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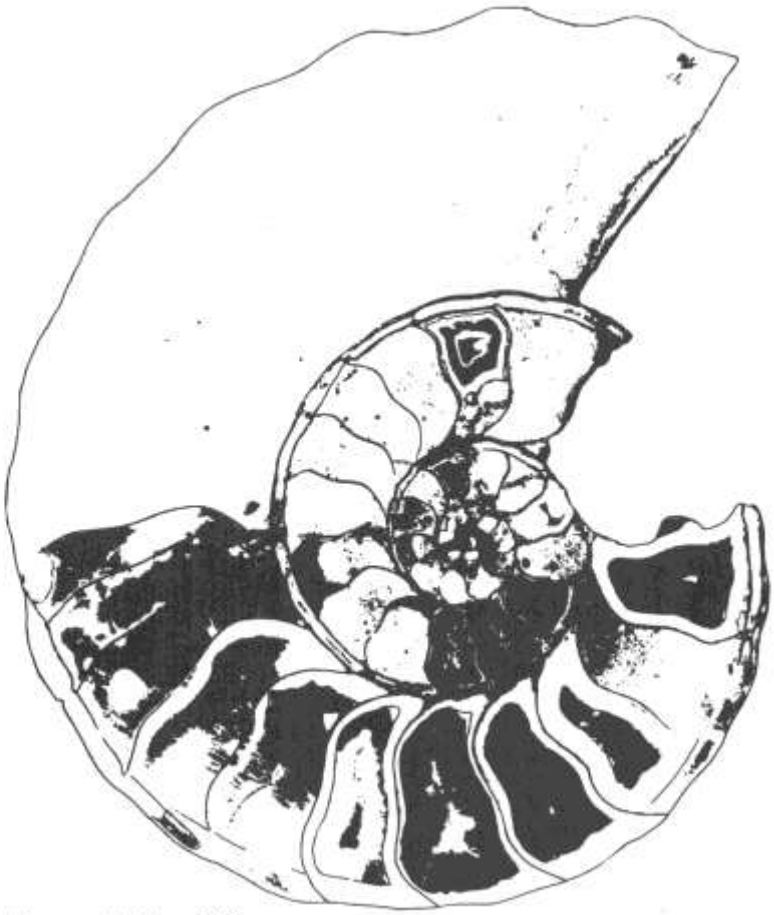

Metoicoceras gibbosum Hyatt, × 0.68
see p. iv

New Mexico Bureau of Mines & Mineral Resources

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NEW MEXICO INSTITUTE OF MINING & TECHNOLOGY

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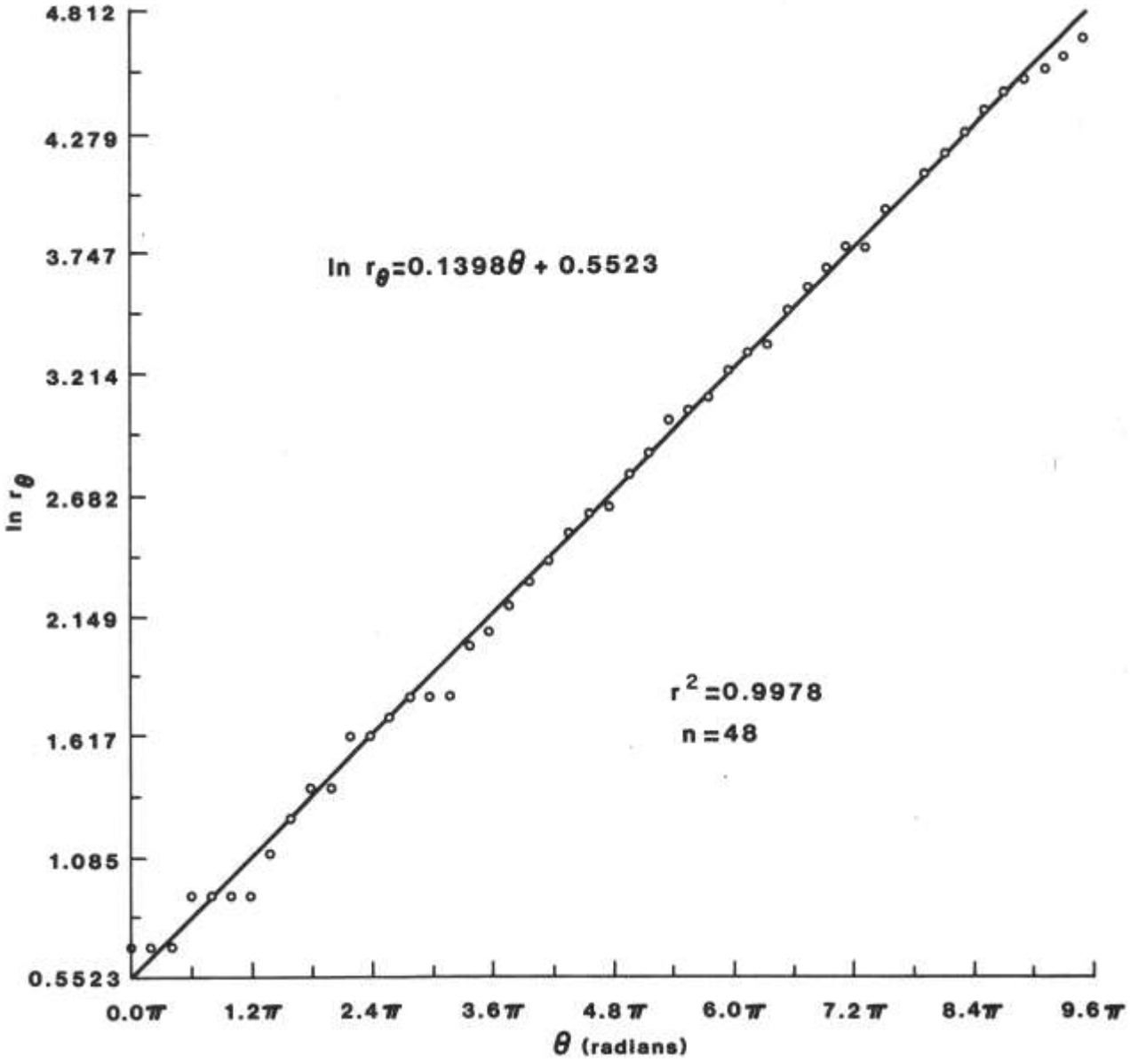

COVER ILLUSTRATION AND GRAPH—High-contrast photoline reproduction of a median longitudinal section through the Upper Cretaceous ammonite *Metoicoceras gibbosum* Hyatt, x 0.68. Radii (re) were measured to the nearest 0.5 mm at 0.2n radian intervals. The natural logarithms of the radii On re) were then plotted against the cumulative angle *(0).* A simple linear regression performed on these data resulted in a slope of 0.1398, an intercept of 0.5523, and a correlation coefficient squared (r^2) of 0.9978. The slope of the line represents the whorl expansion rate of the specimen; the intercept is the initial coiling radius of the specimen; and the correlation coefficient indicates that the linear relationship explains at least 99.78 percent of the observed variability in the data. (The cover photo is by Bradley House.)

