A Statistical Analysis of the Intercuspal Angle of the Phragmodontiform Element of *Phragmodus undatus*

by

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ABSTRACT. -- The intercuspal angle of the phragmodontiform element of the conodont *Phragmodus undatus* Branson and Mehl, 1933 was measured on specimens from samples from two cores drilled in the Cincinnati Region. In the section studied from the core from Minerva, Kentucky, a general trend can be observed that suggests a decrease in the mean intercuspal angle of the population with time. That trend correlates to a similar decrease in the relative abundance of *P. undatus*, which suggests a general shallowing of the water column. The section studied from the core from New Point, Indiana correlates to the upper part of the section studied from the core from Minerva, Kentucky, and extends stratigraphically higher. That section represents relatively deeper water, in which the mean intercuspal angle of the *P. undatus* population does not significantly differ with time. This suggests that a period of stasis developed during which *P. undatus* was in general equilibrium with paleoenvironmental factors as controlled by relative water depth.

INTRODUCTION

Phragmodus undatus Branson and Mehl, 1933 is a long-ranging multielement conodont species, which is widespread in rocks of Middle and Late Ordovician age in North America and parts of Europe. As emended by Bergström and Sweet (1966), the skeletal apparatus of P. undatus is composed of a symmetry transition series of phragmodontiform elements, oistodontiform elements in the M position, and dichognathiform elements in the P_a and P_b positions.

Several authors (Branson and Mehl, 1951; Glenister, 1957; Ethington, 1959) have noted the wide degree of variability occurring in the phragmodontiform element of Phragmodus undatus. Sweet, et al. (1959) subdivided forms on the basis of cusp ornamentation. Pulse and Sweet (1960) mentioned the existence of massive, robust forms that seem to differ greatly from more typical phragmodontiform elements. However, these massive, robust forms possess the sinuous posterior process characteristic of the phragmodontiform element of P. undatus. They suggested that the robust forms may be end-members of a gradational series that may reflect paleoenvironmental conditions.

Figure 1 shows two representations of the phragmodontiform element of Phragmodus undatus. A prominent character of this element is the presence of a large denticle along the posterior process, which rivals or exceeds the size of the cusp. That large denticle and the cusp, taken together, define an intercuspal angle. A general relationship can be perceived between the intercuspal angle of more robust

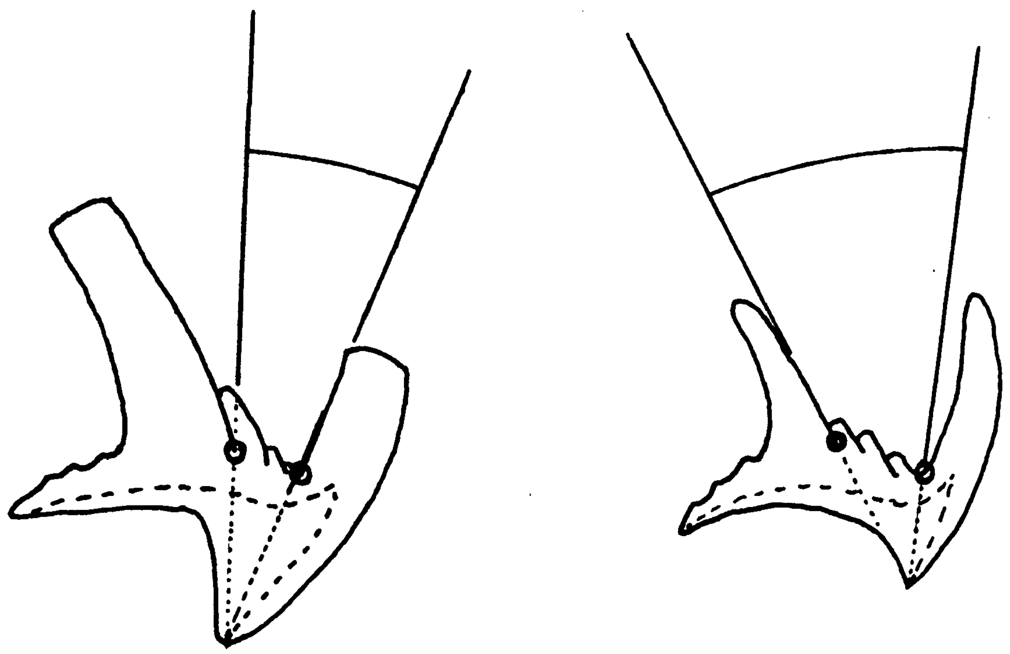

FIGURE 1 -- Representations of the phragmodiform element of Phragmodus undatus, displaying A) a more robust form, B) a more fragile form, and the angle measured on the specimens.

phragmodontiform elements when compared to that of more fragile forms. The intercuspal angle tends to be smaller on more robust forms.

