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Variation in Scales in *Dermophis mexicanus* (Amphibia: Gymnophiona): Are Scales of Systematic Utility?

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A Contribution in Celebration of the Distinguished Scholarship of Robert F. Inger on the Occasion of His Sixty-Fifth Birthday

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Variation in Scales in *Dermophis mexicanus* (Amphibia: Gymnophiona): Are Scales of Systematic Utility?

Abstract

Several workers have suggested that the size, shape, and number of dermal scales in gymnophiones may be of use in identifying taxa. However, an examination of scale morphology within and among individuals, let alone among species, has not been documented. Our data indicate that there are within- and among-individual differences, including ontogenetic variation and sexual dimorphism. We conclude that scales cannot be used as taxonomic characters unless samples are large enough to be tested statistically. Since few species are likely to be sampled adequately, the statistical comparison criterion cannot be used comparatively. Further, excision and preparation of large numbers of scales is somewhat destructive of specimens and inordinately time-consuming. We do not consider scale morphology a useful character for identification of taxa. The biology of scales remains a most provocative problem.

Introduction

The origins, homologies, and conformation of the dermal scales of gymnophiones have attracted the attention of biologists since their initial description by Mayer (1829a,b). Rathke (1852) and Leydig (1853) commented on the presence of scales; Wiedersheim (1879) and Sarasin and Sarasin (1887–1890) carefully described them. Cockerell (1911, 1912), Phisalix (1910, 1912), Dätz (1923), Peyer (1931), Ochotorena (1932), and Marcus (1934) described scales, often in conjunction with consideration of skin glands. More recently Feuer (1962), Gabe (1971), Taylor (1972), Wake (1975), Casey and Lawson (1979), Perret (1982), Fox (1983), and especially Zylberberg et al. (1980) have looked carefully at the structure of gymnophione scales. Zylberberg et al. (1980) present excellent evidence for the homology of gymnophione and teleost scales, and controvert Feuer's (1962) suggestion that the squamulae on scales are arranged in growth series. Werner (1931) suggested that there are generic-level differences in scale morphology, and Taylor (1968, 1969, 1972) suggested that there also are species-level differences. Zylberberg et al. (1980) state that Taylor's work demonstrates the utility of scales in classifying gymnophiones (caecilians), though they also comment on the marked similarity of the two species that they studied.

However, there has been no thorough assessment of variation in scale morphology, number, and distribution within individuals and within populations, let alone comparing variation in species, though "variation" has been noted (Feuer, 1962; Taylor, 1972; Zylberberg et al., 1980). Taylor controlled for variation to some degree, as did Feuer, by examining only the largest scales from the terminal primary annulus, but they did not compare even several large scales from an individual to assess variation. Taylor also considered the number of scale rows present to be potentially useful as a character, but he did not examine ontogenetic series.

It seems requisite to understand how much variation occurs among scales in individuals and within populations before one can select scales and compare them among species. We examined specimens from a Guatemalan population of *Dermophis mexicanus* in order to make a preliminary assessment of variation in scales. We considered scale size, shape, and number within and among annuli of an individual, and among individuals of both sexes and of comparable and different sizes (and, presumably, ages). While collaborating with

Dr. Louise Zylberberg on studies of scale ontogeny and scale microstructure in *Dermophis mexicanus,* we here report preliminary information about adult scale structure and present information on scale variation that indicates that (1) one must consider multiple scales in multiple annuli, preferably from several individuals, in order to determine whether their morphology and distribution characterize species; (2) there is ontogenetic variation in scale size and number; and (3) variation is such that the taxonomic utility of scales is minimal to non-existent.

