SYSTEMATICS OF XANTUSIID LIZARDS OF THE GENUS *LEPIDOPHYMA* IN NORTHEASTERN MEXICO

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ABSTRACT. Discriminant analyses of variation among 30 scale characters indicate that the 21 populations of *Lepidophyma* from northeastern Mexico form six morphological groups. Two of 27 population samples from southern Mexico approach the northern groups in discriminant space. When viewed in terms of univariate differences and geographic distribution, the northern population groups constitute four unique morphological entities that are considered to represent species units. The most distinctive is *Lepidophyma gaigeae* occurring in limestone habitats in the Sierra Madre Oriental of Hidalgo and Querétaro. *Lepidophyma occulor* is known from four localities in the semi-arid Jalpan region of Querétaro and San Luis Potosí, and the cavernicolous *L. micropholis* is confined to the Sierra del Abra of Tamaulipas and San Luis Potosí. The wide-ranging *L. sylvaticum* includes four moderately divergent population groups: northern Madrean (Tamaulipas to San Luis Potosí), southern Madrean (San Luis Potosí to Hidalgo), Veracruzan, and western (Mesa Central of San Luis Potosí to Nuevo León).

The karyotypes of *L. gaigeae* and *L. occulor* are unique within the genus, while most *L. sylvaticum* are chromosomally identical to *L. micropholis*. A heteromorphism in microchromosomes was observed in six females of one population of *L. sylvaticum*, and could represent either ZW sex chromosomes or allodiploidy. This same population plus one in Querétaro have statistically significantly skewed sex ratios that may be associated with hybridization.

RESUMEN. Los análisis discriminatorios de variación entre 30 caracteres de las escamas, indican que las 21 poblaciones de *Lepidophyma* del noreste de México forman seis grupos morfológicos. Dos de los muestreos de la población del sur de México se aproximan a los grupos del norte en espacio discriminatorio. Cuando se examinan en términos de diferencias univariadas y de distribución geográfica, los grupos de la población del norte constituyen cuatro entidades morfológicas únicas que se considera representan unidades de especie. La más distintiva es *Lepidophyma gaigeae* que vive en habitats de piedra caliza en la Sierra Madre Oriental de Hidalgo y Querétaro. *Lepidophyma occulor* se conoce de cuatro localidades de la región semiárida de Jalpan de Querétaro y San Luis Potosí, y el cavernícola *L. micropholis* se encuentra confinado a la Sierra del Abra de Tamaulipas y San Luis Potosí. *L. sylvaticum* de amplia distribución en y cerca de la Sierra Madre Oriental incluye cuatro grupos poblacionales moderadamente divergentes: norte (Tamaulipas a San Luis Potosí), sur (San Luis Potosí a Hidalgo), Veracruz, y occidental (Mesa Central de San Luis Potosí a Nuevo León).

Los cariotipos de *L. gaigeae* y *L. occulor* son únicos dentro del género mientras que la mayoría de *L. sylvaticum* son cromosómicamente idénticos a *L. micropholis*. Se observó heteromorfismo de microcromosomas en seis hembras de una población de *L. sylvaticum* y podría representar ya sea cromosomas sexuales ZW o alodiploidía. Esta misma población, más una en Querétaro han torcido estadísticaniente en forma significativa las proporciones en los sexos que pudieran ser asociadas con hibridización.

INTRODUCTION

Lizards of the xantusiid genus *Lepidophyma* range from Panama to Nuevo León, Mexico, living principally in wet tropical lowland forests in the south, but becoming increasingly restricted to montane and/or rimose habitats in the semi-arid regions to the north. In the rugged ranges of the Sierra Madre Oriental, and in the canyons and valleys along both of its flanks, are a morphologically diverse array of *Lepidophyma* populations. While most of these populations remain taxonomically unallocated, four have been named, and two of these names have been alternatively associated with species occurring to the south (e.g., Smith, 1942; Walker, 1955).

In this paper, the problems of discordant morphological variation, geographic isolation, and small sample sizes of the populations of *Lepidophyma* in northeastern Mexico are handled by treating each locality as a separate sample, and employing multivariate analyses of variation to identify groups of morphologically similar populations. Additional multivariate comparisons with populations to the south, and analyses of univariate differences among all population groups are used to diagnose morphological species. Names are then assigned to the units on the basis of included type or topotypic material, the species of *Lepidophyma* recognized in northeastern Mexico are summarized in brief accounts, including comments on chromosomal variation and skewed sex ratios in certain populations, and a key is presented.

MATERIALS AND METHODS

A total of 152 specimens of *Lepidophyma* from Mexico north of 19°N latitude were used in the analyses. This includes all material studied from the area, except that referable to *L. gaigeae*. One sample (N = 20) of the over 500 known specimens of the species was used as a reference population. In addition, 31 population samples (N = 188) from southern and western Mexico were utilized in the comparative analyses. The selection of 19°N latitude as the southern limit of the study area is based on a distributional hiatus for the genus in the transvolcanic region (ca. 19–20°N), and on preliminary observations suggesting that the populations occurring to the north of this distributional gap share a number of unique morphological similarities.

The localities of the specimens were determined on available maps, and geographic samples were constituted with all specimens from a given locality (or in a few instances by pooling adjacent localities separated by less than 20 km) to form a total of 21 population samples of *Lepidophyma* from northern Mexico (Fig. 1). The specimens and localities are listed in specimens examined, below.

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The analyses use a total of 30 scale characters, 20 meristics, and 10 ratios of the relative size or proportions of individual scales. No significant sexual dimorphism, ontogenetic variation, or correlation was detected among the 30 characters. The characters were selected largely on the basis of their purported diagnostic strength in the genus (Bezy, 1973; Bezy et al., 1982; Mosauer, 1936; Smith, 1942, 1973; Smith and Alvarez del Toro, 1977; Taylor, 1939; Walker, 1955; Werler, 1957; Werler and Shannon, 1957).

Scale terminology follows Savage (1963). The characters are defined below.

