



MICROEVOLUTIONARY DYNAMICS OF THE EARLY DEVONIAN CONODONT *WURMIELLA* FROM THE GREAT BASIN OF NEVADA

Peter D. Roopnarine, Michael A. Murphy, and Nancy Buening

ABSTRACT

The morphologically smooth basal platform margin of one conodont element (P1) in the spathognathodontid ozarkodinidids is a key diagnostic feature for taxon identification. Differences in the shape of this margin have been used as the basis for genealogical delineation and the interpretation of evolutionary dynamics, yet very little is known of the morphological or ontogenetic processes that generate shape variation within the group over geological time. Furthermore, the absence of reliably recognizable geometric landmarks along this margin prevents the application of standard geometric morphometric techniques. This paper addresses these problems by developing a new method for the quantitative description of margin shape, analyzing the ontogeny of shape change within specific stratigraphic intervals, and describing the pattern of evolution of margin shape over geological time.

Specimens of the genus *Wurmiella* were obtained from the Windmill Limestone (Pragian) of central Nevada. The resulting morphometric data were used to discriminate three species within the samples, *Wurmiella wurmi*, *W. tuma*, and a currently undescribed species, *W. n. sp.* The taxa are differentiated both on the basis of overall shape, as well as differences in margin allometry as described by spline shape and size (recorded separately as centroid size). An examination of evolutionary pattern in the *W. wurmi* samples, using a random walk-based technique, demonstrates that three independent aspects of margin shape evolved differently. The overall arch and relative position of the basal cavity were highly constrained and static, while the shape of the margin anterior to the basal cavity underwent an episode of significant directional evolution.

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KEY WORDS: conodont, *Wurmiella*, microevolution, morphometrics

INTRODUCTION

The long-term utilization of conodonts as one of the primary elements of Paleozoic and Triassic biostratigraphy has resulted in a database of stratigraphic information that far exceeds that available for any other Paleozoic or early Mesozoic metazoan taxon (Sweet 1988). The geographically and sedimentologically widespread distributions of many conodont taxa, the group's long stratigraphic history, and the stratigraphic density of the conodont fossil record make these organisms ideal targets for evolutionary paleobiological questions. The present paper applies these properties of the conodont record to long-standing questions of microevolutionary dynamics, an exercise not unique to this paper (for example, Murphy et al. 1981), but one that has not been disseminated broadly into the mainstream paleobiological literature. In turn, current ideas and techniques of morphometric analysis and the analysis of fossil time-series (Roopnarine et al. 1999; Roopnarine 2001) are applied here to the study of the Lower Devonian genus *Wurmiella* from the Great Basin of Nevada.

Microevolutionary Studies

Patterns of microevolutionary change are of central importance to our understanding of organismal diversification over geological time. While the time-scale of microevolution challenges the finest temporal resolutions available from the fossil record, the major theory of diversification (that is, the origin of species by natural selection) claims that microevolution is fundamental to the production of new diversity. On the other hand, more recent macroevolutionary hypotheses such as species selection (Stanley 1975) and the possible random nature of mass extinction events (Gould 2002) have called into question the degree to which microevolutionary processes might exert any control over long-term patterns of diversity. The fossil record remains one of the primary sources of information capable of resolving the conflict between a strict Darwinian view versus hierarchical approaches to selection as a structuring agent in diversification. Accessing this information, however, requires work at the finest stratigraphic resolutions available, detailed quantitative morphological analyses, and objective assessments of microevolutionary series.

Evolutionary change and character variation can be expected to be largely continuous and quantitative as temporal intervals approach generational timescales. Two questions of great importance to understanding the role of microevolution in

macroevolutionary phenomena are 1) the extent to which character variability within ancestral populations determines variation among descendant species, and 2) whether within-species evolution is at all relevant to the differences among species. The first question addresses variation at the organismal level, such as ontogenetic change and the processes of ontogenetic change, for example allometry, heterochrony and heterotopy. The second returns to one of the central arguments of punctuated equilibrium theory, and that is the restriction of major morphological change to times of speciation (Gould 2001). Whether most of the geological span of a species is characterized by constrained stasis (Roopnarine 2001) or oscillatory 'no net change' evolution, the implication is that speciation, as identified by a significant morphological discontinuity, is essentially independent of intraspecific evolution. These issues should be addressed by high resolution, quantitative studies of intraspecific morphological change, coupled with methods appropriate for the classification of microevolutionary modes. This paper addresses both these issues, examining within-sample variation, as well as stratophenetic change in *Wurmiella*.

The highly variable P1 element forms the basic means of taxonomic differentiation in ozarkodine conodonts (Sweet 1988) (Figure 1). The shape and outline of the lower profile of the element is a key feature supporting taxonomic and phylogenetic hypotheses (Murphy et al. 1981) and is the focus of analysis in this paper. The lower profile, however, is a curved or sinuous structure with very few discrete landmarks and therefore does not lend itself to a typical geometric morphometric approach (Bookstein 1991). Here we present a new method combining a landmark approach and a spline-based description of the P1 element's basal platform in lateral profile. The technique relies on the presence of two geometrically homologous landmarks on the element's platform to convert spline coordinates to Bookstein-style shape coordinates for subsequent analysis of within-sample dispersion and allometry, and among-sample discrimination. Finally, the evolutionary mode of the stratigraphically ordinated samples is classified using the Hurst-estimation method outlined in Roopnarine (2001).

SYSTEMATIC PALEONTOLOGY

Phylum CHORDATA Bateson, 1886
 Class CONODONTA Pander, 1856
 Order OZARKODINIDA Dzik, 1976
 Family SPATHOGNATHODONTIDAE Haas, 1959

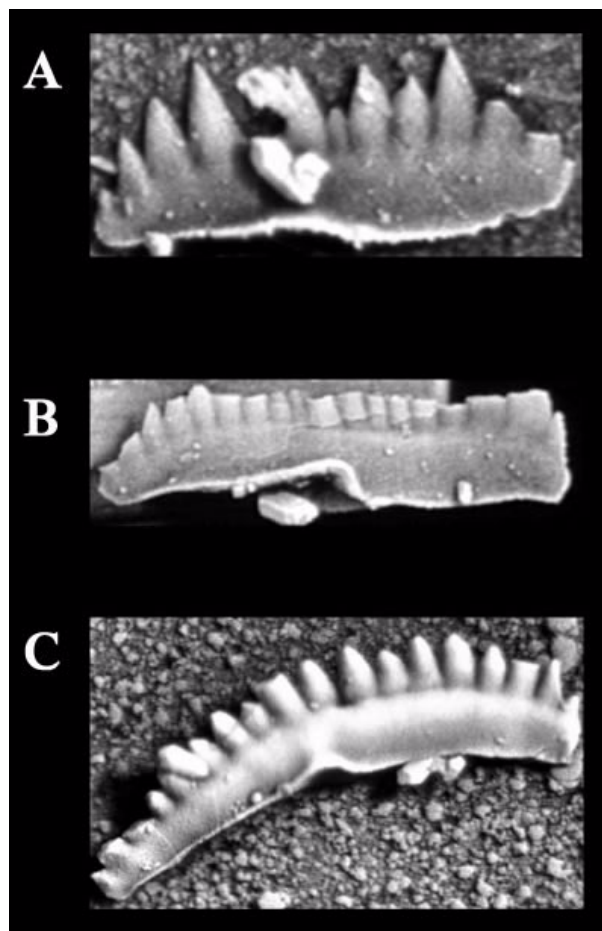


Figure 1. *Wurmiella* P1 elements. A) *Wurmiella tuma*; B) *W. wurmi*; C) *W. n. sp.* All specimens approximately x90.

Genus WURMIELLA Murphy, Valenzuela-Ríos, and Carls, 2004

Type Species. *Wurmiella tuma* (Murphy and Cebecioglu 1986).