Materials and Methods

Scales were extracted from the annuli of five *Dermophis mexicanus* from San Marcos, Guatemala (see table 1 for specimen data). All scales from dorsal to ventral midlines on the left side of the first primary annulus containing scales, the first and fifth secondaries containing scales, every 10th succeeding annulus in both series, and the terminal annuli in the series were extracted and counted for all five specimens (see table 2). Numbers of rows of scales were counted before the scales were extracted. Scales from the right sides of the respective annuli of three specimens (A, C, and E) were extracted, placed on slides, stained with alizarin red-S solution, air-dried, and coverslipped. Scales were then measured and photographed. Pieces of skin including several annuli were taken from various regions of the body of a female specimen 335 mm in total length (TL). Segments were sagittally sectioned, serially mounted, and stained with hematoxylin-eosin, Heidenhain's azan, or picroponceau. Variation in size, structure, and orientation therefore was observable at higher resolution than in the gross preparations. Additional scales were mounted on stubs, sputter-coated with gold-palladium alloy, and examined and photographed with an ISI-DS-130 dual-stage scanning electron microscope.

TABLE 1. Specimens of *Dermophis mexicanus* examined for scale morphology.

Specimen	Total length (mm)	No. of primary annuli	No. of secondary annuli	Sex
A	386	108	67	♂
B	385	103	75	♀
C	377	100	61	♀
D	260	106	66	♀
E	255	101	66	♂

Results

Scale Number, Size, and Shape

Scales first occur in approximately the 10th primary annulus in large adults and the 20th to 30th of small adults. Most anterior annuli are very shallow. Annular depth first increases laterally, and scales lie in the deeper regions of the annuli of four of the five specimens examined. Scales are small (see table 3) and irregularly shaped (figs. 1A, 2A). Following the 30th annulus, scale number increases steadily. Scales are distributed both more dorsally and more ventrally in increasingly posterior annuli. Scales are distributed in a single overlapping row.

Between primary annuli 30 and 50, both scale number and size increase greatly. Scales occur throughout each annulus, except mid-ventrally, and are arrayed in two rows of variably overlapping scales. One row appears to be associated with the anterior wall of the opened annulus, the other with the posterior wall. Dorsomedial scales are not attached to either wall. Following the 50th primary annulus, the number of scales and their distribution is fairly constant (see table 2). Most of the scales are larger (see table 3) than those occurring more anteriorly, though some very small scales also occur in each annulus (fig. 1D–F, table 3). Small scales are distributed throughout the annuli, interspersed among the larger ones. The shapes of the scales show considerable variation regardless of size (figs. 1–2).

Secondary annuli consistently contain scales, except for the anteriormost small shallow lateral one or two. Scale number per annulus increases more rapidly in secondaries than in primaries. The number is relatively stable by the 20th to 30th secondary annulus. The pattern of increase in scale size and distribution is similar to that described above for primary annuli, and scale shapes are similarly variable. The numbers of scales in secondary annuli are slightly fewer than in the primary annuli with which they are associated. There are few differences in counts among specimens B–E, but specimen A, the large male, has more than twice as many scales in primary annuli than in secondaries. A comparison of our photographs of scales from within a single annulus of a *Dermophis*