Abstract

A statistical method for evaluating and comparing planispiral growth patterns among invertebrates is presented. This method is predicated on simple logarithmic growth and employs simple and multiple linear regression combined with analysis of variance and covariance techniques. The method is first discussed in general terms and then is used to study planispiral growth in two Ordovician nautiloid genera, *Plectolites* Flower and *Litoceras* Hyatt. The analysis of coiling in these two genera indicates that the coiling angle (or whorl expansion rate) of the shell alone is a sufficient criterion by which to distinguish one from the other. Preliminary results indicate that this method can also be applied to fusulinids and ammonoids and, presumably, to other planispirally coiled invertebrates.

Introduction

In this paper we present a general statistical model for comparing and studying growth patterns in planispirally coiled invertebrate species. We then use this general model to study and evaluate growth patterns in several specimens belonging to two genera of fossil nautiloids. The statistical methods are predicated on simple logarithmic growth of the shells.

Planispiral coiling among shelled invertebrate species is a rather widespread phenomenon; it occurs in such diverse taxonomic groups as the Foraminifera, Brachiopoda, Gastropoda, and Cephalopoda. Although shell coiling developed independently in these distinct lineages and differences in coiling form and functional significance are readily noted, most types of planispiral coiling have enough geometric characteristics in common to make rigorous comparisons both between and within groups possible (Raup, 1966).

The problem of defining these geometric parameters is well documented in the literature (Moseley, 1838; Thompson, 1942; Raup, 1966, 1967; Raup and Michelson, 1965). As a result of these studies, shell growth among the majority of planispirally coiled invertebrate species has been shown to be variations on a single mathematical model, the logarithmic or equiangular spiral (Thompson, 1942; Raup, 1966). Several different logarithmic models have been proposed for analyzing planispiral growth. Of the two most widely used models (Moseley, 1838; Raup and Michelson, 1965), we have chosen to use Moseley's simple logarithmic model, as explained by Thompson (1942, p. 789).

The simple logarithmic or equiangular spiral is a curve with the property that the angle, a , between the radius vector and the tangent vector is constant (fig. 1). From this property alone the relationship between the radius vector, *r(0)* at angle *0*, and a can be immediately derived. Referring to fig. 1:

$$\text{ctn}\,\alpha = \text{cotangent}\,\alpha = \frac{ar}{rd\theta}$$

$$\ell n\, r(\theta) = \theta \text{ctn}\,\alpha + C \qquad (1)$$

where: C is a constant
θ is the angle in radians
$r(\theta)$ is the radius vector at θ (units arbitrary).

Although we will usually use the equation in the form of (1), note that

$$r(\theta) = C e^{\theta \text{ctn}\alpha} \qquad (2)$$

Hence, C = r(0) is the initial coiling radius at 0 = 0 radians. The angle 0 is the total angular measurement; therefore, each complete revolution of the shell adds 2n radians to *0*. Note that the shell diameter, *d(0),* can be

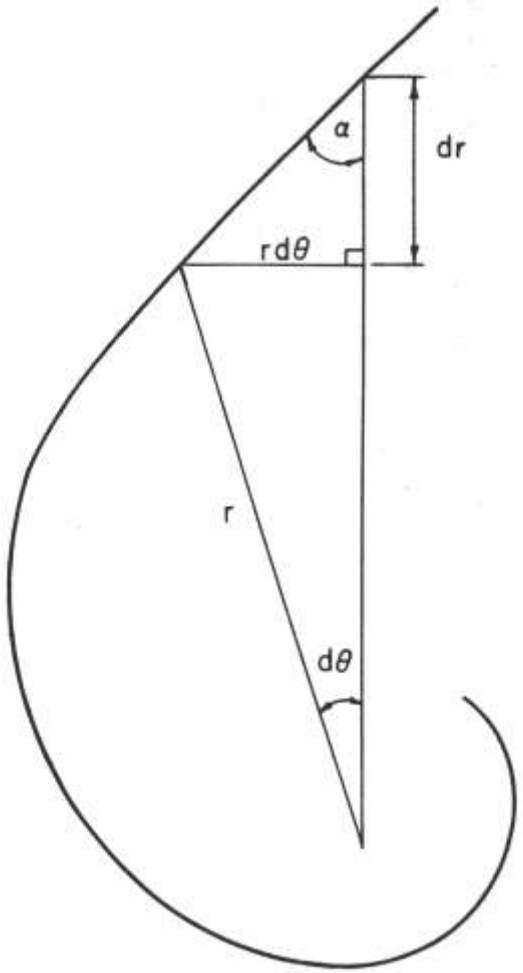

FIGURE 1—SCHEMATIC DIAGRAM OF AN EQUIANGULAR SPIRAL SHOWING THE RELATIONSHIP BETWEEN THE RADIUS (r), ANGLE (θ), AND THE CONSTANT ANGLE OF THE SPIRAL, α (Thompson, 1942).

substituted for the shell radius, r(9), without changing the basic equation (1) or (2). (See fig. 2A.)

In Raup's (1967) analysis of planispiral coiling in ammonoids, he used the logarithmic model of Raup and Michelson (1965). In this model, three summary parameters (W—whorl expansion rate; *D—relative* distance between generating curve and axis of coiling; S—shape of generating curve) are used to geometrically define planispiral coiling. Fig. 2B is reproduced from Raup (1967) and shows how his parameters are theoretically obtained. Although fig. 2B shows the measurements as being made from a cross section of an ammonoid, the actual measurements were made from lateral views in the ammonoid volume of the *Treatise on Invertebrate Paleontology* (Moore, 1957) and, therefore, only present a picture of mature or last-whorl growth and do not account for any ontogenetic variation in growth pattern. Raup's parameters are also difficult to interpret directly in terms of shell morphology.