The systematics of *Ozarkodina* (Branson and Mehl 1933) was reviewed recently (Murphy et al. 2004) and the group of forms that have an apparatus similar to that of *O. excavata* (Branson and Mehl 1933) were classified in the genus *Wurmiella*. These authors envisioned four long-ranging lineages as constituting the main taxonomic units within the genus (Murphy et al. 2004). Here we use Murphy et al.'s (2004) conclusions as our working hypothesis as we consider the two lineages that occur in the middle Lochkovian, *W. wurmi* and *W. tuma*, and identify a third, *W. n. sp.*, that was unrecognized by those authors (Figure 1).

The genus is characterized by the simple blade with rather even sized denticles and generally small expansion of the basal platform of the P1 element and the similarity of its apparatus, especially the Pb elements with their very high cusps, the

even curvature of the M elements and the incrementally larger posterior denticles of the Sc element.

Wurmiella wurmi (Bischoff and Sannemann 1958)

Holotype by original designation = *Spathognathodus wurmi* Bischoff and Sannemann, 1958, pl. 14, fig. 5.

Diagnosis. A species of *Wurmiella* with a combination of the following characteristics in the P1 element: biconcave to convexo-concave lower profile in lateral view, moderate shoulder with or without a denticle on the shoulder on the inner side of the blade or without a shoulder; ledge at the base of the denticle row; 17-27 denticles depending on the size and stratigraphic level of the specimen.

Description. P1 element gently twisted, slightly more strongly near the extremities; basal cavity small, asymmetrical, with inner side more expanded; basal grooves appressed at their distal ends and with straight anterior segment in smaller specimens; lower profile in lateral view biconvex to convexo-concave; upper margin in lateral view biconvex; cross section of blade (below the denticles) low walled, thick at maturity; ledge normally developed on inner side at base of denticles; flanks of blade inflated below ledge and with a narrow pinch zone close to the lower margin; height of both parts (anterior and posterior) of blade about equal; thicker (wider) and higher denticles concentrated near the centers of anterior and posterior parts of blade; at the position of basal cavity ledge bulges laterally to form shoulder on inner side of some specimens and in some specimens on both inner and outer sides; denticle number varies from 17-27, counting all germ denticles and depending on the size of element; denticles straight, stout, with elliptical cross sections, and blunt to moderately sharp tips.

Comparison. *Wurmiella wurmi* differs from *W. excavata* in the greater number of denticles and the biconcave lower margin of the blade that is angulate in *W. excavata*; from *W. n. sp.* in having a biconcave lower margin as opposed to a uniformly arched one, and a basal platform with a well-developed inner lip and shoulder above it.

Discussion. We have recognized three common morphs in this taxon that may be of restricted stratigraphic distribution and, thus, broad diagnosis. They are 1) the type or tau morph (τ) with a well-developed inner shoulder and strongly biconvex lower profile; 2) the alpha morph (α) with a denticle developed on the shoulder; and 3) the beta morph (β) without a shoulder and fewer denticles.

***Wurmiella* n. sp.**

Diagnosis. A *Wurmiella* species based on P1 elements with the following combination of characters: arched lower profile; element bowed or twisted in upper view; basal cavity small, asymmetrical, only slightly or not at all expanded on the inner side.

Description. Element gently bowed in basal view, slightly more strongly near the extremities; basal cavity very small to small, asymmetrical with expansion at base on outer side of blade; basal grooves appressed or open to inverted in some morphs; lower profile moderately arched with somewhat stronger curvature in posterior portion of the element; flanks moderately inflated with narrow pinched zone at base; blade height short with posterior shorter than anterior half; upper profile biconvex with broader and higher denticles concentrated around the position of the cusp and in the anterior one third of element; a slight ledge may be developed at base of denticles; denticle number varies from 17-22 counting all germ denticles depending somewhat on size of element.

Comparison. Differs from *W. excavata* in the more strongly arched and bowed blade and greater number of denticles; from *W. wurmi* in having an arched as opposed to a biconcave lower profile, and in lacking a shoulder.

METHODS**Samples and Collection**

Conodont samples were collected from more than 70 superposed beds within the Lower Devonian Windmill Limestone (Lochkovian) (Johnson 1970) at the SP-VII section, Coal Canyon, northern Simpson Park Range, central Nevada (Berry and Murphy 1975; Murphy and Berry, 1983). The SP-VII section exposes a regressive sequence that begins in the upper part of the deep-water, graptolitic Roberts Mountains Formation and the overlying allodapic carbonate and interbedded shale slope deposits of the Windmill Limestone (Johnson and Murphy 1984). The section is very fossiliferous in both formations with a well-documented sequence of graptolite (Berry and Murphy 1975), conodont (Murphy and Matti 1983), brachiopod (Johnson 1973), and ostracode (Evola 1983) faunas that have served as the basis for zonation of the middle Lochkovian and as a standard of reference for the interval (Murphy and Valenzuela-Ríos, 1999). The SP-VII section has been correlated previously to the Copenhagen Canyon section of the Monitor Range (COP IV-V), the latter section serving as a standard reference for the region (Murphy and Berry 1983). The section spans approximately

10 million years of the Lower Devonian (graptolite Zones *uniformis*, *praehercynicus*, and *hercynicus*).

Specimens of *Wurmiella* were recovered from more than 50 beds, of which 15 with adequate sample sizes (> 10 specimens) were selected as the basis of the present statistical work. The lowest stratigraphic level sampled is denoted as sample 200, but thereafter stratigraphic levels (samples) are enumerated 8 to 15 in ascending stratigraphic order, with sublettering (for example, 9H) indicating successively higher samples. *W. wurmi* was not included in the derivation of the graphic correlation relationship between sections SP-VII and COP IV-V.

Standard Spline Analysis

The smooth morphology of the element basal platform margins, and the absence of all but two geometrically homologous Type I landmarks (Bookstein 1991) (Figure 2) means that much of the information of morphological variation is encompassed in the outline of the margin. A cubic spline was used to describe the platform margin outline and hence capture the variation (Roopnarine et al. 2001).

Individual elements were imaged in lateral view with a Pulnix electronic CCD camera mounted on a Wild dissecting microscope. Elements were imaged in a consistent lateral orientation with the element blade coplanar to the camera. This was accomplished by mounting micropaleontological slides on a stage capable of movement in three dimensions. The lateral margin of the platform was digitized using TnImage for Linux; the number of points used to describe a particular margin depended solely on the complexity of the margin and therefore varied among individual specimens. The digitized points were then converted to Bookstein-style shape coordinates by the sequence of translation, rotation and rescaling (Bookstein 1991), the anterior and posterior ends of the basal cavity (the two Type I landmarks), which spans the length of the element; these points serve as the anchors of the baseline (Figure 3). The shape of each margin was then reconstructed by fitting a cubic spline to the shape coordinates, and the spline standardized by computing new coordinates at fixed x-axis intervals. Intervals of 0.02, ranging from 0 to 1, were used for this study, resulting in each margin being described by 51 standard spline coordinates, of which two are redundant among specimens (the baseline anchors). The result is that all specimens vary in the y-dimension only. Use of a cubic spline to reconstruct the margin outline ensures a smooth reconstruction while minimizing the curvature between points; the result is