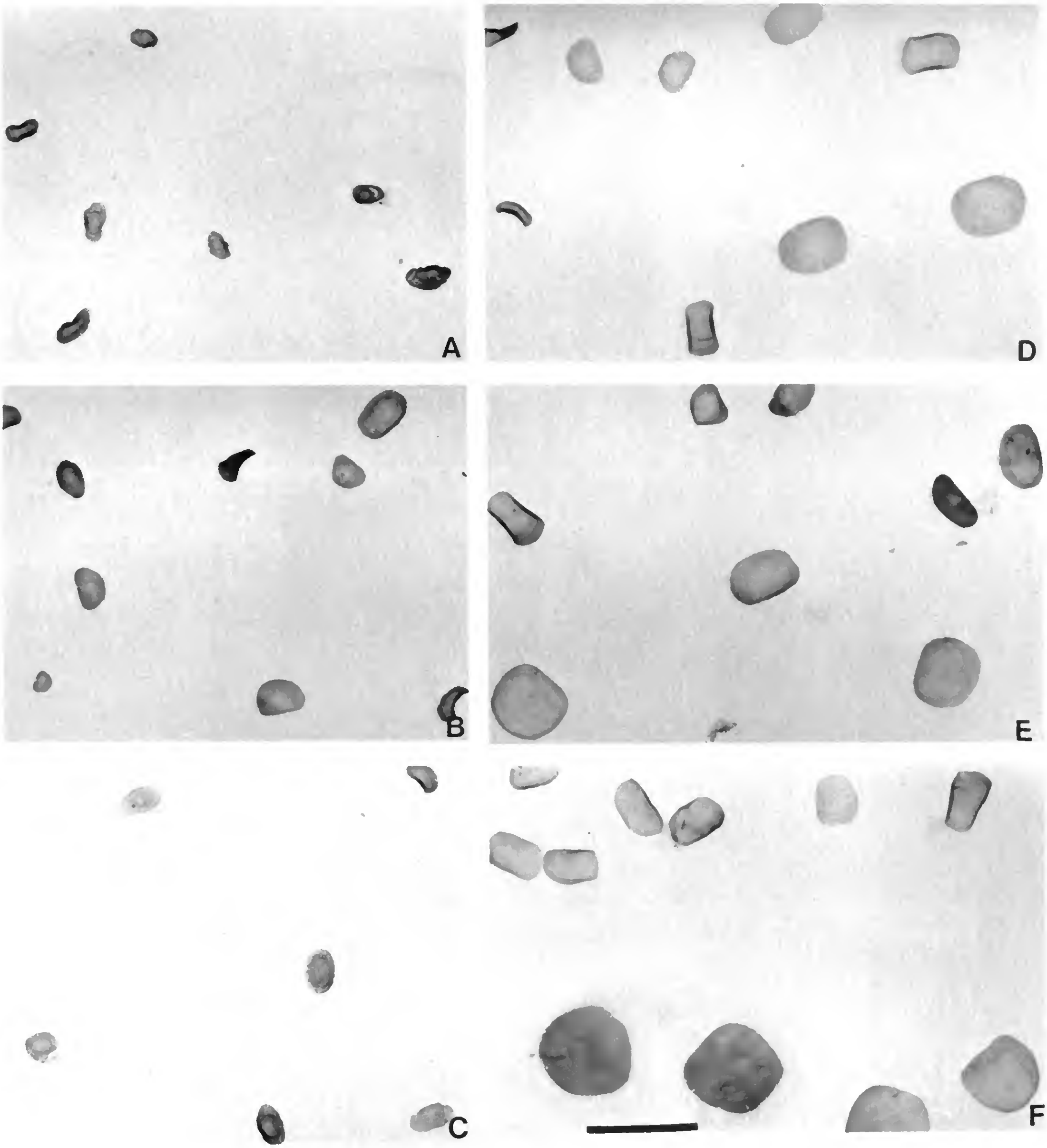

FIG. 1. Scales from primary annuli of a 377-mm (total length) female *Dermophis mexicanus*. A comparison of these photographs shows the size and shape variation of scales within and among annuli. All scales photographed to same scale; bar = 2.0 mm. **A,** Scales from 30th primary annulus behind head; **B,** scales from 40th annulus; **C,** scales from 50th annulus; **D,** scales from 60th annulus; **E,** scales from 80th annulus; **F,** scales from 90th annulus.

mexicanus with the photographs of the scales of a great number of species of caecilians presented by Taylor (1972) shows that all of the diversity among most species, regardless of genus or even family, is equally present within an annulus of an individual, at least of *D. mexicanus.*

Ontogenetic Variation

Ontogenetic variation in scale numbers is suggested by our data. Specimens D and E are a recently matured male and female, respectively,