If the gradation between more fragile and more robust phragmodontiform elements of Phragmodus undatus represents a function of the paleoenvironment, as suggested by Pulse and Sweet (1960), then a measure of the mean intercuspal of the phragmodontiform element for populations of P. undatus through a stratigraphic interval, may reflect some relation to paleoenvironmental factors. This paper will attempt to establish a general trend in a character of the phragmodontiform element of P. undatus, and relate this trend to proposed paleoenvironmental conditions as evaluated by relative-abundance analysis in concordance with lithic features and the general tectonic setting of the region.

DATA

Sources of data for this study are samples from two long cores drilled in the Cincinnati Region (Figure 2). One core was drilled by the Indiana Geological Survey at New Point, Indiana. The core was made available to the Ohio State University in 1965, where it was sampled at

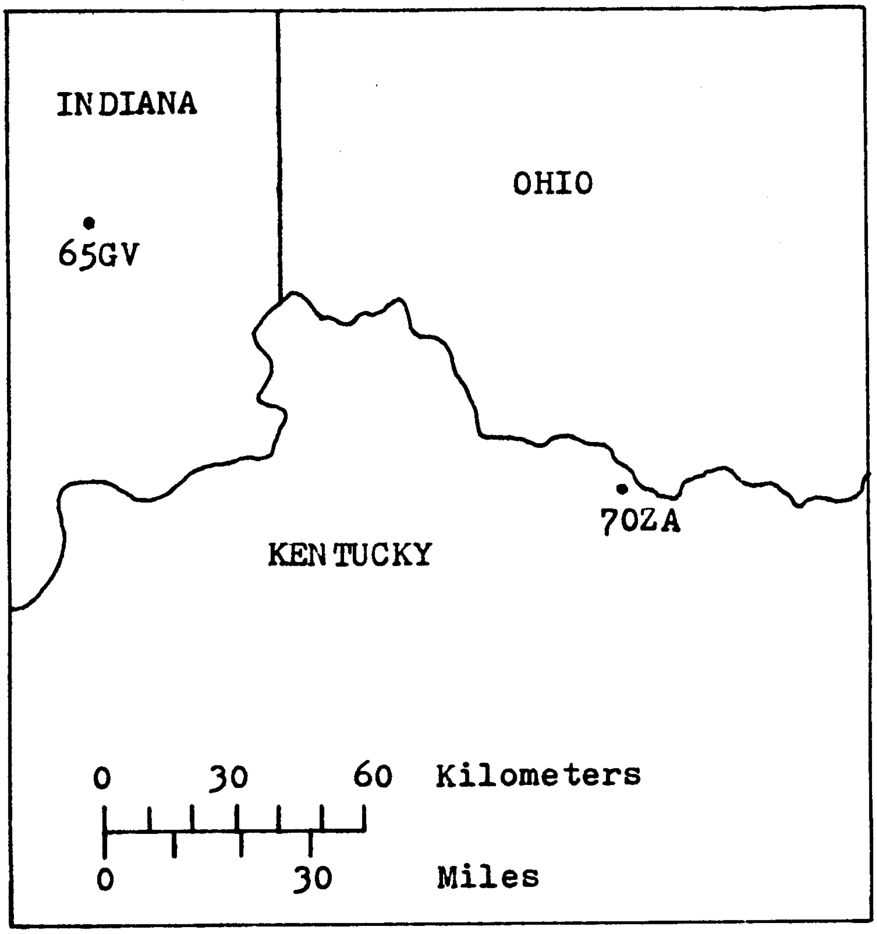

FIGURE 2 -- Locations of the cores from which sample data were taken. 65GV- New Point, Indiana. 70ZA- Minerva, Kentucky.

approximately five-foot intervals, given the designation OSU 65GV, and added to the collections of the Micropaleontological Laboratories. The other core was drilled in 1970 by Cominco American, Inc. at Minerva, Kentucky. It was also sampled at approximately five-foot intervals, and was added to the collections under the designation OSU 70ZA.