1. FPT — Femoral pores (total both sides).
2. LTR — Lateral rows of tubercles (axilla to groin).
3. DBPVR — Dorsals between paravertebral rows of tubercles.
4. IWD1 — Dorsal interwhorls in first caudal segment.
5. IWV1 — Ventral interwhorls in first caudal segment.
6. PTMP — Pretympanics (total both sides) separating postocular from second postorbital supralabial.
7. DBPVT — Distance between large paravertebral tubercles within-row, expressed in number of mid-dorsal scales.
8. GC1IL — Gulars contacting first pair of infralabials.
9. GUL — Gulars (fold to second infralabials).
10. PVTL — Large tubercles in paravertebral row (axilla to groin).
11. VL — Ventrals (gular to vent; includes preanals).
12. 4TL — Fourth toe lamellae (ventral).
13. 4TLD — Fourth toe lamellae divided (i.e., with ca. mid-ventral sutures).
14. DOR — Dorsals occiput to rump (above vent).
15. DAPVR — Dorsals in row immediately above paravertebral row (axilla to groin).
16. PVR — Total scales in paravertebral row (axilla to groin).
17. PVS — Scales in paravertebral row (a–g) smaller than 1.5 dorsals.
18. PVT1 — Scales in paravertebral row (a–g) larger than 1.5 dorsals.
19. PVT2 — Scales in paravertebral row (a–g) larger than 2.0 dorsals.
20. PVT3 — Scales in paravertebral row (a–g) larger than 3.0 dorsals.
21. RPOL — Length of postocular/length of orbit.
22. RPAW — Width of posterolateral preanal/width of posteromedial preanal.
23. RPFML — Prefrontal: length along midline/length along lateral border.
24. RPFL1 — Prefrontal: length of mid-line suture/length along lateral border.
25. RMW — Width of median (prefrontal)/anterior width of interparietal.
26. RNL — Length of nasal/length of postparietal.
27. RML — Length of median (prefrontal)/length of frontal.
28. RAPPSL — Length (total both sides) of all anomalous sutures on postparietals/length of postparietals.

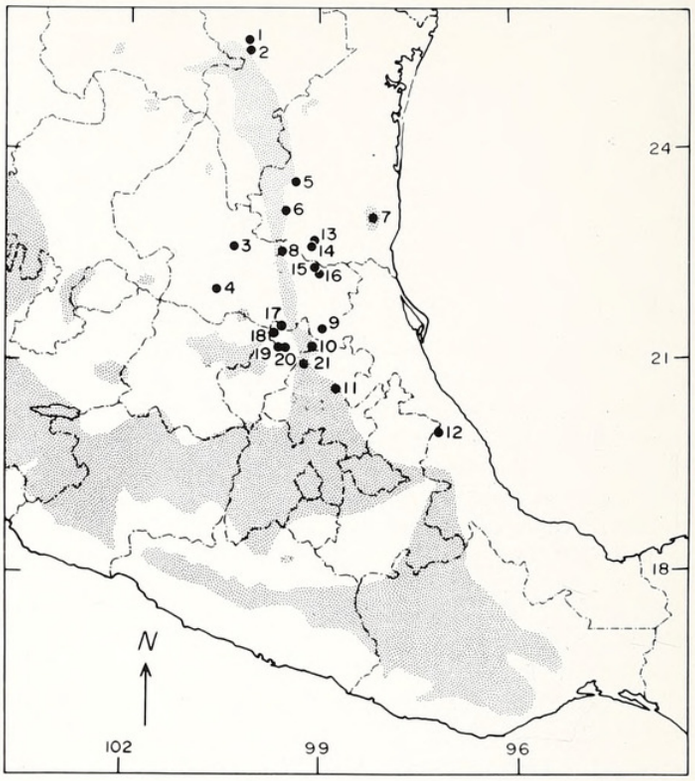

Figure 1. Location of the 21 population samples of *Lepidophyma* in Mexico north of 19°N. Stippled area indicates approximate distribution of pine-oak woodland (after Leopold, 1959). Population numbers are those used throughout the paper (see Specimens Examined for localities).

29. RPNH — Height of postnasal/height of anterior loreal.
30. RSLH — Height of second postorbital supralabial/height of first postorbital supralabial.

Variation in the 30 characters was analyzed univariately with BMDP1D for simple data description, and multivariately with BMDP7M for stepwise discriminant analysis (Dixon, 1981). In all discriminant analyses the *a priori* groups were individual population samples rather than population groups or species.

RESULTS AND DISCUSSION

In the following sections the results of discriminant analyses of populations of *Lepidophyma* from northern Mexico are used to identify northern population groups, which in turn are compared with populations from southern Mexico. The northern population groups are then viewed relative to their univariate differences and geographic relationships to arrive at the definition of unique morphological units. Finally, names are allocated to these units (morphospecies) on the basis of included topotypic and/or type material, and each species is briefly summarized.

NORTHERN MEXICO POPULATIONS

The initial discriminant analysis utilized 30 characters and 18 of the 21 populations from northeastern Mexico (Fig. 1,

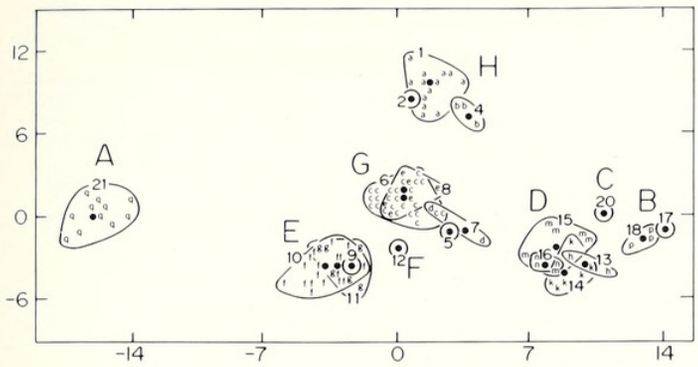

Figure 2. Nineteen population samples of *Lepidophyma* from northeastern Mexico plotted on the first two canonical variables for 25 characters. Population centroids are indicated by dots, and the number of the sample is placed along the line enclosing all included specimens (lower case letters). Upper case letters indicate population groups identified by the analysis.