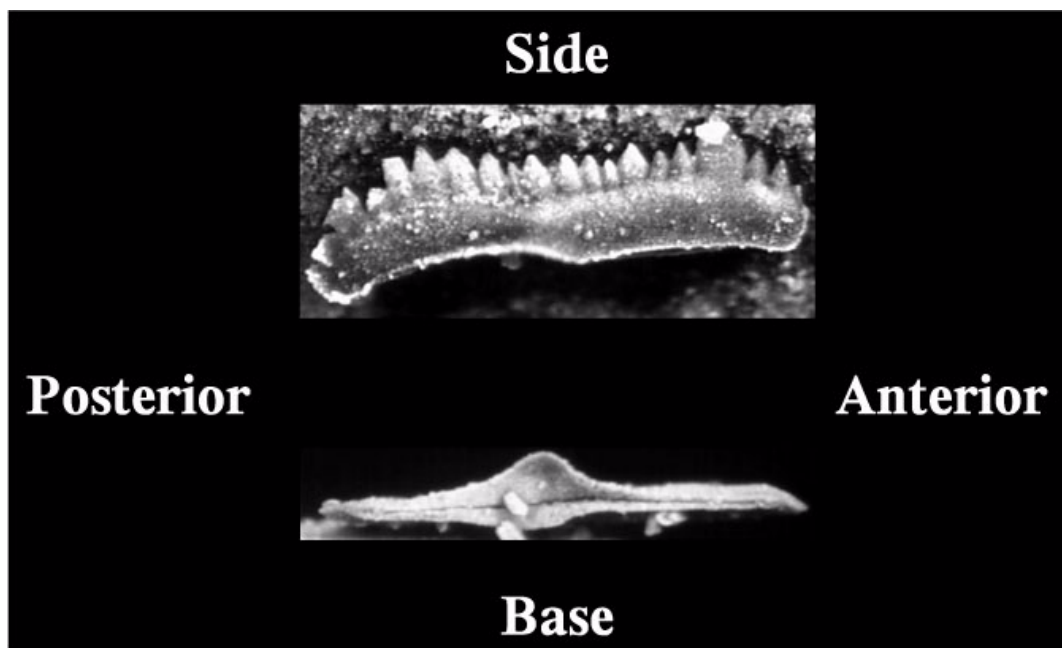


Figure 2. Lateral (upper) and basal (lower) views of a P1 element of *Wurmiella wurmi*. Double-headed arrows indicate the landmarks (anterior and posterior) at which the left and right lateral margins meet, representing the anterior and posterior tips of the basal cavity.

that no extraneous information is added to the description of the outline. The standard spline approach also eliminates the necessity of a fixed number of digitized points per outline, as generally required if digitization follows a fixed angle sampling approach or the outline is divided into a fixed number of equally spaced points.

Singular Value Decomposition and Cross-Validation Analysis

Sample homogeneity/heterogeneity was assessed using singular value decomposition (SVD) of mean centered standard spline matrices (Sampson et al. 1996). Each sample was centered by representing specimens as deviations from the sample mean spline. The structure of this matrix of deviations was then examined with SVD analysis, the resulting eigenvectors of which characterize the major regions of dispersion of the splines within the sample. Each specimen was also given a score or location on each eigenvector (a function of the variable loadings on the eigenvector), the value of which reflects the shape of the spline (Figure 4). The resulting distribution of specimen scores is therefore a measure of sample homogeneity, and this is tested further with a cross-validation analysis of the SVD.

The cross-validation analysis proceeds by removing specimens from the sample one at a time (with subsequent replacement) and reconducting the SVD with each removal. Any specimen that is a statistical outlier is expected to exert significant

influence on the results of the full-sample SVD (Reyment and Jöreskog 1996). Its removal will result in significant alteration of the SVD eigenvectors, and this is detected as a reduction in the correlation between reduced-sample SVD eigenvectors and full-sample eigenvectors.

Ontogenetic Allometry

The exact manner in which the P1 element increases in size remains unknown, but the lamellar cross-sectional patterns of many conodont elements suggest that they grow by expansion around the basal cavity. Growth is not by simple accretion, since element shape changes, and structures such as denticles are added as size increases. Quantifying element shape and shape variation within a sample presents an opportunity to describe ontogenetic shape change in a precise manner for the first time.

The relationship between size and shape of the platform margin was examined as the relationship between centroid size, SVD scores, and spline shape coordinates. The correlations between significant SVD eigenvectors (determined as proportion of sample variance explained by each eigenvector) and centroid size were measured, a significant correlation indicating significant shape change with changing size, that is, allometry. Following the detection of allometry, the actual associated changes in shape are measured with a multivariate regression of the shape coordinates on

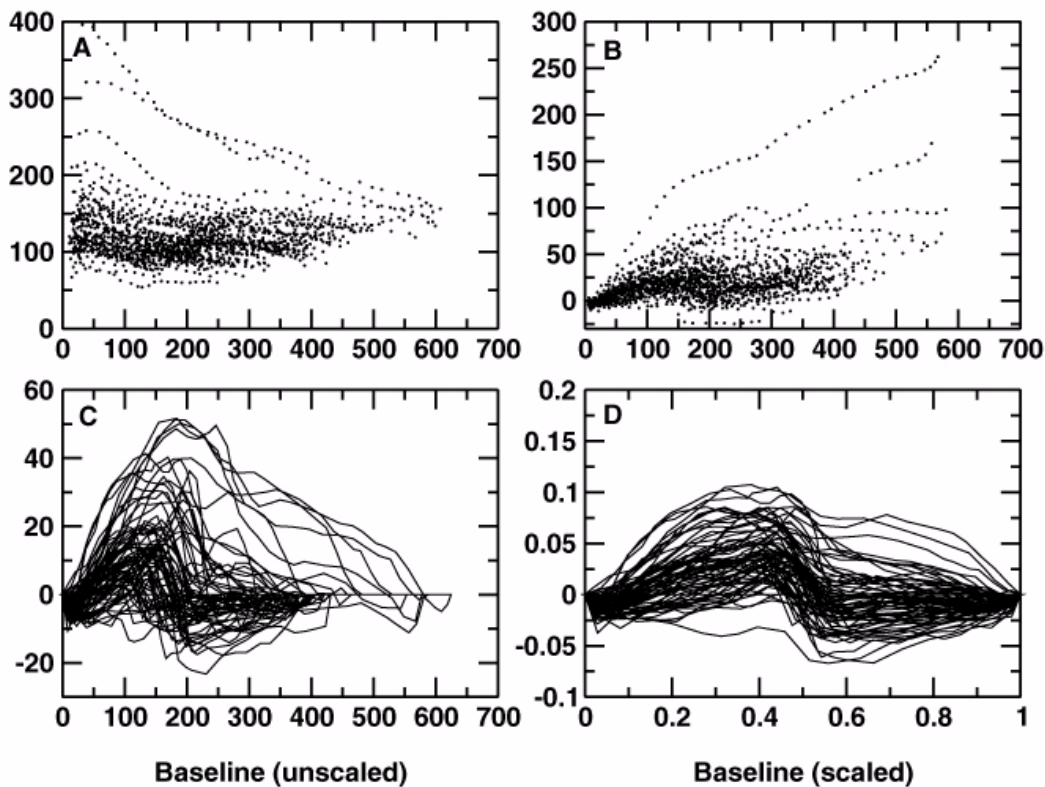


Figure 3. Conversion of digitized coordinates to outline shape coordinates. A) raw digitized coordinates; B) translated raw coordinates; C) rotated coordinates; D) rescaled shape coordinates. Axes are coordinate axes only and have no biological meaning until the baseline is established for the x-axis.

centroid size and calculation of predicted spline shapes throughout the size range of the sample.

Mode of Evolution

Describing the mode of evolution of *W. wurmi* during the time represented by the SP-VII section is a three-step procedure. First, all the samples must be aligned stratigraphically and placed on a common temporal scale. In this case, the samples were placed on a composite stratigraphic scale derived from the graphic correlation of SP-VII with another section of the Windmill Limestone, COP IV-V (Copenhagen Canyon area). COP IV-V has served as the standard reference section for much of the biostratigraphic work that has been conducted on the Windmill Limestone sections in this area (Murphy and Berry 1983). Second, the samples are ordinated within a common multivariate space to facilitate standard inter-sample comparisons. This was accomplished with a canonical variates analysis (CVA) of the sample SVD scores, which tests both inter-sample discrimination (with a prior multivariate analysis of variance [MANOVA]) and ordines specimens according to their canonical or Mahalanobis distances.