Original studies of these cores used data measured in feet. That format is maintained in this paper to facilitate cross-referencing to other applicable papers on the region.

Section 70ZA was described by Sweet, et al. (1974). Of the 1210-foot depth to which the core was drilled, samples from the upper 800 feet were used in this paper. Those samples represent an interval from 135 feet below the base of the Lexington Limestone to the top of the Fairview Formation. Section 65GV was included in a general exposition of conodonts from Middle Ordovician strata in the Cincinnati Region by Bergström and Sweet (1966). Samples from an interval in the Upper Ordovician part of that section from 65GV500 through 65GV835 were used in this study. The sections studied have been correlated with each other graphically and on the basis of relative-abundance analysis, which involved species of *Phragmodus*, *Plectodina*, *Aphelognathus*, *Oulodus*, and *Rhipidognathus* (Sweet, personal communication). Figure 3 is a schematic representation of that correlation.

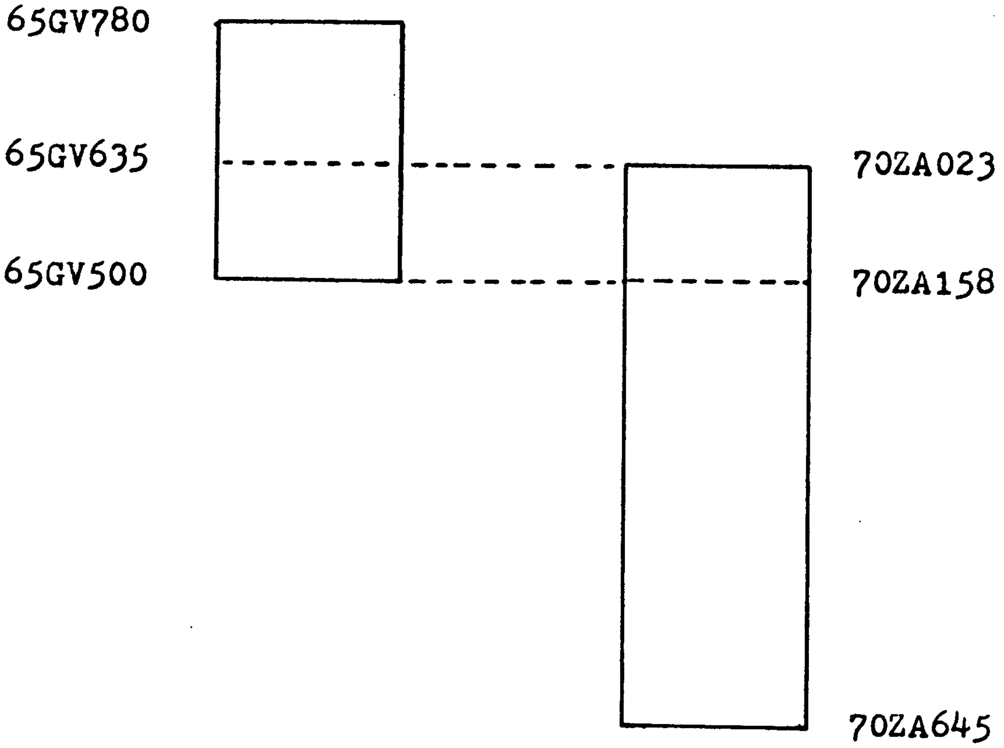

FIGURE 3 -- Schematic representation of the correlation between samples from sections 70ZA and 65GV, based on graphic correlation and relative-abundance analysis. Note the difference in the sequential designation of samples from the two sections.

An initial pilot study of twenty samples was performed, using the four types of elements that make up the skeletal apparatus of Phragmodus undatus. Samples from the two sections of study were surveyed at approximately fifty-foot intervals. Various angular measurements, lengths, and denticle counts were tabulated to inspect for apparently-significant trends. Only the mean intercuspal angle of the phragmodontiform element showed any apparently-significant trend. However, the absence of other apparently-significant trends may be a reflection of the lower frequency of measurements per sample carried out on characters of the other elements in the P. undatus apparatus. That lower frequency of measurements for non-phragmodontiform elements is a result of the less numerous occurrence of oistodontiform and dichognathiform elements in the P. undatus apparatus. As a result, fewer of those elements occur in the samples, and those that do occur are often unusable for various measurements, due to the incomplete preservation of the element. Apparently-significant trends may occur in the oistodontiform and dichognathiform elements of P. undatus, but they were not observed in the pilot study conducted from the two sections available for this study.

