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ABSTRACT—It has been proposed previously that the northern Mississippi Valley Sunwaptan trilobite genus *Dikelocephalus* comprises 26 species. Morphometric analyses demonstrate that many of the criteria that had been used to define species of *Dikelocephalus* are invalid and additional analysis of biostratigraphically and biogeographically constrained collections is necessary before the taxonomic status of *Dikelocephalus* can be fully resolved. Our results indicate that infrageneric morphological variation in *Dikelocephalus* is continuous and lacks gaps that could be the basis for establishing multiple species. Many of the characters shown to be taxonomically insignificant in *Dikelocephalus* are also widely used in the definition of other trilobite taxa. This suggests that the species-level taxonomy of many trilobites may be substantially oversplit. Recognition of widespread oversplitting will have important consequences for biostratigraphic zonations, paleogeographic distributions, and estimates of taxonomic diversity.

INTRODUCTION

ALTHOUGH THOUSANDS of trilobites have been described, the population paleobiology of trilobite species remains poorly known. Many aspects of trilobite taxonomy will remain obscure until the patterns and controls of variation within species have been identified and evaluated. Taxonomic errors result when intraspecific variations, such as ontogenetic, sexual dimorphic, or phenotypic differences, are mistaken for interspecific differences. This leads to oversplit taxa containing species based on minor and inconsistent differences. The monographs on the Upper Cambrian dikelocephalid and saukiid trilobites by Ulrich and Resser (1930 and 1933, respectively) contain notorious examples of this kind of error. To revise the taxonomy of such groups it is necessary to assess the degree of intraspecific variation within well-represented species, whose stratigraphic setting and taphonomic context is well documented. *Dikelocephalus* fulfills these criteria and has been selected for detailed analyses of controls on variation within the Dikelocephalacea.

This paper describes a biometric analysis of the suite of syntype specimens upon which Ulrich and Resser (1930) based their species designations. Results show that: 1) many, if not all, of Ulrich and Resser's species designations are invalid; 2) it is not possible to resolve the taxonomic status on the basis of the material examined by Ulrich and Resser; and 3) studies of well-localized collections will be necessary before the systematics of *Dikelocephalus* can be finally resolved. These results have important implications for trilobite systematics because the vast majority of trilobite species have been described using small numbers of specimens without adequate documentation of intraspecific variation. Detailed studies of trilobites at low taxonomic levels are also needed to evaluate suggestions that levels of intraspecific variation differed in Cambrian and post-Cambrian species (McNamara, 1986; Foote, 1990; Hughes, 1991).

Dikelocephalus.—*Dikelocephalus* occurs in large numbers only in Sunwaptan (uppermost Cambrian; Ludvigsen and Westrop, 1985) deposits of the northern Mississippi Valley (central to western Wisconsin, southeastern Minnesota, and northeastern Iowa) (Hughes, 1993). It is rarely found outside this area (Grant, 1965; Winston and Nichols, 1967; Westrop, 1986). *Dikelocephalus* was first described by Owen (1852) (Figures 1.1, 1.17), and was subsequently figured and discussed by Hall (1863), Winchell (1874), and Walcott (1914). Ulrich and Resser (1930) published a monograph in which they restricted the genus to the generic type-species *D. minnesotensis* Owen, 1852, and established an additional 25 new species of *Dikelocephalus* from the northern Mississippi Valley (examples of their syntypes are shown in Figure 1). Although subsequent workers (Twenhofel, 1945; Raasch, 1951; Taylor and Halley, 1974; Westrop, 1986) criticized Ulrich and Resser's work principally on the grounds that the species-level taxonomy was too finely subdivided, no comprehensive revision has been attempted, although additional species have been described (Bell et al., 1952). As part of a new investigation of the genus, Labandeira (1983a, 1983b) produced a biometric analysis of Ulrich and Resser's (1930) type-suite, Hesselbo (1987a, 1987b) examined some taphonomic aspects of *Dikelocephalus*, and Hughes (1988, 1990, 1991, 1993, in press) conducted a field-based study into the populational paleobiology and geological setting of the genus. This paper addresses: 1) the validity of Ulrich and Resser's classification based only on the type-suite of specimens analyzed by those authors; and 2) the degree of structurally based variation in *Dikelocephalus* based principally on Ulrich and Resser's type-suite, as well as additional, subsequently collected specimens. The fact that only Ulrich and Resser's type-suite was used in the first part of this study was determined by the relative paucity of additional collected specimens of *Dikelocephalus* and by the lack of recognition of Ulrich and Resser's (1930) species designations by subsequent trilobite systematists. Full descriptions of patterns of variation within new collections made from single beds are described elsewhere (Hughes, 1991, in press). This paper is based on the measurements and statistical analyses of Labandeira and was written by both authors in close collaboration.

APPROACH

Ulrich and Resser's taxonomy emphasized the differences among specimens. All morphological variation was automatically considered of taxonomic importance (see Raasch, 1951, for a critical discussion of Ulrich and Resser's taxonomic approach). In the present study characters were examined that could be compared biometrically among all members of their type-suite. This approach permits discrimination between discrete and continuous variation and consequently identifies those characters of likely taxonomic significance. Many of the characters used in this study were also discussed as important features of interspecific differentiation by Ulrich and Resser (1930).

Ulrich and Resser examined approximately 350 specimens, which are now housed in the Milwaukee Public Museum and the National Museum of Natural History (Washington, D.C.). Specimens are from over 25 localities scattered throughout the

northern Mississippi Valley. Sclerites from different localities and sometimes different lithofacies were frequently determined as conspecific (see Raasch, 1951). Specimen locality data were presented in Labandeira (1983b) and the exact locations and details of preservation and taphonomy were provided by Hughes (1993, in press). *Dikelocephalus* fossils are generally preserved as composite molds, but occasional cuticular preservation shows that cuticle thickness is negligible relative to overall sclerite size. Thus, measurements may be taken from either the part or counterpart. Although specimens are free from tectonic distortion, some have been modified by diagenesis (Hughes, 1993); such specimens were excluded from this analysis. Compaction has not greatly influenced the analyses reported herein, because specimens from both sandstone and siltstone lithologies did not exhibit any separation in morphologic trends.

Material analyzed included all of Ulrich and Resser's well-preserved specimens plus a few additional specimens held in the Field Museum of Natural History in Chicago and the Greene Museum of the University of Wisconsin at Milwaukee. The data set is given in Appendix 1. Measured sclerites include cranidia (146 specimens), free cheeks (91 specimens), hypostomes (34 specimens), and pygidia (138 specimens): a total of 409 specimens. Some cranidial and librigenal measurements originated from the same individuals. Isolated thoracic tergites cannot be identified to segment because they vary gradually in shape along the thorax; hence, they were not measured. Thirty variables were assessed including 21 linear measurements and nine angular measurements (see Table 1). The terminology used in the measurement of the free cheeks extends that introduced by Shaw (1956) and Temple (1975). A new morphological landmark has been recognized and designated as point sigma (σ), which is the projection of the posterior facial suture onto the lateral margin. Point sigma, in combination with point omega and the librigenal margin, expresses slenderness of the basal genal spine region (Labandeira, 1983b).

Angular measurements were determined using a protractor. Glabellar and pleural furrow orientation was measured with respect to a sagittal or exsagittal axis. Although most furrows are curvilinear abaxially, their adaxial traces are straight and angles were measured at the intersection of the furrow with the axial furrow. Measurements are given to the nearest degree and results are plotted as rose diagrams (Figures 2, 4).

Linear distances within undistorted sclerites of *Dikelocephalus* were measured by vernier calipers (Fowler® type 6921). These measurements were taken between morphological landmarks and read to the nearest tenth of a millimeter. In many cases measurements were taken from incomplete specimens where one side of an axially symmetrical structure was missing. In such cases the measurement obtained from the complete half was doubled in order to provide an estimate of the total distance. This technique was verified using complete specimens where doubled half-measurements and full-measurements yielded identical values.

Data from linear dimensions were analyzed bivariately using the Pearson product-moment correlation coefficient to determine the extent to which two variables covary during growth. Assessment of the validity of Ulrich and Resser's (1930) species designations was done by use of a stepwise discriminant analysis (SDA), with results plotted on scatter plots to illustrate membership (or the lack thereof) of specimens to Ulrich and Resser's a priori species groups. Finally, interrelationships among all linear characters were explored using a KYST2A (Kruskal et al., 1978) nonmetric Multidimensional Scaling (MDS) program and the results were expressed graphically as bivariate and three-dimensional plots of distance among specimens fitted to Cartesian coordinates. The complete SDA and MDS printouts are deposited, along with extensive new collections of *Dikelocephalus,* in the Geology Museum of the University of Wisconsin at Madison.

RESULTS

Univariate analyses.—Angular measurements (Figures 2–4) all show unimodal distributions. Possible bimodality is present in the angular orientation of the third pleural furrow of the pygidium (Figure 4), but this is evident on the left-hand side only and cannot be considered taxonomically significant. Although the distributions are unimodal, several are platykurtic (e.g., Figure 3a). In the case of the free cheek this reflects the allometric growth of the palpebral lobe (Raasch, 1951; Hughes, 1991, in press).

Bivariate analyses.—Bivariate analyses (Figures 5–10) examine the relations between pairs of variables during growth. The greatest number of characters were used in the bivariate analyses, some of which were not included in the multivariate analyses because of an unacceptable level of missing data. Our results demonstrate that specimens define a single rectilinear trendline for every bivariate plot. The projection of these trends passes close to the origin of both axes, suggesting that growth relationships approach isometry. (However, even small departures from isometry may cause notable morphological differences between small and large specimens, e.g., Sdzuy, 1966, p. 70.) Some growth relationships show very tight clustering about the trendline; others show a much more scattered distribution, and hence lower correlation coefficients. Wide scatters indicate that the growth controls of some characters are more flexible than of others. Within the cranidium the palpebral chord length and frontal area length are the most variable; as for the pygidium, the most variable character is the length of the postaxial region (Labandeira, 1983b; also see Hughes, in press). The coefficient of determination (R^2) is a measure of the proportion of the variation of one variable that is determined by the variation of the other (Sokal and Rohlf, 1973, p. 269). The cranidium and hypostome show average R^2 values (the average of every pairwise R^2 cross-correlation of each variable in that sclerite type) of 0.957 and 0.955, respectively, the pygidium shows an average of 0.931, and the free cheeks show an average of 0.914. These figures indicate that the free cheeks exhibit greater variability than any other sclerite type analyzed. Strong positive values for all the coefficients of determination suggest that overall size is the principal variation within the data set. This is to be expected because the sample encompasses a wide range of holaspid molt instars.

Because none of the bivariate relationships indicates anything other than a single trendline, there are no grounds to suggest that the sample contains more than a single species.

Multivariate analyses.—Two multivariate techniques were used to analyze each of the four sclerite types of *Dikelocephalus.* The first technique was a stepwise discriminant analysis (SDA), a classification technique that establishes whether each of Ulrich and Resser's (1930) species could be statistically recognized. The second technique, nonmetric multidimensional scaling (MDS), is an exploratory technique to assess the morphospace occupied by each sclerite in multidimensional space. Both techniques assume data normality (Manly, 1986), a condition satisfied by our data set (see Figures 2–10). A summary of the philosophy, methodology, and data set results is presented below.

Stepwise discriminant analysis was used to partition specimens assigned to each of Ulrich and Resser's species into a species-group that is characterized by minimum intragroup variance and maximum intergroup variance (Dillon and Goldstein, 1984). Each species-group is defined a priori by those

TABLE 1—Biometric variables analyzed in *Dikelocephalus* (from Labandeira, 1983b). Variables with asterisks were deleted from the multivariate analyses.

Sclerite	Linear dimension	Angular orientation
Cranidium	1. Preglabella furrow midpoint, prepalpebral sinus	22–25. Angular orientations of glabellar furrows (S0, S1, S2 and S3), with respect to the sagittal axis
	2. Preglabella furrow midpoint, postpalpebral sinus	
	3. Palpebral chord length	
	4. Occipito-glabellar length	
	5. Occipital glabellar width	
	6. Frontal area length*	
	7. Palpebral cranidial width	
Librigena	8. Prepalpebral sigma distance	26. Angle subtended by point sigma, prepalpebral point, and point omega
	9. Prepalpebral omega distance	
	10. Postpalpebral omega distance	27. Angle subtended by prepalpebral point, postpalpebral point, and point omega
	11. Palpebral chord length	
Hypostoma	12. Posterior hypostome width	
	13. Hypostome length	
	14. Median body length*	
	15. Intermacular width	
Pygidium	16. Maximum pygidial width	28–30. Angular orientations of the first, second, and third pleural furrows, with respect to the sagittal axis
	17. Total pygidial length	
	18. Total length of rhachis	
	19. Anterior width of rhachis	
	20. Basal interspinal distance*	
	21. Sagittal pleural region length	

specimens that Ulrich and Resser assigned to the particular species whose namesake represents the species-group. Thus, each species-group possesses a characteristic group centroid in canonical multidimensional space that is defined mathematically by an unique classificatory, or discriminant, function. For each species-group, and for each of the four data sets (cranidia, librigenae, hypostomata, and pygidia), all specimens (including specimens from the same species that originally contributed to establishing the discriminant function) are statistically compared to the species-group centroid for inclusion or exclusion (Klecka, 1980). A seemingly counterintuitive but mathematically reasonable potential result of this technique is a situation whereby all specimens contributing to the formation of a group centroid for a particular species-group are actually excluded from that species-group when they are subsequently compared in stepwise fashion to all other group centroids later in the analysis. This, in fact, occurred in four instances (Table 2) and is explained by the fact that an a priori species-group can have intragroup variance so great that specimens from other such "species-groups" can approximate the a priori species-group centroid better than its original defining specimens. Finally, when data set specimens are compared to each of the species-group centroids, the results are statistically strengthened by using a jackknifed classification, wherein specimens are assigned to species-groups without the bias of the assigned specimen entering into the discriminant function that defines the species-group to which it a priori belongs. In several instances jackknifed classifications resulted in lower correct species assignments than unjackknifed classifications.

The SDA used in this study was a BMDP7M program (Jennrich and Sampson, 1988), in which each variable was initially *z*-transformed (i.e., standardized by its mean) to eliminate the scaling effects of variables in the analysis of specimens. *Z*-transformation, however, does not eliminate features of shape associated with size, a pattern that was evident in the multivariate analyses. For each of the four sclerite analyses, the program default settings were used: the tolerance was 0.01, the maximum number of steps was 10, and there were equal prior probabilities for each a priori group. The default F-to-enter and F-to-remove values of 4.0 and 3.996, respectively, were used for analyses of hypostomata and pygidia; they were altered for analyses of the cranidia (3.30, 2.297) and librigenae (1.45, 1.43); in these instances the F values did not exceed the 0.05 alpha level. For the cranidial, hypostomatal, and pygidial data sets, variables

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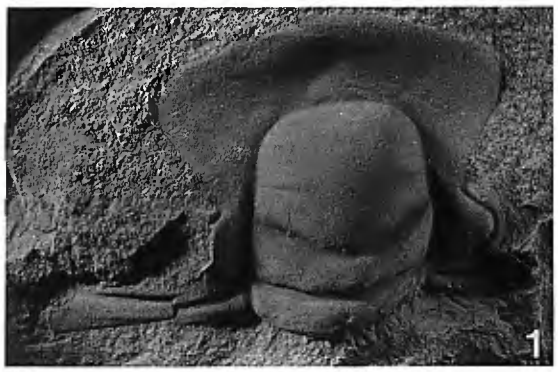
FIGURE 1—A selection of holotypes and syntypes of *Dikelocephalus* species described by Ulrich and Resser (1930). All specimens were coated with ammonium chloride prior to photography. *1,* dorsal view of cranidium, syntype of *D. minnesotensis,* USNM 447020, ×1, Fairy Glen, Stillwater, Washington County, Minnesota, figured by Owen, 1852. *2,* dorsal view of cranidium, syntype of *D. barretti,* MPM 11176, ×1, Button Bluff, Richland County, Wisconsin. *3,* dorsal view of cranidium, syntype of *D. juvenalis,* USNM 58601, ×3, Trempealeau, Trempealeau County, Wisconsin, figured by Walcott, 1914. *4,* dorsal view of cranidium, syntype of *D. weidmani,* MPM 9557, ×, Mondovi, Buffalo County, Wisconsin; *5,* anterior view of MPM 9557, ×1; *6,* lateral view of MPM 9557, ×1. *7,* dorsal view of cranidium, syntype of *D. marginatus,* USNM 71800, ×2, LaGrange Moutain, Redwing, Goodhue County, Minnesota. *8,* ventral view of cephalon, syntype of *D. raaschi,* MPM 18673, ×1, Spring Green, Sauk County, Wisconsin. *9,* dorsal view of cranidium and conjoined free cheeks, syntype of *D. subplanus,* MPM 18682, ×1, Richland Center, Richland County, Wisconsin. *10,* dorsal view of free cheek, syntype of *D. barretti,* MPM 18688, ×1.5, Button Bluff, Richland County, Wisconsin. *11,* ventral view of hypostome, syntype of *D. norwalkensis,* USNM 72706, ×2, Wilton, Monroe County, Wisconsin. *12,* dorsal view of dental wax cast of external mold of pygidium, holotype of *D. postrectus,* USNM 102269, ×1.5, Reedsberg, Sauk County, Wisconsin. *13,* dorsal view of internal mold of pygidium, holotype of *D. postrectus,* MPM 18691, ×1.5, Reedsberg, Sauk County, Wisconsin. *14,* dorsal view of pygidium, syntype of *D. subplanus,* MPM 18684, ×1, Richland Center, Richland County, Wisconsin. *15,* dorsal view of pygidium, syntype of *D. ovatus,* USNM 71740, ×0.5, Prairie-du-Sac, Sauk County, Wisconsin. *16,* dorsal view of pygidium, syntype of *D. hotchkissi,* USNM 58600, ×0.5, Gibraltar Bluff, Columbia County, Wisconsin. *17,* dorsal view of dental wax cast of pygidium with abnormality in right posterior pleurae, syntype of *D. minnesotensis,* USNM 17863, ×0.5, Fairy Glen, Stillwater, Washington County, Minnesota.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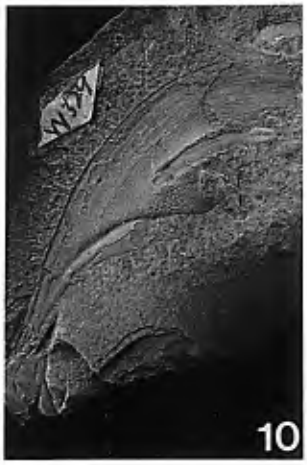
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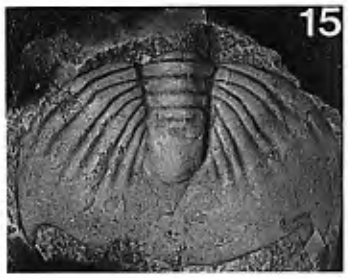
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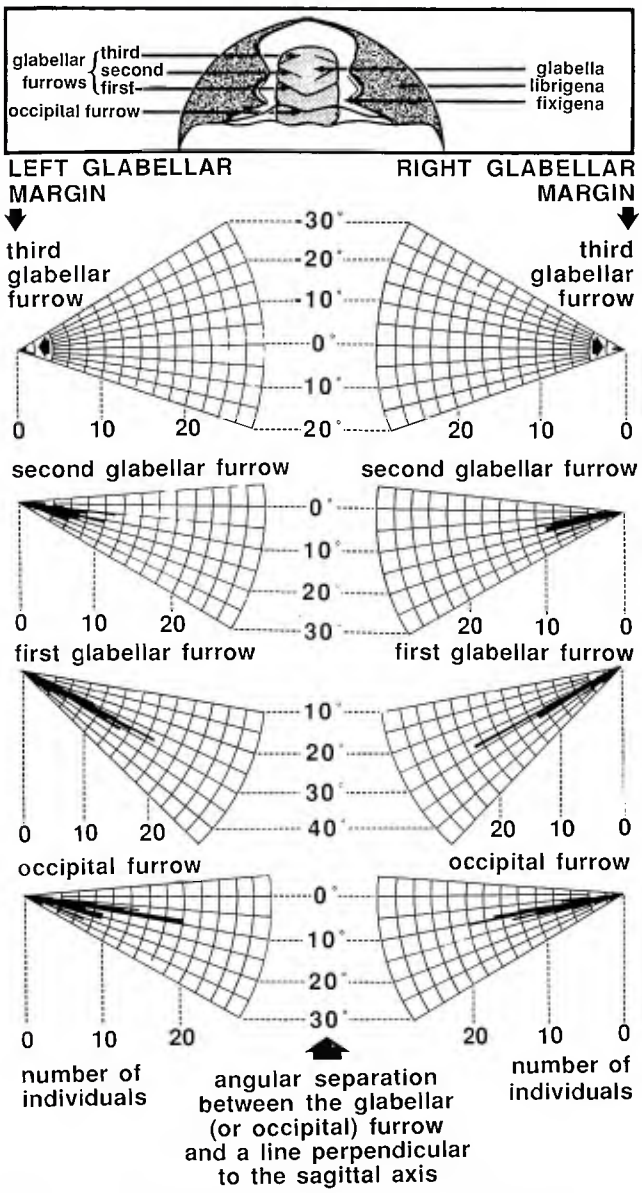


FIGURE 2—Angular orientation of occipital and glabellar furrows among Ulrich and Resser's (1930) syntype-suite.