Raup (1967) does briefly discuss ontogenetic variation in relation to his parameters. He uses one specimen of *Paracravenoceras ozarkense* Gordon as an example; Raup and Chamberlain (1967) also briefly discuss ontogenetic variation in relation to W, and in their fig. 2 fit several best-fit lines at different growth stages to a plot of ln *r(*q*)* versus q for a specimen of *Hammatoceras insigne* (Zeiten). Care must be taken so that false ontogenetic variation is not introduced by the model or the experimenter. In the case of *Hammotoceras insigne*, the ontogenetic variation is sinusoidal about the best-fit line for the entire growth of the shell. Our research using the simple logarithmic model indicates that this sinusoidal variation may well be an artifact introduced by the experimenter.

We have chosen Moseley's simple logarithmic model over the logarithmic model of Raup and Michelson because: 1) The parameters used can easily be interpreted in terms of shell morphology (the slope of the best-fit line represents the whorl expansion rate; the arc-cotangent of the slope yields the constant angle of the spiral, **a,** and the intercept yields the initial coiling radius or diameter. 2) The model is linear in terms of these parameters and, therefore, can more easily be treated by rigorous statistical methods and can be used to make comparisons within and between groups. 3) The simple model allows us to account for ontogenetic variations and to study it in greater detail. 4) The simple logarithmic model can be applied to partial and/or broken shells (Thompson, 1942).

ACKNOWLEDGMENTS—We are indebted to Rousseau H. Flower, Senior Emeritus Paleontologist, New Mexico Bureau of Mines and Mineral Resources, for suggesting the project and making his extensive nautiloid collection available to us. The New Mexico Bureau of Mines and Mineral Resources and the Department of Mathematics at New Mexico Institute of Mining and Technology provided computer time.

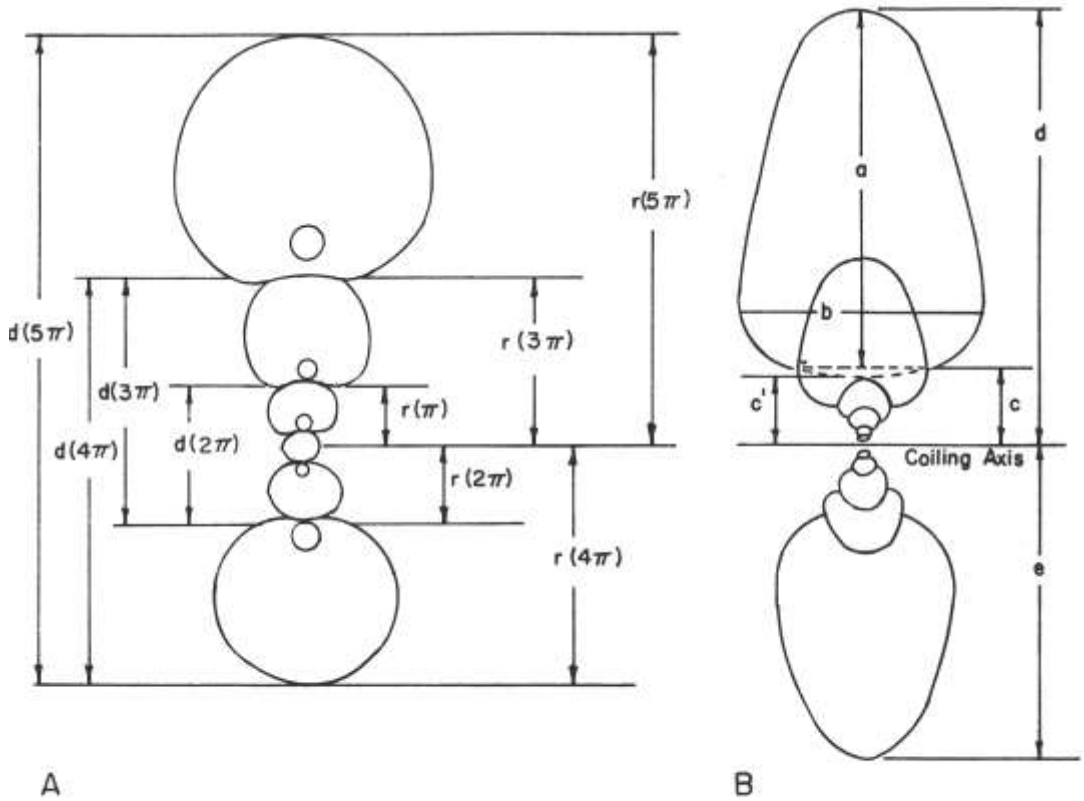

FIGURE 2—LINEAR DIMENSIONS MEASURED FOR THIS STUDY COMPARED WITH THOSE USED BY RAUP (1967). **A)** Cross section of *Plectolites* n.sp.1, X2; **B)** cross section from Raup (1967, fig. 1) showing measurements used to calculate $W = (d/e)^{1}$, $D = (c/d)$, and $S = (b/a)$.

Methods

In the application of the simple logarithmic model to specific samples we need to estimate the unknown constants *C* and ctn a in equation (1). We use simple linear regression to do this for any particular specimen. However, comparing the parameters obtained from different specimens within a genus and making such comparisons between genera is also of interest. To do this, we use a technique known as analysis of covariance. Rather than take the conventional viewpoint whereby analysis of covariance extends analysis of variance (Dunn and Clark, 1974), we look at analysis of covariance as a special case of multiple regression (Draper and Smith, 1966).

Our underlying model equation throughout is of the form

$$Y_{ijk} = \mu_i + \alpha_{ij} + \beta_{ij} X_{ijk} + \epsilon_{ijk}, \quad 1 \le i \le I,\ 1 \le j \le J_i,\ 1 \le k \le K_{ij} \qquad (3)$$

where Y_{ijk} represents the natural logarithm of the radius of specimen *j* within genus *i* at angle X_{ijk} (or, equivalently, at whorl *k).* In this equation m_i represents the intercept for genus *i;* a_{ij} represents the deviation from the genus intercept for specimen, *j* (note $\sum_{j=1}^{J_i} \alpha_{ij} = 0$); b_{ij} is the slope for specimen *j* within genus *i;* and e_{ijk}, is an error term (usually assumed to be a normal random variable with mean 0 and variance 0^2).

In the most general form of the equation (3), we have enough flexibility to permit a different line for each specimen. One might obtain individual lines of the general form indicated in fig. 3A, where for purposes of illustration we suppose we have two genera, each with two specimens.