For the purposes of this study, samples were used in which fifteen phragmodontiform elements could be measured. Fifteen measurements yield a sufficient degree of variability so as to be representative of the population, while at the same time enabling a sufficient number of samples to be utilized in order to represent reasonably, the interval of study of each section. Under that criterion, specimens were measured in samples with fewer than fifteen measurable forms, but data from such samples were not used in the data analysis.

Two-hundred-thirty-nine samples were surveyed, of which 36 contain no specimens of Phragmodus undatus. Twenty-seven of those samples occur in the 135-foot interval of section 70ZA below the base of the Lexington Limestone. The remainder of samples lacking elements of P. undatus are scattered throughout the intervals of study in the two sections. Of the remaining 203 samples, 89 contain fewer than fifteen measurable phragmodontiform elements. The resulting 114 samples represent an average stratigraphic interval of eight feet.

The data set for section 70ZA consists of 84 samples, which cover the 622-foot interval between sample 70ZA645 and 70ZA023. Section 65GV is represented in this study by an interval 275 feet thick between 65GV505 and 65GV780. Correlation indicates that there is a 135-foot interval of overlap between the two sections.

Intercuspal angles were measured to the nearest degree using a graduated stage on a monocular microscope. Sample means were calculated and plotted versus core depth to inspect for apparently-significant trends (Figures 4B and 5B). Statistical analyses, including analysis of variance and linear regression, were then performed using SAS, BMDP, and SPSS statistical packages.

RESULTS

Core depth versus mean intercuspal angle was graphed for sections 70ZA and 65GV (Figures 4B and 5B). Visually, the 70ZA data seem to vary around a more or less constant mean angle throughout the lower and middle parts of the section. The upper section however, appears to mark an