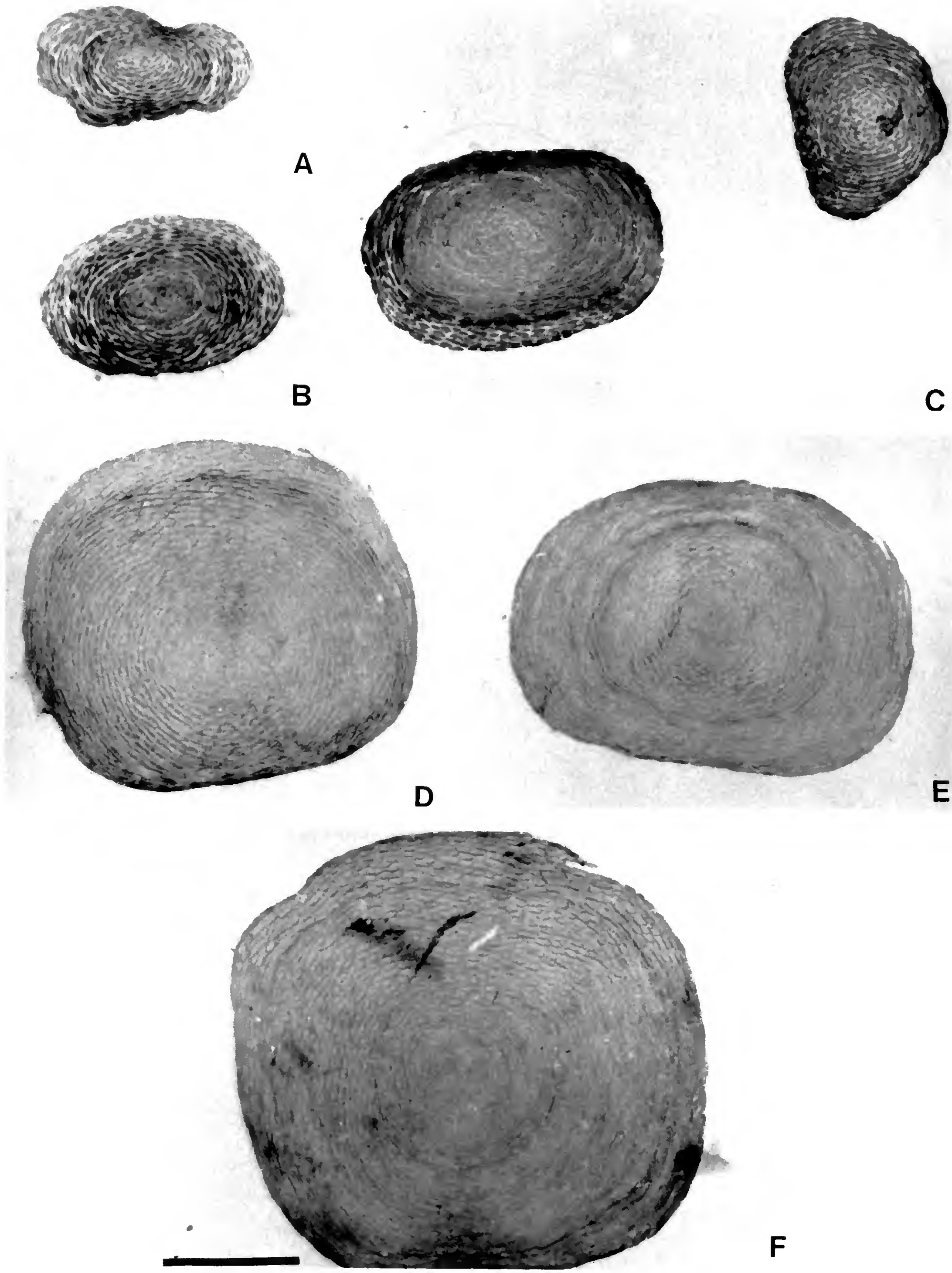

FIG. 2. Large scales from primary annular scale array shown in Figure 1. Note conformation and variation. All photographed to same scale; bar = 0.5 mm. **A,** Scale from 30th annulus; **B,** scale from 40th annulus; **C,** scales from 50th annulus; **D,** scale from 60th annulus; **E,** scale from 80th annulus; **F,** scale from 90th annulus.