First we can test whether the lines within each genus have the same slope, that is, whether the deviation from a common slope shown in fig. 3A is due to chance alone. The hypothesis is that. $b_{ij} = b_{il} = b_i$, for all *j* and *l*. We can introduce this restriction into equation (3) to estimate the common slope b_i, and we can then carry out a statistical test to see if this restricted model can be applied. If we can accept a common slope model for each genus, we are now faced with lines of the form indicated in fig. 3B.

We can also test whether the intercepts are all the same within a genus; that is, we can see if we can accept the conclusion that au = 0 for *j* =1, ..., J_i. Once again we can introduce this restriction into equation (3) and see if the conclusion that au = 0 is warranted. If this conclusion is correct for both genera, we have a single line for each genus, each with a different slope and a different intercept (fig. 3C).

Finally, we can see whether the two lines for the genera have the same slopes and/or intercepts, once again by introducing corresponding restrictions into equation (3). We can reject the equal intercept model within each group and still test the equal slope model between genera.

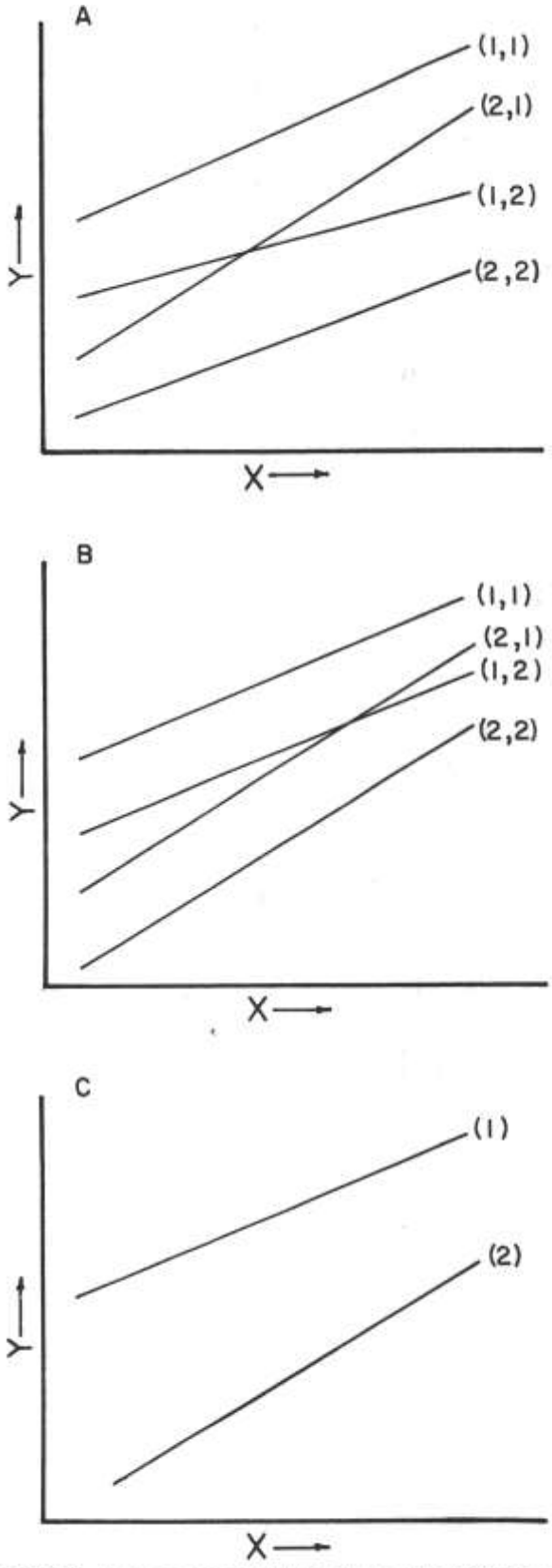

FIGURE 3—ILLUSTRATION OF POSSIBLE LINEAR RELATIONSHIPS THAT CAN ARISE IN ANALYSIS OF COVARIANCE MODELS. A) Slopes and intercepts differ in both groups; B) slopes within groups are the same, intercepts differ; C) slopes within groups are the same, and intercepts within groups are the same.

To carry out these statistical tests, we use ANOVA (analysis of variance) tables associated with general regression models. The approach is to combine the restricted and unrestricted ANOVA tables, rather than to carry out the usual calculations alluded to in discussions of analysis of covariance (Dunn and Clark, 1974). The former approach is especially fruitful if one has access to standard multiple-regression computer programs.

To see how the tests are carried out, we first fit the unrestricted model to get ANOVA table 1A.

If we have one genus only with, for example, *J* specimens and *K1* measurements for specimen *j*, then $N = \sum_{j=1}^{J} K_j$, and $M_1 = 2J-1$ assuming a simple linear model for each specimen.

If we introduce *p* independent restrictions, we get a restricted model and associated ANOVA table 1B.

If, as above, we have one genus with *J* specimens and we want to test the equality of the *J* slopes, we get J-1 independent restrictions and $\mathbf{M_2} = J+1$.

TABLE 1—Analysis of variance tables: **A)** unrestricted ANOVA, **B)** restricted ANOVA.

A	source of variability	sum of sqs.	d.f.	mean square
	regression	SSR_1	M_1	$MSR=SSR_1/M_1$
	dev. from regression	SSE_1	$N-M_1-1$	$MSE_1=SSE_1/(N-M_1-1)$
	total	SST	N-1	

B	source of variability	sum of sqs.	d.f.	mean square
	regression	SSR_2	$M_2=M_1-p$	$MSR_2=SSR_2/M_2$
	dev. from regression	SSE_2	$N-M_2-1$	$MSE_2=SSE_2/(N-M_2-1)$
	total	SST	N-1	

To test whether or not the restrictions introduced apply, we compare

$$\frac{(SSR_1 - SSR_2)}{p} \Big/ MSE_1$$

with a tabulated F-value that has *p* and $N-M_1,-1$ degrees of freedom; we accept or reject the hypothesis leading to the restricted table based on whether the calculated value is smaller or larger than the tabulated value.

The sample

The sample on which our statistical analysis was run consisted of 18 specimens (table 2) belonging to two genera of Ordovician nautiloids. Both genera, *Plectolites* Flower and *Litoceras* Hyatt, are members of the Family Trochlitidae of the Order Tarphyceratida. These two genera were chosen for study because 1) they are among the most numerous and best preserved of the coiled nautiloids housed in the paleontology collections of the New Mexico Bureau of Mines and Mineral Resources, and 2) descriptions of many of the specimens have been published (Flower, 1968).