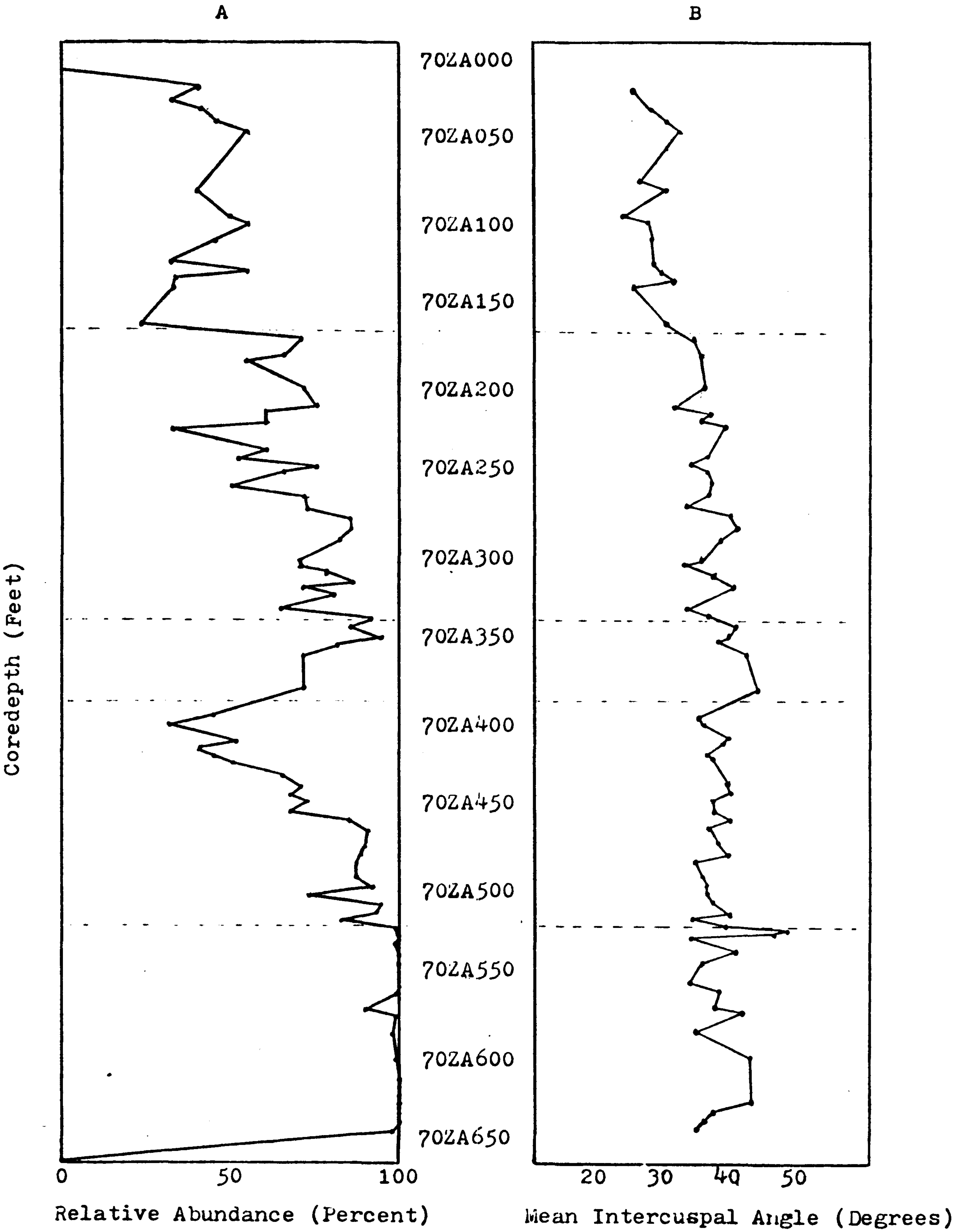

FIGURE 4 -- Graphs of core depth versus A) relative abundance and B) mean intercuspal angle for section 70ZA.

interval in which the mean intercuspal angle has decreased. Inspection of the 65GV data reveals an essentially similar, though less marked pattern. However, the mean intercuspal angles as a whole are generally lower, and a shift to higher values occurs at the top of the section.

One-way analysis of variance procedures were run on data from both sections to determine if the mean intercuspal angle varies significantly in any part of either section. Use of analysis of variance procedures is based on three assumptions: 1) observations are assumed to have been randomly selected from the population; 2) sample populations are assumed to be normally distributed; and 3) variances of the sample populations are assumed to be equal.

Within the established criterion of fifteen measurable phragmodontiform elements per utilized sample, angles were measured without systematic order. Specimens on most slides were originally grouped according to element form within each species. A few slides contain elements arranged in no apparent order. In order to take into account any systematic ordering of form elements, specimens were selected without apparent order. While that is not necessarily random, the absence of systematic order in selecting forms for measurement approaches randomness. Any departures from randomness tend to cancel out and thus enable the assumption to hold.