TABLE 2. Numbers of scales in annuli of *Dermophis mexicanus*. Scales were extracted from the dorsal midline to the venter of the left side of each specimen.

Speci-men	Primary annulus number											
	1	5	10	20	30	40	50	60	70	80	90	100
A	0	0	33	93	112	134	150	151	150	167	168	142
B	0	0	0	27	59	60	80	95	99	90	92	80
C	0	0	6	14	54	90	106	115	102	98	95	81
D	0	0	0	0	0	6	14	25	36	42	52	51
E	0	0	0	0	20	37	45	51	52	50	57	24

	Secondary annulus number									
	1	5	10	20	30	40	50	60		70
A*	2	0	11	64	114	117	126	141	39	
B*	1	23	30	73	70	88	75	86		90
C	3	13	50	85	114	112	115	85		
D*	1	3	5	27	29	37	43	51	8	
E*	1	4	11	41	47	55	54	62	10	

Secondary annulus numbers are positioned to show their association with primary annuli; i.e., the first secondary occurs at approximately the 20th primary in an anterior-to-posterior series. Specimen designations A–E refer to specimens in Table 1.

* Terminal secondary annulus for A is 67; B, 75; D, 66; E, 66. Numbers of scales in terminal annuli for A, C, D, and E are indicated; number for B is 18.

probably three years old (Wake, 1980). They have roughly half the number of scales per annulus of comparable primaries and secondaries of larger specimens (see table 2) that are perhaps six years old (Wake, 1980). Scale distribution is similar to that in the larger specimens. These data indicate that scales may be added throughout life, and that they may be perennial, as in teleosts. The data further suggest that scale development within the pocket of an annulus is not synchronous, so Feuer's (1962) ideas about the concentric rings on annuli as indicators of age are questionable on grounds other than those mentioned by Zylberberg et al. (1980). An appropriate sample is necessary to corroborate these suggestions.

Our measurements indicate that scales in the smaller specimens are also smaller. The largest scales found in specimen E are approximately two-thirds the size of the largest scales in specimen A (1.1 × 0.9 mm vs. 1.6 × 1.6 mm); means of scale measurements from terminal primary annuli are 0.66 × 0.66 mm for E, 0.92 × 0.82 mm for A. Since we have no information on scale growth, two hypotheses about the increase of scale size with age must be tested. Either scales do grow throughout life, perhaps by the addition of concentric squamulae to a growing base plate (as suggested by Feuer, 1962, but partially refuted by Zylberberg et al., 1980), or the scales that are added later in life, as indicated by the increase in numbers in larger specimens, achieve larger size during a short growth period, resulting in diverse sizes of scales within each annulus.

TABLE 3. Sizes of scales (mm) in annuli of *Dermophis mexicanus* specimen C.

Annulus number	$\bar{x}$ of dimensions (height × width) of 10 scales per annulus	Range
Primary		
20	0.65 × 0.40	0.6 × 0.4–0.7 × 0.4
30	0.68 × 0.36	0.4 × 0.3–1.2 × 0.6
40	0.65 × 0.43	0.4 × 0.3–0.9 × 0.5
50	0.93 × 0.48	0.4 × 0.3–1.5 × 0.7
60	1.16 × 0.89	0.8 × 0.6–1.4 × 1.1
70	1.14 × 0.83	0.7 × 0.3–1.4 × 1.0
80	1.18 × 0.92	0.6 × 0.4–1.5 × 1.3
90	1.40 × 1.09	0.9 × 0.6–1.7 × 1.7
Secondary		
1	0.70 × 0.40	0.5 × 0.4–0.8 × 0.4
10	0.76 × 0.42	0.4 × 0.3–1.1 × 0.5
20	0.81 × 0.64	0.6 × 0.5–1.2 × 0.8
30	0.93 × 0.73	0.5 × 0.4–1.4 × 1.0
40	1.20 × 1.10	0.9 × 0.8–1.4 × 1.3
50	1.26 × 0.93	0.5 × 0.4–1.6 × 1.3
60	1.39 × 1.25	0.6 × 0.6–1.7 × 1.6