Evolutionary pattern, and consequently mode, cannot be determined from visual inspection of stratophenetic series, nor from straightforward statistical comparisons of net differences over a stratigraphic interval. The likelihood of random walks meeting criteria of directionality under such conditions, yet with no underlying deterministic mechanisms, precludes such approaches (Bookstein 1988). A random walk and randomization technique (Roopnarine 2001) was therefore used to search for non-randomness in the SVD I-III stratophenetic series. Evolutionary mode of *W. wurmi* in the SP-VII section was determined by analyzing the temporal passage of the samples through the conodont lower profile morphospace as described by SVD analysis of the samples. The analysis used here measures the deviation of the stratophenetic series sample means from the expectation of a random walk through the morphospace. It proceeds by measuring the pattern or the information content of the series with an estimation of the Hurst component, which is in fact a measure of the fractal dimension of the passage. The relationship of the calculated Hurst estimate to that expected of a random walk is tested with com-

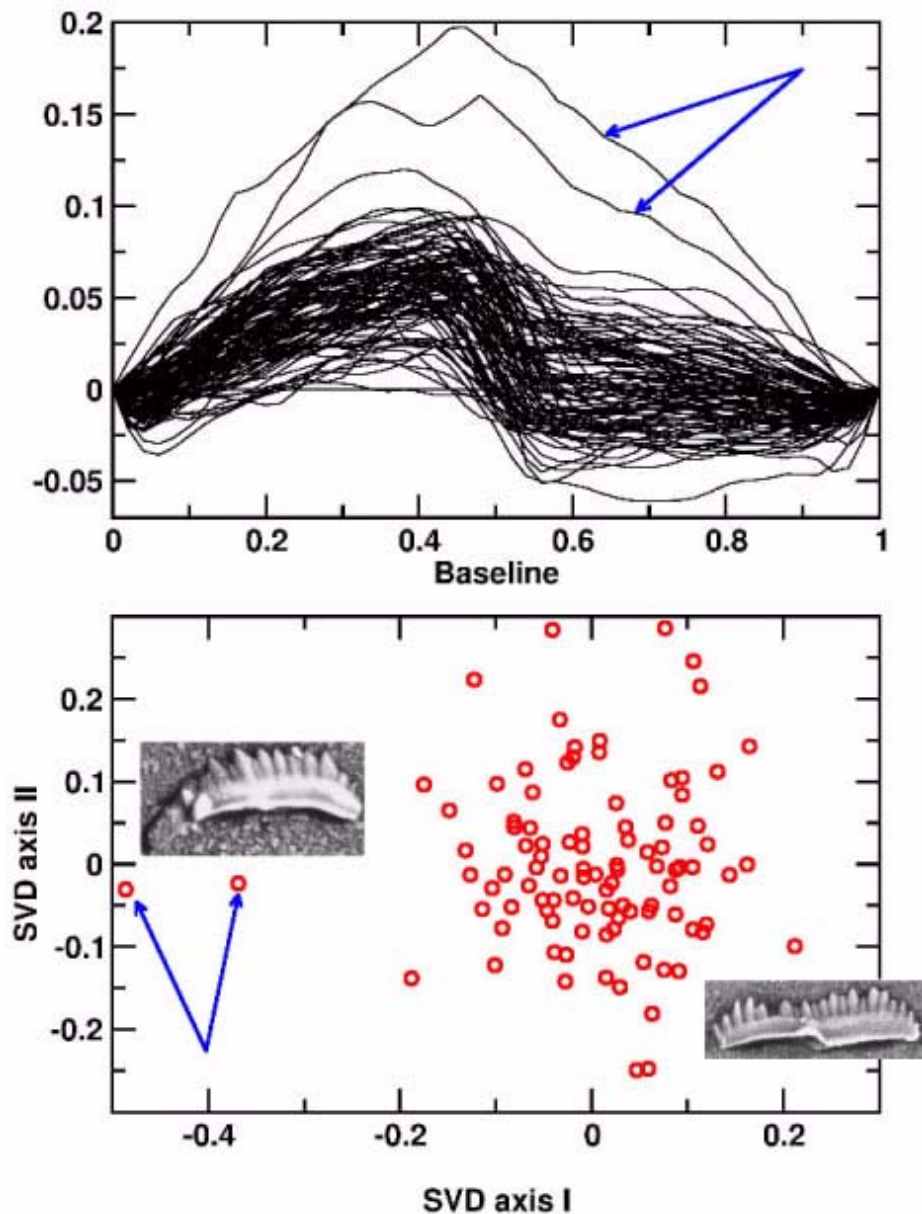


Figure 4. Standardized margin splines (upper) from a single sample illustrating an overwhelmingly common morphology, and the presence of two possible outliers. Y-axis represents variation in profile shape. Lower figure plots the specimen scores on the first two SVD axes, with an example of the common morphology, and the less common arched profile of the two outlying specimens.

parison of the estimate to a distribution of estimates derived from repeated randomization and re-analysis of the stratophenetic series. Any stratophenetic series so analyzed may then be classified as significantly directional, random, or constrained (static). The entire procedure is described in greater detail in Roopnarine (2001).

The standard spline analysis, SVD and cross-validation SVD analyses were performed by programs written in C++ and Octave for Linux, while other statistical analyses were performed with

Stata-SE 7.0 for Linux and SYSTAT 10 for Windows. The Hurst estimation analysis was performed with Enigma-1.0 for Linux (Roopnarine 2001).

RESULTS

Sample Composition and Discrimination

Singular value decomposition analysis and cross-validation SVD were performed on each stratigraphic sample to examine sample homogeneity

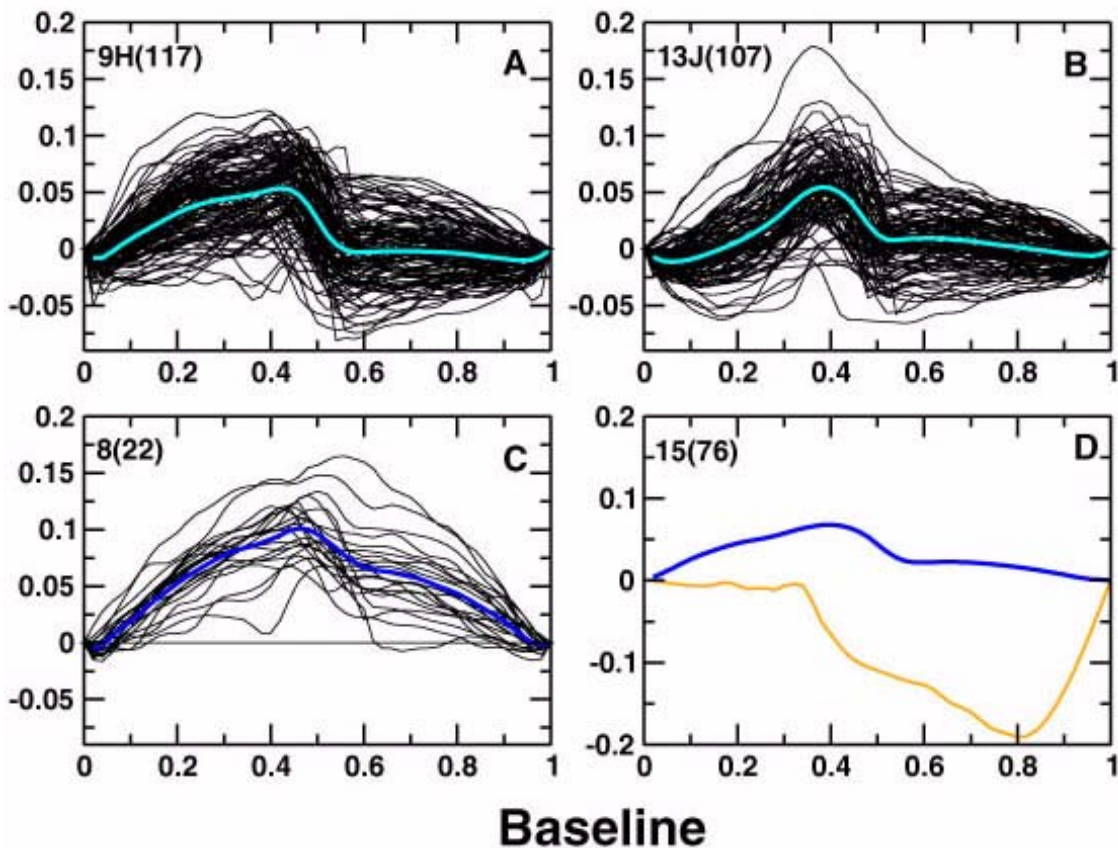


Figure 5. Four morphotypes discovered in the section by the standard spline analysis, corresponding to A) *Wurmiella wurmi*; B) *W. tuma*; C) *W. n. sp.*; and D) a single aberrant individual. Labels in upper left corners of graphs denote stratigraphic samples. Bold aqua and blue lines represent the mean spline of the sample, while the orange spline of the lower right graph illustrates the single aberrant specimen.