Kolmogorov-Smirnov's goodness-of-fit test was used to

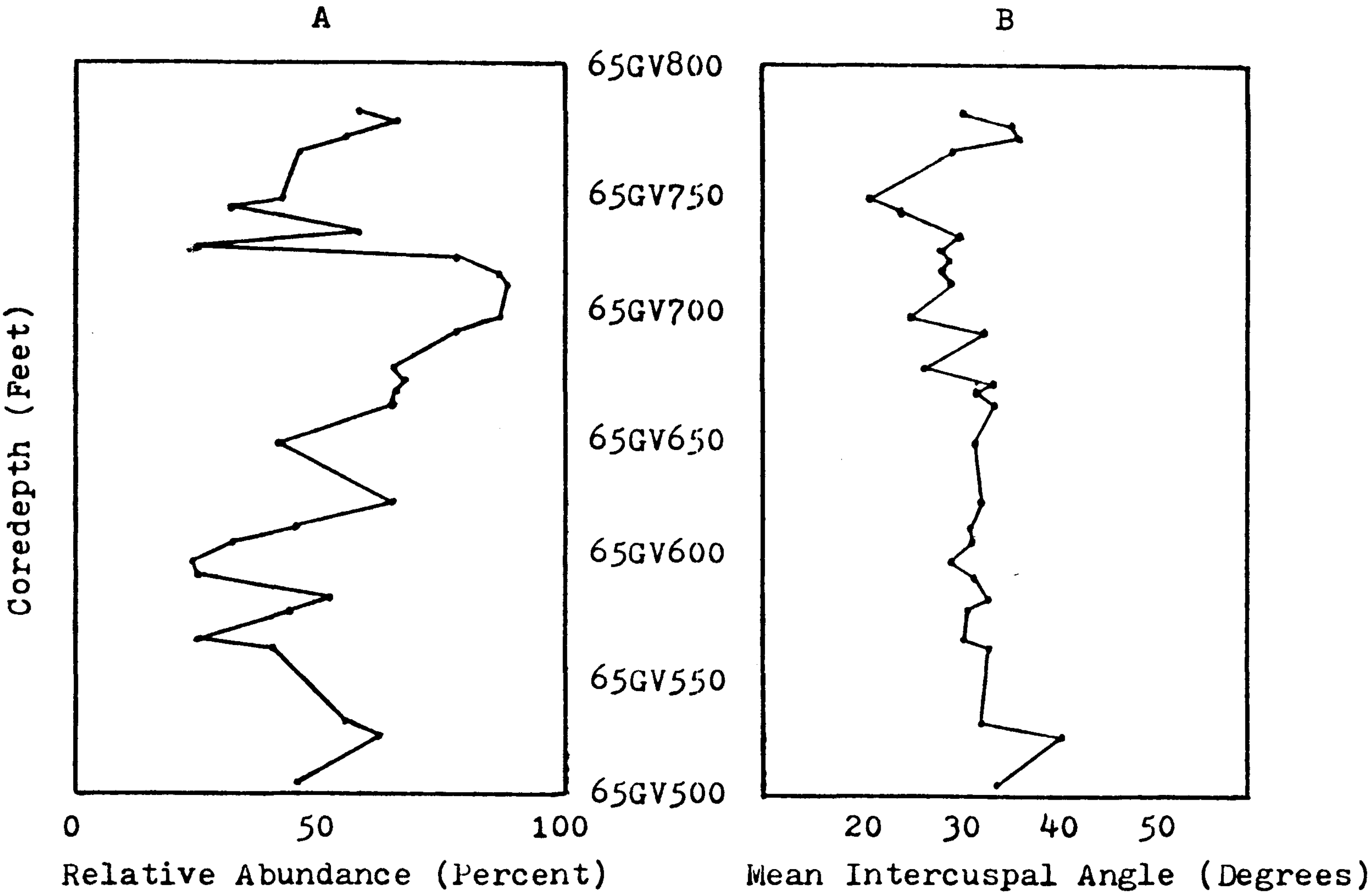

FIGURE 5 -- Graphs of core depth versus A) relative abundance and B) mean intercuspal angle for section 65GV.

evaluate the assumption of normality. That test computes the mean and standard deviation of a sample and compares it to a normal distribution with the same mean and standard deviation. The probability that the sample is normally distributed is computed using the Kolmogorov-Smirnov z-value. Rejection occurs at the five-percent significance level. Spot checks of samples throughout each section yielded generally high probabilities that the samples are normally distributed (Figure 6).

Sample Number	K-S z-value	Probability(Normal)
65GV780	0.660	0.776
65GV715	0.545	0.927
65GV610	0.650	0.792
65GV505	0.626	0.828
70ZA023	0.413	0.996
70ZA129	0.426	0.993
70ZA212	0.636	0.814
70ZA275	0.502	0.963
70ZA333	0.602	0.862
70ZA418	0.791	0.559
70ZA482	0.824	0.505
70ZA531	0.673	0.755
70ZA603	0.872	0.432

FIGURE 6 -- Results of the Kolmogorov-Smirnov test to evaluate the assumption of normality. Rejection occurs at the 5% significance level.

Bartlett's homogeneity-of-variance test was used to evaluate the variance assumption. Sample variances are compared to the mean variance for all samples in a manner distributed approximately as chi-squared. Rejection occurs at the five-percent significance level. For the intervals calculated, the null hypothesis that the variances are all equal could not be rejected (Figure 7).