Sexual Dimorphism

Male specimens of both size classes examined have greater numbers of scales in comparable an-

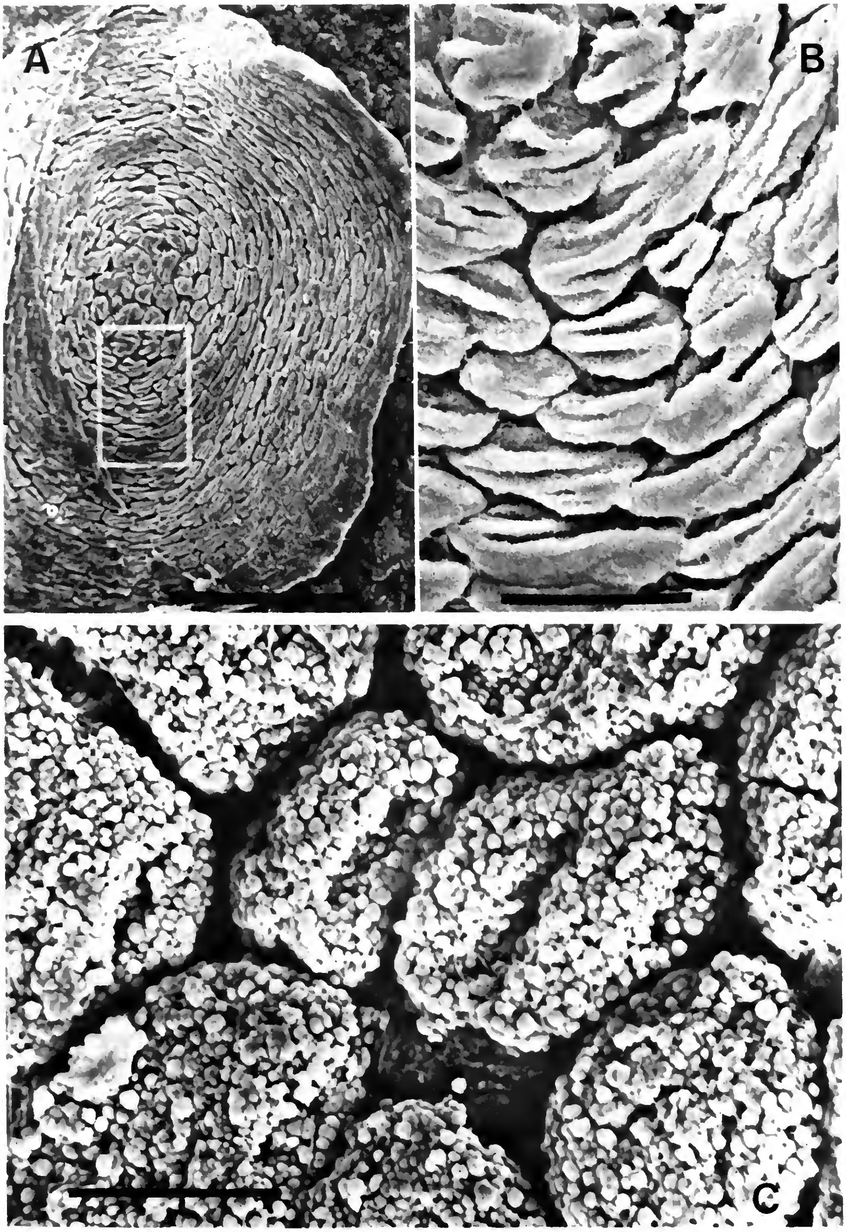

FIG. 3. Scanning electron micrographs of scale of *Dermophis mexicanus*. **A**, Whole scale with mineralized denticles on surface. Area in rectangle shown in **B**. Bar = 1.0 mm. **B**, Close-up of surface denticles. Note complex folding patterns. Bar = 200 μm. **C**, Further magnification of denticles to demonstrate granular spherules of mineralized material. Bar = 10 μm.