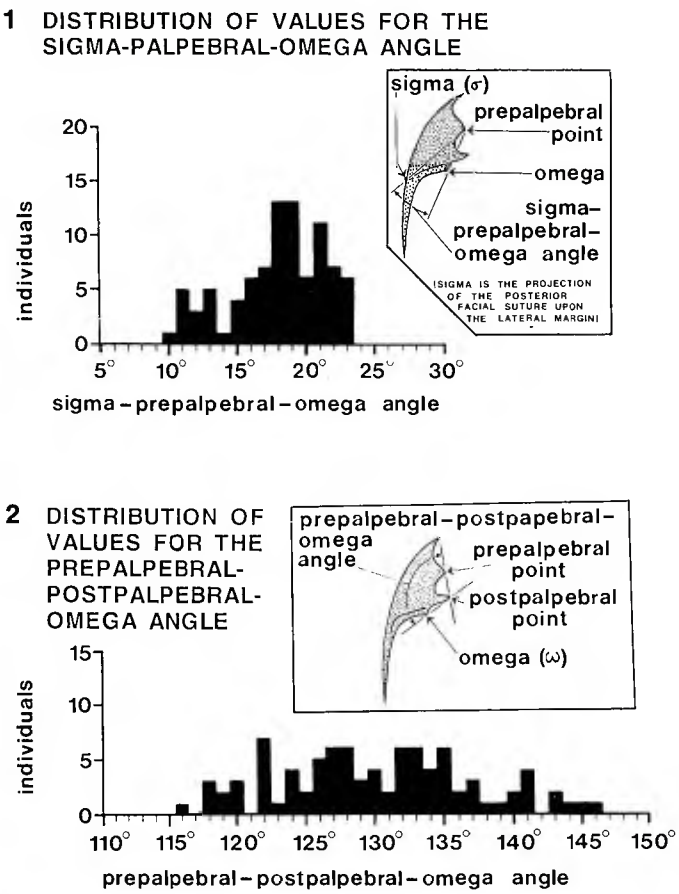


FIGURE 3—Variation in shape of free checks among Ulrich and Resser's (1930) syntype-suite. *1*, distribution of values for the sigma-prepalpebral-omega angle. *2*, distribution of values for the prepalpebral-postpalpebral-omega angle.

with an unacceptable degree of missing data were omitted—namely, palpebral chord length, frontal area length, sagittal hypostome length, and terminal interspinal distance, respectively. Right and left ipsative variables of two cranidial features were individually averaged, resulting in two rather than four variables. (The combination of these four variables into two composite variables incurred minimum information loss.) Additionally, all specimens with missing data were excluded from the analyses. After these cullings, sample sizes were 59 for cranidia, 54 for librigenae, 23 for hypostomata, and 74 for pygidia. (Details of the analyzed data sets are provided in Table 2.) In no instance was the number of specimens for each a priori species group less than the number of original variables of the data set. Because of these restrictions on the number of cases (specimens) and variables, only 11 of Ulrich and Resser's 26 *Dikelocephalus* species were used. The remaining 15 species that were not analyzed either contained too few specimens per species or the quality of the material was too poor for accurate and complete measurement, as in the cases for the species *D. beani, D. inaequalis, D. juvenalis, D. thwaitesi,* and *D. wiltonensis.* Notably, one species, *gracilis,* was sufficiently abundant in all four sclerite analyses that its scatter plot distribution could be used as a visual test for the percentage of total *Dikelocephalus* "discriminant morphospace" occupied by a single, relatively abundant, a priori species.

The SDA results are presented in Figure 11 as scatter plots representing the distribution of Ulrich and Resser's species in canonical space, and in Table 2, which lists the misclassified species identities and the posterior probabilities of classified specimens for each species-group for each of the four sclerite data sets. Because of the relatively high correlation values for all pairwise comparisons of variables in all the four data sets—values ranged from .880 to .993, of which the bulk of the 34 total correlation values clustered between .940 and .985—only plots of Canonical Axis I versus Canonical Axis II were used. Hypostomata are plotted on a single axis because they possessed too few original variables to warrant a bivariate SDA scatter plot.

Results of all SDA scatterplots indicate well-defined clusters, each characterized by a region of high density along the upper- or lower-right margins that gradually disperses in an opposite direction. There are indications that this trend from a denser

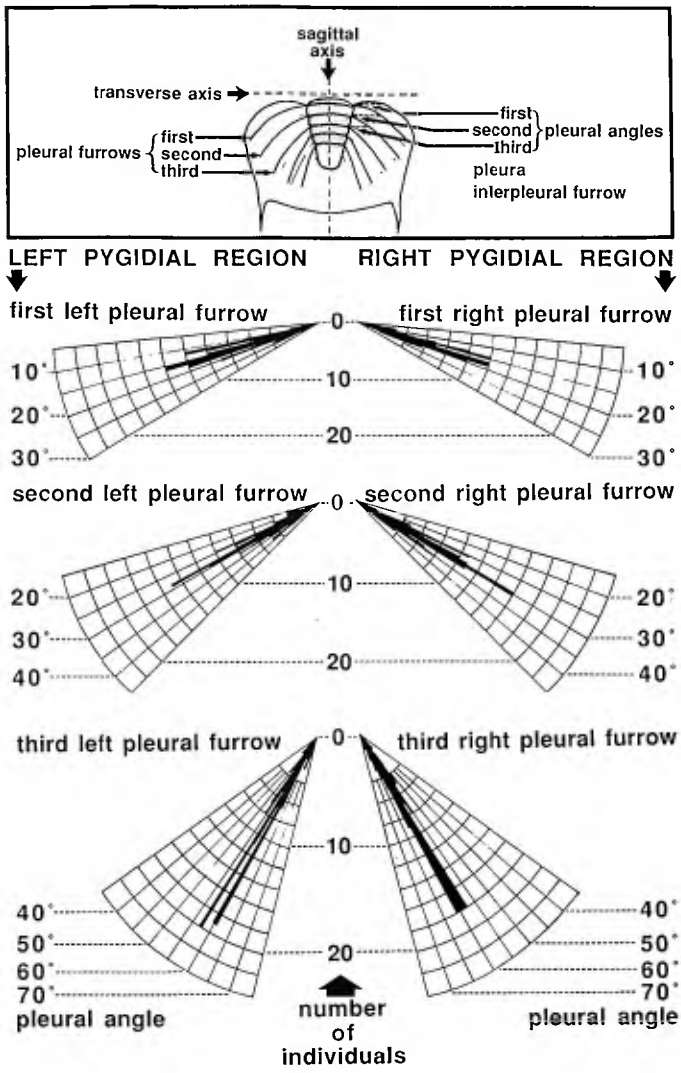


FIGURE 4—Angular orientation of pygidial pleural furrows among Ulrich and Resser's (1930) syntype-suite.

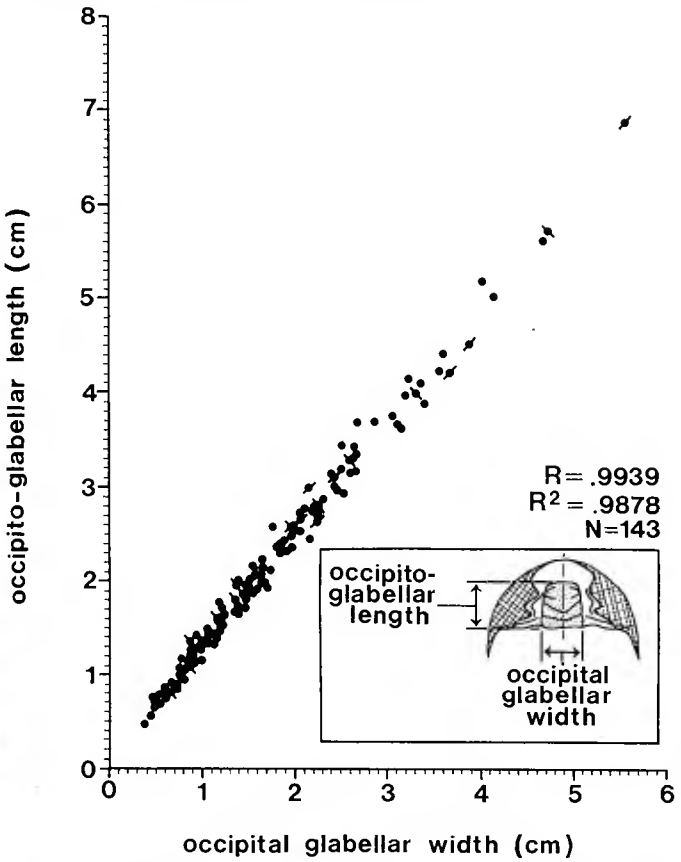


FIGURE 5—Occipital glabellar width versus occipito-glabellar length among Ulrich and Resser's (1930) syntype-suite. Glyphs with bars directed to the left indicate specimens from a single bedding plane collection at Richland Center, Richland County, Wisconsin; bars directed to the right indicate Ulrich and Resser's (1930) figured syntypes.

to a more rarefied region reflects a vector that is indirectly associated with size. One explanation accounting for this trend is the lingering effect of those variables with extreme values that were not completely eliminated by *Z*-transformation. Alternatively, and more likely, this trend is attributable to size-associated shape changes. This trend is also demonstrated by mapping raw data values onto respective discriminant scores for members of each species-group: specimens distal from the region of high density tend to be large in absolute size. However, because SDA is designed to classify specimens rather than reveal latent or obvious data set structure, the pertinent patterns revealed by all four data sets are the following.

1. The a priori species-group with the greatest number of constituent specimens, *D. gracilis* (representing 88 specimens, or 41.9 percent of all four data sets), occupies virtually all of the available canonical morphospace, and thus possesses intragroup variance that is approximately coincident with the intragroup variance of all remaining groups for each sclerite.

2. As specimen number per species-group increases, there generally is greater coverage of available canonical morphospace.

3. Ulrich and Resser on average correctly identified about four out of 11 (36.3%) of their original specimens to the "correct" species, when analyzed a posteriori. For the *D. gracilis* species-group—the species with the greatest representation of specimens—the percentage of correct identifications was 31.8 percent, less than the total average. If it was possible to include all 26 species groups for each sclerite data set, the total percentage of correctly identified specimens would undoubtedly decrease. Although the percentage of correctly identified specimens varied for each sclerite—a high of 50.8 percent for cranidia and a low of 25.9 percent for hypostomata—in no case does Ulrich and Resser's percentage of correctly identified specimens approach that of 0.95 percent, the conventionally accepted level for statistical testing.

4. The data set included specimens preserved in dolomitic siltstones, where they may be cracked, and in very fine sandstones, where original relief is preserved. If preservational differences were responsible for much of the variation among sclerites, then species-groups from similar lithologies would tend to cluster together, and species from sandstones would be expected to show smaller ranges of variation than those from siltstones. Ulrich and Resser's (1930) *D. norwalkensis* was collected from sandstones only. Our discriminant analysis shows that it displays a similar degree of variation to species-groups from siltstones and that the morphospace envelopes of *D. norwalkensis*

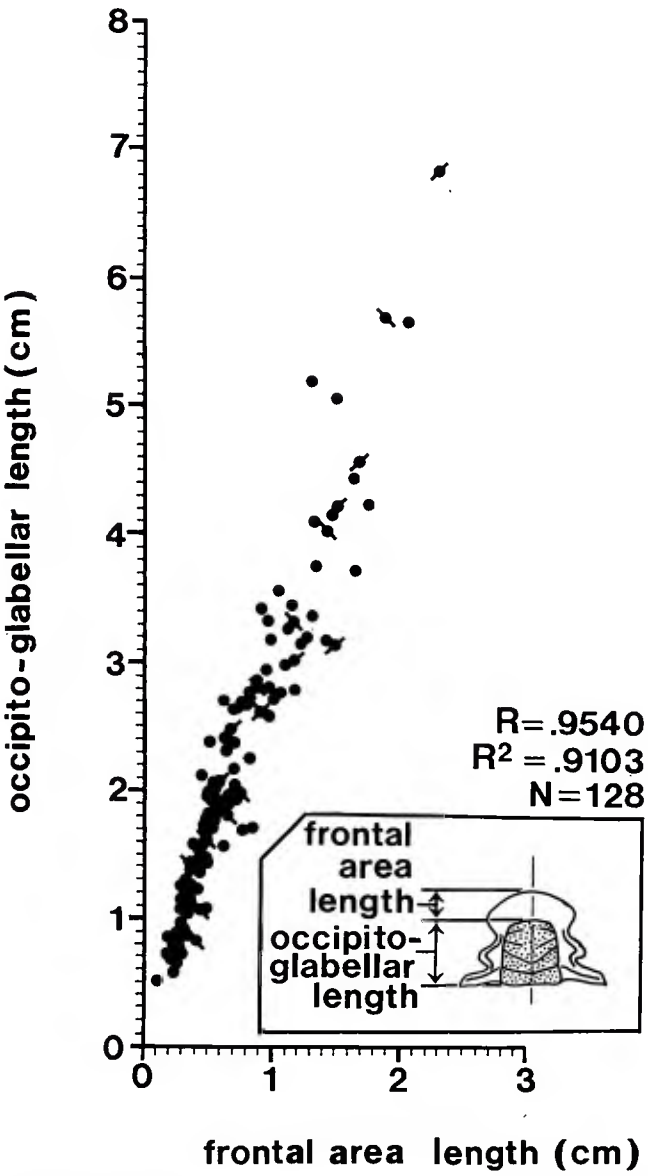


FIGURE 6—Occipito-glabellar length versus frontal area length among Ulrich and Resser's (1930) syntype-suite. Glyphs with bars directed to the left indicate specimens from a single bedding plane collection at Richland Center, Richland County, Wisconsin; bars directed to the right indicate Ulrich and Resser's (1930) figured syntypes.

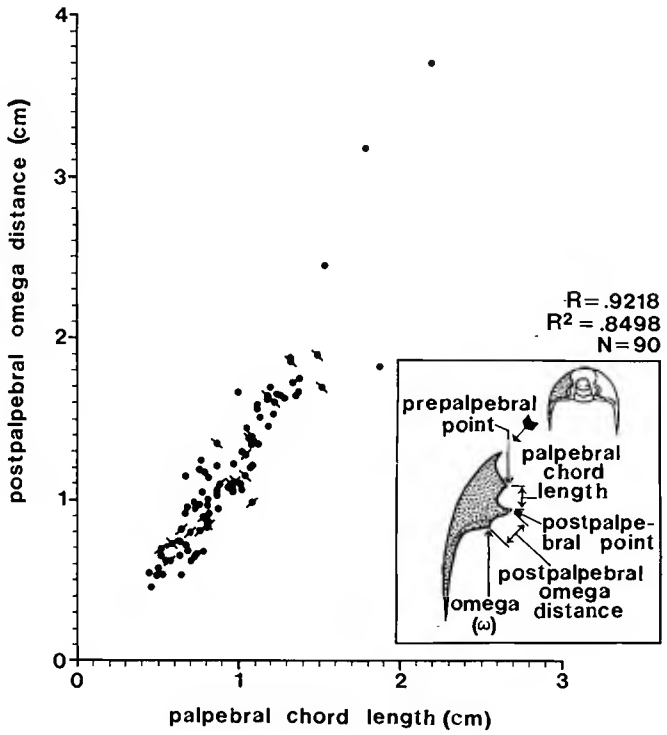


FIGURE 7—Postpalpebral-omega distance versus palpebral chord length among Ulrich and Resser's (1930) syntype-suite. Glyphs with bars directed to the left indicate specimens from a single bedding plane collection at Richland Center, Richland County, Wisconsin; bars directed to the right indicate Ulrich and Resser's (1930) figured syntypes.

overlap with the envelopes of several other species (Figure 11 cranidia and pygidia). This indicates that preservational differences are of limited importance in considering variation within *Dikelocephalus*.

Although as a classification technique SDA can be extremely informative regarding the a posteriori placement of specimens into a priori groups, it is not an exploratory technique that can reveal the internal structure of a data matrix in multidimensional space. An apologist for Ulrich and Resser might argue that our discriminant analysis does not invalidate those author's species because their taxa were defined using additional characters that we could not use in our analysis. The purpose of this paper is to demonstrate that although Ulrich and Resser's species could (however unlikely) be proven valid by analysis of additional localized collections, there was no justification of their species designations based on the material they had at hand. To do this we have used an exploratory technique to reveal the structure of the data matrix within multidimensional space. Such techniques permit evaluation of the pattern of variation within *Dikelocephalus* without reference to a priori species designations. Several exploratory techniques traditionally have been used to elucidate latent biological structure, including cluster analysis, ordination techniques such as principal components analysis, and factor analysis. However, critical reviews of these procedures have indicated that problems exist in the interpretation of results from all these techniques (Kendall, 1975; Chatfield and Collins, 1980). A major problem is the elimination of size-associated variation (Pimentel, personal commun.). For these reasons, MDS was preferred—it is a purely data-analytic technique that lacks the probabilistic framework inherent in most other multivariate techniques (Mardia et al., 1979).

Given a matrix of distances among objects, MDS graphically constructs a spatial network that expresses interobject distances as parsimoniously as possible. For morphometric data the procedure begins with a matrix of raw data "distances" that numerically expresses associations between samples and variables. From the raw data matrix, a matrix of Euclidean distances is calculated. A monotonic, ascending, least-squares regression is made of the Euclidean distances on the raw data distances, such that small raw data distances are scaled to match small Euclidean distances as closely as possible, and similarly for successively larger raw matrix and Euclidean distances. These new regressed distances are termed "disparities." After the first regression step, a goodness-of-fit statistic is calculated between

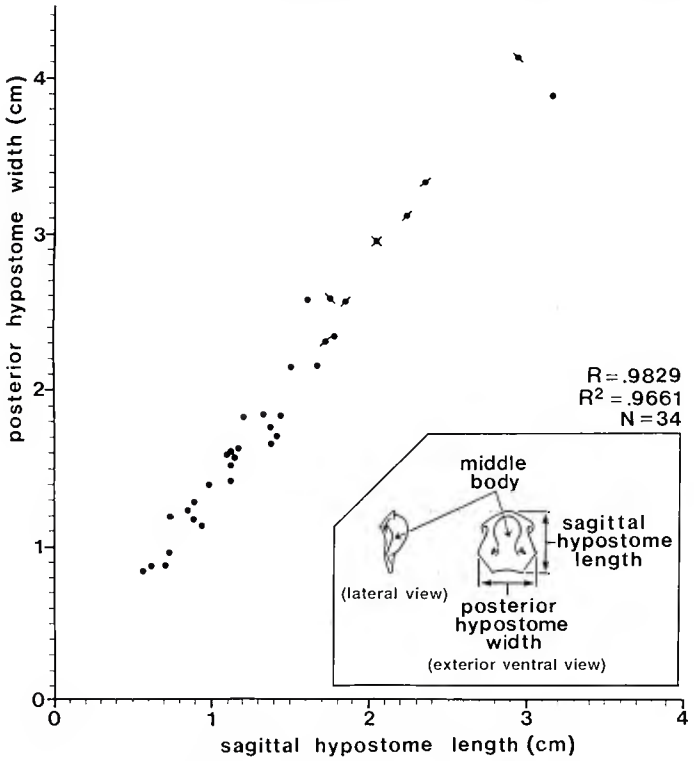


FIGURE 8—Posterior hypostomal width versus sagittal hypostomal length among Ulrich and Resser's (1930) syntype-suite. Glyphs with bars directed to the left indicate specimens from a single bedding plane collection at Richland Center, Richland County, Wisconsin; bars directed to the right indicate Ulrich and Resser's (1930) figured syntypes.

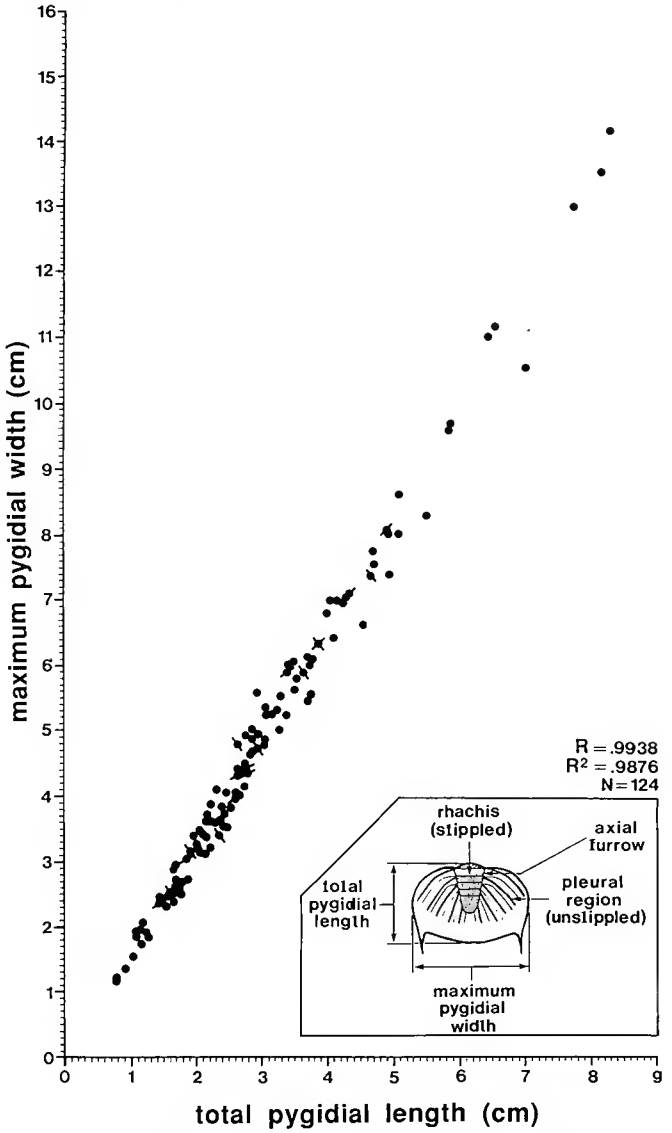


FIGURE 9—Total pygidial length versus maximum pygidial width among Ulrich and Resser's (1930) syntype-suite. Glyphs with bars directed to the left indicate specimens from a single bedding plane collection at Richland Center, Richland County, Wisconsin; bars directed to the right indicate Ulrich and Resser's (1930) figured syntypes.

the configuration distances and the disparities. We used "Stress Formula 1" (Kruskal et al., 1978) as a goodness-of-fit measure, which evaluates the degree to which the configuration matrix has to be stressed in order to obtain the raw data distances (Manly, 1986). During the stressing of the spatial configuration, the dimensional coordinates of each object are altered so as to reflect the reduced stress. The procedure from calculation of Euclidean distance to realignment of the objects in multidimensional coordinates is repeated for successive iterations until stress is sufficiently minimized that a local minimum is established for a best-fit display of the object configuration in multidimensional space. Interpretation of the multidimensionally scaled data is accomplished by identifying vectors that meaningfully express some property inherent in the original data. These properties should become manifest in any of the final MDS configurations, each of which represents a separate run arrived at by varying the initial random "seed" and the number of penultimate and final iterations.