and detect possible outliers. Most samples were homogeneous and without outliers, and the majority of specimens per sample can be assigned to a single variable species. Throughout the section, however, there are three distinct morphotypes. The most common morphotype has a lateral profile that is concave posterior to the basal or central cavity and horizontal anterior to the cavity (Figure 5A). These specimens are assignable to *Wurmiella wurmi*. The second morphotype is distinguishable from *W. wurmi* by having a convex profile posterior to the basal cavity and is assignable to *W. tuma* (Figure 5B), first described by Murphy and Matti (1983) as a subspecies of *Ozarkodina excavata* and was later elevated to species status (Murphy and Cebeçioğlu 1986) on the basis of differences in denticulation frequency. *W. tuma* is stratigraphically restricted, and Murphy and Cebeçioğlu (1986) hypothesized that it is a cladogenetic descendant of what was considered by these authors to be *O. excavata* (= *W. wurmi*). There is no stratigraphic overlap between the two morphotypes, with *W.*

tuma occurring in only a short interval in the upper portion of the section. The third morphotype comprises individuals with significantly concave arches, and while it is dominant in only one sample (8), additional individuals do occur infrequently throughout the section. This morphotype is clearly and statistically distinct from the common *W. wurmi* morphotype in the section, though it has been repeatedly referred to that species in the past (for example, Murphy and Cebeçioğlu 1986). It is designated here as a potentially new species, *W. n. sp.* (Figure 5C). Finally, there is a single aberrant individual in sample 15 that is not yet assignable to a described taxon; similar specimens do not occur anywhere else in the section. This specimen is not included in further analyses.

A multivariate analysis of variance and canonical variates analysis were performed on the pooled SVD scores of each morphotype in order to compare the morphotypes. Results indicate that all morphotypes differ significantly (Wilks' $\lambda=0.441$, $p<0.0001$) (Figure 6) and the morphological dis-

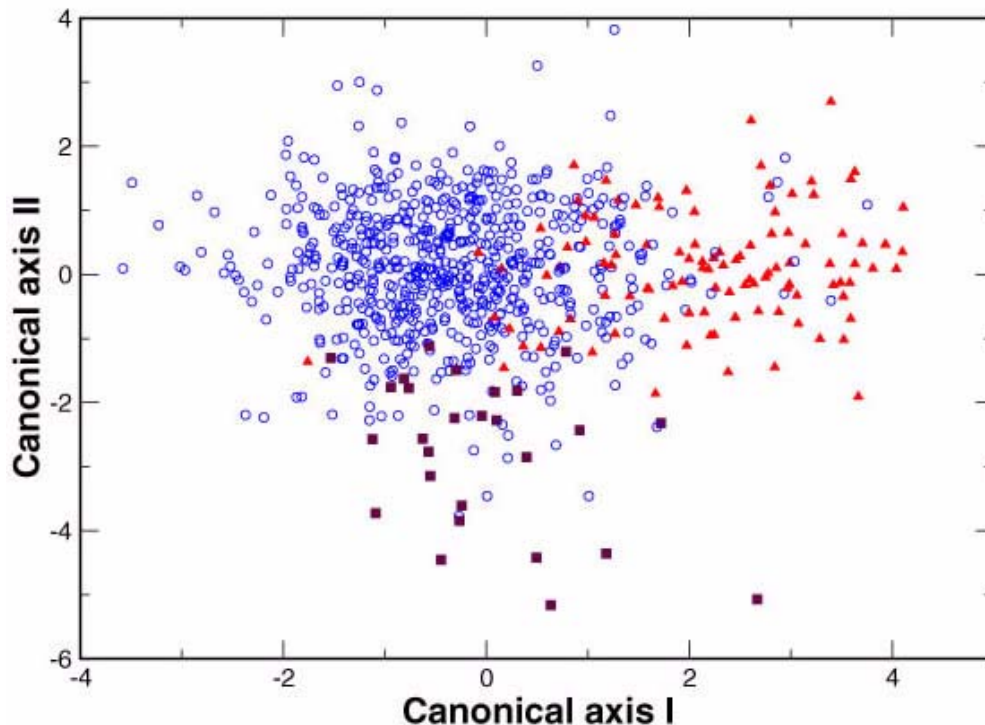


Figure 6. Canonical variates analysis of three dominant morphotypes (Figure 4). The three taxa are morphologically distinct from each other. Symbols, circles - *Wurmiella wurmi*, triangles - *W. tuma*, squares - *W. n. sp.*

continuities suggest that they should be treated as individual taxa. SVD analysis of the multiple *W. wurmi* samples (first morphotype), however, yields no obvious discrimination *within* this taxon, though there is noticeable variation within individual samples.

Allometry

The quantitative description of shape variation and separate recording of size present the opportunity to examine static allometry in each sample. Most samples had broad size ranges and significant relationships between profile variability and size, and it was therefore possible to calculate allometric relationships for these samples and to predict shape throughout a sample's size range. In several cases there was no significant allometry within a sample, and in these instances the shape of a sample was summarized simply as the mean morphotype profile for that sample.

Figure 7 illustrates the allometries of the dominant morphotype in each sample. The first series outlines sample allometries of *W. wurmi* (morphotype 1). The general pattern throughout the samples is a change of margin shape, posterior to the central cavity, from very straight, to slightly basal-concave at the mean size. Further growth is relatively isometric (for example sample 10Li), or

involves either continued increase of concavity of the posterior margin (for example samples 14L and 15), and/or a posterior shift in the relative position of the central cavity (for example samples 8A-9E). These stratigraphically successive allometric patterns are interesting both from the standpoint of stability or stasis over brief stratigraphic intervals, as well as their fluctuation within the lineage over longer periods of time.

The highly arched *W. n. sp.* is present in significant numbers only in sample 8 and exhibits no allometric change. This may be a function of small sample size but is more likely caused by a narrow size range preserved within the sample. Finally, *W. tuma* (sample 13J) does exhibit allometry, with the concavity of the central cavity becoming more pronounced with increasing element size and also shifting to a more anterior relative position.

Microevolutionary Mode of *Wurmiella wurmi*

Samples of *Wurmiella wurmi* were discriminated from the other taxa on the basis of the canonical variates analysis (above). The pooled samples were subjected to a single SVD analysis in order to examine intraspecific variation and microevolutionary dynamics. The first three eigenvectors accounted for the majority of the variance in the pooled sample (58.23%) (Figure 8) and are