For the 70ZA section, a series of analysis-of-variance tests was run in order to establish intervals during which the mean intercuspal angle of the samples did not significantly differ. Initially, that test was conducted

Section	Sample Interval	Chi-square	Probability(=Variances)
65GV	780-715	9.288	0.433
65GV	710-610	7.261	0.629
65GV	605-505	8.914	0.467
70ZA	023-129	16.198	0.071
70ZA	134-212	10.198	0.356
70ZA	217-275	8.287	0.527
70ZA	281-333	6.042	0.751
70ZA	339-418	11.965	0.233
70ZA	423-477	11.967	0.233
70ZA	482-531	13.893	0.140
70ZA	533-603	7.473	0.608
70ZA	558-645	13.402	0.160

FIGURE 7 -- Results of the Bartlett test to evaluate the assumption of equal variances between populations. Rejection occurs at the 5% significance level.

on the entire section. The null hypothesis that the means are all equal was rejected at a confidence level exceeding 99 percent. Concurrently, Tukey's studentized-range test evaluated mean angles that did not significantly differ at a five-percent significance level. That enabled the section to be split into intervals characterized by approximately equivalent mean intercuspal angles (Figure 4B). Figure 8 shows the results of various analysis-of-variance runs and the associated mean intercuspal angles for each interval.

The resulting divisions then were compared to a plot of core depth versus the relative abundance of *Phragmodus*

Section	Sample Interval	Probability(=means)	Interval Mean
65GV	780-505	0.0001*	31.207
70ZA	023-645	0.0001*	35.883
70ZA	023-165	0.1003	28.152
70ZA	172-339	0.1524	35.530
70ZA	347-382	0.2185	40.440
70ZA	398-526	0.4030	37.091
70ZA	531-645	0.0001*	38.351

* Default value for very small probabilities.

FIGURE 8 -- Results of analysis of variance procedures and the appropriate mean angular values for each interval. Rejection occurs at the 5% significance level.

undatus as a component of the characteristic Midcontinent fauna of the Cincinnati Region. A general similarity in pattern can be recognized from the two plots of Figure 4. Both dependent variables tend to decrease upsection.

A simple linear-regression analysis utilizing least-squares procedures was run on the intercuspal angles, with relative abundance as the regressor variable. An r-correlation coefficient of 0.254 was obtained for the data. The t-test for the null hypothesis that there is no correlation between the two variables yielded a probability approaching zero. The relationship between the variables is significant to a confidence level exceeding 99.99 percent with 1258 degrees of freedom.

Data from section 65GV were treated in a manner similar to the treatment of data from section 70ZA. An initial analysis-of-variance test was run on the entire section. The null hypothesis that all sample means are equal was rejected at a confidence level exceeding 99 percent. However, Tukey's studentized-range test indicated that rejection was occurring on the basis of four extreme values, located throughout the section. Three values are low and occur in the upper part of the section, while the other value is high and occurs near the base of the section studied. Without those extreme values, analysis of variance would fail to reject the null hypothesis at a significance level of five percent. That suggests that, except for a few isolated circumstances, a period of stasis with respect to the mean intercuspal angle of the population developed during the interval.

A plot of core depth versus the mean intercuspal angle for data from section 65GV was compared to a plot of core depth versus the relative abundance of Phragmodus undatus as a constituent of the Midcontinent fauna (Figure 5). The relative abundance ranges from 24 percent to 89 percent in the interval of the section studied. Fluctuations occur persistently and tend to display no prolonged trends. The mean intercuspal angle tends to vary about a relatively constant value during the same interval. No obvious correlation can be discerned from the graphs.

A regression analysis was run on the intercuspal angles using relative abundance as the regressor variable.

An r-correlation coefficient of 0.042 was obtained for the data. The t-test on this value failed to reject the null hypothesis that there is no correlation between the variables at the ten percent significance level with 448 degrees of freedom. Linear correlation between the mean intercuspal angle and the relative abundance of *Phragmodus undatus* can not be maintained for the interval of section 65GV.

DISCUSSION

As summarized by Sweet (1979) and maintained by other authors (Seddon and Sweet, 1971; Bergström, 1971; Barnes et al., 1973; Barnes and Fahraeus, 1975), *Phragmodus undatus* represents a relatively deeper water species of the Midcontinent fauna.