Initial calculation of *z*-standardized Euclidean distances from the raw data matrix was performed by a SPSS® Proximities Program (SPSS®, 1990). The generated diagonal matrix then was used as input into a nonmetric MDS program, KYST2A (Kruskal et al., 1978). KYST2A imposes an absolute limitation of 59 inputted cases because the number of dissimilarity matrix cells cannot exceed 1,800. (Fifty-nine cases yield a diagonal matrix of 1,770 cells.) Rather than using a cutoff level, which eliminates dissimilarities with smaller values and thus distorts the resulting final configuration into an arguably uninterpretable horseshoe shape (Kruskal and Wish, 1977), we chose to cull our cranidial, librigenal, and pygidial data sets such that only 59 cases were used as input into KYST2A for each of these data sets. For the cranidia, this was done by excluding all specimens with missing data, leaving a remainder of 60, of which the last case was deleted. For 86 librigenal cases with complete data, deletion of approximately every third specimen left a requisite 59 cases. For 123 pygidia, subtraction of approximately every other case resulted in 59 cases available for input into KYST2A. Thirty-four all data-complete hypostome specimens were used, corresponding to an input matrix of 561 cells.

Table 3 presents relevant input and output parameters for our MDS runs. The number of iterations needed to arrive at the penultimate MDS configuration ranged from 220 (librigenae) to 392 (pygidia); the final configuration was achieved in 36 (hypostomata) to 126 (pygidia) iterations. An expected result of using close to the maximum allowable data values for three of

TABLE 2—Results of stepwise discriminant analysis of 11 *Dikelocephalus* species erected by Ulrich and Resser (1930), to accompany Figure 11.

Sclerite	Ulrich and Resser's (1930) *Dikelocephalus* species	Number of samples for species at left	Jackknifed incorrect[1] classification and frequency	Total percent correct for species	Percent correct for sclerite
Cranidium	*barretti*	6	*gracilis* (2) *granosus* (1) *raaschi* (1)	33.3	
	gracilis	32	*barretti* (2) *granosus* (5) *norwalkensis* (8) *raaschi* (2)	46.9	
	granosus	6	*barretti* (1) *gracilis* (2) *norwalkensis* (2)	16.6	
	norwalkensis	9	*barretti* (1)	88.9	
	raaschi	6	*barretti* (1) *granosus* (1)	66.7	
					50.8
Librigena	*edwardsi*	10	*gracilis* (3) *marginatus* (3) *subplanus* (1)	30.0	
	gracilis	19	*edwardsi* (3) *marginatus* (2) *ovatus* (1) *raaschi* (3) *subplanus* (1) *wisconsinensis* (3)	31.6	
	marginatus	5	*edwardsi* (2) *subplanus* (1) *wisconsinensis* (1)	20.0	
	ovatus	5	*raaschi* (4)	20.0	
	raaschi	6	*gracilis* (1) *ovatus* (2) *wisconsinensis* (1)	33.3	
	subplanus	5	*gracilis* (2) *marginatus* (3)	0	
	wisconsinensis	4	*raaschi* (1) *subplanus* (2)	25.0	
					25.9
Hypostoma	*edwardsi*	3	*gracilis* (1) *norwalkensis* (2)	0	
	gracilis	8	*edwardsi* (1) *norwalkensis* (2) *ovatus* (3)	25.0	
	norwalkensis	4	*edwardsi* (2)	50.0	
	ovatus	4	*edwardsi* (1) *gracilis* (1) *raaschi* (1)	25.0	
	raaschi	4	*ovatus* (2)	50.0	
					30.4
Pygidium	*edwardsi*	5	*norwalkensis* (1) *subplanus* (4)	0	
	gracilis	29	*edwardsi* (3) *minnesotensis* (5) *norwalkensis* (2) *ovatus* (4) *subplanus* (2) *wisconsinensis* (8)	17.2	
	minnesotensis	10	*gracilis* (1) *norwalkensis* (1) *subplanus* (1) *wisconsinensis* (2)	50.0	
	norwalkensis	12	*edwardsi* (2) *subplanus* (3)	58.3	
	ovatus	6	*wisconsinensis* (2)	66.7	
	subplanus	6	*edwardsi* (2)	66.7	
	wisconsinensis	6	*minnesotensis* (1) *norwalkensis* (1) *ovatus* (1) *subplanus* (3)	0	
					33.8

[1] Based on other species groups in the same sclerite data set; samples could have been assigned to other species if they were present in the same data set.

our four data sets was a high number of iterations needed to reach a statistically significant local minimum from which a final configuration was constructed. In all cases a minimum was achieved, with associated stress levels ranging from 0.001 (hypostomata) to 0.012 (librigenae), indicating a high goodness-of-fit between the data and the MDS axes (see Part 5 of Figures 12 to 15). (A stress of 0 represents exact equality between the data and the encompassing axes.) The final MDS configurations shown in Figures 12–15 have been rotated to principal components.

For each sclerite, the final MDS scatter plots are provided in three two-dimensional versions and a summary three-dimensional version (Figures 12–15). The final MDS configuration for all sclerites consisted of cylindrical clouds of points with few or no outliers, which were either rectilinear (hypostomata and pygidia) or curvilinear (cranidia and librigenae) in overall shape. In all four sclerites there is a trend from smaller sized specimens exhibiting interpoint compactness to larger sized specimens that display greater dispersion. However, this trendline, which is principally oriented subparallel to Dimension 1 in all four sclerites, corresponds with important shape-related sclerite characters (see Part 6 of Figures 12–15). Thus, in order to interpret the MDS final configuration in terms of trilobite structure, we have chosen for each sclerite to map relevant shape-associated trends onto their respective Dimension 1 versus Dimension 2 scatter plots. These trends express overall sclerite shape and variability in the shape of selected measured intrasclerite fea-

tures, such as glabellar or rhachial shape. In all cases, ratios of relevant original measured variables (from Labandeira, 1983b) were used to construct the trendlines on the Dimension 1 versus Dimension 2 scatter plots.

The resulting patterns, while straightforward, nevertheless illustrate the continuous nature of intraspecific variation for all sclerites analyzed in *Dikelocephalus* (Hughes, 1991). Among the cranidia (Figure 12), the major axis defines a curvilinear trend where glabellae are wide and squarose (lower right) to narrow and prolonged (upper left). For librigenae (Figure 13), the dominant trend is also curvilinear and consists of morphs that have a larger separation between the postpalpebral point and point omega (left) and those that have a smaller separation between these two landmarks (right). The only observed structural trend for hypostomata (Figure 14) is a continuum of forms possessing a squarose hypostoma with a proportionately smaller middle body (right) to those with anteriorly to posteriorly prolonged hypostomata with a proportionately larger middle body (left). Pygidia (Figure 15) exhibit a strong rectilinear trend from morphs with anteriorly to posteriorly elongated pygidia and proportionately wider rhachises (right) to morphs with less squarose pygidia and proportionately narrower rhachises (left). These patterns of continuous variation in sclerite form support our contention that Ulrich and Resser's species-level circumscription of their *Dikelocephalus* type-suite was unwarranted. Rather, *Dikelocephalus* is a structurally variable trilobite representing a continuum of morphs in time and space.

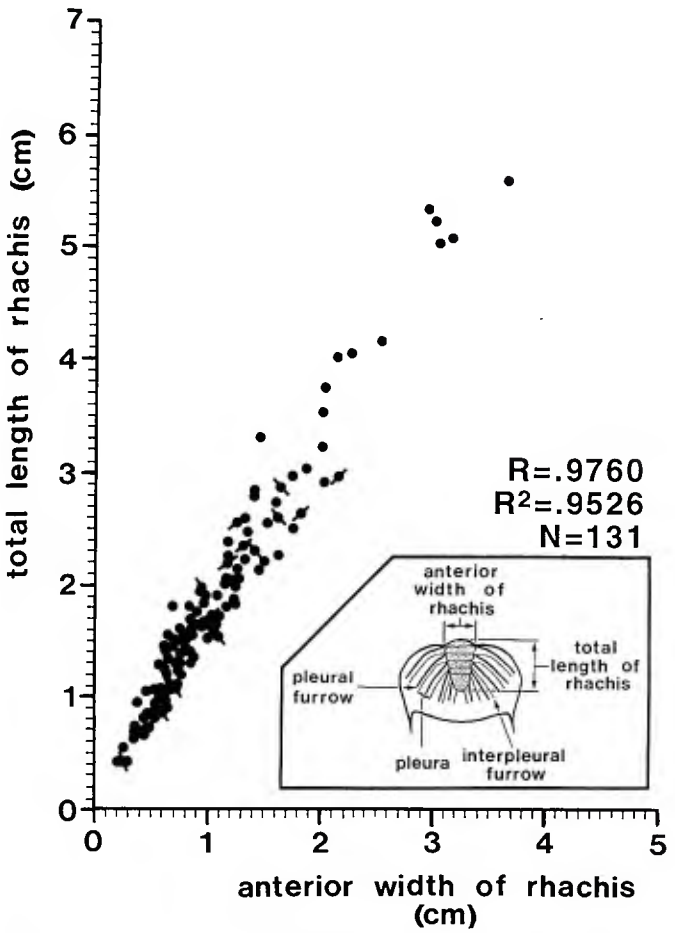


FIGURE 10—Anterior width of rachis versus total rachial length among Ulrich and Resser's (1930) syntype-suite. Glyphs with bars directed to the left indicate specimens from a single bedding plane collection at Richland Center, Richland County, Wisconsin; bars directed to the right indicate Ulrich and Resser's (1930) figured syntypes.

VARIATION AND TAXONOMY

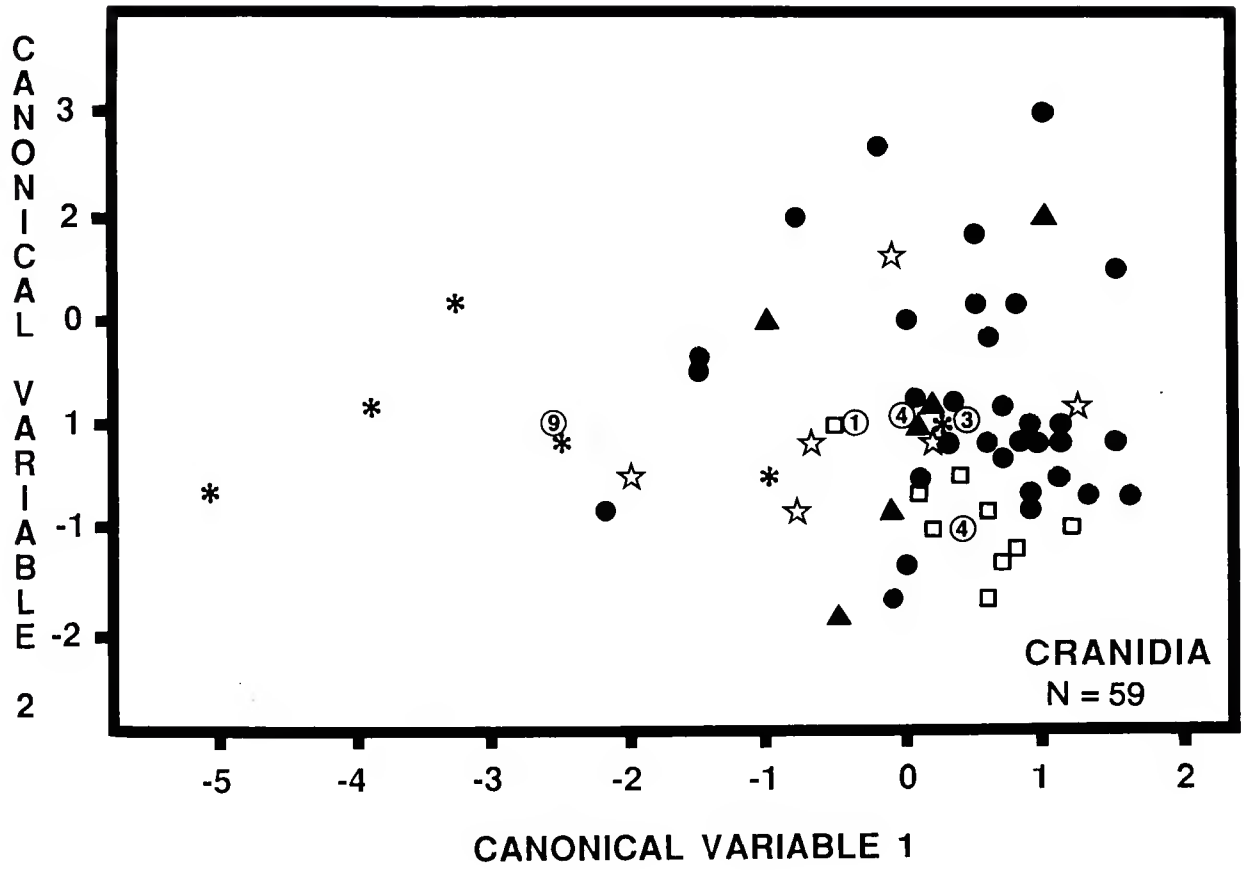
We consider species to represent "the smallest aggregation of populations . . . diagnosable by a unique combination of character states in comparable individuals" (Nixon and Wheeler, 1990, p. 218). Such phylogenetic species cannot be further subdivided even if they show considerable continuous variation within the lineage (Wiley, 1978). Morphological continuity is emphasized as positive evidence for the integrity of species. Because Ulrich and Resser's (1930) pooled sample of *Dikelocephalus* exhibits complete continuity in all bivariate and multivariate analyses, there is insufficient grounds for the recognition of more than a single species. While it is not possible to discriminate distinct species from this morphometric analysis, it is clear that there is substantial morphological variation within the sample. The inability to detect any subgroups within the data set suggests that the patterns of variation within *Dikelocephalus* are complex but intraspecific.

Where possible, Ulrich and Resser (1930) supported their shape-based species diagnoses using variation of meristic characters. It is possible that the distribution of such characters may define monophyletic subgroups within the genus. For example, a median occipital tubercle is present in approximately half the sample. The occurrence of the tubercle could potentially be used to discriminate species or dimorphs of *Dikelocephalus,* although ironically Ulrich and Resser (1930) did not use this character in their species diagnoses. Analysis of the patterns of variation within and among collections from individual bedding planes is necessary before the taxonomic significance of such characters can be assessed. Hence, it would be inappropriate to base formal taxonomic revision on the present study. Ulrich and Resser (1930) used approximately 350 specimens in their study. The present study demonstrates that only documentation of patterns of growth and locality-related variability in *Dikelocephalus* will permit comprehensive revision of the systematics of the genus (Hughes, in press). At low taxonomic levels the availability of large numbers of specimens from spatiotemporally well-constrained localities is a necessary condition for determining systematic relationships. To sufficiently demonstrate these relationships it must be established whether patterns of morphological variation within and between populations are continuous or discontinuous and whether such patterns are not more appropriately explained by hypotheses involving ontogenetic processes, dimorphic differences, or other types of intraspecific variation.

Characters that have been proved unreliable taxonomic indicators in *Dikelocephalus* are commonly used in the diagnoses of other trilobite taxa. For example, the relative length of the frontal area is considered as taxonomically significant in many trilobites, such as the discrimination of three genera of Ordovician olenids by Ludvigsen and Tuffnell (1983). (Also see Henningsmoen, 1957, for other examples of the use of frontal area

TABLE 3—Structure of the four sclerite data sets inputted into the KYST2A multidimensional scaling analysis. An absolute maximum matrix sample size of 100 and maximum of 1,800 matrix data values are limitations of KYST2A.

Sclerite data set	Sample size	Matrix values	Iterations			Stress minimum
			Default	Penultimate	Final	
Cranidia	59	1,770	600	290	56	0.0048
Librigenae	59	1,770	600	220	55	0.012
Hypostomata	34	561	800	284	36	0.001
Pygidia	59	1,770	600	392	126	0.002



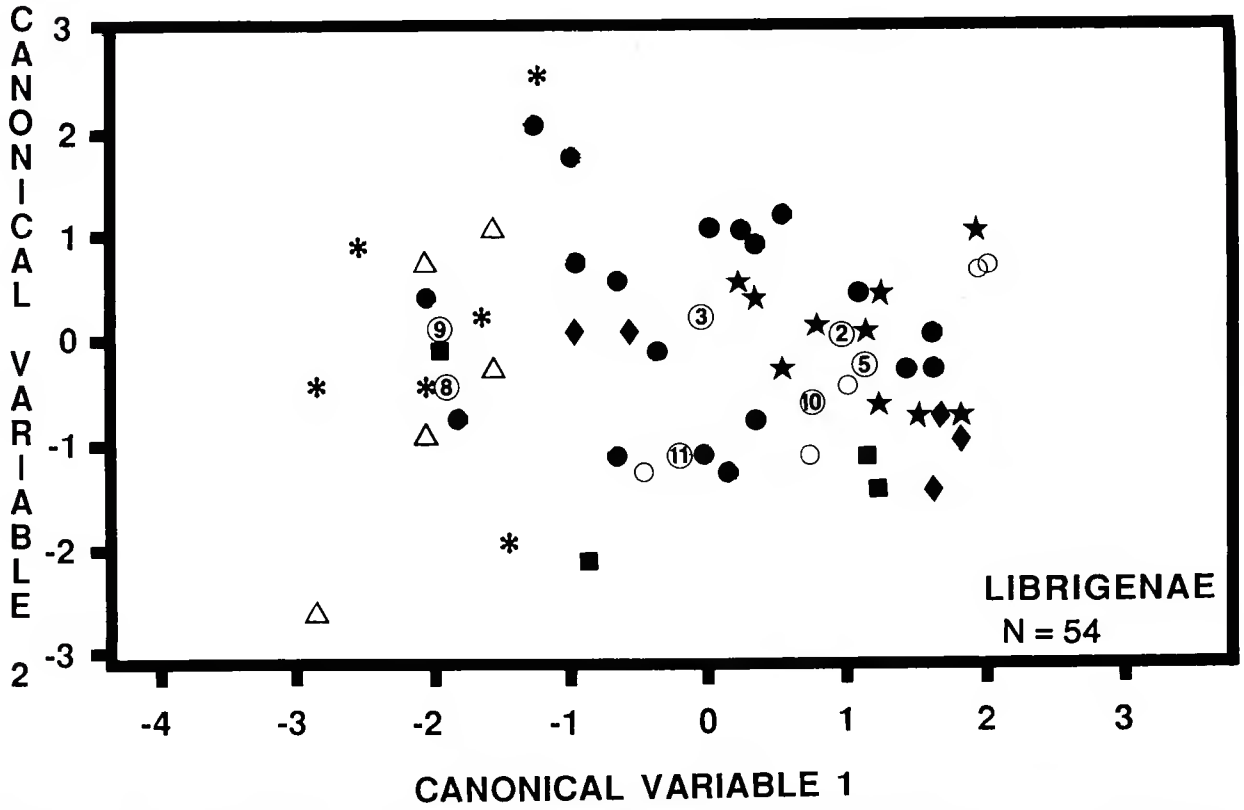
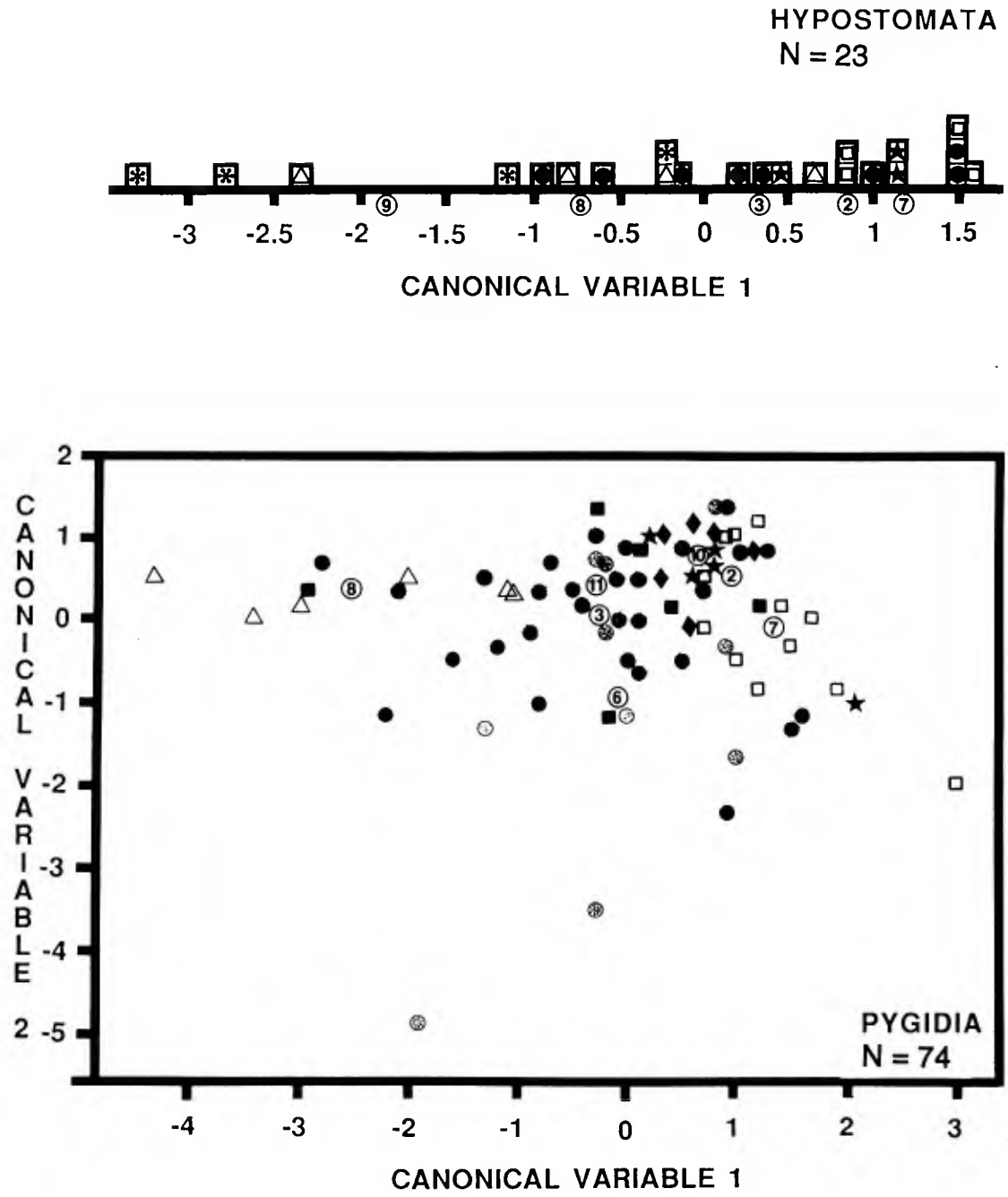


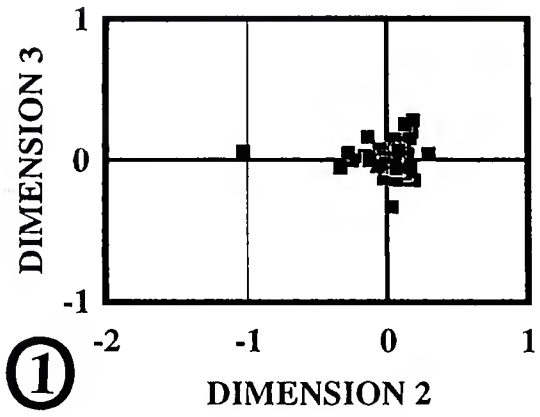
FIGURE *11*—Canonical variable scatter plots and histogram of *Dikelocephalus* specimens representing the four sclerites indicated and comprising 11 of the 26 species established by Ulrich and Resser (1930). See Appendix for raw data values used in this analysis.