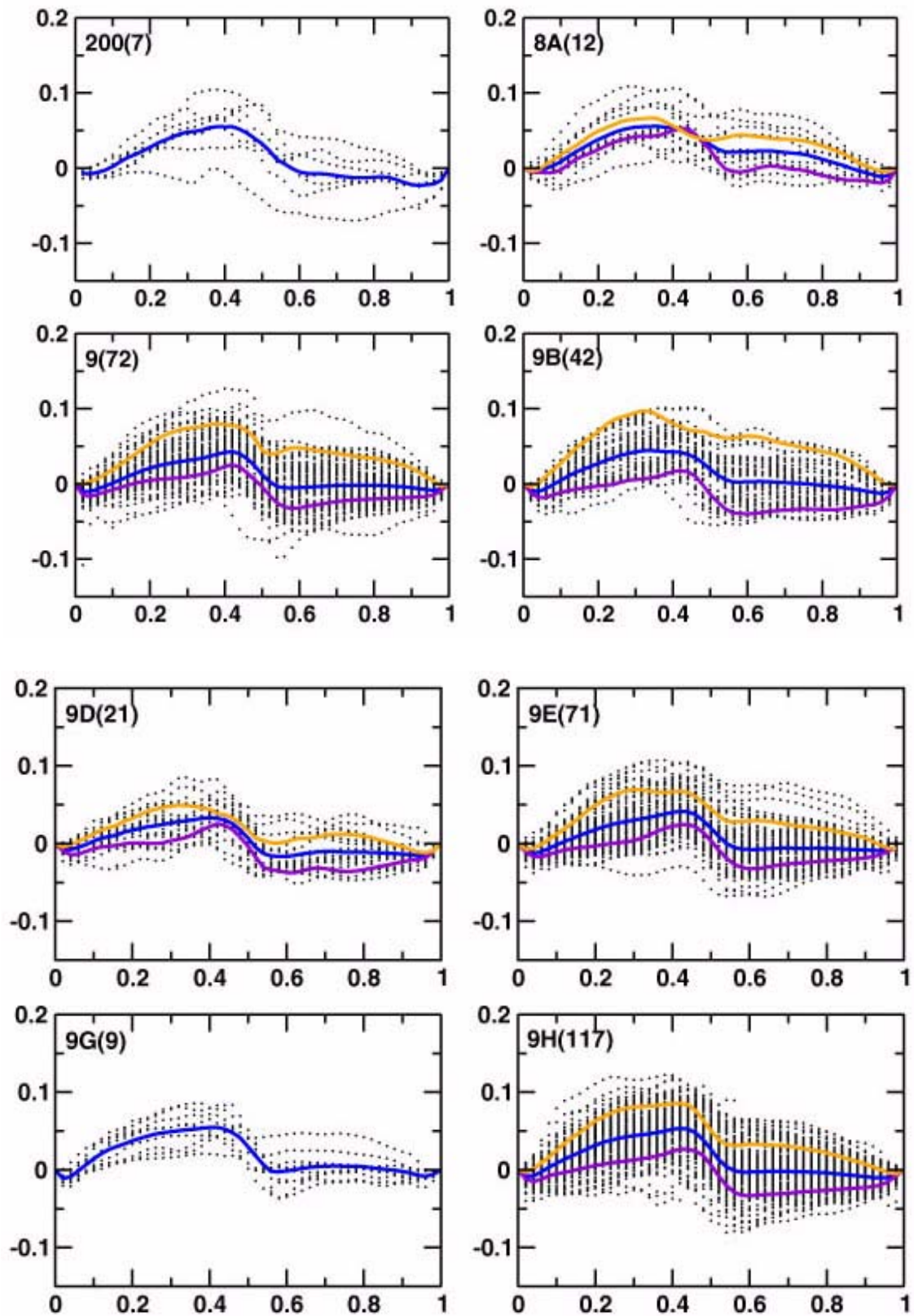


Figure 7. Allometric development in individual, single-taxon samples. Black dots represent individual specimens, whereas solid lines are least squares predictions derived from spline regressions on centroid size: violet-estimate of shape at lowest end of size range, blue-sample mean spline, orange-estimate from upper end of size range. Sample numbers are in the upper left corner. Samples 8 and 13J represent *Wurmiella. n. sp.* and *W. tuma* respectively, while all other samples are assignable to *W. wurmi*. Axes as in earlier spline figures.

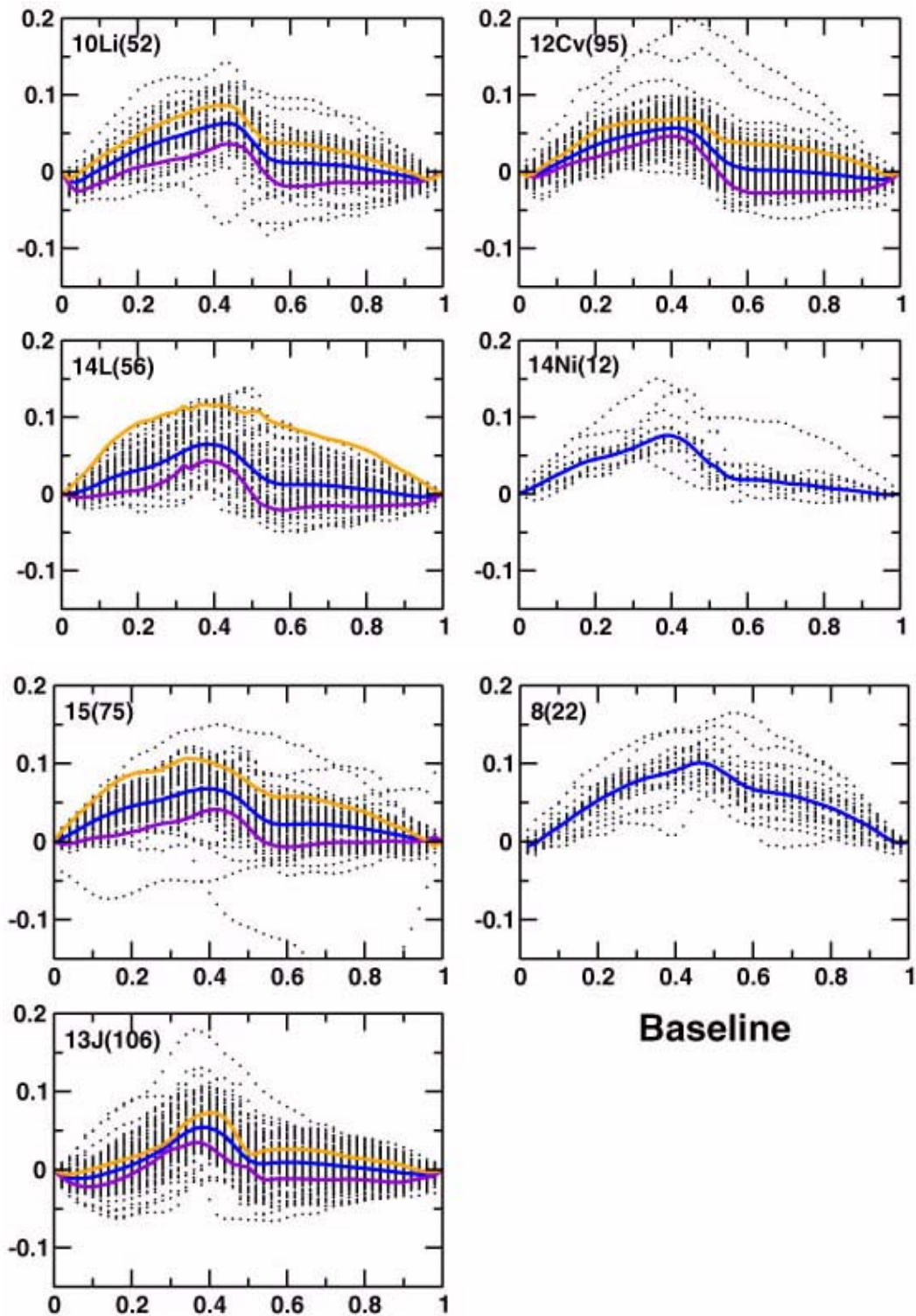


Figure 7 (continued).

the only eigenvectors considered for further analysis. The nature of the SVD analysis ensures that the eigenvectors are orthogonal, so they may be treated as independent characters in the analysis of microevolutionary pattern.