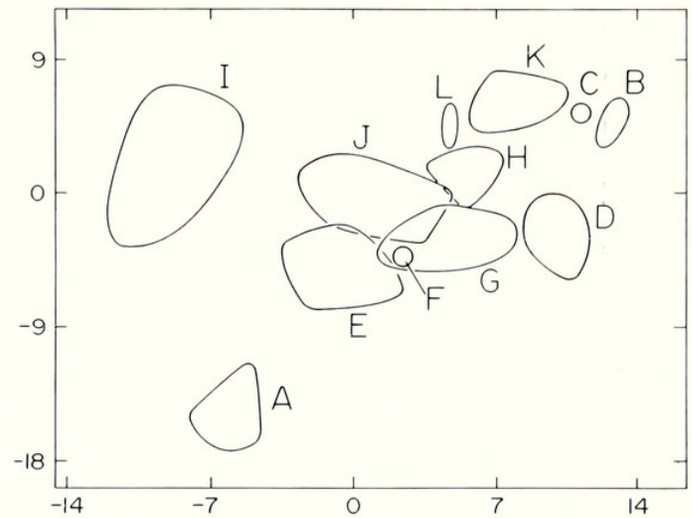

Figure 3. Twelve population groups of *Lepidophyma* from Mexico plotted on the first two canonical variables for 30 characters. Lines enclose all individuals comprising each of the eight northern (A–G) and four southern (I–L) population groups.

Table 1). In samples 3, 5, and 19 there are no individuals on which all of the characters could be scored. The analysis resulted in high resolution of the populations in that 99 percent (127/128) of the individuals were "correctly" assigned by the posterior classification to the locality sample of which they were a member (one specimen of sample 7 was misassigned to 6). A second analysis was performed excluding five characters (IWD1, IWV1, RPFML, RPFL1, RML) in order to allow inclusion of sample 5 (Fig. 2). Samples 3 and 19 were not included in any of the multivariate analyses due to the limitations of the data available from them. While both analyses produced similar results, the reduction in characters of the second lowered the accuracy of the posterior classification (96%; 126/131).

From the second analysis, eight population groups were identified on the basis of overlap or juxtaposition of the included samples and the distance between groups in discriminant space (Fig. 2). The first canonical variable accounts for 57 percent of the variation, is most heavily loaded with LTR, PVS, PVR, DOR, and GUL (in order of decreasing weight), and places group A at one end, and B, C, and D at the other, with E, F, G, and H occupying intermediate positions. The second coordinate has heavy loadings for PVS, PVR, PVT1, LTR, and FPT, accounts for 21 percent of the variation, and effectively separates groups E, G, and H from one another.

The sample comprising group A (21) is highly isolated in discriminant space from all other populations, suggesting it is not a member of the same morphological complex. Group D is a discrete cluster of four overlapping populations (13–16) that is approximately equidistant from B (17, 18) and C (20). The three populations of group E (9–11) form a moderately tight cluster that is only weakly separated from the loosely associated populations of G (5–8) and the one specimen (12) comprising the intermediate group F. The three populations of group H (1, 2, 4) are well separated from their nearest discriminant neighbor, group G.

COMPARISONS WITH SOUTHERN GROUPS

Twenty-seven samples from southern Mexico were compared with the 18 northern populations to identify those that might be closest morphologically to northern groups. The initial discriminant anlaysis utilized 30 characters and a total of 288 specimens arrayed in 45 populations (Fig. 3), and produced high resolution of the populations in that the accuracy of the posterior classification was 98 percent. The first canonical variable is most heavily loaded with PVS, DBPVT, LTR, GUL, and PVR, and expresses 43 percent of the total dispersion; the second expresses 21 percent and is dominated by LTR, PVS, PVTL, FPT, and RPAW. The graph (Fig. 3) was used primarily to identify those southern population groups that are multivariately most similar to the northern ones and which are further resolved in subsequent analyses containing fewer populations.

All but one (F) of the eight northern groups identified in the previous analysis remain separated from each other, although they are approached or overlapped by three southern groups (J, K, L) (Fig. 3). Northern groups B, C, and D were well separated from both southern and northern populations and thus are not included in the subsequent analyses. Southern group I is also strongly separated from all populations, and its nearest discriminant neighbor is another southern group (J). Consequently, it was also excluded from further analysis. In the following analyses, northern groups E through H are compared in greater detail first with K and L, and then with J.

The 10 populations of northern groups E, F, G, and H were analyzed together with the four populations of southern groups K and L (Fig. 4). The posterior classification was 98 percent (121/123) accurate, one specimen of sample 11 being misassigned to 10 (both group E) and one of sample 43 to 44 (both group K). The first canonical variable accounts for 60 percent of the total dispersion, is heavily loaded with

Table 1. Variation among 30 scale characters for 21 population samples of *Lepidophyma* from northern Mexico. Sample size is (*in parentheses*) under each of the population numbers (POP). In each cell the upper number is the mean; the middle, the standard error; and the lower, the range. See text for character abbreviations and locality data.