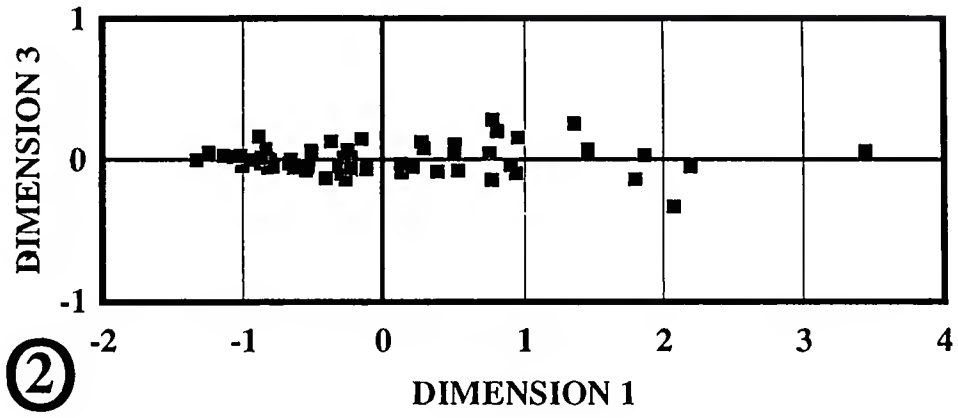


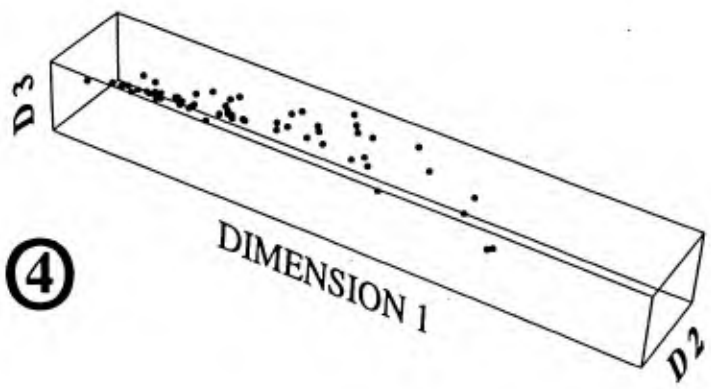
LEGEND FOR DISCRIMINANT ANALYSIS PLOTS

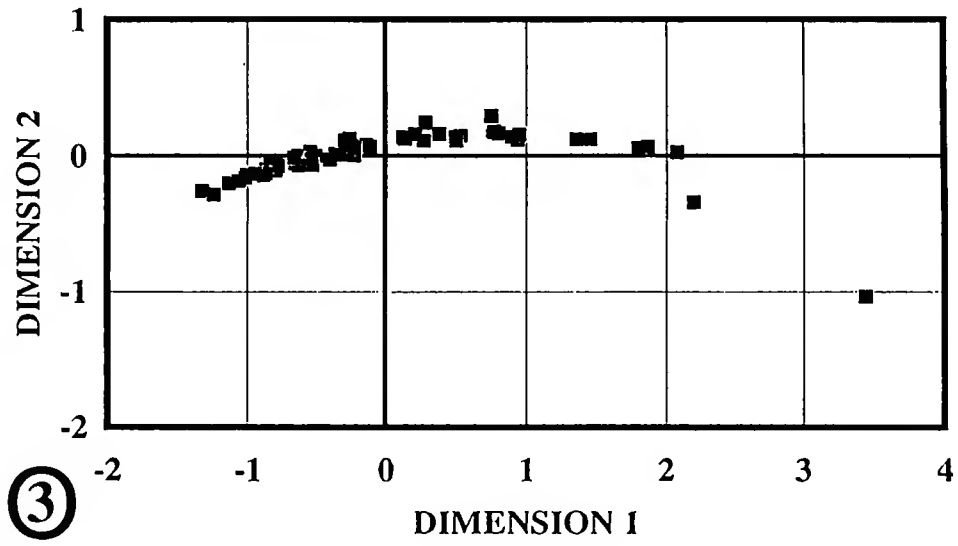
Dikelocephalus species	species-group centroids	specimen symbol
barretti	1	☆
edwardsi	2	★
gracilis	3	●
granosus	4	▲
marginatus	5	○
minnesotensis	6	⊛
norwalkensis	7	□
ovatus	8	△
raaschi	9	✻
subplanus	10	♦
wisconsinensis	11	■

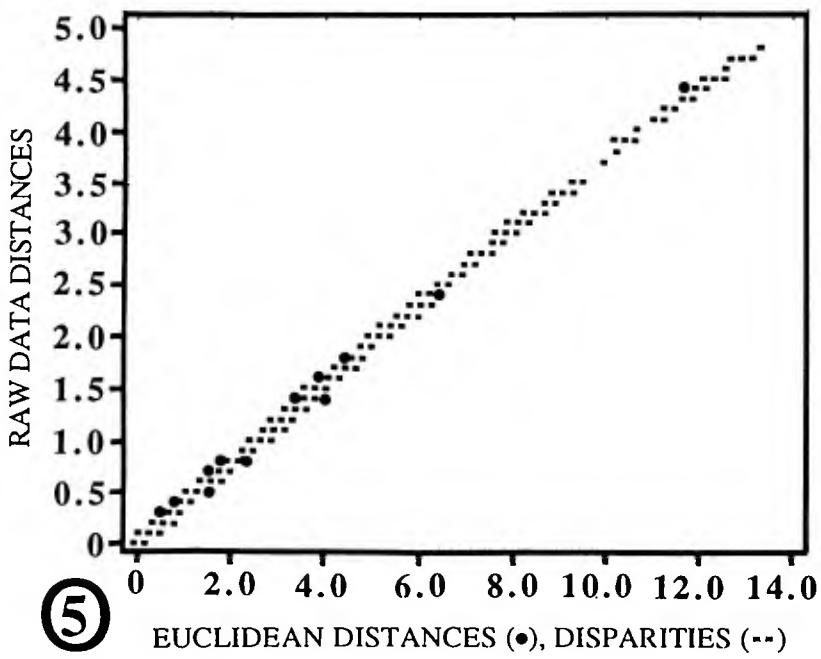
FIGURE *11*—Continued.











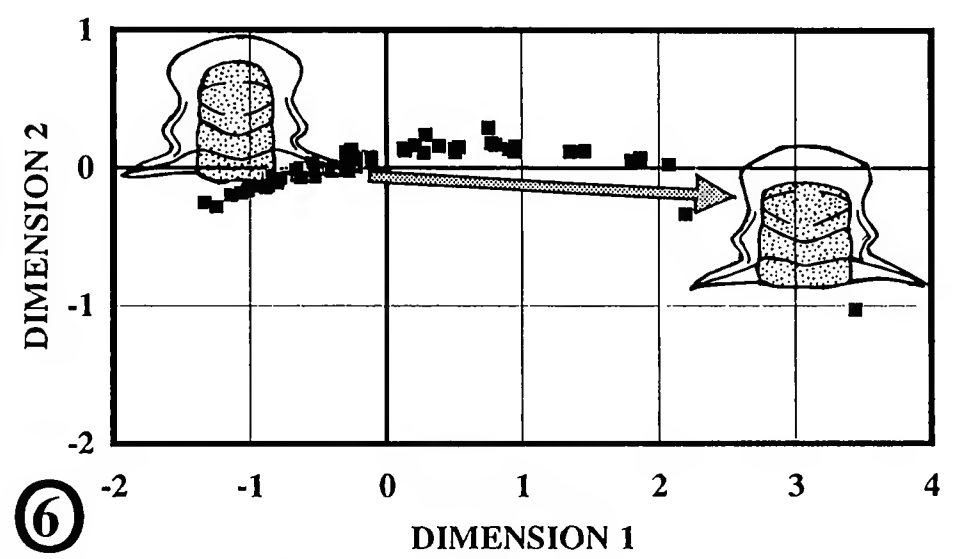
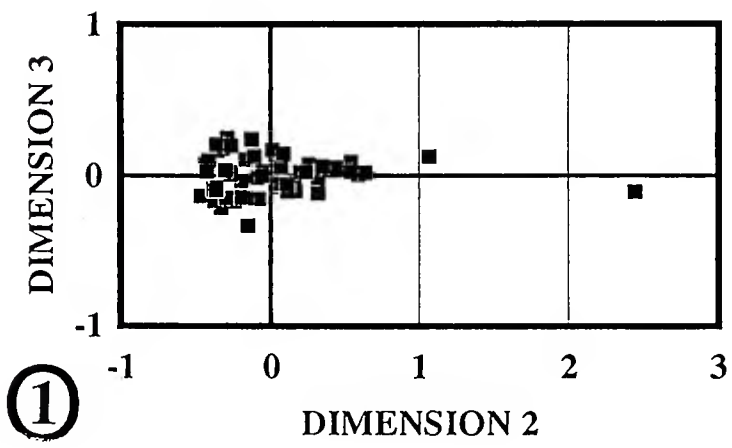
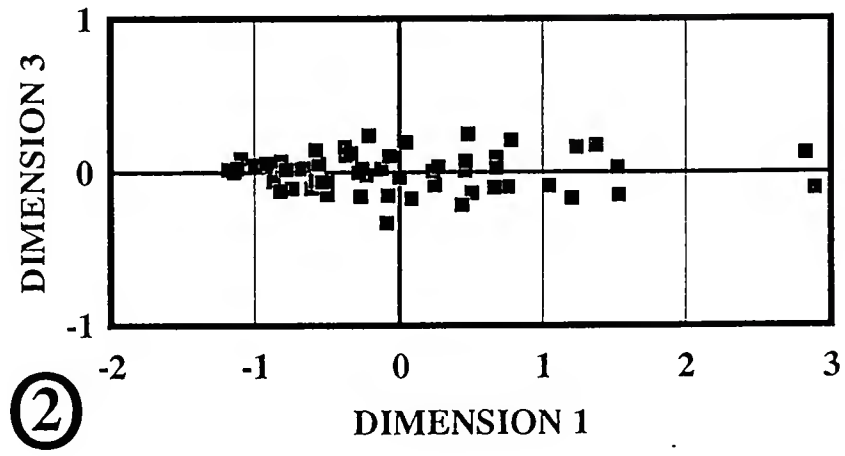
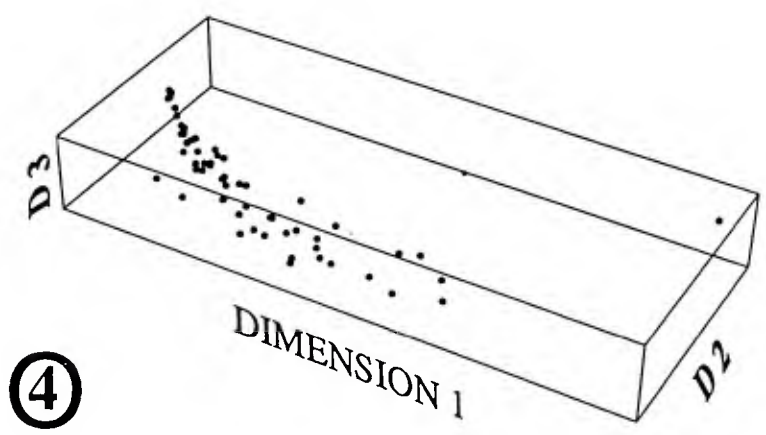


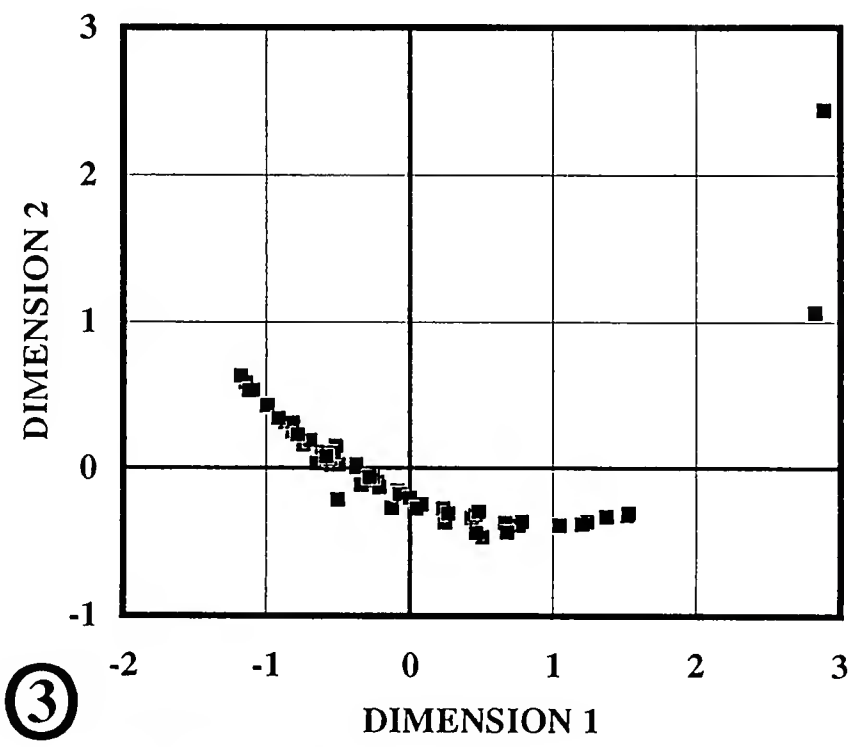
FIGURE *12*—Results of nonmetric multidimensional scaling for 59 specimens of *Dikelocephalus* cranidia. *1,* scatter plot of Dimension 2 versus Dimension 3. Data points represent individual specimens. *2,* scatter plot of Dimension 1 versus Dimension 3. *3,* scatter plot of Dimension 1 versus Dimension 2. *4,* final three-dimensional configuration. *5,* graph showing a least-squares regression of initial (raw) data distances on the X-axis, versus Euclidean distances (dots) and disparities (dashes) on the Y-axis. Disparities are raw data distances scaled to match Euclidean distances as closely as possible. *6,* interpretation of pattern revealed by Dimension 1 versus Dimension 2. Relevant original raw data was mapped onto the scatter plot, indicating a trend from cranidia with wide and squarose glabellae (lower right) to morphs with narrow and anteriorly to posteriorly prolonged glabellae (upper left). Endmember outlines showing relative cranidial proportions are exaggerated to visually convey the sense of cranidial change along the trendline. See Appendix for raw data used in this analysis.

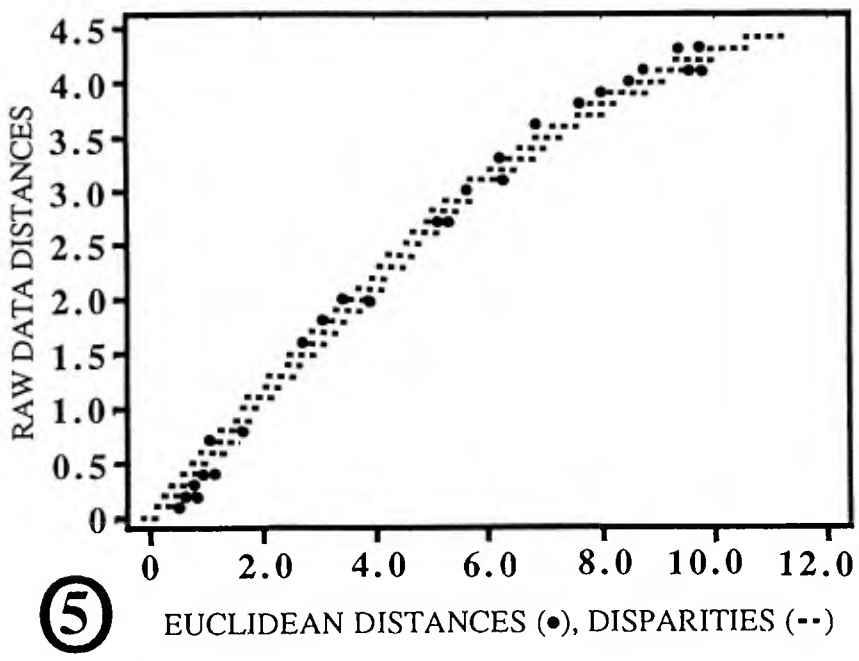
length in olenid taxonomy.) In *Dikelocephalus* the frontal area length shows wide but continuous variation and this character cannot be used to distinguish species within the genus. The possibility that such a wide range of variation may represent an intraspecific feature often has not been considered in systematic studies of trilobites. The high variability of this character in *Dikelocephalus* does not necessarily invalidate the use of relative length of the frontal area as a taxonomic character generally in trilobites. However, the possibility of continuous variation in the frontal area must be excluded before frontal area length can be used in taxonomic diagnoses of any trilobite. As in *Dikelocephalus,* an instance where the length of the frontal area was used inappropriately was the separation of *Parabolinoides contractus* and *P. hebe.* Bell and Ellinwood (1962) considered these two taxa to be represented by short and long frontal areas, respectively. In contrast, large numbers of specimens were used











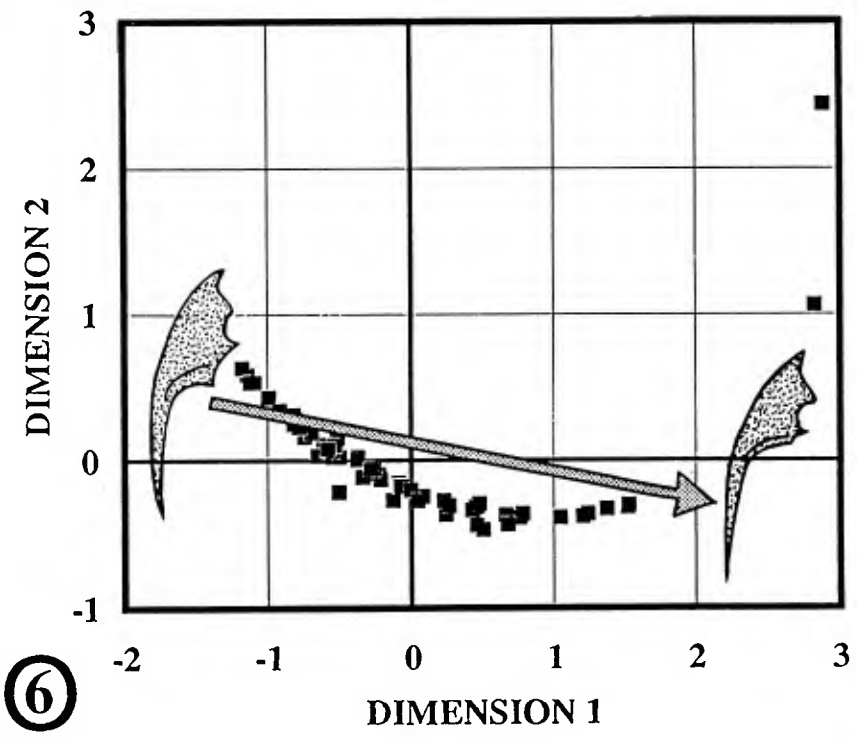
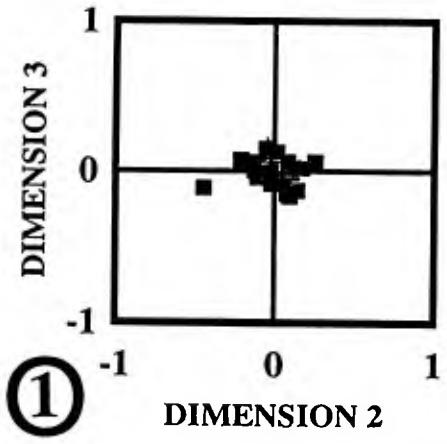
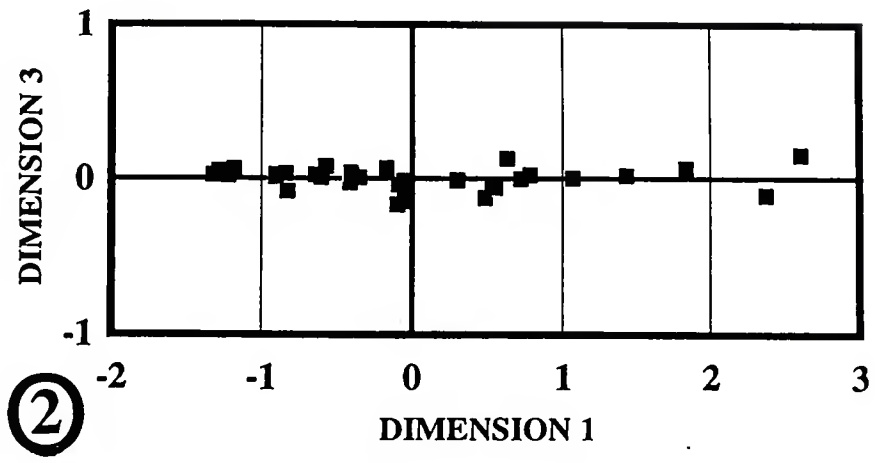
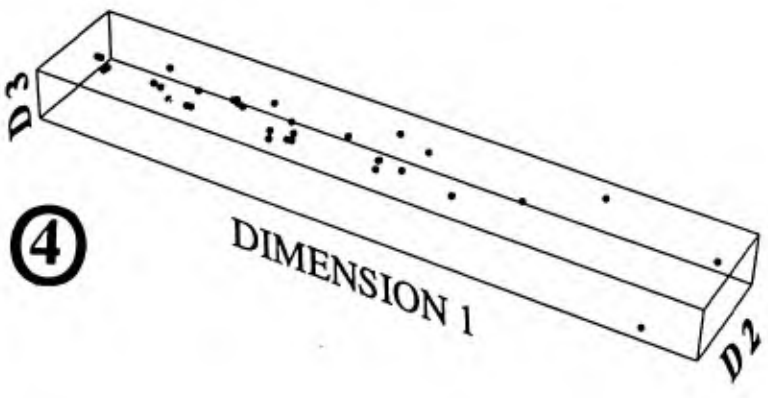
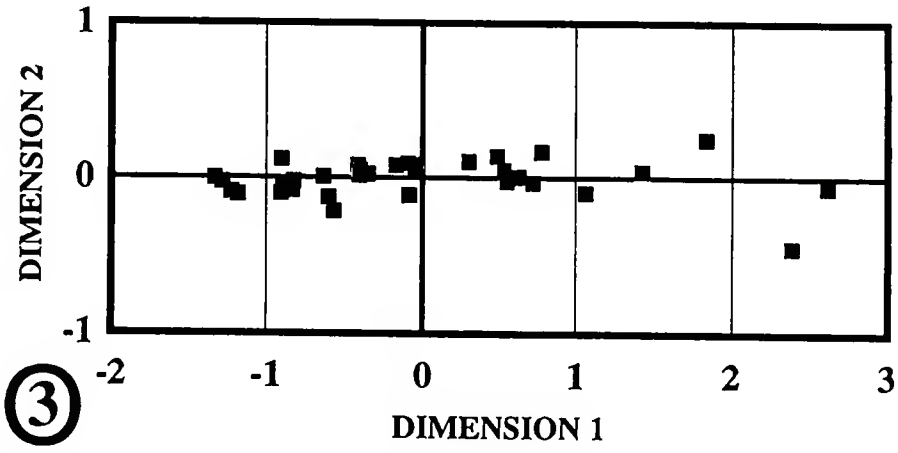