Although published measurements (Flower, 1968) were available for many of the specimens, we remeasured every specimen in order to minimize measurement error and to get the data in a form more usable for equation (1). Because the simple logarithmic model is a proportional model (scale does not affect the resulting slope), all of our measurements were made from photographs of cross sections, with recourse to the actual specimen if discrepancies resulted. Fig. 2A, which was drafted from the cross section of *Plectolites* n.sp.1, shows how our measurements were made. We assumed that diameters would be the more accurate measurements to use; unlike radii, they do not presuppose knowledge of the exact center of coiling. This assumption is one that could be statistically evaluated.

In the case of the genus *Plectolites,* two simple regressions were performed on the entire subsample, one using radii, the other using diameters. The results of these two regressions are summarized in table 3. An F-test was performed that indicated no significant difference exists at the 95-percent confidence level between the results obtained from radii and those obtained from diameters. We decided to use radii measurements because 1) the specimens from both genera were generally well preserved, 2) radii provide at least one more parameter (degree of freedom) per specimen, and 3) the 95-percent confidence interval on the slope of the line obtained using radii is more restrictive than that obtained from diameters.

The problem of determining the true angle 9 for use in equation (1) is particularly difficult, because often the innermost whorls are not preserved in fossil material. Even in well-preserved material, determining the angle that the plane of the section makes with respect to 0 radians of the coiled shell is generally not possible. To circumvent this problem, we simply noted that p radians exist between any two consecutive radii of a cross section (fig. 2A). Whorls of the cross section were numbered consecutively, with the innermost whorl given the number 1/2, the next given the number 1, and so on. If the innermost whorls were not preserved, an educated guess was used to start the numbering. These whorl numbers were later converted to radians by multiplying them by 2n.

Since the exact relationship between the plane of the section and 0 radians could not be determined precisely, all of the resulting curves are translated in one direction or the other with respect to the origin; hence, the intercept does not provide the true initial coiling radius.

The actual measurements of radii to the venter of each whorl were made in millimeters with the aid of a

TABLE 2—Observed values of radii to the venter (mm) in the 18 study specimens. NMBM—New Mexico Bureau of Mines and Mineral Resources; CU—Columbia University; USNM—United States National Museum; MCZ—Museum of Comparative Zoology; BYU—Brigham Young University (unnumbered); NF—Nyfriesland, Spitsbergen; e—estimated.

whorl number (θ)	$\frac{1}{2}(\pi)$	$1(2\pi)$	$1\frac{1}{2}(3\pi)$	$2(4\pi)$	$2\frac{1}{2}(5\pi)$	$3(6\pi)$	$3\frac{1}{2}(7\pi)$
specimen							
Plectolites n.sp.1 NMBM 1468	4.3	5.7	11.2	16.8	27.1	----	----
P. n.sp.2 BYU	5.2	6.2	14.4	19.8	37.9	54.0	----
P. n.sp.3 NMBM 1559	7.0	9.6	18.3	27.7	44.8	65.0	----
P. n.sp.4 CU 28782	9.0	14.4	24.5	36.0	----	----	----
P. n.sp.5 NMBM 1564	8.7	22.1	30.3	53.0	63.8	----	----
P. costatus Flower Holotype, CU 28783	9.1	11.4	22.7	31.8	51.5	----	----
P. n.sp.6 NMBM 1522	----	10.4	22.9	37.7	58.1	----	----
P. n.sp.7 NMBM 1563	9.3	13.1	23.5	35.5	54.5	----	----
P.(?)*kirki* Flower Holotype, USNM 140356	----	----	27.0	40.6	64.3	----	----
Litoceras adamsi Flower USNM 140353	3.1	8.6	10.4	17.7	24.0	39.3	----
L. adamsi Flower Paratype, MCZ 9403	6.1	7.3	14.4	18.4	30.0	43.7	----
L. adamsi Flower Holotype, MCZ 4402	4.6	8.7	12.4	19.3	----	44.0	----
L. adamsi Flower NMBM 375	7.8	10.1	17.2	22.7	33.9	----	----
L. adamsi Flower Paratype, NMBM 373	6.5	10.3	14.4	21.5	32.6e	50.3	----
L. n.sp BYU	7.5	12.0	18.8	28.5	----	----	----
L. adamsi Flower Holotype, MCZ 9404	7.3	16.4	19.9	34.0	49.3	----	----
L. adamsi Flower Paratype, NMBM 376	7.1	8.6	15.0	20.4	----	----	----
L.(?) n.sp. NF 2743-44	5.2	6.7	15.4	24.1	29.3	42.7	54.9

vernier caliper and dividers. We drew a line on the photograph representing the intersection of the sagittal plane with the cross section, then pricked holes in a backing sheet at the center of coiling and at the radius to the venter of each whorl. These holes were used as points of reference for the measurements. Three readings for each radius were obtained, and the average of these three readings (to the nearest 0.1 mm) was used in the computations. To see if the radii measurements were transposed correctly, the successive radii were added and checked against the measurement of the respective diameter (fig. 2A).

TABLE 3—Radii-diameter comparison for *Plectolites* specimens.

based on:	b	S_b	d.f.	95% C.I. on b
radii	0.14457	0.12593	41	(0.12167, 0.16747)
diameters	0.16340	0.12240	32	(0.11208, 0.17472)

b = slope of regression line
S_b = standard deviation of the slope
d.f. = degrees of freedom
95% C.I. on b = 95% confidence interval on the slope

Analysis of nautiloid fossils

The data described in the previous section were used to examine several hypotheses about the genera *Litoceras* and *Plectolites.* We began by considering each specimen alone. For each specimen we fit a line of the log of the radius versus the angle *9.* The equations for the 18 individual lines are shown in table 4A.

Pooling the sums of squares for each specimen within a genus by adding the sums of squares for deviation from regression and the associated degrees of freedom for each of the simple linear models, we obtained the two ANOVA tables given in table 5A.

Our next objective was to test whether the variations observed between slopes within each genus were in fact real or due to chance alone. That is, we wished to test the hypothesis that *fly* $b_{1j} = b_1$, for all *j* and also $b_{2j} = b_2$ for all *j*.

To carry out this test, we fit a line to the data from each specimen within a genus where a common slope was used but different intercepts were possible for each specimen. The results of this fitting procedure are shown in table 4B.

To test the hypothesis of equal slopes within each genus, we formed the adjusted sum of squares by combining the ANOVA tables in table 5.