POP	FPT	LTR	DBPVR	IWD1	IWV1	PTMP	DBPVT	GC1IL	GUL	PVTL	VL	4TL	4TLD	DOR	DAPVR	PVR
1	31.3	18.1	3.17	3.0	2.1	2.1	2.83	.3	45.0	15.9	36.1	25.3	8.1	161.2	83.2	44.8
(*15*)	.37	.59	.093	0	.09	.07	.080	.13	.59	.21	.15	.33	.56	1.88	.99	1.13
	29–34	15–22	2.5–4.0	3	2–3	2–3	2.5–3.5	0–1	42–49	15–17	35–37	24–29	4–12	150–174	77–91	39–53
2	29.0	19.0	2.50	3.0	2.0	3.0	2.50	1.0	46.0	17.0	35.0	26.0	7.0	164.0	83.0	43.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	29	19	2.5	3	2	3	2.5	1	46	17	35	26	7	164	83	43
3	29.0	—	3.50	2.0	2.0	2.0	3.00	1.0	46.0	—	—	20.0	5.0	—	—	—
(*1*)	0	—	0	0	0	0	0	0	0	—	—	0	0	—	—	—
	29	—	3.5	2	2	2	3.0	1	46	—	—	20	5	—	—	—
4	27.0	17.0	3.38	2.5	1.5	2.3	3.00	.3	45.0	16.0	35.3	23.0	6.3	172.5	91.0	47.0
(*4*)	.41	0	.125	.58	.29	.25	0	.25	.71	.41	.25	.41	.25	3.43	1.47	1.08
	26–28	17	3.0–3.5	2–3	1–2	2–3	3.0	0–1	43–46	15–17	35–36	22–24	6–7	163–178	87–94	44–49
5	28.0	31.0	5.00	—	—	1.0	4.50	3.0	56.0	15.0	38.0	31.0	15.0	207.0	98.0	63.0
(*1*)	0	0	0	—	—	0	0	0	0	0	0	0	0	0	0	0
	28	31	5.0	—	—	1	4.5	3	56	15	38	31	15	207	98	63
6	27.8	29.3	3.89	3.2	1.8	2.0	3.08	.5	48.3	16.8	35.8	26.3	14.6	182.1	93.5	51.0
(*32*)	.45	.40	.122	.52	.11	.15	.106	.11	.49	.35	.23	.33	.53	1.96	1.26	.87
	24–35	24–34	3.0–5.0	2–4	0–3	0–4	1.0–4.0	0–2	43–55	15–23	34–39	23–30	9–23	166–217	83–112	42–62
7	28.0	29.0	4.83	3.3	2.0	2.0	3.50	.3	51.0	16.7	35.3	25.3	13.3	206.3	107.0	57.0
(*4*)	1.53	1.00	.167	.58	0	0	.289	.25	1.78	.33	.88	.67	.88	5.36	5.51	5.57
	26–31	27–30	4.5–5.0	3–4	2	2	3.0–4.0	0–1	48–55	17–18	34–37	24–26	12–15	196–214	96–113	46–64
8	26.2	27.8	4.08	3.5	2.5	2.2	3.08	1.0	45.5	18.0	36.0	27.7	14.2	191.3	97.8	53.8
(*6*)	.40	1.14	.201	.55	.22	.31	.201	0	1.09	1.83	.37	.56	.98	2.91	2.12	3.28
	25–27	25–31	3.5–5.0	3–4	2–3	1–3	2.5–4.0	1	43–50	15–27	35–37	26–30	11–18	180–199	91–104	42–64
9	26.0	36.0	4.00	3.0	2.0	2.0	2.50	0	42.0	27.0	37.0	24.0	14.0	191.0	89.0	56.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	26	36	4.0	3	2	2	2.5	0	42	27	37	24	14	191	89	56
10	26.1	33.7	4.64	3.1	1.9	1.6	1.71	.6	44.0	24.9	34.8	25.5	17.7	180.1	91.0	52.2
(*22*)	.31	.44	.082	.47	.06	.15	.146	.11	.42	1.47	.24	.14	.52	1.33	1.25	1.18
	24–30	31–38	4.0–5.0	2–4	1–2	0–2	1.0–3.0	0–1	41–49	15–39	33–37	24–27	13–23	165–188	78–99	40–66
11	25.2	34.2	4.25	4.0	2.2	2.2	3.25	1.1	47.8	19.0	36.6	25.7	18.8	184.6	95.5	61.4
(*10*)	.55	.51	.112	.67	.20	.13	.186	.18	.83	1.09	.16	.45	.57	2.57	1.86	1.63
	23–28	32–36	3.5–4.5	3–5	1–3	2–3	2.5–4.0	0–2	45–54	15–25	36–37	23–28	16–21	167–192	88–104	56–73
12	31.0	35.0	5.00	4.0	2.0	3.0	4.00	0	47.0	17.0	36.0	28.0	18.0	205.0	103.0	53.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	31	35	5.0	4	2	3	4.0	0	47	17	36	28	18	205	103	53
13	32.7	29.3	5.67	5.0	3.0	.7	4.67	.3	62.0	16.0	36.3	25.3	12.3	243.3	126.7	70.3
(*3*)	1.45	1.20	.167	0	0	.67	.333	.33	3.21	.58	.33	.88	1.20	4.41	7.26	4.81
	30–35	27–31	5.5–6.0	5	3	0–2	4.0–5.0	0–1	57–68	15–17	36–37	24–27	10–14	235–250	115–140	61–77
14	32.6	30.6	6.27	4.7	2.5	1.2	4.68	.4	62.4	16.2	35.9	26.5	13.9	244.2	122.5	73.4
(*11*)	.62	.59	.124	.47	.16	.25	.122	.16	.88	.23	.21	.43	.64	1.50	2.14	2.00
	29–36	28–35	6.0–7.0	4–5	2–3	0–2	4.0–5.0	0–1	58–68	15–17	35–37	24–29	11–17	235–251	112–134	65–85
15	29.5	29.2	4.92	3.7	1.8	1.8	5.00	.5	56.8	15.8	36.3	26.0	13.2	237.5	128.0	62.5
(*6*)	.56	.40	.239	.52	.17	.17	0	.34	.70	.31	.21	.45	.65	2.43	2.36	2.14
	28–31	28–31	4.0–5.5	3–4	1–2	1–2	5.0	0–2	55–60	15–17	36–37	25–28	11–15	231–245	119–135	52–66
16	29.8	30.2	4.80	4.0	2.2	2.0	4.90	.8	58.6	15.6	36.0	27.0	16.8	239.4	120.4	60.8
(*5*)	.80	.49	.123	0	.20	0	.100	.20	.81	.40	.32	.71	.66	1.40	2.42	2.43
	28–32	29–31	4.5–5.0	4	2–3	2	4.5–5.0	0–1	56–61	15–17	35–37	25–29	15–19	236–244	112–127	56–70
17	19.0	22.5	5.00	3.5	2.0	2.0	4.00	0	67.0	17.0	37.5	25.0	6.0	228.5	113.0	54.0
(*2*)	1.00	1.50	0	.71	0	0	0	0	4.00	0	.50	0	0	4.50	1.00	1.00
	18–20	21–24	5.0	3–4	2	2	4.0	0	63–71	17	37–38	25	6	224–233	112–114	53–55
18	19.0	21.3	4.67	3.0	1.7	2.0	4.00	0	61.0	15.7	35.3	24.7	7.3	239.3	118.3	60.7
(*3*)	1.15	.67	.441	0	.33	0	0	0	.58	.67	.33	.33	.88	1.33	1.86	4.63
	17–21	20–22	4.0–5.5	3	1–2	2	4.0	0	60–62	15–17	35–36	24–25	6–9	238–242	116–122	53–69
19	19.5	24.0	5.00	4.0	2.0	2.0	4.50	—	66.0	17.0	36.5	24.0	8.5	—	—	—
(*2*)	.50	0	0	0	0	0	.500	—	1.00	1.00	.50	0	.50	—	—	—
	19–20	24	5.0	4	2	2	4.0–5.0	—	65–67	16–18	36–37	24	8–9	—	—	—
20	19.5	21.5	3.00	3.0	2.0	2.5	4.00	0	60.0	15.5	35.5	22.0	4.5	216.5	101.0	53.5
(*2*)	1.50	1.50	0	0	0	.50	0	0	1.00	.50	.50	0	1.50	3.50	1.00	4.50
	18–21	20–23	3.0	3	2	2–3	4.0	0	59–61	15–16	35–36	22	3–6	213–220	100–102	49–58
21	33.5	46.5	4.02	2.2	2.0	3.8	2.54	.5	36.4	11.3	34.3	26.3	11.1	133.5	64.2	51.2
(*20*)	.28	.54	.057	.38	0	.24	.098	.11	.41	.73	.19	.32	.46	1.09	.69	1.08
	32–37	43–50	3.5–5.0	2–3	2	2–6	2.0–3.0	0–1	33–39	6–18	33–36	25–30	7–16	126–142	59–68	44–58

Table 1. Continued.