In Middle and Upper Ordovician rocks of the Cincinnati Region, the exterior subprovince of the North American Midcontinent Province is represented by a conodont fauna consisting primarily of species of *Phragmodus*, *Plectodina*, *Aphelognathus*, *Oulodus*, and *Rhipidognathus* (Sweet, 1979). The southern part of that region is dominated by *Aphelognathus*, *Oulodus*, and *Rhipidognathus*, in rocks regarded by Kohut and Sweet (1968) as having been deposited in relatively shallow water, based on lithic features and relative abundance. The northern part of the Cincinnati Region is considered to have been a relatively deeper-water depositional site, and its conodont fauna is dominated by *Phragmodus* and *Plectodina*. Occurrences of *Plectodina* and *Phragmodus* suggest that *Plectodina* inhabited shallower waters than *Phragmodus*, and that *Phragmodus* was the relatively deeper-water species of the Cincinnati Region.

Samples from the lower part of section 70ZA, beginning at the base of the Lexington Limestone, are dominated almost completely by elements of *Phragmodus undatus*. Relative-abundance values range from 91 percent to 100 percent, with a majority of values at 99 percent and 100 percent. Successively younger rocks in the section contain generally decreasing percentages of *P. undatus* and increasing percentages of other species characteristic of the exterior subprovince of the North American Midcontinent Province. That trend suggests that environmental conditions, altered by a general shallowing of water in the region, favored successively shallower water species. Those specimens of *P. undatus* present under changing environmental conditions would tend to represent forms better suited to the altering circumstances.

A plot of the mean intercuspal angle of the phragmodontiform element of *Phragmodus undatus* reflects a general trend in samples of section 70ZA. A decrease in the mean intercuspal angle within the interval of the section studied correlates with the decrease in relative abundance of *P. undatus*. That correlation suggests that relatively smaller-angled forms were better adapted to increasingly shallower-water conditions and were able to persist in the area longer, thus contributing increasingly greater percentages to the population mean intercuspal angle. Larger-angled forms would tend to migrate to deeper waters more suitable to their morphology.

The portion of section 65GV studied represents an interval equivalent to the upper 135 feet of section 70ZA, but extends an additional 145 feet above. A comparison of mean intercuspal angles during the interval of stratigraphic overlap shows the 65GV section to have a greater value by about three degrees. That conforms with the expectation that a generally shallower water area, as represented by section 70ZA, contains a population with a smaller mean intercuspal angle.

The interval represented by section 65GV contains populations with a mean intercuspal angle that remains essentially constant within the limits of variation. During the same interval, the relative abundance of *Phragmodus undatus* fluctuates within a range from 25 percent to 89 percent. No correlation is apparent between the mean intercuspal angle and the relative abundance. That suggests that the interval of section 65GV represents a situation different from that of section 70ZA. A period of stasis seems to have occurred, in which *P. undatus* existed in approximate equilibrium with respect to paleoenvironmental factors as affected by water depth. Relative-abundance values suggest that the water depth at this site experienced no long-ranging trends during the interval studied. No paleoenvironmental factors persisted in such a way as to further drive away relatively larger-angled forms in an already angle-reduced population. The result is a sequence of populations with approximately equal mean intercuspal angles, generally reduced from the means of prior populations as paleoenvironmental factors favored smaller-angled forms during the prior interval. No further reductions in the mean intercuspal angle of the population occurred as water depth stabilized around a general level.

The data suggest that paleoenvironmental factors as controlled by water depth, influenced the population of Phragmodus undatus such that the mean intercuspal angle decreased. However, no indication is apparent from the data to specify what factors were responsible for that trend in P. undatus. Seddon and Sweet (1971), and Barnes and Fahraeus (1975) suggested that temperature, salinity, and possibly food availability may have exerted strong controls upon the life habits and morphology of conodonts. Hydrostatic pressure, abundance of dissolved gases, and water turbulence may have posed additional problems. The relative effects of any of those factors can not be determined from the data evaluated in this paper. More extensive studies will have to be done on this problem in order to evaluate the various effects of different factors.

CONCLUSION

Data from one measured character of the conodont *Phragmodus undatus* suggest a general relationship to paleoenvironmental factors as affected by a shallowing of the water column. A persistent shallowing of the Cincinnati Region during Middle and Upper Ordovician is reflected by lithic characters and an increasing percentage of relatively shallow-water species in successively younger rocks. Those specimens of *P. undatus* that persisted in relatively shallower water tend to have smaller intercuspal angles. It is probable that other characters of the species were susceptible to the paleoenvironmental stresses occasioned by a shallowing of the water column. Such characters may help to suggest causal relationships between character trends and paleoenvironmental factors.

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