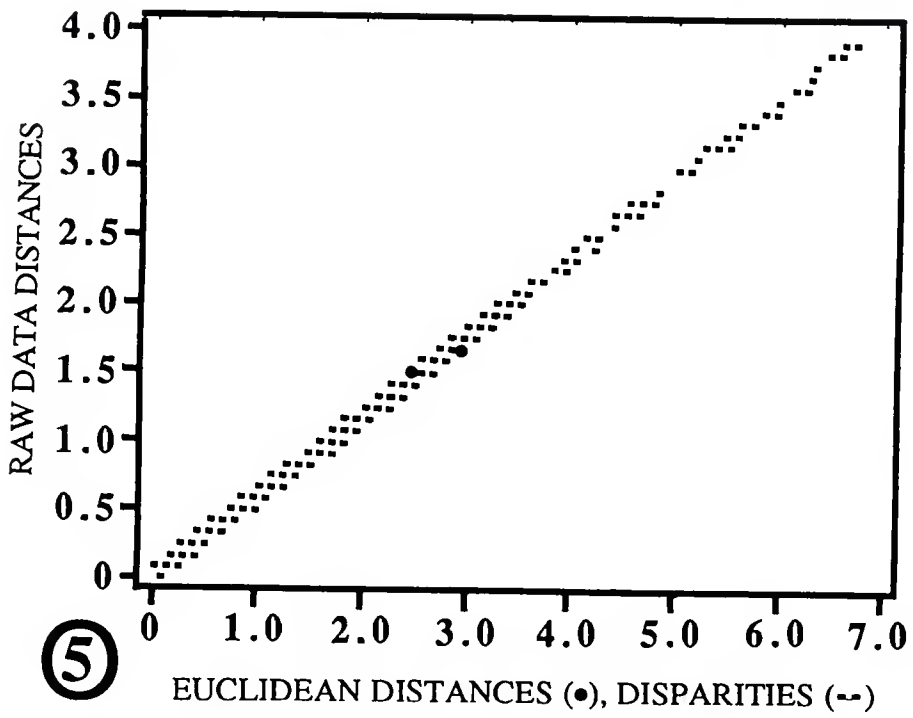
FIGURE *13*—Results of nonmetric multidimensional scaling for 59 specimens of *Dikelocephalus* librigenae. *1*, scatter plot of Dimension 2 versus Dimension 3. Data points represent individual specimens. *2*, scatter plot of Dimension 1 versus Dimension 3. *3*, scatter plot of Dimension 1 versus Dimension 2. *4*, final three-dimensional configuration. *5*, graph showing a least-squares regression of initial (raw) data distances on the X-axis versus Euclidean distances (dots) and disparities (dashes) on the Y-axis. Disparities are raw data distances scaled to match Euclidean distances as closely as possible. *6*, interpretation of pattern revealed by Dimension 1 versus Dimension 2. Relevant original raw data was mapped onto the scatter plot, indicating a trend from librigenae with a relatively wide separation between the postpalpebral point and point omega (right) and those forms with a relatively narrow separation between these two points (left). Endmember outlines showing relative librigenal proportions are exaggerated to visually convey the sense of librigenal change along the trendline. See Appendix for raw data used in this analysis.











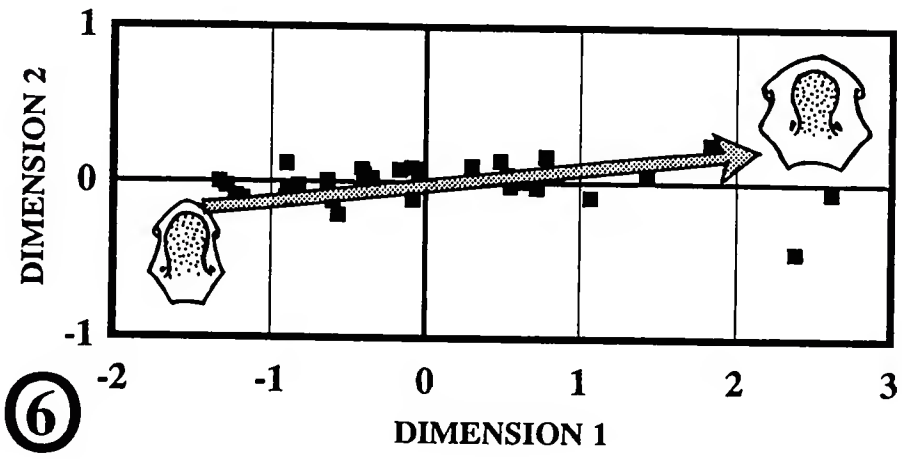
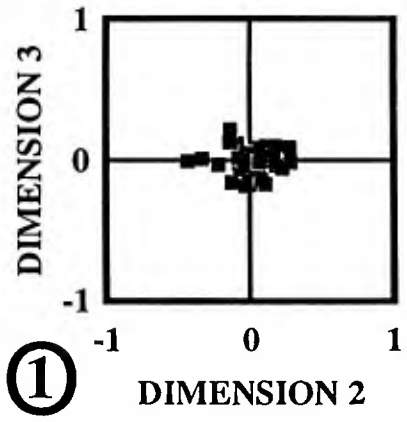
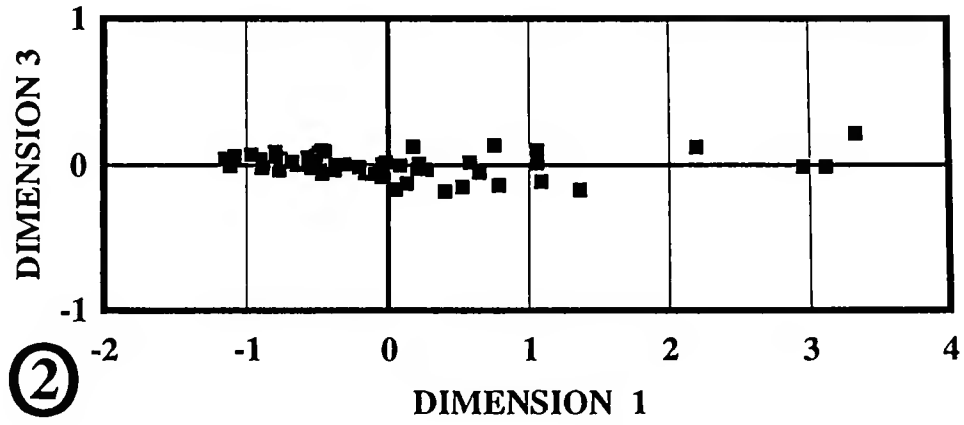


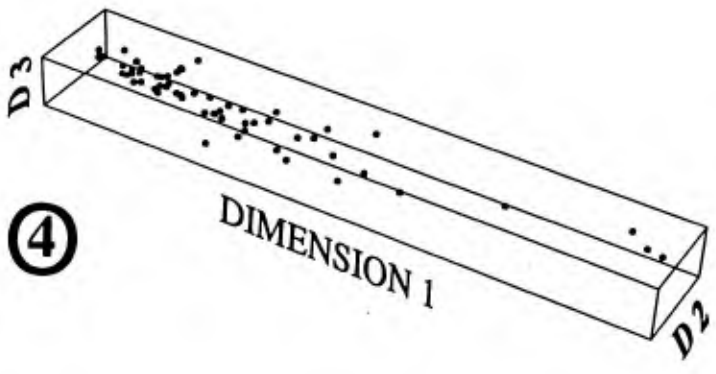
FIGURE *14*—Results of nonmetric multidimensional scaling for 34 specimens of *Dikelocephalus* hypostomata. *1*, scatter plot of Dimension 2 versus Dimension 3. Data points represent individual specimens. *2*, scatter plot of Dimension 1 versus Dimension 3. *3*, scatter plot of Dimension 1 versus Dimension 2. *4*, final three-dimensional configuration. *5*, graph showing a least-squares regression of initial (raw) data distances on the X-axis versus Euclidean distances (dots) and disparities (dashes) on the Y-axis. Disparities are raw data distances scaled to match Euclidean distances as closely as possible. *6*, interpretation of pattern revealed by Dimension 1 versus Dimension 2. Relevant original raw data was mapped onto the scatter plot, indicating an apparent trend of hypostomata possessing a more squarose shape and a relatively smaller middle body (right) to those with an anterior to posterior prolonged hypostome and a relatively larger middle body (left). End-member outlines showing relative hypostomatal proportions are exaggerated to visually convey the sense of hypostomatal change along the trendline. See Appendix for raw data used in this analysis.

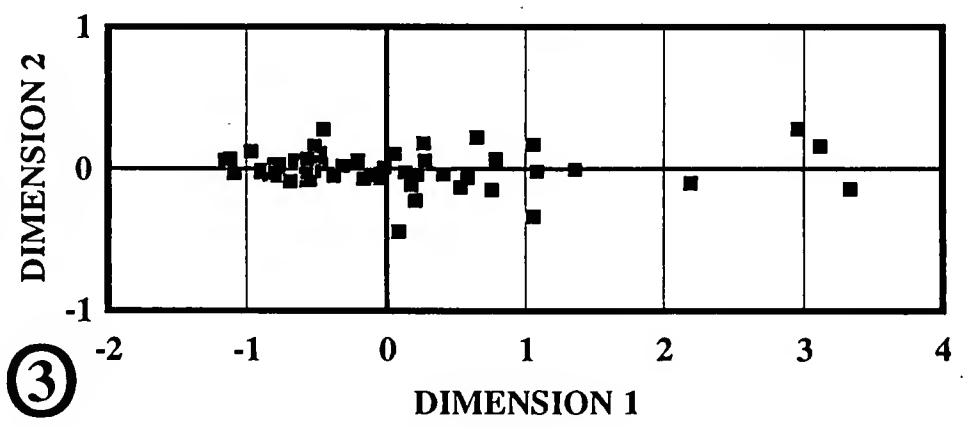
by Longacre (1970) to document continuous intergradation of frontal area lengths between these two species—thus demonstrating that any taxonomic distinction must rely on other differences.

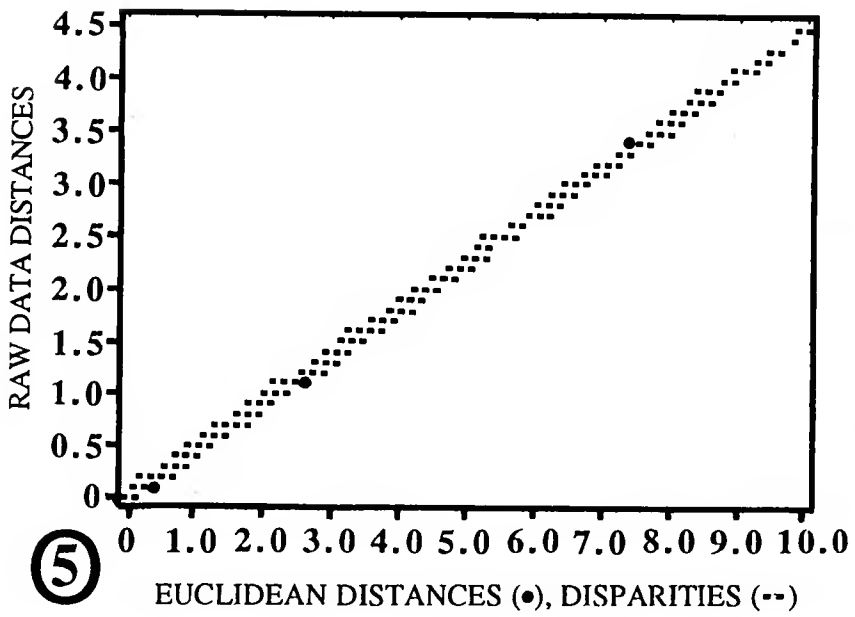
The shape of the pygidium was considered taxonomically significant in *Dikelocephalus* by Ulrich and Resser (1930). The present analyses indicate that the shape of the pygidium varies continuously among the total sample and cannot be used for species recognition. Pygidial shape has commonly been considered species-specific in trilobites. For example, Jaanusson (1953, p. 389, fig. 5) considered pygidial shape as the most important character for distinguishing between several genera and species of middle Ordovician asaphids from Scandinavia. Fortey (1980) and Sheldon (1987) both used morphometric analyses of large numbers of asaphid specimens to demonstrate continuous variation between specimens previously considered as different taxa. Fortey (1980) suggested that two previously recognized species of *Basilicus* were not differentiated by pygidial morphology and











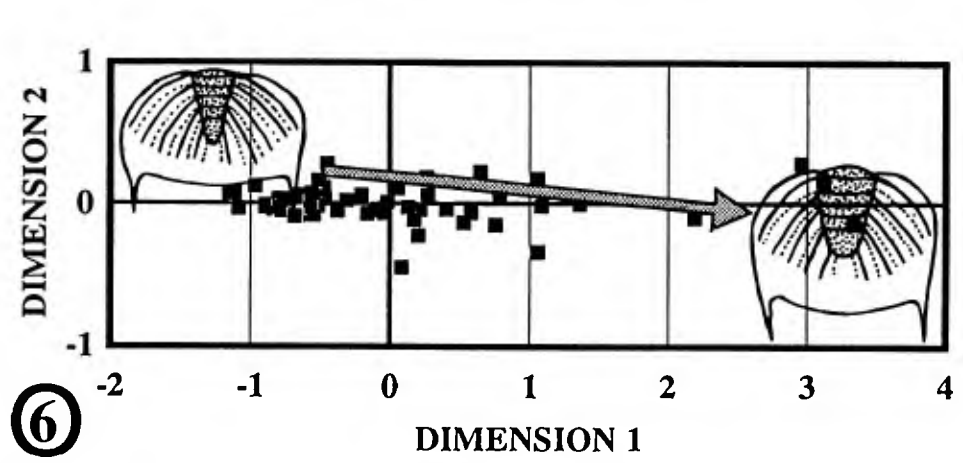


FIGURE *15*—Results of nonmetric multidimensional scaling for 59 specimens of *Dikelocephalus* pygidia. *1,* scatter plot of Dimension 1 versus Dimension 2. Data points represent individual specimens. *2,* scatter plot of Dimension 2 versus Dimension 3. *3,* scatter plot of Dimension 1 versus Dimension 3. *4,* Final three-dimensional configuration. *5,* graph showing a least-squares regression of initial (raw) data distances on the X-axis versus Euclidean distances (dots) and disparities (dashes) on the Y-axis. Disparities are raw data distances scaled to match Euclidean distances as closely as possible. *6,* interpretation of pattern revealed by Dimension 1 versus Dimension 2. Relevant original raw data was mapped onto the scatter plot, indicating a trend from pygidia with relatively wide rhachises and elongated in an anterior to posterior fashion (right) to more squarose pygidia with relatively narrow rhachises (left). End-member outlines showing relatively pygidial proportions are exaggerated to visually convey the sense of pygidial change along the trendline. See Appendix for raw data used in this analysis.

thus were probably synonymous. However, in the absence of biostratigraphically and biogeographically well-constrained collections he did not propose formal synonymy. Marked pygidial variation within species lineages has also been demonstrated in several species lineages of Ordovician asaphids and other trilobites (Sheldon, 1987).

Intraspecific dimorphs have been recognized in Cambrian trilobites on the basis of slight differences in relative proportions within sclerites and interpreted as sexual dimorphs (e.g., Hu, 1971, and references therein; Kopaska-Merkel, 1982). However, the present analysis of relative sclerite proportion in large numbers of *Dikelocephalus* did not detect dimorphism. Using morphometric analysis of large collections, Bruton and Owen (1988) have shown that shape-based "dimorphs" of the Ordovician illaenid *Stenopareia glaber* are simply end-members of a continuous range of intraspecific variation. Most cases of sexual dimorphism in trilobites are poorly supported.

Although the patterns of variation shown within *Dikelocephalus* are not necessarily characteristic of all trilobite species, they clearly have parallels in other trilobite taxa and, apparently, in other fossils, such as planktonic foraminifera (Tabachnick and Bookstein, 1990) and Triassic ammonites (Hohenegger and Tatzreiter, 1992). Hence, taxonomic studies of trilobites species should include analyses and evaluations of patterns of character

variation. In all the cases mentioned above, large numbers of specimens were necessary to detect continuous variation. Morphometric studies at low taxonomic levels strongly suggest that the range of intraspecific variation within trilobites is far greater than previously expected. This suggests a paradox. If a random sample is taken from a clade containing species that all show similar levels of intraspecific variation, at small sample sizes many intraspecific differences will appear discrete and thus could be considered interspecific. As the sample size increases, these differences will be found to vary continuously until only the true interspecific characters emerge as being discrete. Hence, in a comparison of two clades of equal species diversity, the less well known clade may appear to be more diverse. This principle is applicable at all levels of the taxonomic hierarchy and has important implications for studies of taxonomic, as opposed to morphologic, diversity in the Trilobita.

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REFERENCES

BELL, W. C., AND H. L. ELLINWOOD. 1962. Upper Franconian and Lower Trempealeauan Cambrian trilobites and brachiopods, Wilberns Formation, central Texas. Journal of Paleontology, 36:385–423.

——, O. W. FENIAK, AND V. E. KURTZ. 1952. Trilobites from the Franconia Formation, southeast Minnesota. Journal of Paleontology, 26:175–198.

BRUTON, D. L., AND A. W. OWEN. 1988. The Norwegian Upper Ordovician illaenid trilobites. Norsk Geologisk Tidsskrift, 68:241–258.

CHATFIELD, C. A. J., AND A. J. COLLINS. 1980. An Introduction to Multivariate Analysis. Chapman and Hall, London, 246 p.

DILLON, W. R., AND M. GOLDSTEIN. 1984. Multivariate Analysis: Methods and Applications. John Wiley and Sons, New York, 587 p.

FOOTE, M. 1990. Nearest-neighbor analysis of trilobite morphospace. Systematic Zoology, 39:371–382.

FORTEY, R. A. 1980. *Basilicus tyrannus* (Murchison) and the glabellar structure of asaphid trilobites. Bulletin of the British Museum of Natural History (Geology), 34:255–264.

GRANT, R. E. 1965. Faunas and stratigraphy of the Snowy Range Formation (Upper Cambrian) in southwestern Montana and northwestern Wyoming. Geological Society of America Memoir, 96:1–171.

HALL, J. 1863. Preliminary notice of the fauna of the Potsdam Sandstone, p. 119–226. *In* Sixteenth Annual Report of the Regents of the University of the State of New York on the Condition of the State Cabinet of Natural History.

HENNINGSMOEN, G. 1957. The trilobite family Olenidae. Skrifter utgitt av det Norske Videnskaps-Academi i Oslo, 1. Mathematisk-Naturvidenskabelig Klasse, 1:1–303.

HESSELBO, S. P. 1987a. The biostratinomy of *Dikelocephalus* sclerites: implications for the use of trilobite attitude data. Palaios, 2:605–608.

——. 1987b. The Cambrian aglaspidid arthropods from Wisconsin and Utah and their geological setting. Unpubl. Ph.D. thesis, University of Bristol, United Kingdom, 414 p.

HOHENEGGER, J., AND F. TATZREITER. 1992. Morphometric methods in determination of ammonite species, exemplified through *Balatonites* shells (Middle Triassic). Journal of Paleontology, 66:801–816.

HU, C.-H. 1971. Ontogeny and sexual dimorphism in lower Paleozoic Trilobita. Palaeontographica Americana, 7:31–151.

HUGHES, N. C. 1988. Ontogenetic and phenotypic variation in the Upper Cambrian trilobite *Dikelocephalus*. Society of Economic Paleontologists and Mineralogists Annual Midyear Meeting, Abstracts, 5:26.

——. 1990. The Upper Cambrian trilobite *Dikelocephalus minnesotensis* and its geological setting. Unpubl. Ph.D. thesis, University of Bristol, United Kingdom, 483 p.

——. 1991. Morphological plasticity and genetic flexibility in a Cambrian trilobite. Geology, 19:913–916.

——. 1993. Distribution, taphonomy and functional morphology of the Upper Cambrian trilobite *Dikelocephalus*. Milwaukee Public Museum Contributions in Biology and Geology, 84:1–49.