For *Plectolites,* the adjusted sum of squares was 24.936 - 24.86604 = 0.04996, with 17 - 9 = 8 d.f. (degrees of freedom). The calculated F-ratio was (0.04996/8)/0.015 = 0.416, which was less than that

TABLE 5—ANOVA tables for comparisons within genera: **A)** unrestricted model, **B)** restricted model with equal slopes for each genus.

A a. Plectolites

source of variability	sum of sqs.	d.f.	mean square
regression	24.93600	17	1.46682
dev. from regression	0.37511	25	0.01500
total	25.31111	42	

R^2 = (multiple correlation coefficient)^2 = 0.98518

b. Litoceras

source of variability	sum of sqs.	d.f.	mean square
regression	18.87724	15	1.24848
dev. from regression	0.34708	25	0.013883
total	19.22432	40	

R^2 = (multiple correlation coefficient)^2 = 0.98195

B a. Plectolites: $\beta_{1j} = \beta_1$

source of variability	sum of sqs.	d.f.	mean square
regression	24.86604	9	2.76289
dev. from regression	0.44507	33	0.01349
total	25.31111	42	

R^2 = (multiple correlation coefficient)^2 = 0.98242

b. Litoceras: $\beta_{2j} = \beta_2$

source of variability	sum of sqs.	d.f.	mean square
regression	18.78230	8	2.34779
dev. from regression	0.44202	32	0.01381
total	19.22432	40	

R^2 = (multiple correlation coefficient)^2 = 0.97701

TABLE 4—Fitted lines to specimens: **A)** different slopes, **B)** common slopes. This specimen was significantly different when compared with the common slope model for the other eight specimens of *Litoceras.*

	A	B	
Plectolites (i=1)	different slopes	common slopes	name
j=1	y_{11}=0.912+0.152x	y_{11}=0.912+0.152x	Plectolites n.sp.1
2	y_{12}=1.043+0.159x	y_{12}=1.119+0.152x	P. n.sp.2
3	y_{13}=1.449+0.147x	y_{13}=1.397+0.152x	P. n.sp.3
4	y_{14}=1.737+0.149x	y_{14}=1.717+0.152x	P. n.sp.4
5	y_{15}=1.414+0.155x	y_{15}=1.448+0.152x	P. n.sp.5
6	y_{16}=1.685+0.143x	y_{16}=1.600+0.152x	P. costatus Flower
7	y_{17}=1.875+0.180x	y_{17}=2.097+0.152x	P. n.sp.6
8	y_{18}=1.743+0.144x	y_{18}=1.672+0.152x	P. n.sp.7
9	y_{19}=1.986+0.138x	y_{19}=1.811+0.152x	P.(?)kirki Flower
Litoceras (i=2)			
j=1	y_{21}=0.923+0.149x	y_{21}=1.069+0.135x	Litoceras adamsi Flower
2	y_{22}=1.326+0.130x	y_{22}=1.273+0.135x	L. adamsi Flower
3	y_{23}=1.176+0.140x	y_{23}=1.229+0.135x	L. adamsi Flower
4	y_{24}=1.647+0.119x	y_{24}=1.497+0.135x	L. adamsi Flower
5	y_{25}=1.474+0.129x	y_{25}=1.402+0.135x	L. adamsi Flower
6	y_{26}=0.693+0.142x	y_{26}=0.784+0.135x	L. n.sp.
7	y_{27}=1.220+0.145x	y_{27}=1.341+0.135x	L. adamsi Flower
8	y_{28}=1.521+0.119x	y_{28}=1.395+0.135x	L. adamsi Flower
9*	y_{29}=1.333+0.108x		L.(?) n.sp.

tabulated $F_0 5(8,25) = 2.34$ point. Hence, we accepted the hypothesis that all of the slopes in the *Plectolites* specimens are equal at the .05 level.

Similarly, for *Litoceras* we got an adjusted sum of squares of 18.87724 - 18.78230 = 0.09494, with 15 - 8 = 7 d.f. and a calculated F-ratio of 0.97694; $F_{05}(7,25) = 2.40$; once again, we accepted the hypothesis of equal slopes for the specimens of this genus.

The equations in table 4B indicate considerable variation between intercepts for the specimens within each genus. We tested the hypothesis of equal intercepts for each genus. For this test, we obtained a line with a common intercept and a common slope for each genus and carried out an F-test similar to the above. For the genus *Plectolites* we obtained the following equation (the associated analysis of variance is given in table 6):

$$Y = 1.562 + 0.145\ X.$$

Here, the adjusted sum of squares = 24.86604 - 20.14816 = 4.71788, the adjusted d.f. = 9 - 1 = 8, the

$$\text{calculated } F\text{-ratio} = \frac{4.71788}{8} / 0.01349 = 43.72, \text{ and}$$

the tabulated *F95(8,33)* = 2.2.

The calculated F-value indicates that the hypothesis of a common intercept should be rejected at the .05 level. A similar calculation was made for the genus *Litoceras* with the same result; the hypothesis of equal intercepts must be rejected.

The rejection of this hypothesis was not unexpected because of the problems of determining the 9 = 0 point on the specimens and determining where to start numbering the whorls in specimens in which the initial whorls were not preserved. However, in specimens in which numbering problems are minimal (for example, fusulinids), the results of this test could be significant because of the morphological interpretation of the intercept as the initial coiling radius of the shell.

A final statistical test was made to determine if a common slope could be fitted to the data from both genera. Here again an ANOVA table (table 7) was constructed.

The adjusted sum of squares = 45.57522 - 45.4472 = 0.12802, the adjusted d.f. = 18 - 17 = 1, the calculated

$$F\text{-ratio} = \frac{0.12802}{1} / 0.01365 = 9.37875, \text{ and the}$$

tabulated F05(1,65) = 4.00.

The hypothesis that the slopes were equal ($b_1 = b_2 = b$) was rejected at the .05 level. Table 8 shows the 95-percent confidence intervals on the slopes (ctn a) and a, the constant angle of the spiral. The confidence in

TABLE 7—ANOVA tables for comparisons between genera: **A)** two different slopes, $\beta_1 \neq \beta_2$; **B)** common-slope model, $\beta_1 = \beta_2 = \beta$.