POP	PVS	PVT1	PVT2	PVT3	RPOL	RPAW	RPFML	RPFL1	RMW	RNL	RML	RAPPSL	RPNH	RSLH
1	13.9	30.0	20.2	15.7	.229	.603	.459	.382	.117	.136	.100	0	.704	1.079
(*15*)	.98	.55	.81	.21	.0249	.0311	.0409	.0475	.0514	.0086	.0491	0	.0118	.0476
	7–20	26–34	15–28	15–17	.15–.56	.39–.82	.11–.70	.11–.65	0–.56	.09–.20	0–.63	0	.65–.81	.91–1.61
2	15.0	28.0	17.0	16.0	.247	.788	.456	.456	0	.121	0	0	.754	.890
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	15	28	17	16	.25	.79	.46	.46	0	.12	0	0	.75	.89
3	–	–	–	–	.124	–	.401	.351	0	.309	0	0	.723	1.245
(*1*)	–	–	–	–	0	–	0	0	0	0	0	0	0	0
	–	–	–	–	.12	–	.40	.35	0	.31	0	0	.72	1.25
4	15.0	32.0	26.5	16.3	.181	.706	.485	.485	0	.238	0	.221	.907	1.099
(*4*)	1.47	1.08	.87	.48	.0184	.0289	.0321	.0321	0	.0151	0	.2214	.1605	.0560
	12–19	29–34	24–28	15–17	.14–.23	.64–.77	.42–.54	.42–.54	0	.22–.28	0	0–.89	.73–1.39	.98–1.21
5	43.0	20.0	15.0	14.0	.241	.400	–	–	0	.072	–	0	.742	1.156
(*1*)	0	0	0	0	0	0	–	–	0	0	–	0	0	0
	43	20	15	14	.24	.40	–	–	0	.07	–	0	.74	1.16
6	22.1	28.9	21.4	12.0	.181	.539	.564	.357	.272	.171	.375	.007	.781	1.172
(*32*)	1.25	.72	.84	.59	.0075	.0132	.0222	.0362	.0612	.0082	.0865	.0042	.0236	.0218
	12–37	20–35	15–34	4–18	.11–.27	.41–.69	.38–.84	0–.71	0–.84	.11–.29	0–1.26	0–.11	.66–1.40	.86–1.41
7	26.3	30.7	21.3	15.3	.158	.593	.623	.522	0	.133	0	0	.783	1.279
(*4*)	6.23	.67	2.85	.33	.0006	.0382	.0177	.0203	0	.0318	0	0	.0121	.0246
	14–34	30–32	18–27	15–16	.16	.53–.66	.60–.66	.48–.54	0	.08–.19	0	0	.76–.80	1.23–1.32
8	27.5	26.3	19.3	14.0	.181	.545	.513	.344	.213	.164	.319	.46	.727	1.113
(*6*)	4.43	1.65	2.01	1.03	.0145	.0354	.0504	.0800	.1265	.0130	.2134	.3021	.0282	.0359
	12–38	19–30	16–29	9–16	.13–.23	.40–.66	.36–.68	0–.52	0–.77	.13–.22	0–1.32	0–1.65	.64–.81	1.01–1.23
9	24.0	32.0	27.0	0	.154	.300	.754	.422	.623	.132	.682	0	.787	1.253
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	24	32	27	0	.15	.30	.75	.42	.62	.13	.68	0	.79	1.25
10	21.0	31.2	24.0	2.5	.188	.497	.540	.455	.141	.167	.109	.017	.856	1.180
(*22*)	1.67	.94	1.02	.73	.0140	.0190	.0218	.0259	.0585	.0110	.0483	.0173	.0283	.0338
	7–42	22–37	17–33	0–13	.07–.32	.31–.68	.35–.82	.14–.65	0–.95	.09–.27	0–.85	0–.38	.71–1.37	.95–1.55
11	31.5	29.9	19.1	2.9	.176	.589	.475	.480	.045	.172	.022	.140	.803	1.141
(*10*)	1.89	1.04	.99	.75	.0119	.0364	.0322	.0433	.0284	.0160	.0137	.1102	.0209	.0369
	21–40	26–35	16–25	0–6	.10–.22	.39–.75	.27–.69	.27–.81	0–.28	.12–.28	0–.13	0–1.12	.71–.91	.84–1.25
12	20.0	33.0	22.0	9.0	.200	.466	1.071	.283	.729	.106	.739	0	.750	1.141
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	20	33	22	9	.20	.47	1.07	.28	.73	.11	.74	0	.75	1.14
13	42.0	28.3	23.3	15.0	.146	.498	.562	.611	0	.188	0	0	.744	1.168
(*3*)	5.13	2.85	3.84	1.15	.0042	.1159	.0405	.0654	0	.0051	0	0	.0342	.1171
	35–52	25–34	19–31	13–17	.14–.15	.27–.63	.49–.63	.49–.71	0	.18–.19	0	0	.70–.81	.94–1.32
14	42.6	30.7	23.5	15.6	.168	.570	.579	.579	0	.129	0	0	.745	1.176
(*11*)	2.38	.76	1.26	.34	.0062	.0313	.0321	.0321	0	.0027	0	0	.0276	.0701
	32–56	26–34	17–29	14–18	.14–.20	.35–.74	.46–.76	.46–.76	0	.11–.15	0	0	.66–.95	.95–1.76
15	26.7	35.8	30.3	17.7	.140	.728	.528	.528	0	.181	0	0	.754	1.111
(*6*)	2.20	1.22	1.23	.67	.0085	.0584	.0198	.0198	0	.0129	0	0	.0184	.0427
	17–32	33–40	26–35	16–20	.12–.18	.46–.85	.48–.62	.48–.62	0	.14–.22	0	0	.70–.83	.96–1.21
16	29.8	31.0	28.2	16.2	.189	.500	.544	.544	0	.129	0	0	.743	1.114
(*5*)	2.63	.45	.80	.58	.0177	.0185	.0468	.0468	0	.0123	0	0	.0236	.0259
	25–40	30–32	26–30	15–18	.14–.24	.44–.54	.42–.68	.42–.68	0	.10–.15	0	0	.69–.81	1.02–1.17
17	26.5	27.5	31.5	19.5	.151	.537	.670	.670	0	.136	0	0	.677	.954
(*2*)	5.50	4.50	1.50	1.50	.0217	.0020	.0049	.0049	0	.0232	0	0	.0636	.0087
	21–32	23–32	30–33	18–21	.13–.17	.54	.67	.67	0	.11–.16	0	0	.61–.74	.95–.96
18	30.3	30.3	30.3	20.7	.181	.566	.747	.747	0	.156	0	.037	.775	.819
(*3*)	4.91	.33	.33	1.45	.0206	.0496	.0247	.0247	0	.0102	0	.0370	.0039	.0343
	22–39	30–31	30–31	18–23	.15–.22	.55–.66	.70–.77	.70–.78	0	.14–.18	0	0–.11	.77–.78	.76–.88
19	–	–	–	–	.178	–	–	–	–	–	–	–	–	–
(*2*)	–	–	–	–	.0018	–	–	–	–	–	–	–	–	–
	–	–	–	–	.18	–	–	–	–	–	–	–	–	–
20	22.0	31.5	30.0	16.0	.145	.629	.709	.709	0	.090	0	0	.776	.805
(*2*)	4.00	.50	0	0	.0251	.0592	.0443	.0443	0	.0059	0	0	.0281	.0216
	18–26	31–32	30	16	.12–.17	.57–.69	.67–.75	.67–.75	0	.08–.10	0	0	.75–.81	.78–.83
21	36.5	14.6	3.9	0	.208	.407	.491	.405	.094	.199	.137	.052	.744	.745
(*20*)	1.97	1.05	.74	0	.0056	.0168	.0264	.0367	.0400	.0076	.0587	.0323	.0087	.0155
	22–50	8–22	0–11	0	.15–.26	.27–.54	.28–.71	0–.63	0–.62	.15–.26	0–.84	0–.59	.68–.80	.59–.86