——. In press. Ontogeny, intraspecific variation, and systematics of the Late Cambrian trilobite *Dikelocephalus*. Smithsonian Contributions to Paleobiology, 79.

JAANUSSON, V. 1953. Untersuchungen über baltoskandische Asapiden 1. Arkiv för Mineralogi och Geologi, 1:377–464.

JENNRICH, R., AND P. SAMPSON. 1988. Stepwise discriminant analysis, p. 337–356. *In* W. J. Dixon (ed.), BMDP Statistical Software Manual. University of California Press, Berkeley.

KENDALL, M. G. 1975. Multivariate Analysis. Charles Griffin, London, 210 p.

KLECKA, W. R. 1980. Discriminant analysis. Sage University Paper Series on Quantitative Applications in the Social Sciences, 07-001, 71 p.

KOPASKA-MERKEL, D. C. 1982. Sexual dimorphism in five species of the trilobite *Ehmaniella*. Geological Society of America, Abstracts with Programs, 14:534.

KRUSKAL, J. B., AND M. WISH. 1977. Multidimensional scaling. Sage University Paper on Quantitative Applications in the Social Sciences, 07-011, 95 p.

KRUSKAL, J. B., F. W. YOUNG, AND J. B. SEERY. 1978. How to Use KYST, a very flexible program to do multidimensional scaling and unfolding. Bell Laboratories, Murray Hill, New Jersey, privately published, 72 p.

LABANDEIRA, C. C. 1983a. Changing species concepts in American paleontology and revision of *Dikelocephalus*, an Upper Cambrian trilobite from southwestern Wisconsin and eastern Minnesota. Geological Society of America, Abstracts with Programs, 15:260.

——. 1983b. The Paleobiology of the Dikelocephalidae (Trilobita, Upper Cambrian) and systematic revision of the genus *Dikelocephalus* (Owen) with special reference to changing species concepts in North American paleontological thought. Unpubl. M.S. thesis, University of Wisconsin-Milwaukee, 328 p.

LONGACRE, S. A. 1970. Trilobites of the Upper Cambrian ptychaspid biomere, Wilberns Formation, central Texas. Paleontological Society Memoir, 4:1–68.

LUDVIGSEN, R., AND P. A. TUFFNELL. 1983. A revision of the Ordovician olenid trilobite *Triarthrus* Green. Geological Magazine, 120: 567–577.

——, AND S. R. WESTROP. 1985. Three new Upper Cambrian stages for North America. Geology, 13:139–143.

MANLY, B. F. J. 1986. Multivariate Statistical Methods: A Primer. Chapman and Hall, New York, 159 p.

MARDIA, K. V., J. T. KENT, AND J. M. BIBBY. 1979. Multivariate Analysis. Academic Press, London, 521 p.

MCNAMARA, K. J., 1986. The role of heterochrony in the evolution of Cambrian trilobites. Biological Reviews, 61:121–156.

NIXON, K. C., AND Q. D. WHEELER. 1990. An amplification of the phylogenetic species concept. Cladistics, 6:211–223.

OWEN, D. D. 1852. Report of the Geological Survey of Wisconsin, Iowa and Minnesota. Lippencott, Grambo, and Co. Philadelphia, 638 p.

RAASCH, G. O. 1951. Revision of the Croixan dikelocephalids. Transactions of the Illinois Academy of Science, 44:137–151.

SDZUY, K. 1966. Das Kambrium des Frankenwaldes. Senckenbergiana Lethaea, 47:57–86.

SHAW, A. B. 1956. Quantitative trilobite studies II. Measurement of the dorsal shield of non-agnostidean trilobites. Journal of Paleontology, 31:193–207.

SHELDON, P. R. 1987. Parallel gradualistic evolution of Ordovician trilobites. Nature, 330:561–563.

SOKAL, R. R., AND F. J. ROHLF. 1973. Introduction to Biostatistics. W. H. Freeman and Co, San Francisco, 368 p.

SPSS®. 1990. SPSS® Reference Guide, 550–562. SPSS® Inc., Chicago.

TABACHNICK, R. E., AND F. L. BOOKSTEIN. 1990. The structure of individual variation in Miocene *Globorotalia*. Evolution, 44:416–434.

TAYLOR, M. E., AND R. B. HALLEY. 1974. Systematics, environment and biogeography of some Late Cambrian and Early Ordovician trilobites from eastern New York State. U. S. Geological Survey, Professional Paper 834:1–38.

TEMPLE, J. T. 1975. Standardisation of trilobite orientation and measurement. Fossils and Strata, 4:461–467.

TWENHOFEL, W. H. 1945. Several Upper Cambrian fossils from the Upper Mississippi Valley and a giant graptolite from the lower Middle Ordovician of Newfoundland. Journal of Paleontology, 19:633–636.

ULRICH, E. O., AND C. E. RESSER. 1930. The Cambrian of the Upper Mississippi Valley, Part 1. Trilobita; Dikelocephalinae and Osceolinae. Milwaukee Public Museum Bulletin, 12;1–122.

——. 1933. The Cambrian of the Upper Mississippi Valley. Part 2. Trilobita; Saukiinae. Milwaukee Public Museum Bulletin, 12:123–306.

WALCOTT, C. D. 1914. Cambrian geology and paleontology 2. *Dikelocephalus* and other genera of the Dikelocephalina. Smithsonian Miscellaneous Collections, 57:345–430.

WESTROP, S. R. 1986. Trilobites of the Upper Cambrian Sunwaptan Stage, southern Canadian Rocky Mountains, Alberta. Palaeontographica Canadiana, 3:1–179.

WILEY, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology, 27:17–26.

WINCHELL, N. H. 1874. The geology of the Minnesota Valley. Minnesota Geological and Natural History Survey Second Annual Report, 1874:127–212.

WINSTON, D., AND H. NICHOLLS. 1967. Late Cambrian and Early Ordovician faunas from the Wilberns Formation of central Texas. Journal of Paleontology, 41:66–96.

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APPENDIX

Linear and angular measurement data for specimens of *Dikelocephalus,* comprising mostly of material referred to by Ulrich and Resser (1930), and some subsequently collected, additional specimens. Asterisks indicate that a relevant landmark was not clearly present during measurement. Institutional abbreviations: FMNH, Field Museum of Natural History; MPM, Milwaukee Public Museum; USNM, United States National Museum; and UWM, University of Wisconsin-Milwaukee Green Museum.

Cranidial linear measurements.

Catalog number and institution	Preglabellar furrow midpt./ prepalpebral sinus distance		Preglabellar furrow midpt./ postpalpebral sinus distance		Palpebral chord length		Sagittal		Frontal area length	Palpebral cranidial width	Ulrich and Resser's species	Use in multivariate analysis	
	Left	Right	Left	Right	Left	Right	Occipital glabellar width	Occipito glabellar length				SDA	MDS
USNM102264	1.80	1.84	2.99	2.58	0.86	0.90	2.07	2.67	0.79	3.75	*barretti*	X	X
MPM19926	1.07	1.00	1.60	1.51	0.62	0.63	1.19	1.78	0.52	2.15	*barretti*	X	X
MPM19931	0.72	0.74	1.25	1.22	0.56	0.57	0.93	1.14	0.30	1.82	*barretti*	X	X
MPM19932	1.15	1.15	1.67	1.64	0.63	0.64	1.37	1.81	0.67	2.48	*barretti*	X	X
MPM20677	—	1.69	—	2.53	—	0.94	1.77	2.59	0.98	3.61	*barretti*	X	
MPM20678	1.38	—	2.05	—	0.81	—	1.54	2.03	0.73	2.98	*barretti*	X	
MPM18681	0.77	0.90	1.37	1.55	0.67	0.70	1.12	1.40	0.40	2.11	*brevis*		X
MPM19935	0.48	0.45	0.75	0.71	0.33	0.32	0.61	0.80	0.24	1.22	*brevis*		X
MPM19936	—	—	—	—	—	—	0.60	0.78	—	—	*brevis*		
MPM19937	0.82	0.80	1.32	1.29	0.60	0.58	1.00	1.37	—	1.76	*brevis*		
MPM19938	—	0.80	—	1.42	—	0.61	0.98	1.15	0.34	2.01	*brevis*		
MPM19940	0.53	0.55	0.95	0.96	0.47	0.49	0.73	0.88	0.25	1.48	*brevis*		X
MPM20692	0.68	0.68	1.12	1.15	0.54	0.51	0.79	1.19	0.32	1.68	*brevis*		X
USNM102248	0.90	0.87	1.54	1.59	0.73	0.76	1.22	1.57	0.42	2.24	*edwardsi*		
MPM19946	0.75	—	1.32	—	0.64	—	0.90	1.26	0.31	1.80*	*edwardsi*		
MPM20186	0.52	—	1.05	—	0.71	—	0.67	0.85	—	1.54	*edwardsi*		
MPM20679	—	0.55	—	0.85	—	0.34	0.70	0.86	0.35	1.26	*edwardsi*		
MPM20681	1.04	1.07	1.59	1.64	0.62	0.64	1.22	1.56	0.40	2.33	*edwardsi*		X
MPM842-2	0.73	0.76	1.19	1.23	0.51	0.53	0.88	1.20	0.37	1.74*	*gracilis*	X	X
MPM842-3	0.76	0.77	1.27	1.29	0.49	0.50	0.92	1.26	0.35*	1.77	*gracilis*	X	X
MPM842-4	0.53	0.55	0.89	0.88	0.35	0.36	0.69	0.85	0.26	1.31*	*gracilis*	X	X
MPM842-5	0.73	0.80	1.23	1.28	0.60	0.59	0.91	1.21	0.35	1.67	*gracilis*	X	
MPM842-6	—	0.52	—	0.92	—	0.45	0.63	0.86	0.20*	1.25	*gracilis*	X	
MPM842-7	0.68	—	1.13	—	0.58	—	0.82	1.08	0.30*	1.55*	*gracilis*	X	
MPM842-8	—	0.98	—	1.75	—	0.85	1.22	1.73	0.49	2.17*	*gracilis*	X	
MPM842-9	0.83	0.93	1.36	1.45	0.59	0.57	1.10	1.43	0.42	2.07	*gracilis*	X	X
MPM842-10	0.31	0.31	0.59	0.58	0.28	0.26	0.38	0.50	0.13	0.79	*gracilis*	X	X
MPM11158	—	—	—	—	—	—	1.10	1.42	0.36	2.11*	*gracilis*		
USNM102247	1.55	1.46	2.42	2.40	0.99	1.02	1.96	2.48	0.68	3.42	*gracilis*	X	
MPM19954	—	1.60	—	2.45	—	0.97	1.88	2.41	0.65	3.45	*gracilis*	X	
MPM19955	1.88	1.91	3.05	3.02	1.38	1.32	2.66	3.18	0.98	4.54	*gracilis*	X	X

Cranidial linear measurements—Continued.

Catalog number and institution	Preglabellar furrow midpt./ prepalpebral sinus distance		Preglabellar furrow midpt./ postpalpebral sinus distance		Palpebral chord length		Sagittal		Frontal area length	Palpebral cranidial width	Ulrich and Resser's species	Use in multivariate analysis	
	Left	Right	Left	Right	Left	Right	Occipital glabellar width	Occipito glabellar length				SDA	MDS
MPM19956	2.24	—	3.61	—	1.51	—	2.88*	3.72	—	5.22*	*gracilis*		
MPM19957	—	1.44	—	2.34	—	0.92	1.88	2.32	—	3.38*	*gracilis*		
MPM19968	0.71	0.68	1.12	1.08	0.55	0.53	0.89	1.07	0.45	1.65	*gracilis*	X	X
MPM19971	—	0.56	—	0.91	—	0.45	0.65	0.82	0.41	1.23*	*gracilis*	X	
MPM19972	1.20	—	2.06	—	0.97	—	1.38	1.97	0.51	1.97	*gracilis*	X	
MPM19973	1.19	—	1.95	—	1.00	—	1.49	1.82	0.59	2.80*	*gracilis*	X	
MPM19978	0.57	0.57	0.94	0.92	0.39	0.38	0.73	0.91	0.30*	1.41	*gracilis*	X	X
MPM19979	0.40	—	0.70	—	0.31	—	0.50*	0.71	0.19	1.01*	*gracilis*	X	
MPM19985	1.82	—	2.90*	—	1.29	—	2.26	2.70	0.65	4.14*	*gracilis*	X	
MPM19986	0.97	—	1.55	—	0.64	—	1.10	1.41	—	2.19*	*gracilis*		
MPM19987	0.74	0.74	1.28	1.27	0.58	0.56	0.99	1.27	0.32*	1.83	*gracilis*	X	X
MPM19988	0.61	0.61	1.00	1.03	0.46	0.45	0.77	0.99	—	1.56	*gracilis*		
MPM19998	—	2.18	—	3.39	—	1.25	2.51	3.43	0.90	4.50*	*gracilis*	X	
MPM19999	—	1.05	—	1.81	—	0.80	1.41	1.68	0.50	2.43*	*gracilis*	X	
MPM20000	1.12	1.13	1.81	1.86	0.75	0.75	1.44	1.70	0.48	2.50	*gracilis*	X	X
MPM20012	2.18	2.18	3.17	3.15	1.10	1.13	2.67	3.32	0.98	4.39	*gracilis*	X	X
MPM20013	1.27	—	1.86	—	0.67	—	1.51	1.83	0.51	2.90*	*gracilis*	X	
MPM20014	1.98	—	3.06*	—	1.38	—	2.26	2.82	1.01	4.22*	*gracilis*	X	
MPM20021	1.38	1.35	1.99	1.94	0.88	0.90	1.66	1.99	0.58	3.03	*gracilis*	X	X
MPM20109	2.53	—	3.79	—	1.33	—	3.13	3.68	—	5.18	*gracilis*		
MPM20658	0.95	—	1.60	—	0.73	—	1.25	1.65	0.50	2.34	*gracilis*	X	
MPM20659	0.91	0.94	1.63	1.68	0.67	0.66	1.19	1.55	0.42	2.40	*gracilis*	X	X
MPM20660	1.71	—	2.61	—	1.06	—	2.05	2.74*	1.02	3.84	*gracilis*	X	
MPM20661	0.54	—	0.93	—	0.40	—	0.68	0.90	0.28	1.38	*gracilis*	X	
MPM20662	0.74	0.73	1.07	1.07	0.44	0.48	0.85	1.14	0.34	1.74*	*gracilis*	X	X
MPM20663	1.45	—	2.16	—	0.85	—	1.59*	2.15	0.45	—	*gracilis*		
MPM19965	1.08	1.07	1.83	1.82	0.79	0.79	1.42	2.00	0.53	2.73	*granosus*	X	X
MPM19966	1.81	1.89	2.75	2.90	1.25	1.16	2.31	2.87	0.90	4.02*	*granosus*	X	
MPM19967	1.13	1.16	1.94	1.88	0.98	0.93	1.49	1.75	0.55	2.74	*granosus*	X	X
MPM19969	1.47	—	2.29	—	0.85	—	1.82	2.39	0.54*	3.18	*granosus*	X	
MPM20034	0.90	—	1.47	—	0.68	—	1.06	1.42	0.51	1.96	*granosus*	X	
MPM20036	—	—	—	—	—	—	0.79	0.97	0.30	1.53	*granosus*		
MPM20037	0.70	0.65	0.99	0.99	0.41	0.39	0.82	1.09	0.50	1.52	*granosus*	X	X
MPM5981	—	—	—	—	—	—	3.24	4.16	1.49	—	*hotchkissi*		
MPM20043	2.98	—	4.24	—	1.41	—	3.54	4.24	1.76	6.10*	*hotchkissi*		
MPM20044	—	2.21*	—	3.49	—	1.35	2.69	3.72	1.65	5.20*	*hotchkissi*		
USNM102262	1.19	1.17	1.94	1.96	0.92	0.90	1.41	1.75	0.54	2.57	*marginatus*		X
MPM20060	—	0.48	—	0.91	—	0.46	0.61	0.87	0.35	1.20*	*marginatus*		
MPM842-1	0.94	0.92	1.46	1.46	0.59	0.60	1.13	1.38	0.38*	2.25	*minnesotensis*		X
MPM842-11	0.88	0.85	1.34	1.34	0.54	0.51	1.12	1.34	—	2.21	*minnesotensis*		
FMNH10107	2.16	2.09	3.22	3.14	1.08	1.05	2.59	3.17	1.24	4.42	*minnesotensis*		X
FMNH16732	1.89	—	2.84	—	1.13	—	2.52	2.96	0.97*	4.36	*minnesotensis*		
MPM20076a	—	0.87	—	1.40	—	0.56	0.97	1.40	0.45	1.78	*norwalkensis*	X	
MPM20076b	0.36	—	0.74	—	0.33	—	0.53	0.69	0.20	1.20	*norwalkensis*	X	
MPM20077	1.67	—	2.58	—	1.04	—	1.77	2.61*	—	3.41*	*norwalkensis*		
MPM20078	0.40	—	0.65	—	0.32	—	0.49	0.65	0.27	0.95*	*norwalkensis*	X	
MPM20084	1.31	—	2.12	—	0.86	—	1.53	1.98	0.68	3.00*	*norwalkensis*	X	
MPM20086	0.88	—	1.50	—	0.73	—	1.18	1.46	0.49	2.27	*norwalkensis*	X	
MPM20090	—	—	—	—	—	—	0.77	1.08	0.34	—	*norwalkensis*		
MPM20091	—	0.62	—	1.18	—	0.60	0.77	1.06	0.35	1.53	*norwalkensis*	X	
MPM20094	0.44	—	0.80	—	0.38	—	0.55	0.80	0.27	1.08	*norwalkensis*	X	
MPM20096	—	0.71	—	1.22	—	0.56	0.93	1.22	0.42*	1.76*	*norwalkensis*	X	
MPM20097	0.35	0.32	0.62	0.58	0.30	0.26	0.44	0.57	0.26	0.88	*norwalkensis*	X	X
USNM102263	—	2.05	—	3.05	—	1.03	2.44	3.13	1.50	4.39*	*orbiculatus*		
MPM20104	2.83	2.78	4.34	4.35	1.67	1.68	3.60	4.44	1.64	6.64	*orbiculatus*		X
MPM20105	1.90	1.81	2.82	2.76	1.05	1.07	2.20	2.77	1.06	3.94	*orbiculatus*		X
MPM20107	1.85	1.87	2.80	2.81	1.12	1.06	2.22	2.81	0.97	4.05	*orbiculatus*		
USNM102256	1.69	1.74	2.62	2.71	1.12	1.09	2.26	2.66	0.80	3.94	*ovatus*		
MPM20057	2.17	2.19	3.06	3.01	1.01	0.99	2.52	3.20	1.29	4.33	*ovatus*		
MPM20114	1.54	—	2.51	—	1.05	—	1.93	2.32	0.67	3.53*	*ovatus*		X
MPM20118	1.31	—	1.92	—	0.73	—	1.62	1.94	0.53	2.93*	*ovatus*		X
MPM5583	2.07	2.09	3.24	3.23	1.49	1.41	2.60	3.30	1.17*	4.62	*oweni*		
MPM18659	4.35	4.77	6.73	6.75	2.56	2.32	5.57	6.85	2.29	9.73	*oweni*		X
MPM19060	—	—	—	—	—	—	2.43	3.57	1.05	4.55	*oweni*		
MPM20130	—	3.74	—	5.65	—	1.98	4.76	5.71	1.90	8.21	*oweni*		
MPM20132	1.97	—	3.19	—	1.43	—	2.46	2.98	—	4.50*	*oweni*		
MPM20137	0.96	0.92	1.68	1.61	0.82	0.94	1.45	1.86	—	2.33	*oweni*		
MPM20138	—	—	—	—	—	—	2.10*	2.78*	0.84	—	*oweni*		

Cranidial linear measurements—Continued.