A

source of variability	sum of sqs.	d.f.	mean square
regression	45.57522	18	2.53196
dev. from regression	0.88709	65	0.01365
total	46.46231	83	

R^2 = (multiple correlation coefficient)^2 = 0.98091

B

source of variability	sum of sqs.	d.f.	mean square
regression	45.84720	17	2.67336
dev. from regression	1.01511	66	0.01538
total	46.46231	83	

R^2 = (multiple correlation coefficient)^2 = 0.97815

tervals for the two genera do not overlap, and hence the growth rates of the shells of the two genera are distinct. This result leads inescapably to the conclusion that shell growth is a genetically controlled factor that can be used to quantitatively differentiate between the genera *Plectolites* and *Litoceras.*

The equation of the line for *Plectolites* n.sp.1 in table 4A (different-slope model) has the same slope and intercept as the equation of the corresponding line in table 4B (common-slope model). This result is partly due to round off, but this specimen also was the best preserved in the collection; hence, more precise location of its center of coiling was possible.

Once the estimated regression lines have been obtained for a particular taxon, they can be used to help determine whether another specimen should be assigned to that taxon. For example, the regression line for *Litoceras(?)* n.sp. (table 4) is significantly different at the .05 level from that obtained for the genus *Litoceras.* In fact, when this specimen was included in the *Litoceras* group, we had to reject the hypothesis of equal slopes (that is, $b_{21} = b_{22} = ... = b_{29} = b_2$. The differing regression lines suggest that assignment of this species to the genus *Litoceras* is indeed questionable. However, our *Litoceras* sample is heavily weighted by the presence of seven specimens assigned to *L. adamsi.* The common slope we obtained for the genus *Litoceras* might, in fact, represent the species *L. adamsi.*

Even though all of the multiple correlation coefficients, squared, were on the order of 0.98 or larger, which indicates that the linear relationship explains at least 98 percent of the observed variability in the data,

TABLE 6—ANOVA table for *Plectolites,* common-slope and common-intercept model.

source of variability	sum of sqs.	d.f.	mean square
regression	20.14816	1	20.14816
dev. from regression	5.16295	41	0.12593
total	25.31111	42	

R^2=(multiple correlation coefficient)^2= 0.79602

TABLE 8—Confidence intervals on ctn α and α for the two genera.

genus	ctn α	std. dev.	95% C.I. on ctn α	95% C.I. on α
Plectolites	0.152	0.00396	(0.144,0.160)	(81.81°, 80.91°)
Litoceras	0.135	0.00379	(0.128,0.143)	(82.71°, 81.86°)

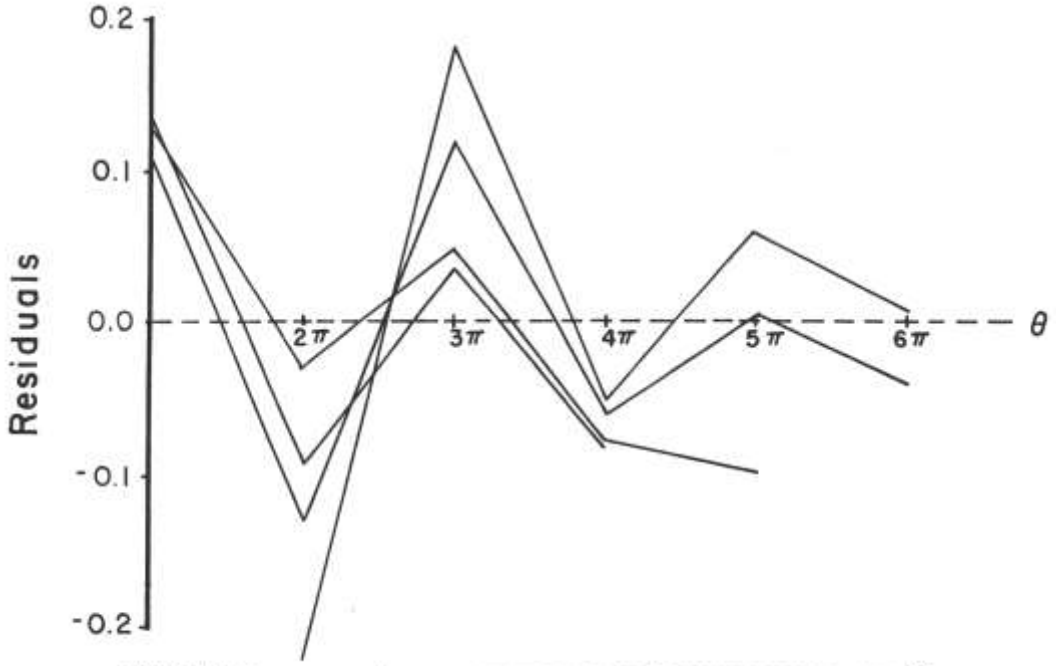

FIGURE 4—RESIDUALS FOR *LITOCERAS* SPECIMENS, GROUP 1, VERSUS THE WHORL ANGLE (θ).

an examination of the residuals (observed values minus fitted values) was instructional. Observed cumulative distributions of residuals were graphed on normal probability paper and fell approximately along a straight line, supporting the assumption of normality of the residuals in both genera.

Figs. 4 and 5 show the residuals for the *Litoceras* specimens. Two different groups were noted because the initial whorl could not always be determined. These graphs were used to estimate where the measured whorls started. The residuals were then adjusted by translating the set in fig. 5 one-half whorl to the right and replotting the data. A similar analysis was carried out for the *Plectolites* specimens. These adjustments do not affect the preceding analyses on the slopes; essentially they adjust for the nonequal intercepts. The adjusted residuals were then averaged and are shown in fig. 6 for both genera.

The data in fig. 6 indicate a periodic effect that dies out as the radius increases. The periodicity is most likely an artifact introduced because the plane of the cross-sectional cut does not coincide precisely with a true diameter of the shell; that is, it does not intersect the center of coiling. Suppose the center is misplaced by an amount δ where $\delta > 0$ implies displacement to the left.