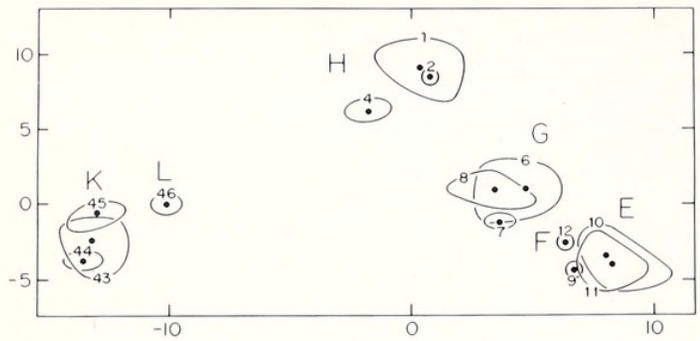

Figure 4. Fourteen samples of *Lepidophyma* of two southern (K and L) and four northern (E–H) population groups plotted on the first two canonical variables for 30 characters. Dots are centroids; sample numbers are along lines enclosing all included specimens.

4TLD, LTR, PVS, PVR, and RMW; the second explains 16 percent of the variation and is most weighted with PVS, PVR, PVT1, FPT, and PVT2. Southern groups K and L are strongly separated from H, their nearest discriminant neighbor among northern groups. However, one population of group H (4) is separated from the other two populations of the group in the direction of group L. The relationships of population 4 are discussed further on p. 7.

The 17 populations of group J were analyzed together with northern groups E through H (Fig. 5). The accuracy of the posterior classification was 98 percent (128/131), two specimens of sample 11 being misclassified as 10 (both group E). The first variable accounts for 42 percent of the total dispersion and is influenced most by PVS, PVR, PVT1, FPT, and LTR; the second expresses 26 percent and has heavy loadings for PVS, PVT1, PVR, LTR, and DAPVR. The five groups are separated from one another, although one population of group J (27) is separated from the remainder of the group and is placed intermediate between J and E and F, and two individuals of sample 37 (group J) approach group G.

GROUP ANALYSES

The multivariate relationships of the 46 populations described above are here considered in respect to univariate similarities or differences between population groups (Table 2) and to geographic distributions (Fig. 6) in order to arrive at the definition of morphologically diagnosable units of *Lepidophyma* occurring in northern Mexico. It is anticipated that the resultant units should consist of groups of populations that are overlapping or juxtaposed in discriminant space, that can be diagnosed by one or more univariate characters, that are not linked to other groups by univariately, multivariately, and geographically intermediate populations, and that thus represent morphospecies. For a genus such as *Lepidophyma,* in which sympatry is rare, discordant variation common, and populations often disjunct and represented by small sample sizes, such morphologically defined units are initial species hypotheses to be tested by securing additional samples and information (e.g., allozyme data).

Groups E, F, and G are positioned nearest each other in the four discriminant analyses (Figs. 2–5) and they overlap

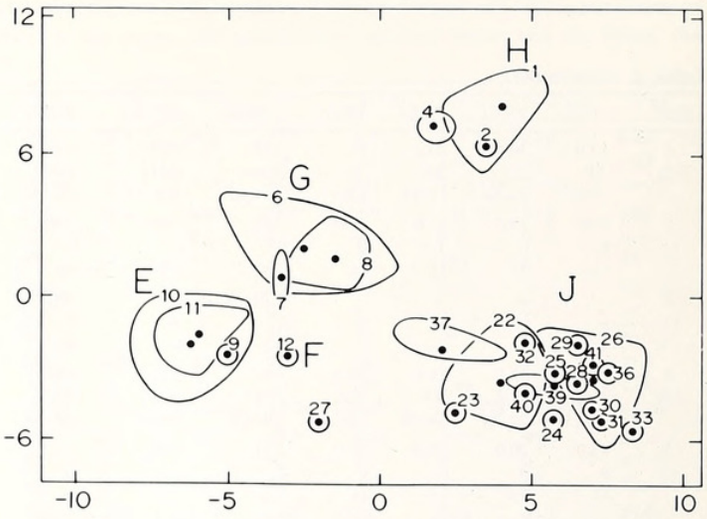

Figure 5. Twenty-seven samples of *Lepidophyma* of one southern (J) and four northern (E–H) population groups plotted on the first two canonical variables for 30 characters. Presentation as in Fig. 4.

in all individual characters (Table 2). The three appear to represent a single species unit EFG distributed along the Sierra Madre Oriental from southern Tamaulipas to Veracruz (Fig. 6).