Catalog number and institution	Preglabellar furrow midpt./ prepalpebral sinus distance		Preglabellar furrow midpt./ postpalpebral sinus distance		Palpebral chord length		Sagittal		Frontal area length	Palpebral cranidial width	Ulrich and Resser's species	Use in multivariate analysis	
							Occipital glabellar width	Occipito glabellar length					
	Left	Right	Left	Right	Left	Right						SDA	MDS
MPM20149	2.62	2.66	3.87	3.91	1.42	1.41	3.38	4.11	1.33	5.76	*oweni*		
MPM20755	4.12	—	5.62	—	1.72	—	4.67	5.66	2.05	8.55*	*oweni*		X
USNM101433	2.70	2.68	4.27	4.27	1.85	1.78	3.68	4.22	1.51	6.40	*raaschi*		
MPM18673	2.70	2.89*	4.64	4.78	2.06	2.17	3.86	4.56	1.69	6.34	*raaschi*	X	X
MPM20157	2.77	—	4.21	—	1.57	—	3.22	4.01	1.46	5.81	*raaschi*	X	X
MPM20162a	2.06	2.02	3.36	3.30	1.34	1.35	2.61	3.29	1.15	4.62	*raaschi*	X	
MPM20162b	1.37	1.28	2.09	1.98	0.67	0.72	1.65	1.98	0.76	2.88	*raaschi*	X	X
MPM20163	—	—	—	—	—	—	2.24	2.82	0.90	—	*raaschi*	X	X
MPM20164	1.03	—	1.67	—	0.72	—	1.19	1.62	0.51	2.24*	*raaschi*		
USNM102261	1.25	1.20	2.00	1.95	0.74	0.72	1.57	2.06	0.58	2.82	*retrorsus*	X	
MPM20172	0.82	—	1.27	—	0.54	—	0.89*	1.38	0.39	1.79*	*retrorsus*		X
USNM101435	1.36	1.30	2.11	2.11	0.87	0.91	1.65	2.08	0.58	3.07	*subplanus*		
MPM20206	1.42	—	2.34	—	0.93	—	1.75	2.13	—	3.21*	*subplanus*		
MPM20219	—	—	—	—	—	—	0.57	0.72	0.30*	1.07*	*thwaitesi*		
MPM20220	0.45	—	0.68	—	0.30	—	0.47	0.77*	0.28*	0.98	*thwaitesi*		
MPM9557	—	1.79	—	2.80	—	1.20	2.17	3.01	1.19	4.07	*weidmani*		
MPM20236	0.95	—	1.48	—	0.58	—	1.07	1.48	0.50	1.95*	*wiltonensis*		
MPM20240	—	—	—	—	—	—	2.67	3.43	1.16	4.31	*wiltonensis*		
MPM20241	—	1.40	—	2.19	—	0.90	1.56	2.17	0.72	2.96	*wiltonensis*		
USNM102252	1.71	1.70	2.53	2.51	0.90	0.92	1.99	2.62	0.93	3.56	*wisconsinensis*		X
MPM20687	—	2.11	—	3.07	—	1.07	2.44*	3.00	1.11	4.22*	*wisconsinensis*		
MPM20123	3.37	3.37	5.10	5.12	1.97	1.95	4.02	5.21*	1.31	7.08	unassigned		X
MPM25654	—	1.94	—	2.98	—	1.11	2.41*	3.16	1.44	4.21*	unassigned		
MPM27676	—	3.40	—	4.58	—	1.26	4.15	5.07	1.50	6.81*	unassigned		
MPM27677	0.81	0.83	1.40	1.44	0.63	0.67	1.07	1.35	0.42	2.07	unassigned		X
MPM27678	0.49	0.48	0.84	0.83	0.36	0.38	0.60	0.77*	—	1.31	unassigned		
MPM27679	0.63	0.66	1.05	1.06	0.45	0.46	0.80	0.95	0.30	1.51*	unassigned		X
MPM27680	—	0.77	—	1.23	—	0.55	0.91	1.23	0.38	1.79	unassigned		
MPM27714	1.80	—	2.78	—	1.09	—	2.25	2.78	1.20	3.97*	unassigned		
UWM27100	—	1.51	—	2.19	—	0.83	1.67	2.23	0.85	2.98*	unassigned		
UWM27104	1.32	—	2.19	—	0.82	—	1.58	2.06	0.60	2.95	unassigned		
UWM27107	1.61	1.52	2.50	2.41	0.94	0.93	1.98	2.36	0.70	3.44	unassigned		X
UWM27114	2.22	2.20	3.28	3.25	1.21	1.23	2.68	3.35	1.32	4.59	unassigned		X
UWM27115	1.18	1.15	1.87	1.86	0.75	0.79	1.53	1.90	0.61*	2.67	unassigned		
FMNH14393	2.87	2.85	3.91	3.93	1.26	1.28	3.04	3.78	1.37	5.54	unassigned		X
FMNH10106a	1.29	1.28	1.86	1.85	0.76	0.75	1.54	1.90	0.67	2.57	unassigned		X
FMNH10106b	3.09	—	4.53	—	1.66	—	3.53*	—	2.07	6.26	unassigned		
FMNH24108	—	—	—	—	—	—	1.72	1.95*	0.73	3.10	unassigned		
FMNH24109	—	—	—	—	—	—	2.08	2.46	—	3.96	unassigned		
FMNH28467	2.68	—	3.92	—	1.31	—	3.32*	—	1.77	5.96	unassigned		
FMNH28529	1.23	1.26	1.95	2.00	0.87	0.83	1.48	1.99	0.56	2.77	unassigned		X
FMNH39205	1.64	1.57	2.56	2.49	1.00	0.96	1.98	2.66*	0.71	3.61	unassigned		X
FMNH39209	1.06	1.02	1.70	1.72	0.89	0.84	1.21	1.60	0.48	2.34	unassigned		X
FMNH39211	0.98	—	1.48	—	0.72	—	1.18	1.58	0.67	2.30	unassigned		
FMNH39213	—	—	—	—	—	—	3.13	3.66	—	—	unassigned		
FMNH39214	—	1.17	—	1.61	—	0.57	1.38	1.69	0.82	2.40*	unassigned		
FMNH39215	1.28	1.32	1.73	1.75	0.54	0.60	1.39	1.70*	0.90	2.56	unassigned		

Cranidial angular measurements.

Catalog number and institution	Angular displacement of occipital and glabellar furrows from sagittal axis								Furrow number	Ulrich and Resser's species
	Left				Right					
	1	2	3	4	1	2	3	4		
USNM102264	20	39	13		18	33	13		3	*barretti*
MPM19926	21	40	20		—	38	19		3	*barretti*
MPM19931	6	20	3		6	23	3		3	*barretti*
MPM19932	12	30	11		13	34	14		3	*barretti*
MPM20677	—	31	18	5	18	29	20	—	4	*barretti*
MPM20678	11	34	6	−21	10	29	8	−21	4	*barretti*
MPM18681	12	31	17		12	33	—		3	*brevis*
MPM19935	3	25			4	24			2	*brevis*
MPM19936	4	28	3		5	30	5		3	*brevis*
MPM19937	4	26	16		8	28	14		3	*brevis*
MPM19938	8	35			9	37			2	*brevis*
MPM19940	16	31			14	33			2	*brevis*
MPM20692	7	35	15		8	37	11		3	*brevis*
USNM102248	15	30	7		15	29	12		3	*edwardsi*
MPM19946	12	35	15		10	35	14		3	*edwardsi*
MPM20186	5	22	11		4	19	9		3 (?4)	*edwardsi*
MPM20679	19	37	26		16	40	25		3	*edwardsi*
MPM20681	22	33	13		21	32	17		3	*edwardsi*
MPM842-2	11	27	11	17	12	33	13	15	4	*gracilis*
MPM842-3	8	20	0		9	31	2		3	*gracilis*
MPM842-4	10	27	11		11	28	13		3	*gracilis*
MPM842-5	11	33	17		13	32	14		3	*gracilis*
MPM842-6	14	28	18	−14	15	31	19	−12	4	*gracilis*
MPM842-7	5	23	6		6	36	−6		3	*gracilis*
MPM842-8	8	32	13		7	29	3		4	*gracilis*
MPM842-9	7	28	7		9	13	8		3	*gracilis*
MPM842-10	5	28	5		6	29	7		3	*gracilis*
MPM11158	7	28	—		9	25	6		3	*gracilis*
USNM102247	9	30	8		8	32	10		3	*gracilis*
MPM19954	16	27	10	−17	11	28	13	−18	4	*gracilis*
MPM19955	14	36			17	37			2	*gracilis*
MPM19956	7	24	6		—	—	—		3	*gracilis*
MPM19957	10	25	—		12	31	8		3	*gracilis*
MPM19968	7	29	20		7	29	19		3	*gracilis*
MPM19971	16	27	6		18	27	3		3	*gracilis*
MPM19972	6	27	6	−11	—	29	6	—	4	*gracilis*
MPM19973	9	29	5	−10	10	28	—	—	4	*gracilis*
MPM19978	14	22	4	−18	12	21	4	—	4	*gracilis*
MPM19979	10	28	22	−8	12	32	15	−11	4	*gracilis*
MPM19985	14	26	11	−10	16	30	10	−5	4	*gracilis*
MPM19986	7	27	—		8	28	—		3	*gracilis*
MPM19987	16	29	17		13	28	15		3	*gracilis*
MPM19988	13	25	24		12	24	18		3	*gracilis*
MPM19998	9	—	—		9	33	6		4	*gracilis*
MPM19999	10	26	12	−9	12	27	15	—	4	*gracilis*
MPM20000	14	31	18	—	11	31	18	−18	4	*gracilis*
MPM20012	9	27	6		10	27	7		3	*gracilis*
MPM20013	10	29	12		12	32	—		3	*gracilis*
MPM20014	9	39	15		9	40	13		3	*gracilis*
MPM20021	10	27	12	11	9	30	12	—	4	*gracilis*
MPM20109	8	27	—	—	10	34	7	8	4	*gracilis*
MPM20658	18	30	12	−28	15	30	11	−29	4	*gracilis*
MPM20659	9	28	5	−22	10	31	7	−19	4	*gracilis*
MPM20660	14	24	6		12	30	5		3	*gracilis*
MPM20661	9	31	8		12	33	10		3	*gracilis*
MPM20662	11	31	17	−29	11	35	14	−21	4	*gracilis*
MPM20663	6	29	14	−16	—	31	19	—	4	*gracilis*
MPM19965	10	33	19		12	34	15		3	*granosus*
MPM19966	16	31	13		16	30	12		3	*granosus*
MPM19967	10	29	12		8	31	11		3	*granosus*
MPM19969	7	29	15		9	36	16		3	*granosus*
MPM20034	16	38	8		16	40	9		3	*granosus*
MPM20036	10	30	8		10	27	6		3	*granosus*
MPM20037	17	29	14		20	30	14		3	*granosus*
MPM5981	16	29	11		—	—	—		3 (4?)	*hotchkissi*
MPM20043	11	33	7		10	33	9		3	*hotchkissi*
MPM20044	13	—	—		14	—	—		—	*hotchkissi*
USNM102262	9	22	6		8	20	—		3	*marginatus*
MPM20060	5	33	14		5	42	8		3	*marginatus*
MPM842-1	21	31	20	13	21	29	19	10	4	*minnesotensis*
MPM842-11	18	29	18		19	28	19		3	*minnesotensis*
FMNH10107	10	30	−9		13	26	−12		3	*minnesotensis*
FMNH16732a	6	18	5		8	17	—		3	*minnesotensis*
MPM20076a	15	25	—		15	24	15		3	*norwalkensis*

Cranidial angular measurements—Continued.

Catalog number and institution	Angular displacement of occipital and glabellar furrows from sagittal axis								Furrow number	Ulrich and Resser's species
	Left				Right					
	1	2	3	4	1	2	3	4		
MPM20076b	21	28	20		25	33	20		3	*norwalkensis*
MPM20077	—	26	21		—	28	18		3	*norwalkensis*
MPM20078	6	24	8		6	27	10		3	*norwalkensis*
MPM20084	15	33	14		16	28	14		3	*norwalkensis*
MPM20086	10	27	2		9	24	0		3	*norwalkensis*
MPM20090	9	25	10		10	28	10		3	*norwalkensis*
MPM20091	7	31	5		9	30	4		3	*norwalkensis*
MPM20094	18	32	18		17	28	19		3	*norwalkensis*
MPM20096	10	28	15		10	26	16		3	*norwalkensis*
MPM20097	12	28	15		14	28	13		3	*norwalkensis*
USNM102263	11	28	6		18	32	8		3	*orbiculatus*
MPM20104	9	31	10		11	40	12		3	*orbiculatus*
MPM20105	11	34			11	29			2	*orbiculatus*
MPM20107	10	27	11		11	29	9		3	*orbiculatus*
MPM18676	8	24	0	−15	10	25	5	−17	4	*ovatus*
MPM20057	9	30	0		11	26	8		3	*ovatus*
MPM20114	5	30	7		8	28	—		3	*ovatus*
MPM20118	11	28	9		—	31	9		3	*ovatus*
MPM5983	10	25	—		10	27	14		3	*oweni*
MPM18659	9	28	14		11	28	13		3	*oweni*
MPM19060	—	30	—		6	29	—		3	*oweni*
MPM20130	9	30	15		9	36	—		3	*oweni*
MPM20132	9	27	3		10	31	5		4 (5?)	*oweni*
MPM20137	6	39			5	40			2	*oweni*
MPM20138	10	26	11		—	24	9		3	*oweni*
MPM20149	8	35	8		0	27	7		3	*oweni*
MPM20755	5	30	4		8	31	4		3	*oweni*
USNM101433	5	39	12		6	35	11		3	*raaschi*
MPM18673	6	—			4	20			2	*raaschi*
MPM20157	7	28			8	26			2	*raaschi*
MPM20162a	15	37	—		14	34	—		3	*raaschi*
MPM20162b	3	29	—		1	26	7		3	*raaschi*
MPM20163	21	37	11		19	37	10		3	*raaschi*
MPM20164	4	25	9		—	37	9		3	*raaschi*
USNM102261	19	38	12		13	31	8		3	*retrorsus*
MPM20172	13	31	17		—	—	19		3	*retrorsus*
USNM101435	7	36	2		10	36	4		3	*subplanus*
MPM20206	10	26	2		11	28	11		3	*subplanus*
MPM20219	13	37	—		10	28	13		3	*thwaitesi*
MPM20220	6	28			5	30			2	*thwaitesi*
MPM9557	11	28	12		12	32	14		3	*weidmani*
MPM20236	21	31	—		20	—	21		3	*wiltonensis*
MPM20240	11	36	—		13	33	12		3	*wiltonensis*
MPM20241	13	34	12		14	33	12		3	*wiltonensis*
USNM102252	12	32	14	13	15	36	17	—	4	*wisconsinensis*
MPM20687	—	—	—		5	14	0		3	*wisconsinensis*
MPM20123	9	25	7		8	30	3		3	unassigned
MPM25654	—	—	—	—	5	18	6	9	4	unassigned
MPM27676	14	32	8		13	42	5		3	unassigned
MPM27677	13	26	14	14	29	15	15	4	4	unassigned
MSM27678	16	26	12		13	23	11		3	unassigned
MSM27679	11	19	11	11	9	20	8	8	4	unassigned
MSM27680	10	26	10		10	22	12		3	unassigned
MSM27714	15	29	10		13	30	—		3	unassigned
UWM27100	12	23	—		12	27	10		3	unassigned
UWM27104	13	29	9		13	27	—		3	unassigned
UWM27107	11	30	25	9	9	27	26	7	4	unassigned
UWM27114	14	29	9		14	28	11		3	unassigned
UWM27115	14	31	9		14	32	12		3	unassigned
FMNH14393	7	17			7	14			2	unassigned
FMNH10106a	9	22	13	0	9	21	12	0	4	unassigned
FMNH10106b	22	9	−12	—	25	10	−6		4	unassigned
FMNH24108	9	18	—		9	23	0		3	unassigned
FMNH24109	11	20	—		10	21	−3		3	unassigned
FMNH28467	—	22	9		—	—	10		3	unassigned
FMNH28529	11	25	6		8	24	3		3	unassigned
FMNH28529	11	25	6		8	24	3		3	unassigned
FMNH39205	12	22	8		16	32	9		3	unassigned
FMNH39209	9	16	—		6	23	10		3	unassigned
FMNH39211	11	24			—	—			2	unassigned
FMNH39213	7	10	−10		7	—	—		3	unassigned
FMNH39214	5	—			2	23			2	unassigned
FMNH39215	7	18			5	23			2	unassigned

Librigenal measurements.

Catalog number and institution	Prepalpebral sigma distance	Prepalpebral omega distance	Palpebral chord length	Postpalpebral omega distance	Sigma-prepalpebral omega angle	Prepalpebral–postpalpebral omega angle	Total genal spine length	Ulrich and Resser's species	Use in multivariate analyses	
									SDA	MDS
USNM102268	1.97*	1.18	0.51*	0.70	13°	135°		*barretti*		
MPM18656	3.03*	1.83	0.89	1.08	22°	127°		*brevis*		X
MPM18657	2.91*	1.93	1.09	0.99	19°	143°		*brevis*		X
MPM19941	2.77	1.81	0.88	0.95	19°	133°		*declivis*		
USNM102249	2.18	1.34	0.76	0.82	19°	135°		*edwardsi*	X	X
USNM102250	2.66	1.80	0.94	1.07	13°	132°		*edwardsi*	X	X
MPM18666b	2.00	1.32	0.56	0.62	11°	133°		*edwardsi*	X	
MPM19947	2.31	1.35	0.64	0.74	18°	146°		*edwardsi*	X	X
MPM19952	2.41	1.56	0.81	0.96	20°	128°	2.34	*edwardsi*	X	X
MPM20178a	3.76	1.81	0.98*	1.10*	22°	—		*edwardsi*	X	
MPM20178b	3.57	1.79	0.96	1.09	21°	125°	3.77	*edwardsi*	X	X
MPM20179	2.73	1.43	0.82	0.86	12°	132°		*edwardsi*	X	X
MPM20180	2.22	1.39	0.78	0.68	17°	141°		*edwardsi*	X	
MPM20182	1.63	1.00	0.52	0.55	22°	122°	1.69	*edwardsi*	X	X
USNM102246	2.43	1.45	0.81	0.85	17°	124°		*gracilis*	X	X
MPM19964	3.62	1.98	1.04	1.14	22°	122°		*gracilis*	X	
MPM19976	3.21	2.04	1.08	1.21	19°	128°		*gracilis*	X	X
MPM19983	3.05	1.95	1.01	1.10	18°	130°		*gracilis*	X	
MPM20002	1.83	1.18	0.63	0.65	21°	135°		*gracilis*	X	
MPM20018	3.59	2.55	1.12*	1.57	15°*	141°		*gracilis*	X	X
MPM20023	3.49	2.30	1.19	1.45	13°	127°	2.49	*gracilis*	X	X
MPM20027	3.19	1.92	1.02	1.07	—	132°		*gracilis*	X	
MPM20033	3.09	1.74	0.77	0.97	18°	133°		*gracilis*	X	X
MPM20062	2.32	1.55	0.72	0.98	23°	126°		*gracilis*	X	X
MPM20072a	5.54	2.90	1.43	1.63	21°	129°		*gracilis*	X	X
MPM20072b	5.37	2.82	1.33	1.72	18°	135°		*gracilis*	X	X
MPM20670	3.97	2.40	1.12	1.35	19°	143°	3.55	*gracilis*	X	X
MPM20671	2.46	1.35	0.67	0.72	16°	137°	1.93	*gracilis*	X	
MPM20672	3.19	1.57	0.78*	1.05	20°*	129°*	2.72	*gracilis*	X	X
MPM20673	3.38	1.98	0.88	1.22	19°	137°	3.89	*gracilis*	X	X
MPM27716	3.32	2.00	1.08	1.20	18°	126°		*gracilis*	X	
MPM27724	3.21	2.04	0.97	1.22	10°	120°	3.56	*gracilis*	X	X
MPM27724	2.13	1.24	0.68	0.68	21°	134°	2.41	*gracilis*	X	X
MPM27717	1.78	1.07	0.75	0.67*	12°	144°*		*granosus*		
MPM11904a	2.34	1.26	0.64	0.82	16°	124°		*marginatus*	X	X
MPM11904b	2.50*	1.43	0.70	0.80	17°	126°		*marginatus*	X	X
MPM20063a	2.12	1.39	0.72*	0.63*	18°*	138°		*marginatus*	X	
MPM20063b	2.21	1.33	0.71	0.62	20°	132°		*marginatus*	X	X
MPM20064	2.16	1.84	0.82	1.14	16°	124°		*marginatus*	X	X
MPM20071	5.51*	3.43*	1.89*	1.82*	18°*	119°*		*minnesotensis*		
MPM27743	2.33	1.32	0.67	0.80	20°	118°		*minnesotensis*		X
FMNH10106	4.53	2.25	1.08	1.34	26°*	124°*		*minnesotensis*		X
MPM18002	4.27	2.59	1.36	1.67	17°	118°		*norwalkensis*		
MPM20076	1.76*	1.28*	—	—	13°*	—	2.06	*norwalkensis*		
MPM20093	1.80	1.14	0.50	0.57	11°	140°		*norwalkensis*		X
MPM20101	2.55	1.65	0.82	0.92	18°	133°		*norwalkensis*		X
MPM20111	4.16	2.38	0.99	1.67	22°	118°		*ovatus*	X	
MPM20113	4.33	2.58	1.11	1.59	21°	122°		*ovatus*	X	X
MPM20116a	—	—	1.19	1.62	—	—		*ovatus*		
MPM20116b	4.79	2.60	1.14	1.52	18°	137°		*ovatus*	X	X
MPM20116c	4.54	3.03	1.38	1.75	19°	133°		*ovatus*	X	X
MPM20122	9.69	5.45	2.19	3.63	18°	132°		*ovatus*	X	X
MPM20128	4.54	2.73	1.36	1.66	23°	135°		*ovatus*		X
MPM20046	7.12*	3.63*	1.53	2.43*	19°*	120°		*oweni*		
MPM20135	3.94	2.62	1.07	1.37	18°	130°		*oweni*		X
MPM20151	7.35	4.40	1.80	3.19	16°	120°		*oweni*		X
MPM20159	5.10	3.07	1.33	1.87	22°	134°		*raaschi*	X	
MPM20160	5.38	3.15	1.51	1.68	19°	141°		*raaschi*	X	X
MPM20161	5.11	3.22*	1.47*	1.90*	13°*	133°		*raaschi*	X	X
MPM20165	3.80	2.54	1.19	1.64	19°	127°		*raaschi*	X	
MPM20166	3.49	2.17*	0.87	1.35	16°*	145°		*raaschi*	X	X
MPM20167	4.10	2.60	1.23	1.60	17°	128°		*raaschi*	X	X
MPM20175	4.80	2.98	1.30	1.87	21°	125°		*retrorsus*		
MPM20177	3.39	2.24	1.05	1.44	14°	128°		*retrorsus*		X
USNM101436	3.70	2.20	1.04	1.29	18°	128°		*subplanus*	X	X
MPM20201	3.72	2.18	1.09	1.39	17°	122°		*subplanus*	X	
MPM20209	1.98	1.22	0.56	0.62	19°	131°		*subplanus*	X	X
MPM20211	1.53	0.99	0.49	0.53	23°	129°		*subplanus*	X	
MPM20211	1.36	0.91	0.45	0.55	15°	116°	1.76	*subplanus*	X	X
MPM5982	3.16	2.10	—	—	11°	—		*wisconsinensis*		
USNM102253	2.14	1.23	0.59	0.73	11°	135°		*wisconsinensis*	X	X
MPM20245	1.76	0.96	0.51	0.65	16°	119°	2.78	*wisconsinensis*	X	X
MPM20247	4.25	2.75	1.24	1.66	17°	134°		*wisconsinensis*	X	

Librigenal measurements—Continued.