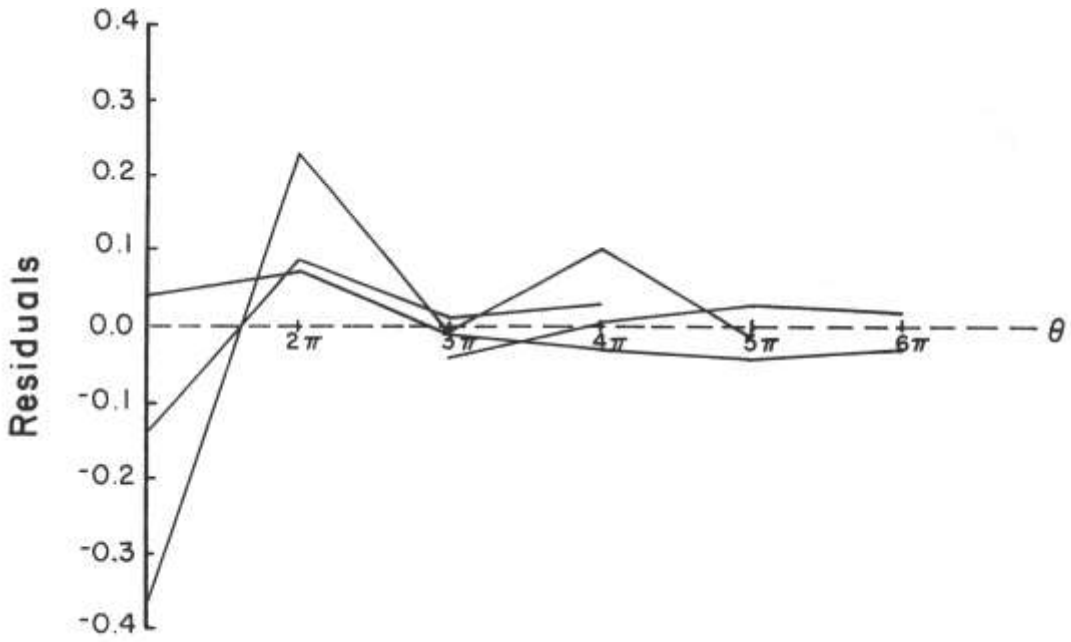

FIGURE 5—RESIDUALS FOR *LITOCERAS* SPECIMENS, GROUP 2, VERSUS THE WHORL ANGLE (θ).

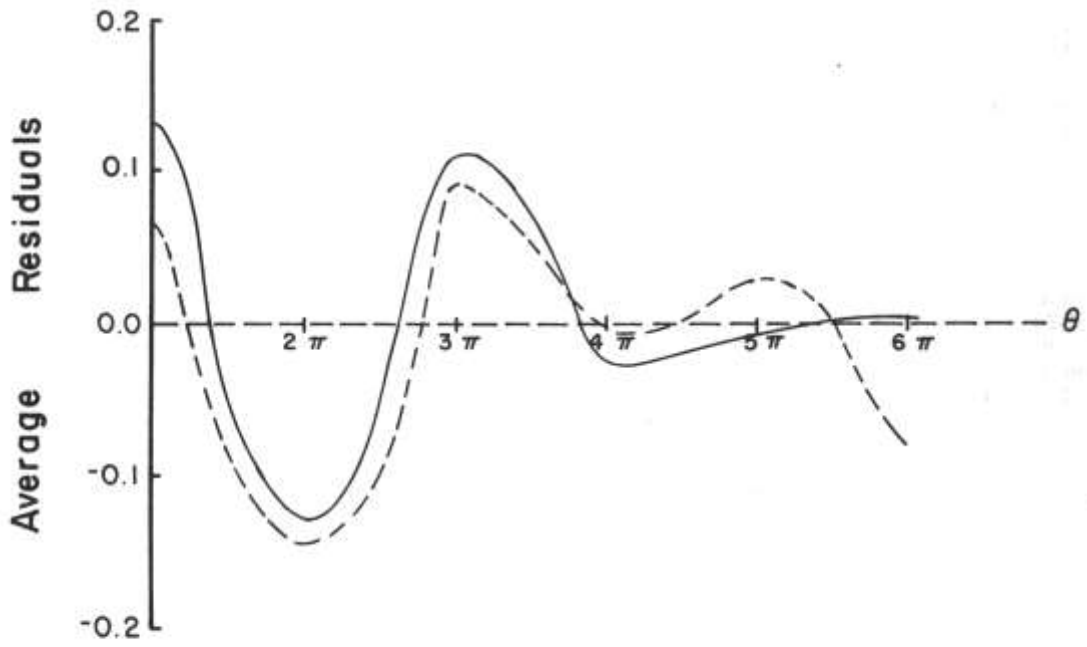

FIGURE 6—AVERAGE ADJUSTED RESIDUALS FOR BOTH GENERA WITH TRANSLATION, VERSUS THE WHORL ANGLE (θ).

——— = *Plectolites*, - - - - - = *Litoceras*

Then we essentially measure

$$r_1(\theta) = r(\theta) + \delta\cos(\theta), \qquad \text{at } \theta = 0, \pi, 2\pi, \ldots$$

If δ is small,

$$\begin{aligned} \ell n[r_1(\theta)] &= \ell n[r(\theta)\{1 + \frac{\delta\cos(\theta)}{r(\theta)}\}] \\ &= \ell n[r(\theta)] + \ell n[1 + \frac{\delta\cos(\theta)}{r(\theta)}] \\ &\cong \ell n[r(\theta)] + \frac{\delta\cos(\theta)}{r(\theta)} \end{aligned}$$

Thus, a cosine term is added to the log of the true value. Furthermore, since $r(q)$ increases with q, the amplitude of the term is damped out. In fact, one could estimate 6 and recalculate the true radii. We did not do this because the slope and intercept estimates would not be changed by a significant amount.

Summary and conclusions

We have presented a general statistical method for comparing and interpreting planispiral coiling among invertebrate species. Our statistical model is predicated on simple logarithmic growth of the shell and uses simple linear regression and analysis of variance and covariance techniques to evaluate planispiral coiling. We chose to use the simple logarithmic model of Moseley (1838), as explained by Thompson (1942), because the parameters used in this model are easily interpreted in terms of shell morphology and because statistical tests indicate that the simple logarithmic model is adequate to explain the coiling phenomenon.

We applied this statistical method to data from 18 specimens from two genera of fossil nautiloids, *Plectolites* and *Litoceras.* The statistical analysis of this data indicates that coiling angle of the shell is a sufficient criterion for distinguishing these genera from each other and for determining the generic assignments of species.

Although our analysis has been a univariate analysis of planispiral coiling, other aspects of shell growth can be expressed in terms of our general model: growth of the siphuncle, growth of shell height and width, radius to dorsum, and volume between septa (Denton and Gilpin-Brown, 1966). Preliminary results indicate that our model adequately fits published data for the ammonoid genera *Cravenoceras* Bisat and *Rhadinites* Saunders (Saunders, 1973) and for the fusulinid genera *Millerella* Thompson, *Eostaffella* Rauser-Chernoussova (King, 1973), *Schwagerina* Moller, and *Pseudoschwagerina* Dunbar (Williams, 1966).

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