The nearest geographic and discriminant neighbor of group H among northern populations is group G (Figs. 2 and 6), from which it differs (=no overlap in range of variation) in LTR (Table 2). The decision as to whether H should be considered specifically distinct from EFG is complicated by

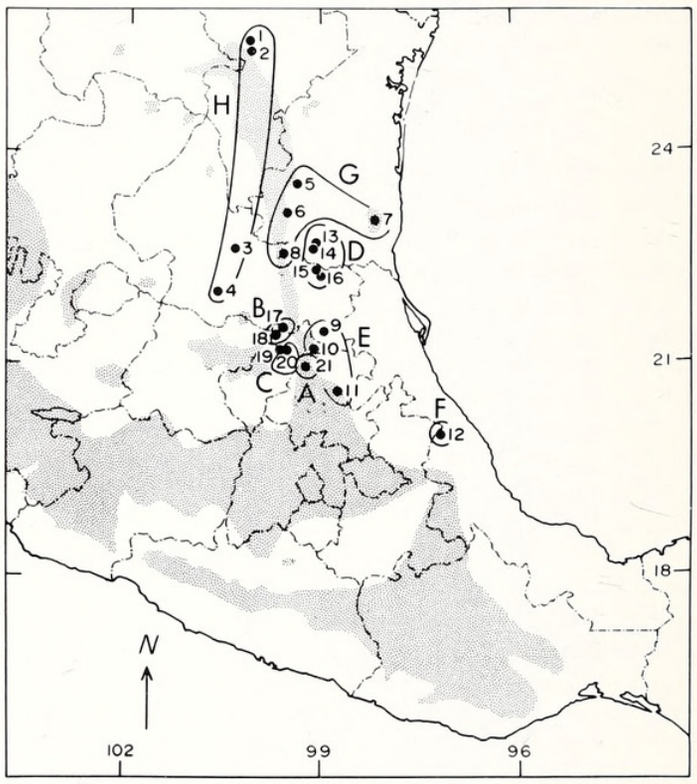

Figure 6. Distribution of eight population groups of *Lepidophyma* in northeastern Mexico. Lines enclose the samples (numbers) included in the groups (letters).

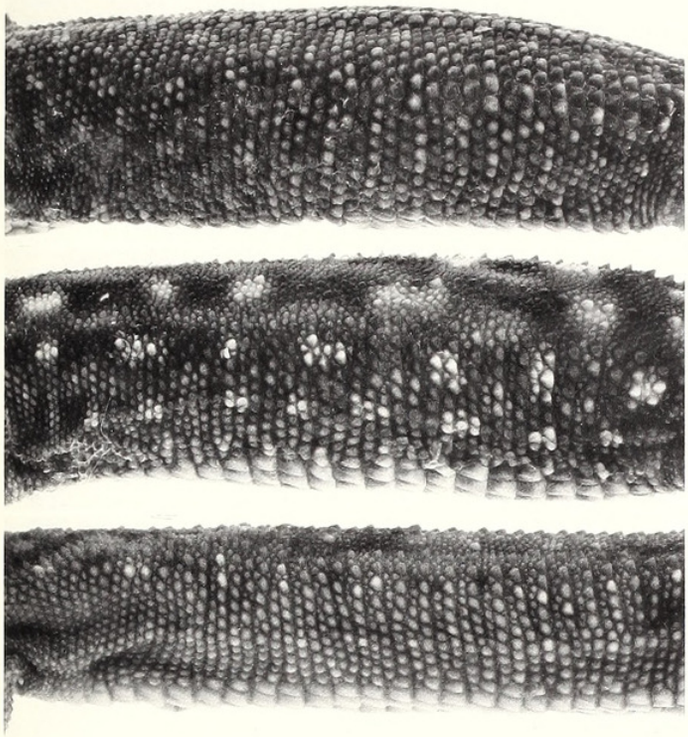

Figure 7. Lateral body surface of specimens of *Lepidophyma* of groups A (*upper*, sample 21, AMNH 13879) and E (*middle*, sample 11, LACM 106742; and *lower*, sample 10, LACM 109771).

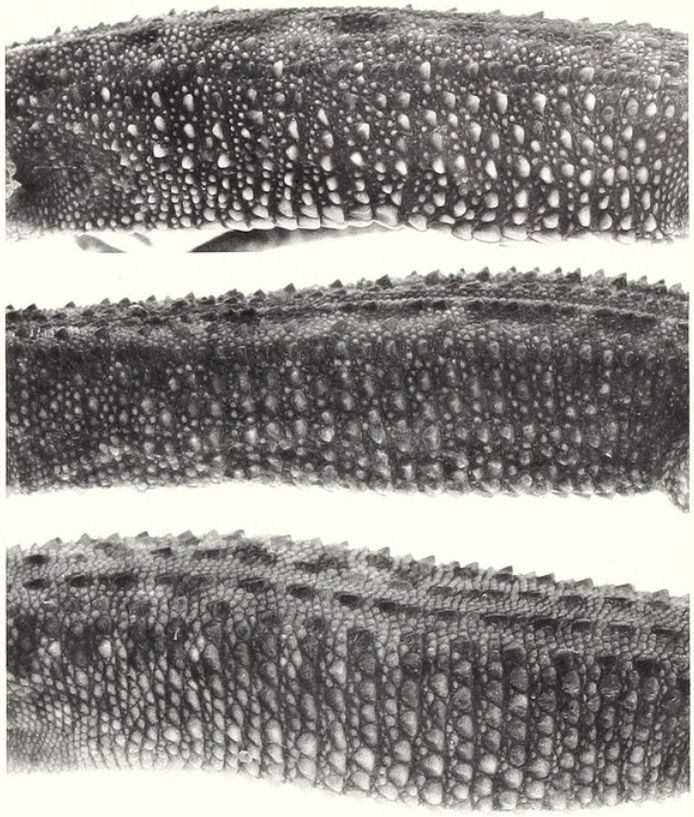

Figure 8. Lateral body surface of specimens of *Lepidophyma* of groups G (*upper*, sample 6, UMMZ 102980; *middle*, sample 8, LACM 131145) and H (*lower*, sample 2, EAL 4644).

the presence of intermediate states, observed in the lateral tubercle rows, that are not expressed in the LTR counts. In some specimens, the low number of lateral tubercle rows that characterizes group H results from a slight reduction of some of the rows in terms of the distance they extend above the ventrals and the relative size of the tubercles which compose them (Figs. 7–8). While uniform criteria were employed throughout the study to determine which rows to include in the counts, for some of the specimens in groups G and H the decision was difficult and repeatability of the counts was low. The difference in LTR between H and EFG is thus less discrete than suggested by the counts and is bridged by intermediate morphological states. While additional specimens and information (e.g., allozyme data) are needed to fully evaluate this situation, it seems best not to place emphasis on the differences in LTR number, and to recognize a single species unit composed of groups E, F, G, and H.