Sample distributions for each eigenvector are illustrated in Figure 9. Sampling is not distributed evenly along the stratigraphic section, due primarily to the relative scarcity of *W. wurmi* between stratigraphic composite units (SCU) 75 and 150;

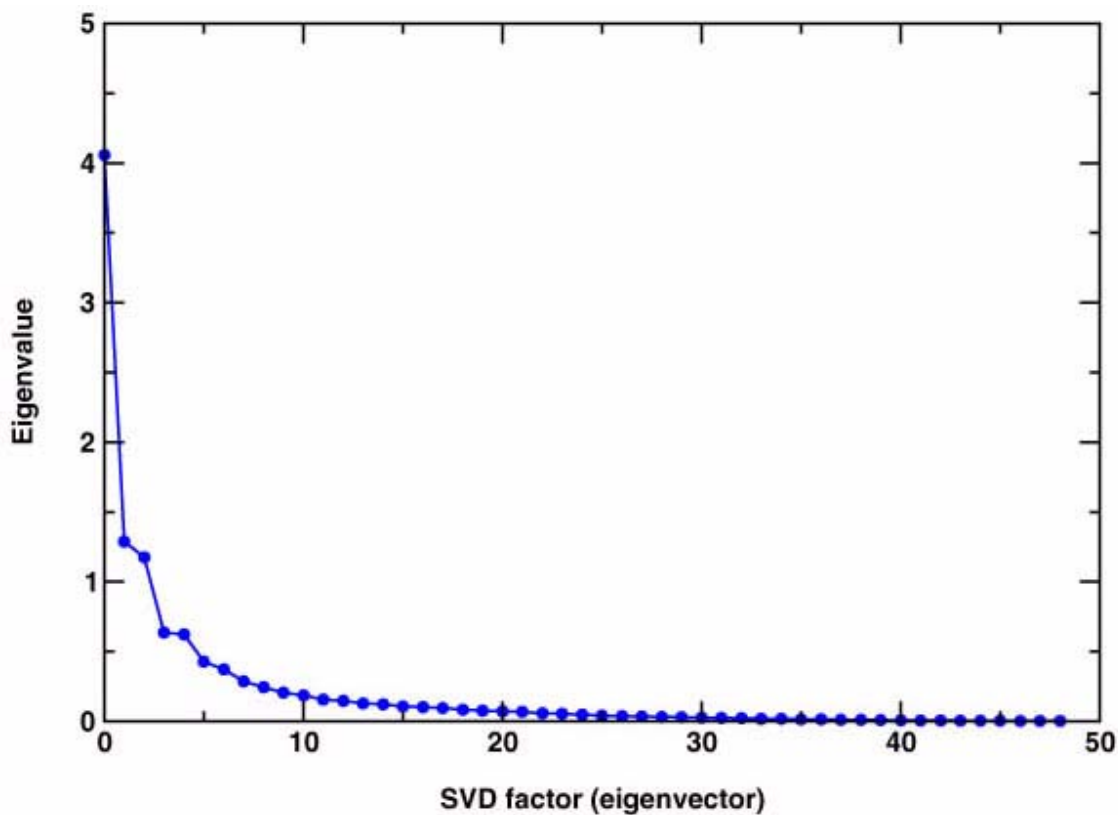


Figure 8. SVD eigenvalue magnitude versus eigenvector number showing rapid decline after the first eigenvector, and then after the second and third eigenvectors.

samples in that interval are generally specimen-poor, though current sampling efforts may remedy that situation in the near future. Each SVD axis represents a different aspect of margin shape, and it is obvious that the axes are not reflecting similar patterns of evolutionary change. For example, the first axis is a measure of the overall arch or concavity of the platform, the second axis contrasts concavity of the margin anterior and posterior to the basal cavity, and the third axis reflects the relative position of the cavity as well as the shape and concavity of the margin posterior to the cavity (Figure 9).

Visual inspection of the stratophenetic series in Figure 9 suggests several microevolutionary features. None of the characters seem to undergo net evolutionary change, though there are some suggestions of directionality. Analyses of the series using the Hurst estimation procedure (Roopnarine 2001) result in SVD I and III being categorized as static series. The SVD I trajectory moves very little as the series is analyzed (Figure 10A), and its very low Hurst estimate values are strongly suggestive of a morphology that is not varying randomly but is perhaps constrained. SVD III varies more than SVD I, and could be described as a classic stasis,

or 'no net change' type of pattern (Figure 10C). SVD II, however, exhibits significant directionality in the stratigraphic interval 25-50 SCU (Figure 10B), and this is documented by its trajectory's high values and relatively low probabilities of being generated by a random process (95% c.i. of minimum P value of the trajectory, $0.548 \leq P \leq 0.042$). Beyond that interval, however, the series becomes significantly constrained.

DISCUSSION

Species Discrimination

A quantitative description of the *Wurmiella* P1 element's basal platform in lateral profile, using the standardized cubic spline approach outlined in this paper, is useful for understanding the nature and levels of variation both within and among species of *Wurmiella*. Examination of the homogeneity of individual stratigraphic samples resulted in the detection of three distinct morphotypes within the SP-VII section, two assignable to the described species *W. wurmi* and *W. tuma*, and another belonging to an as yet undescribed species, *W. n. sp.* The standardized spline also leads to qualitative descriptions of the morphological differences

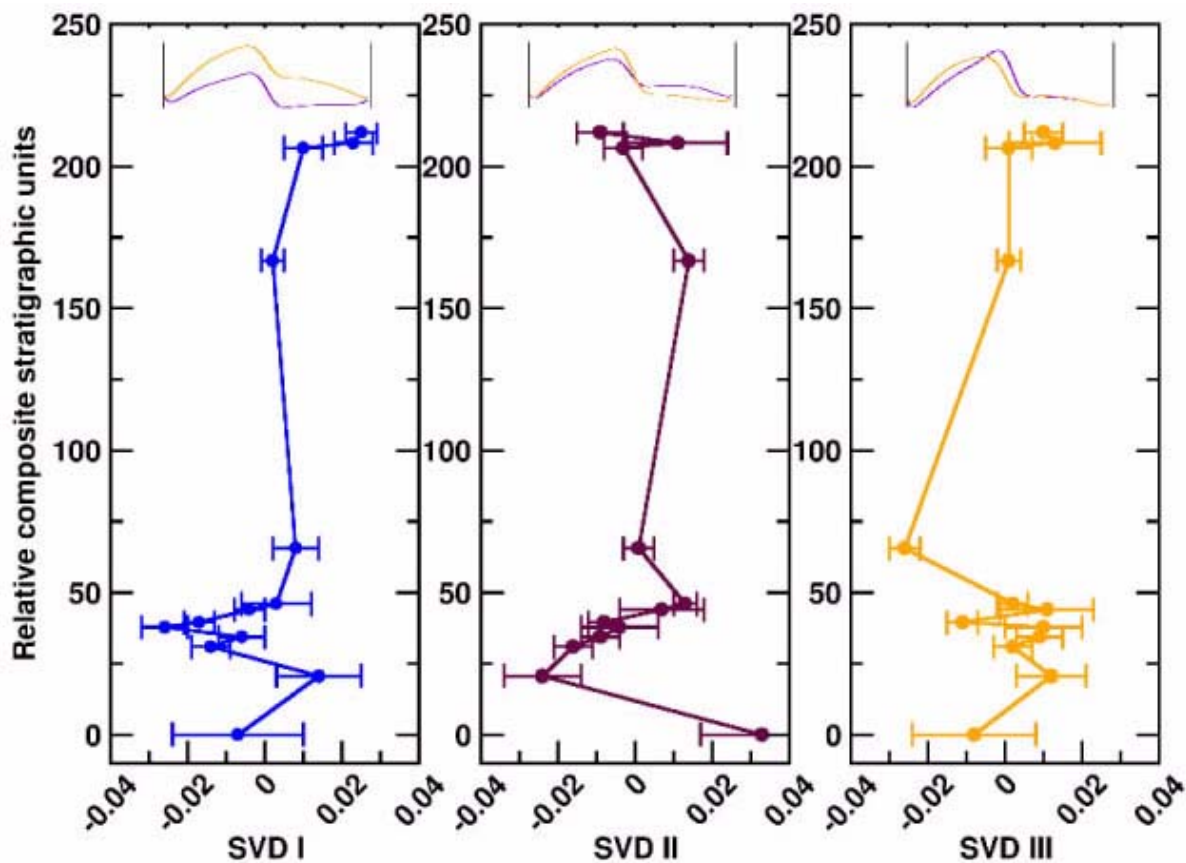


Figure 9. Stratophenetic illustrations of shape variability in *Wurmella wurmi* described by the first three SVD eigenvectors. Splines inset at the top of each column illustrate the range of variation described by the eigenvector and hence the aspect of margin shape being described.

among the taxa. *W. wurmi* differs from *W. tuma* primarily in the shape of the basal cavity in lateral view; the cavity is represented by a noticeably “pinched” region of the profile in *W. tuma*, while in *W. wurmi* it marks a change in the curvature of the profile between anterior and posterior regions. The new species is distinctly different, with a significant overall crownward arching of the entire element.

