kahler and Kahler, type species *Pseudoschwagerina* (*Zellia*) *heritschi* var. *heritschi* Kahler and Kahler, *Rugososchwagerina* Miklukho-Maklay, type species *Schwagerina yabei* Staff, and *Acervoschwagerina* Hanzawa, type species *A. endoi* Hanzawa. *Pseudofusulina* is also recognized as distinct from *Schwagerina*.

Text-fig. 12A–H shows the spiral plots for topotype specimens of the type species of the eight genera; text-fig. 12I shows the envelopes of variation in the types of *Schwagerina*, *Pseudofusulina*, *Paraschwagerina*, and *Pseudoschwagerina*; and text-fig. 13 shows the envelopes for plots of chamber-height and diameter for the same four genera.

The spiral types and proloculum sizes are as follows:

Schwagerina, normal-negative, medium proloculum
Pseudofusulina, negative, large proloculum
Zellia, negative, perhaps just sigmoidal, medium to large proloculum
Paraschwagerina, moderately sigmoidal, small proloculum
Rugososchwagerina, strongly sigmoidal, small proloculum
Pseudoschwagerina, strongly sigmoidal, large proloculum
Acervoschwagerina, strongly sigmoidal, medium proloculum
Robustoschwagerina, strongly sigmoidal, large proloculum.


7·0
5·0
1·0
0·5
0·1
diameter in mm.
one volution interval
A
B
C
D
E
A Rugososchwagerina yabei
B Paraschwagerina gigantea
C Zellia h. heritschi
D Pseudofusulina huecoensis
E Schwagerina princeps


10·0
5·0
1·0
0·1
Diameter in mm.
one volution interval
F
G
H
I
B
D
E
F Robustoschwagerina tumida
G Acervoschwagerina endoi
H Pseudoschwagerina uddeni

There is a morphological series of spiral form from negative in *Pseudofusulina* through *Schwagerina*, *Zellia*, and *Paraschwagerina* to strongly sigmoidal in the pseudoschwagerinid genera. Except in these very sigmoidal types there is no sharply defined juvenile stage. Up to a diameter of about 0·5 to 0·6 mm. there is almost no difference in the spiral parameters of the eight species. In particular the so-called 'tightly coiled' juvenaria of *Paraschwagerina* and *Robustoschwagerina* are not more tightly coiled than the early stages of *Schwagerina*, but simply smaller. The maximum value of the spiral parameter is reached between diameters of 0·8 and 1·5 mm. in the sigmoidal spirals. This contrasts with the maximum chamber-height which is reached much later.

It is concluded that while in these complexes the spiral form is a potentially useful character at generic level it does not, by itself, provide an adequate means for subdivision. Because of the wide intraspecific variation it is not likely to be a useful specific character.

DESCRIPTIVE PROCEDURES

The following procedures for routine taxonomic work on fusulines are suggested:

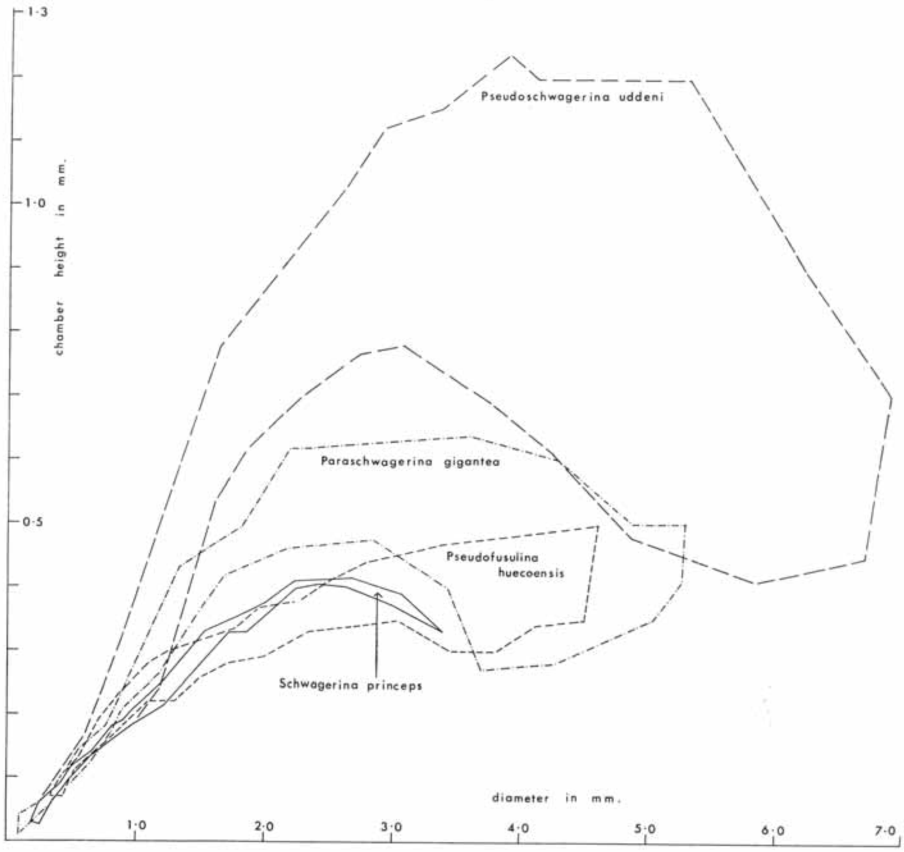
1. Measurements of radius, diameter, chamber-height, length, and other characters should be made at every half volution on at least twenty specimens from every sample.

2. Plots should be made for each sample of the growth relations between diameter and length, as well as other characters such as tunnel width, protheca thickness, and septal separation. A convenient plotting scale for length and diameter of medium-sized fusulines is 1 mm. = 50 mm. with reduction to 1 mm. = 20 mm. for publication.

3. Plots of spiral form should be made for each sample. Convenient scales for all fusulines are 1 volution equal to 20 mm. and an interval of 1·0 on the logarithmic scale for diameters equal to 100 mm. with reduction by one-half for publication. Common points should be at values of log (D) equal to −1·0, −0·9, −0·8, etc.

4. As many plots as possible should be published in preference to tables of measurements, which are much less informative. However, at least one measurement for each figured specimen should be given as a check on stated magnification. Tables of measurements could usefully be deposited with the specimens. It is important to state the number of specimens used in each plot.

TEXT-FIG. 12. Spiral curves for topotype specimens of the type species of eight genera (A–H) and total variation envelopes for four of them (I). Most of the measurements were made on photographs from the following sources: 'Treatise on Invertebrate Paleontology', Part C, Protista 2 (1964), *R. yabei*, *R. tumida*, and *A. endoi*; Dunbar and Skinner (1937), *P. gigantea*, *P. huecoensis*, and *P. uddeni*; Ross (1963), *P. gigantea*, *P. uddeni*; Williams (1963), *P. huecoensis*; Kahler and Kahler (1937), *Z. h. heritschi*. Diameters of *S. princeps* and early stages of one specimen of *P. gigantea* were obtained by interpolating from figures given by Dunbar and Skinner (1936, 1937).



TEXT-FIG. 13. Total variation envelopes for chamber-height and diameter curves of topotype specimens of the type species of four genera.

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