Catalog number and institution	Prepalpebral sigma distance	Prepalpebral omega distance	Palpebral chord length	Postpalpebral omega distance	Sigma-prepalpebral omega angle	Prepalpebral–postpalpebral omega angle	Total genal spine length	Ulrich and Resser's species	Use in multivariate analyses	
									SDA	MDS
MPM20248	3.40	1.87	0.77	1.19	15°	123°		*wisconsinensis*	X	X
MPM11179	2.43	1.56	0.79	0.90	20°	134°		unassigned		X
MPM27684	4.04	2.46	1.22*	1.54	21°	130°		unassigned		X
MPM27686	2.89	1.65	1.22*	1.54	21°	130°		unassigned		
MPM27691	2.62	1.60	0.73	0.95	23°	136°		unassigned		X
MPM27693	2.98	1.74	0.79	1.17	23°	127°		unassigned		X
MPM27695	3.07	1.79	0.86	1.06	21°	136°		unassigned		X
MPM27696	2.97	1.80	0.86	1.05	20°	141°		unassigned		X
MPM27697	3.35	1.86	0.97	1.05	21°	130°		unassigned		
MPM27700	2.63	1.50	0.81*	0.88*	19°	140°		unassigned		X
MPM27701	4.24*	2.47*	1.14*	1.65*	21°	126°*		unassigned		X
MPM27702	1.45	0.86	0.45	0.45	18°	128°		unassigned		X
UWM27103	3.72	2.32	1.03*	1.30*	21°	122°		unassigned		X
FMNH24113	2.73	1.57	0.68	0.97	25°	126°		unassigned		X
FMNH39207c	2.93	1.71	0.81	1.02	27°	127°		unassigned		
FMNH39207d	2.53	1.40	0.56	0.92	23°	122°		unassigned		X

Hypostomal measurements.

Catalog number and institution	Intermacular width	Posterior hypostome width	Sagittal hypostome length	Middle body sagittal length	Hypostome depth	Ulrich and Resser's species	Use in multivariate analyses	
							SDA	MDS
MPM19927	0.51	1.19	0.89	0.66	intermediate	*barretti*		X
MPM19928	0.78	1.52	1.11	0.84	intermediate	*barretti*		X
MPM19944	0.53	1.23	0.85	0.66	deep	*edwardsi*	X	X
MPM19945	0.54	1.28	0.90	0.71	intermediate	*edwardsi*	X	X
MPM20679	0.74	1.61*	1.11	0.88	intermediate	*edwardsi*	X	X
MPM19942	0.92	1.76	1.38*	1.03	shallow	*declivis*		X
MPM19990	0.80	1.84*	1.43*	1.06	shallow	*gracilis*	X	X
MPM20010	1.14	2.16	1.68*	1.30	intermediate	*gracilis*	X	X
MPM20011	0.90	1.85	1.33	1.00	intermediate	*gracilis*	X	X
MPM20688	1.04	2.14	1.52*	1.22	intermediate	*gracilis*	X	X
MPM20689	0.41	0.86	0.61	0.45	intermediate	*gracilis*	X	X
MPM20690	0.41	0.84	0.55	0.42	intermediate	*gracilis*	X	X
MPM27734	0.76	1.60*	1.10	0.85	shallow	*gracilis*	X	X
MPM27754	0.56	1.56	1.14	0.84	intermediate	*gracilis*	X	X
MPM20050	0.77	1.62	1.16	0.88	deep	*halli*		X
MPM20045	1.07	2.34	1.78	1.36	shallow	*hotchkissi*		X
FMNH11873	1.14	2.58	1.62	1.21	intermediate	*minnesotensis*		X
MPM20083	0.41	0.88	0.71	0.50	deep	*norwalkensis*	X	X
MPM20089	0.60	1.14	0.94	0.72	deep	*norwalkensis*	X	X
MPM20094	0.61	1.42*	1.11	0.83	deep	*norwalkensis*	X	X
MPM20102	0.40	0.96	0.74	0.55	deep	*norwalkensis*	X	X
USNM102258	1.10	2.30	1.72	1.26	shallow	*ovatus*	X	X
MPM20120	1.56	3.86	3.21	2.29	intermediate	*ovatus*	X	X
MPM27732	0.66	1.40	0.98	0.68	shallow	*ovatus*	X	X
MPM27733	0.92	1.64	1.38	0.98	shallow	*ovatus*	X	X
MPM18660	1.42	3.11	2.24	1.70	shallow	*oweni*		X
USNM101432	1.69	3.32*	2.37	1.86	shallow	*raaschi*	X	X
USNM101434	1.20	2.95	2.04	1.64	shallow	*raaschi*	X	X
MPM20155	0.92	1.70	1.42	1.14	intermediate	*raaschi*	X	X
MPM20168	1.84	4.12*	2.98	2.28	shallow	*raaschi*	X	X
MPM20175	1.24	2.57*	1.75	1.33	intermediate	*retrorsus*		X
MPM9559	1.12	2.56	1.84	1.45	intermediate	*weidmani*		X
FMNH39207	0.61	1.20	0.73	0.55	deep	unassigned		X
FMNH39204	0.85	1.83	1.20	0.90	shallow	unassigned		X

Pygidial measurements.

Catalog number and institution	Total pygid. length	Maximum pygid. width	Total length of rhachis	Anterior width of rhachis	Terminal interspinal distance	Sagittal pleural region length	Angular displacement of pleural furrows from sagittal axis						Ulrich and Resser's species	Use in multivariate analyses	
							Left			Right					
							1	2	3	1	2	3		SDA	MDS
USNM102265	2.75*	4.38*	1.67	1.03	—	1.08	17	26	55	15	25	56	*barretti*		X
USNM102266	—	—	2.60	1.32	—	—	13	29	54	12	30	55	*barretti*		
USNM102267	3.38	5.91	2.19	1.19	5.06	1.19	12	17	39	11	22	40	*barretti*		X
MPM19933	2.64	4.81	1.60	1.04	3.79*	1.04	9	27	58	10	23	63	*barretti*		
MPM18658	1.46	2.38	0.81	0.55	2.00	0.65	21	38	67	21	35	66	*brevis*		X
MPM19939	2.42	3.55	1.46	0.70	2.92*	0.96	—	—	59*	—	29	52	*brevis*		
USNM102251	1.58	2.48	0.87	0.55	2.06	0.71	20	34	57	19	30	56	*edwardsi*	X	X
MPM19949	1.69	2.98	1.07	0.60	2.42*	0.62	18	33	61	—	—	—	*edwardsi*	X	
MPM19950	1.53*	2.34	0.87	0.47	1.88*	0.66	12	29	57	—	31	61	*edwardsi*	X	X
MPM20182	2.04	—	1.30	0.74	—	0.74	—	—	60	22	35	61	*edwardsi*		
MPM20183	1.38	—	0.82	0.42	—	0.56	—	—	58	12	34	51	*edwardsi*		
MPM20184	2.36	3.40*	1.57	0.63	2.80	0.79	14	30	57	18	30	57	*edwardsi*	X	X
MPM20185	1.43	2.40	0.84	0.46	1.80	0.59	11	20	61	15	30	60	*edwardsi*	X	
MPM19958	4.13	7.00	2.58	1.50	5.36	1.55	15	26*	58	13	32	54	*gracilis*	X	
MPM19959	2.00	3.28	1.10	0.69	2.51	0.90	16	30	55	22	33	64	*gracilis*	X	X
MPM19960	—	7.64	2.89	1.64	—	—	15	25	60	17	28	56	*gracilis*		
MPM19961	4.64	7.40*	2.60	1.62*	6.10	2.04	—	23	60	7	23	55	*gracilis*	X	X
MPM19962	2.91	4.74	1.99	0.92	3.48	0.96	14	29	61	16	30	57	*gracilis*	X	
MPM19963	3.60	5.90	2.30	1.42	—	2.18	—	—	59	16	23	58	*gracilis*	X	
MPM19970	1.92	3.14	1.22	0.65	3.02	0.70	—	—	48	14	23	47	*gracilis*	X	X
MPM19981	1.02	1.58	0.58	0.27	1.36	0.44	22	37	60	23	—	58	*gracilis*	X	
MPM19982	1.23	1.84	0.70	0.36	1.66	0.53	17	34	60	16	39	61	*gracilis*	X	
MPM19994	2.94	4.97	1.84	0.97	4.10	1.10	15	32	50	14	28	55	*gracilis*	X	X
MPM19995	2.09	3.66	1.28	0.77	3.04	0.81	10	30	60	10	31	59	*gracilis*	X	
MPM20016	3.71	6.02	2.22	1.50	4.38	1.49	17	26	62	18	—	61	*gracilis*	X	X
MPM20017	3.01	4.88	1.83*	0.83*	3.22	1.18	16	27	57	—	—	—	*gracilis*	X	
MPM20024	3.36	5.23	2.08	1.15	4.10	1.28	20	29	54	19	31	61	*gracilis*	X	X
MPM20025	1.66	2.60	0.93	0.55	2.14	0.73	20	34	57	20	34	55	*gracilis*	X	X
MPM20030	2.62	4.41	1.67	0.95	2.94*	0.95	17	33	60	21*	28	62	*gracilis*	X	
MPM20031	3.07	5.25	2.03	1.13	4.14	1.04	13	24*	54	15	26	56	*gracilis*	X	
MPM20032	2.82	4.65	1.72	1.09	3.59	1.10	—	—	54	18	35	53	*gracilis*	X	X
MPM20039	5.05	8.60	3.25	2.01	7.13	1.80	16	25	57	13	25	60	*gracilis*	X	X
MPM20040	2.84	4.69	1.71	1.03	3.83	1.81	19	30	44	21	27	43	*gracilis*	X	
MPM20064	4.53	6.64	2.85	1.41	5.57	1.68	15	24	56	14	30	58	*gracilis*	X	
MPM20065	3.04	5.38	1.87	1.23	4.02	1.17	23	28	60	22	29	62	*gracilis*	X	X
MPM20666	2.62	4.35	1.54	1.00	3.21	1.08	17	31	60	17	32	58	*gracilis*	X	X
MPM20667	2.02	3.25	1.12	0.74	2.31	0.90	17	32	58	15	31	60	*gracilis*	X	
MPM20668	2.34	3.60	1.40	0.85	2.96*	0.94	20	30	63	21	24	52	*gracilis*	X	X
MPM20669	0.90	1.38	0.45	0.26	0.94	0.45	16	33	55	20	—	56	*gracilis*	X	
MPM20693	3.75	6.13	2.28	1.63	4.38	1.47	13	33	—	—	—	58	*gracilis*	X	
MPM20694	3.51	5.80	2.08	1.28	4.69	1.43	20	40	54	18	39	51	*gracilis*	X	
MPM27750	2.85	4.89	1.69	0.98	4.38	1.16	23*	38	—	22	39	64	*gracilis*	X	X
MPM27757	2.77	4.43	1.67	1.03	3.35	1.10	15	38	60	17	38	58	*gracilis*	X	X
MPM20035	3.22	5.30	1.98	0.92	4.46*	1.34	16	28	57	16	31	60	*granosus*		
MPM27718	2.59	4.06	1.63	0.89	3.38	0.96	—	—	—	11	24	55	*granosus*		
MPM27719	3.29	5.56*	1.93	0.95*	—	1.36	—	—	—	18	31	52	*granosus*		X
MPM5984	6.51	11.17	4.07	2.25	8.86	2.44	20	35	57	17	29	54	*hotchkissi*		X
MPM20047	5.83	9.58	3.79	2.00	8.16	2.04	14	32	62	—	28	59	*hotchkissi*		
MPM20058	6.44*	11.02	4.19	2.55	—	2.25	18	24	45	—	25	45	*intermedius*		
MPM20061	1.45	2.42	0.97	0.39	1.95	0.48	13	38	65	14	34	62	*marginatus*		X
MPM20065	3.02*	4.80*	2.02	1.24	—	1.00	—	33	66	—	27	60	*marginatus*		X
MPM20066	3.75	5.58	2.48	1.35	4.10	1.27	21	29	56	19	30	53	*minnesotensis*	X	
MPM20067	4.68*	7.78*	2.99	1.76	—	1.69	18	29	54	18	32	54	*minnesotensis*	X	X
MPM20069	5.87	9.69	4.03	2.12	—	1.84	12	27	54	12	26	58	*minnesotensis*	X	
MPM27743	3.48	5.62	2.40	1.18	4.12	1.08	—	27	58	—	28	57*	*minnesotensis*	X	X
MPM27752	2.40	3.75	1.51	0.77	2.90	0.89	16	36	66	19	43	59	*minnesotensis*	X	
MPM27753	2.15	3.61	1.34	0.83	2.76	0.81	12	31	57	14	30	59	*minnesotensis*	X	X
MPM27754	2.20	3.62	1.31	0.82	2.36*	0.89	13	25	61	17	28	60	*minnesotensis*	X	
MPM27756	0.80	1.20	0.45	0.27	0.94*	0.40	15	37	62	17	37	67	*minnesotensis*	X	
UWM27112	5.05	8.04	3.08	—	6.84*	1.97	—	—	—	15	28	51	*minnesotensis*		
FMNH16732	2.89*	5.60	1.90	1.10	—	0.79	12	29	56	—	—	—	*minnesotensis*	X	
FMNH16732	8.15	13.54	5.37	2.97	11.64	2.62	19	29	53	17	26	54	*minnesotensis*	X	X
MPM20072	—	—	2.28	1.18	—	—	17	26	59	16	33	59	*norwalkensis*		
MPM20087	1.08	1.89	0.65	0.34	—	0.43	12	25	53	15	29	56	*norwalkensis*	X	X
MPM20088	2.39	3.62	1.60	0.79	—	0.79	—	—	57	17	29	59	*norwalkensis*	X	
MPM20092	2.63	4.02	1.72	0.82	—	0.91	17	29	60	21	30	59	*norwalkensis*	X	
MPM20098	1.74*	2.50*	1.07	0.58	—	0.67	19	32	63	24	31	59	*norwalkensis*	X	X
MPM20099	2.27	3.60	1.47	0.62	2.70*	0.80	13	29	55	—	—	—	*norwalkensis*	X	X
MPM20100	1.64	2.52	1.06	0.49*	—	0.58	—	—	—	—	30	53	*norwalkensis*	X	
MPM20187	2.47	3.53	1.83	0.64*	—	0.64	—	28	59	18	26	59	*norwalkensis*	X	X
MPM20188	2.36	—	1.63	0.75	—	0.73	—	32	61	13	30	57	*norwalkensis*		
MPM20189	2.12	3.14	1.30	0.59	2.32	0.82	22	—	61*	—	32	60	*norwalkensis*	X	
MPM20190	1.75*	2.62	1.06	0.45	2.10	0.69	—	—	60	—	28	63	*norwalkensis*	X	X

Pygidial measurements—Continued.

Catalog number and institution	Total pygid. length	Maximum pygid. width	Total length of rhachis	Anterior width of rhachis	Terminal interspinal distance	Sagittal pleural region length	Angular displacement of pleural furrows from sagittal axis: Left 1	Left 2	Left 3	Right 1	Right 2	Right 3	Ulrich and Resser's species	Use in multivariate analyses: SDA	MDS
MPM20197	0.79	1.18	0.44	0.22	0.78*	0.34	12	26	58	16	38	63	*norwalkensis*	X	
MPM20215	2.51	3.84	1.57	0.83	—	0.94	—	—	58	—	35	57	*norwalkensis*	X	X
MPM20218	1.12	1.96	0.64	0.35	1.40	0.58	—	26*	62	17	30	63	*norwalkensis*	X	X
MPM19950	1.43	2.48	0.72	0.47	1.78	0.71	13	26	60	14*	31	62	*norwalkensis*		
MPM20106	5.50	8.29	3.57	2.00	6.85	1.93	16	29	57	19	29	59	*norwalkensis*		
MPM20109	2.07	3.44	1.31	0.73	—	0.76	18	33	63	18	35	59	*norwalkensis*		X
USNM102259	4.29	7.07	2.66	1.83	5.49	1.63	18	28	56	14	26	57	*ovatus*	X	
USNM102260	4.87	8.08	3.00	2.17	6.51*	1.87	14	25	58	11	28	60	*ovatus*	X	
MPM20110	4.68	7.59	2.93*	2.02	5.33	1.75	23	30	65	19	31	66	*ovatus*	X	
MPM20112	3.26	5.04	1.81	1.17*	3.82*	1.45	21	27	55	—	33	52	*ovatus*	X	X
MPM20115	3.44	6.10	2.13	1.45	—	1.31	15	36	62	—	—	62	*ovatus*	X	X
MPM20700	2.72	4.92	1.89	1.21	4.00	0.83	18	32	60	19	34	60	*ovatus*	X	
MPM5599	8.25	14.16	5.12	3.06	10.82*	3.13	18	28	57	—	30	58	*oweni*		X
MPM20121	—	15.64	5.69*	3.60	—	—	23	—	51	21	—	—	*oweni*		
MPM20123	—	13.00	5.08	3.02	—	—	18	30	57	14	26	65	*oweni*		
MPM20127	2.02	3.23	1.09	0.69	2.41	0.93	20	—	57	18	42	58	*oweni*		
MPM20150	7.70	13.02	5.25	3.01	10.20	2.45	24	39	68	22	38	67	*oweni*		X
MPM18691	1.86*	3.06	0.94	0.57	2.08	0.92	15	29	57	12	30	60	*postrectus*		
USNM101431	4.27	7.04	2.55	1.27	5.65	1.72	10	25	55	15	25	54	*raaschi*		X
MPM20117	4.89	8.04	3.32	1.46*	6.26	1.57	10	24	63	—	—	—	*raaschi*		X
MPM20171	1.05	1.90	0.67	0.42	1.58	0.38	16	38	64	18	33	62	*retrorsus*		
MPM20173	2.45	4.08	1.54	0.79	—	0.91	13	34	55	—	—	—	*retrorsus*		
MPM20174	2.12	3.40*	1.26	0.72	2.54*	0.86	15	—	53	17	—	52	*retrorsus*		X
MPM20176	2.72	4.50	1.55	1.09	3.33*	1.63	16	39	63	25	38	64*	*retrorsus*		X
USNM101437	2.56	3.99	1.61	0.86	3.48	0.95	12	25	60	12	23	59	*subplanus*	X	
MPM20193	1.59	2.52	0.88	0.55	2.07	0.71	19	29	58	20	30	58	*subplanus*	X	
MPM20203	2.05*	3.16	1.21	0.70	2.68*	0.84*	11	34	66	14	29*	66	*subplanus*	X	X
MPM20204	1.21*	1.91	0.73	0.37	—	0.48*	—	35	59	14	36	58	*subplanus*	X	
MPM20205	1.15*	2.08*	0.68	0.38*	—	0.47	12	29*	51	—	—	59	*subplanus*	X	
MPM20208	1.14	1.76	0.71	0.42	1.38*	0.43	18	30	64	18	32	62	*subplanus*	X	X
MPM20223	—	—	1.65	0.89	—	—	20	32	61	20	35	60	*thwaitesi*		
MPM5601	4.08	6.46*	2.52	1.75	4.87	1.56	16	27	48	18	32	48	*wisconsinensis*	X	
USNM102254	3.85	6.83	2.36	1.31	5.09	1.49	13	31	55	13	32	55	*wisconsinensis*	X	X
USNM102255	1.91	3.19	1.06	0.66	2.61	0.85	16	29	53	15	29	56	*wisconsinensis*	X	
MPM20683	1.66	2.57	0.92	0.64	1.93*	0.74	15	—	63*	10	33	64	*wisconsinensis*	X	X
MPM20685	1.78	2.70	1.09	0.53	1.90	0.69	12	40	58	13	—	62	*wisconsinensis*	X	X
MPM20686	2.39	3.86	1.43	0.80	3.06	0.96	18	30	57	18	34	60	*wisconsinensis*	X	
MPM27661	6.97	10.56	—	—	—	—	—	—	—	23	35	54	unassigned		
MPM27684	1.67	2.39	1.01	0.56	1.80	0.66	16	26	56	16	29	57	unassigned		
MPM27685	1.64	2.90	0.93	0.51	—	0.71	12	32	60	—	—	—	unassigned		X
MPM27708	2.15	3.72	1.55	0.62*	2.64	0.71	16	22	58	—	—	—	unassigned		X
MPM27762	3.39	6.04	2.01	1.21	5.12	1.38	—	—	62	15*	29	65	unassigned		
UWM27101	1.69	2.74	1.08	0.59	2.16	0.61	—	33	57	19	34	62	unassigned		
UWM27102	4.07	7.00	2.84	1.40	—	1.23	—	—	—	13	26	55	unassigned		X
UWM27106	4.21	6.98	2.78	1.61*	5.20	1.43	—	—	60	17	33	61	unassigned		X
UWM27110	1.93	3.42	1.13	0.65	2.88*	0.80	13	28	56	—	26	61	unassigned		
FMNH11873a	1.86	2.76	1.01	0.61	2.24	0.85	17	24	—	15	30	55	unassigned		X
FMNH11873b	3.69	5.42	2.15	1.27	—	1.42	20	35	51	19	35	53	unassigned		
FMNH16732	2.89*	5.60	1.90	1.10	—	0.79	12	29	56	—	—	—	unassigned		
FMNH10106	8.15	13.54	5.37	2.97	11.64	2.82	19	29	53	17	26	54	unassigned		
FMNH10107a	2.03	3.51	1.23	0.63	2.88	0.80	11	25	52	17	27	—	unassigned		X
FMNH10107b	2.36	3.68	1.39	0.80	—	0.97	12	22	—	13	25	53	unassigned		X
FMNH24107	3.13	5.22*	2.02	—	4.26	1.11	18	—	52	—	—	—	unassigned		
FMNH24110	2.81*	5.02	1.63*	0.96	—	1.18	—	—	—	—	—	49	unassigned		
FMNH24111	—	2.71*	1.20*	0.75	—	—	16	22	37	15	27	—	unassigned		
FMNH24112	3.68*	6.14	2.21	1.34	5.80	1.47	17	31	51	15	33	50	unassigned		
FMNH28468	3.97*	6.81	2.35	—	5.50	1.62	—	—	—	—	—	—	unassigned		
FMNH32708	2.11	3.25	1.36	0.66	2.49	0.75	14	28	57	17	24	61	unassigned		X
FMNH39206	—	3.50	1.55	0.79	—	—	17	28	57	—	27	59	unassigned		
FMNH39207a	2.71	4.17	1.73	0.90	3.24*	0.95	17	35	62	19	31	58	unassigned		X
FMNH39207b	1.71*	2.65	0.98	0.60*	1.95	0.73	—	30	57	—	—	63	unassigned		
FMNH39208	2.11	3.25	1.36	0.66	2.49	0.75	14	28	57	17	24	61	unassigned		
FMNH39210	2.20	3.90	1.39	0.75	—	0.91	16	25	60	—	28	60	unassigned		X
FMNH39212	2.29	4.12	1.52	0.70	—	0.77	11	17	60	11	19	61	unassigned		X
Pers. coll.	4.95	7.42*	3.04	1.89	—	1.91	18	30	59	20	29	58	unassigned		