Ontogenetic Variation

The use of a geometric morphometric approach to description of the profile, including the calculation of Bookstein-type shape coordinates, allows a clean separation of geometric shape and scale. Rescaling according to geometric shape and scale. Rescaling according to baseline length removes scale information from the configuration of landmarks for each specimen thus placing all specimens on a fixed scale for the purposes of shape comparison. Scale information is recorded separately as the centroid size (Bookstein 1991) of the standardized but unscaled spline coordinates. Information regarding size may nevertheless be present in scaled geometric analyses because of the allometric covariation of shape coordinates and

centroid size. Allometric information was recovered in this study by examining the covariation of shape and centroid size, and reconstructing (via regression) “average” splines at three points in the size range for any single stratigraphic sample of an individual species. The points used were the minimum and maximum sizes, as well as mean size. Comparison of the resulting splines lead to a set of very interpretable graphics of shape change, during development, of any of the species at a particular stratigraphic level.

Using this analysis, one developmental feature common to both *W. wurmi* and *W. tuma* becomes obvious immediately; increasing size is associated with an increase in the degree of crownward arching of the element (Figure 7). The lack of detectable allometry in the single sample in which *W. n. sp.* is dominant (8) prohibits a similar comparison, but it is interesting to note that qualitative extrapolation of the growth trend of *W. wurmi* leads to both an increase in the degree of arching, as well as a shallowing of the basal cavity, a condition seen in all specimens of *W. n. sp.* We cannot yet determine the roles that these developmental

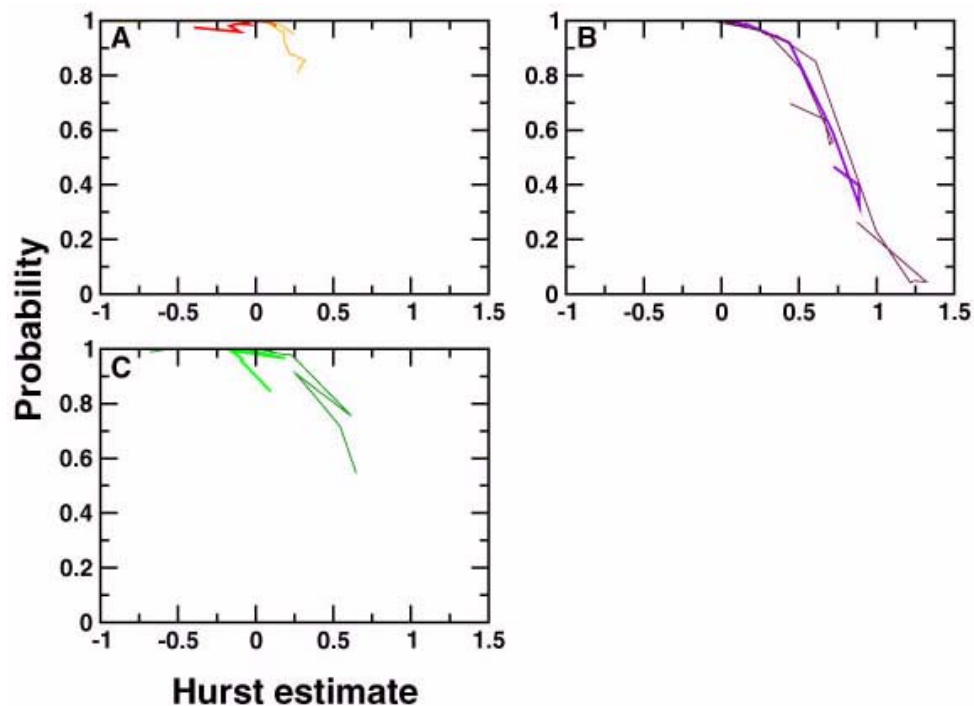


Figure 10. Hurst estimate analysis of the evolutionary pattern described by each stratophenetic series in Figure 9. Hurst estimates measure deviations from randomness (random walk), with values $\gg 0.5$ indicating increasing directionality, while values $\ll 0.5$ indicating increased constraint. Probability on the y-axis is the probability that that portion of the series is non-directional. Bold lines are mean Hurst estimates, while fainter lines are 5% and 95% confidence intervals. A and C (SVD I and SVD III) range between random oscillation and significant constraint, while B (SVD II) exhibits a significant episode of directionality early in the series.

characters may have played in the evolution of the *Wurmiella* clade, because we do not currently have a phylogenetic hypothesis of sister-species relationships for the genus. Nevertheless, this is the type of morphological information, which is required for the addition of hypotheses of evolutionary process to hypotheses of phylogenetic pattern.

Microevolutionary Mode

The distribution of *W. wurmi* samples throughout the section allows an examination of the pattern(s) of microevolution exhibited by the species. The description of this mode uses a random walk as a null model of evolutionary change (Bookstein 1988; Roopnarine 2001). Of the three most significant factors of the SVD analysis, two conformed to the expectation of stasis (SVD I and SVD III), and one exhibited an interval of significant directional change (SVD II). SVD I, a description of the overall crownward arch of the element, varied very little, undergoing no net change through the section. This type of pattern conforms to constrained stasis (Roopnarine 2001), where the degree of variation is less than what would be expected of an unbi-

ased random walk. Such patterns suggest the action of one or more mechanisms that limit variation, such as stabilizing selection or functional constraints (Roopnarine 2001). SVD III, the relative position of the basal cavity, varied broadly and randomly in the lower part of the section, but then also seems to follow a constrained pattern. SVD II, on the other hand, a description of the crownward concavity of the profile posterior to the basal cavity, underwent a period of directional change from samples 9D-10Li. The trend is a subtle, but significant decrease in concavity. Examination of the allometric curves (Figure 7) shows that the trend is rooted in the changing development of the profile, where the posterior section of the profile fails to increase in concavity with increasing size as one moves up the SP VII section. This is a significant conclusion since it links within-sample changes in allometry/development to a longer term microevolutionary trend.

The long geological history, generally high abundance, and morphological richness of conodonts and their fossil record combine to make them ideal subjects for long-term microevolutionary studies. In this study we have been able to use a

single element of the *Wurmiella* apparatus, preserved in a single stratigraphic section, to discriminate three species, describe ontogenetic changes in individual samples of each species, describe patterns of character evolution in one of the species (*W. wurmi*), and link long-term directional evolution in one of those characters to evolution at the ontogenetic level. The obvious extensions of the present study include 1) broader geographic sampling in order to understand spatial variation of the patterns observed, 2) longer stratigraphic sampling to capture temporal variation throughout the entire geological span of the species, including times of cladogenesis, and 3) a phylogenetic framework of sister-group relationships in which to test hypotheses of the relationship between the microevolutionary observations and a macroevolutionary pattern. These are the basic steps toward understanding some of the questions raised by macroevolutionary theory, namely the role of microevolutionary processes in macroevolutionary patterns, the pattern of microevolution during the non-cladogenetic span of a species, and the distribution of microevolutionary rates during the geological span of a species.

The combination of a good fossil record, careful stratigraphic sampling and analysis, and appropriate methods for quantitative morphological and stratigraphic data analysis, will allow paleobiologists to address evolutionary questions with growing confidence. As paleontology continues to move increasingly from descriptive to analytical phases, the understanding of the quantitative nature of the discipline's unique data will become increasingly fundamental (Roopnarine 2002).

ACKNOWLEDGMENTS

We wish to thank P. Fitzgerald for valuable assistance in the laboratory, and P. Carls and I. Valenzuela-Ríos for useful discussions. C. Tang and L. Leighton kindly reviewed several versions of the manuscript, as did two anonymous reviewers. This work was supported by National Science Foundation grant EAR-9814354 to PDR and MAM.

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