nuli than do females of approximately the same sizes within the classes (see table 2). Consequently the total number of scales is greater in males of both sizes than in comparable females. As noted above, the larger male (A) has approximately twice the number of scales in primary annuli than have the females of comparable size that were sampled, though the difference in numbers of scales in secondaries differs little. Male A also has scales distributed throughout its anterior annuli, rather than just laterally as in the females. Again, the number of specimens examined does not allow a firm conclusion, but the greater number of scales in males of both sizes suggests that males may have more scales than females.

Scale Structure

The scales of *Dermophis mexicanus* are composed of an unmineralized bilaminar fibrous base plate topped with mineralized squamulae (fig. 3). The squamulae are irregularly shaped but basically elongate rhomboids, especially toward the periphery of the scales. Squamulae are less elongate in the center regions of scales. They are arrayed in concentric series and are similar to those of several other species, as shown by Taylor (1972) and Zylberberg et al. (1980). The pattern of the surface structure with many small mineralized spherules (fig. 3C) is similar to that reported by Zylberberg et al. (1980) in both *Ichthyophis* and *Hypogeophis*.

In sagittal section, several scales are apparent in the scale pocket. This is due to the overlapping of scales in each of the two major rows (see above). Because of the curvature of the scales, differences in the thickness and arrangement of both the base plate and the squamulae are shown. This is a consequence of the normal variation in these structures across the diameter of any scale.

Discussion

There is considerable variation in scale size, shape, and number within annuli and among individuals from a single population of *Dermophis mexicanus*. Some of that variation may be correlated with size (or age) and with sex. Controlling for variation by restricting comparison to the largest scale from the terminal annulus, as Taylor (1972) did, does not consider the problem of ontogenetic variation, which our data suggest is substantial, and does not deal with the possibility of sexual differences, which our data also indicate. As noted above, the variation of scale characteristics *within* an annulus of a single individual is comparable to the variation Taylor (1972) attempted to show *among* taxa. We therefore conclude that scale size, shape, and number are not reliable indicators of species (or higher taxonomic category) identity.

This does not preclude the likelihood that large samples of scales that can be treated statistically might indicate differences. This would require that any ontogenetic and sexual variation be accounted for, as well as that within and among annuli of individuals. It is not unreasonable that different species would have different numbers of scales among comparable annuli of similarly sized animals, and that scale size means and ranges might differ. However, we do not have statistically appropriate data for other species to compare to data for *Dermophis mexicanus*.

Taylor (1972) suggested that the numbers of *rows* of scales within annuli might be a useful character. Our data suggest that rows as well as numbers of scales might increase during growth. We also see variation in the number of rows in anterior annuli relative to more posterior ones. However, the increase from one row to two in *Dermophis mexicanus* is not comparable to that of species that may have as many as eight rows of scales in some annuli. Our preliminary survey of such species indicates that there is anteroposterior variation in numbers of rows among annuli. We do not have any information on ontogenetic variation in these species.

More crucially, we are not convinced that the acquisition of such data is necessarily appropriate. Excision of scales from multiple annuli of multiple specimens is somewhat destructive to the specimens. Maintaining, mounting, counting, and measuring the scales is not time-efficient if there are any more reliable indicators for identification. Most species of caecilians are represented by only a few specimens, and very rarely by ontogenetic or population series; therefore, the statistical comparison criterion cannot be utilized throughout a clade. It remains possible, indeed likely, that there are differences in the microstructure of scales among taxa. However, the developmental and physiological data necessary to corroborate this supposition are not yet available, and it is likely that only a few species can be subject to such analysis in the near future. The search for systematic characters should include consideration of the utility and general applicability of the characters in question.

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