In one of the analyses, population 4 is slightly separated from the other two populations of group H (1, 2) in the direction of southern group L from coastal Michoacán (Fig. 4). For a number of characters (e.g., LTR, IWD1, GUL, 4TL, and 4TLD), the mean for population 4 is intermediate between L and the Nuevo León populations (1, 2) (Tables 1 and 2). Nevertheless, population 4 differs from L in four characters (FPT, PTMP, 4TLD, DOR), and from the Nuevo León populations (1, 2) in one (FPT). Evaluation of these differences is hampered by the small sample sizes of population 4 (N = 4) and group L (N = 3). To estimate the range of variation of 4 and L that would be expected with larger sample sizes, three standard deviations of population 1 (N = 15) were added to and subtracted from the means of each of the characters to encompass 99.7 percent of the population (Simpson, Roe, and Lewontin, 1960:139). The estimated range of population 4 overlaps the observed range of population 1 in all characters, but is separated from the estimated range of group L in FPT (23–31 vs. 13–21) and PTMP (1.5–3.0 vs. 3.2–4.8). While additional material is necessary to fully evaluate the relationships of population 4, the information at hand suggests that it should be considered a member of group EFGH. Further collecting along the western flank of the Sierra Madre Oriental seems likely to produce material linking the Sierra Alvarez population (4) geographically and morphologically with the Nuevo León populations (1, 2) (Fig. 6).

Two populations of southern group J (27, 37) approach EFGH in discriminant space (Fig. 5). The two groups differ

Table 2. Variation among 30 scale characters for eight population groups of *Lepidophyma* in northern Mexico. Presentation as in Table 1.

Group	FPT	LTR	DBPVR	IWD1	IWV1	PTMP	DBPVT	GC1IL	GUL	PVTL	VL	4TL	4TLD	DOR	DAPVR	PVR
A	33.5	46.5	4.03	2.2	2.0	3.8	2.54	.5	36.4	11.3	34.3	26.3	11.1	133.5	64.2	51.2
(*20*)	.28	.54	.057	.09	0	.24	.098	.11	.41	.73	.19	.32	.46	1.09	.69	1.08
	32–37	43–50	3.5–5.0	2–3	2	2–6	2.0–3.0	0–1	33–39	6–18	33–36	25–30	7–16	126–142	59–68	44–58
B	19.0	21.8	4.80	3.2	1.8	2.0	4.00	0	63.4	16.2	36.2	24.8	7.0	235.0	116.2	58.0
(*5*)	.71	.66	.255	.20	.20	0	0	0	1.96	.49	.58	.25	.71	3.10	1.69	3.03
	17–21	20–24	4.0–5.5	3–4	1–2	2	4.0	0	60–71	15–17	35–38	24–25	6–9	224–242	112–122	53–69
C	19.5	21.5	3.00	3.0	2.0	2.5	4.00	0	60.0	15.5	35.5	22.0	4.5	216.5	101.0	53.5
(*2*)	1.50	1.50	0	0	0	.50	0	0	1.00	.50	.50	0	1.50	3.50	1.00	4.50
	18–21	20–23	3.0	3	2	2–3	4.0	0	59–61	15–16	35–36	22	3–6	213–220	100–102	49–58
D	31.3	30.0	5.58	4.4	2.3	1.5	4.80	.5	60.2	16.0	36.1	26.4	14.1	241.5	123.9	67.9
(*25*)	.47	.33	.157	.13	.11	.16	.071	.12	.73	.16	.13	.28	.46	1.15	1.48	1.64
	28–36	27–35	4.0–7.0	3–5	1–3	0–2	4.0–5.0	0–2	55–68	15–17	35–37	24–29	10–19	231–251	112–140	52–85
E	25.8	33.9	4.50	3.4	2.0	1.8	2.20	.7	45.1	23.1	35.4	25.5	17.9	181.8	92.4	55.1
(*33*)	.27	.33	.072	.11	.07	.12	.167	.10	.49	1.13	.23	.17	.41	1.24	1.06	1.18
	23–30	31–38	3.5–5.0	2–5	1–3	0–3	1.0–4.0	0–2	41–54	15–39	33–37	23–28	13–23	165–192	78–104	40–73
F	31.0	35.0	5.00	4.0	2.0	3.0	4.00	0	47.0	17.0	36.0	28.0	18.0	205.0	103.0	53.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	31	35	5.0	4	2	3	4.0	0	47	17	36	28	18	205	103	53
G	27.6	29.1	4.01	3.0	1.9	2.0	3.15	.6	48.3	17.0	35.9	26.5	14.5	185.7	95.2	52.1
(*43*)	.37	.36	.107	.08	0	.12	.093	.11	.50	.37	.19	.30	.43	1.95	1.19	.94
	24–35	24–34	3.0–5.0	2–4	0–3	0–4	1.0–4.5	0–3	43–56	15–27	34–39	23–31	9–23	166–217	83–113	42–64
H	30.4	17.9	3.18	2.9	2.0	2.2	2.85	.3	45.1	16.0	35.9	24.9	7.7	163.6	85.5	45.2
(*20*)	.49	.45	.083	.06	.10	.08	.064	.11	.46	.18	.15	.33	.45	1.84	1.00	.89
	26–34	15–22	2.5–4.0	2–3	1–3	2–3	2.5–3.5	0–1	42–49	15–17	35–38	22–29	4–12	150–178	77–94	39–53

Table 3. Variation among 30 scale characters for nine species of *Lepidophyma* from Mexico. Presentation as in Table 1.

Species	FPT	LTR	DBPVR	IWD1	IWV1	PTMP	DBPVT	GC1IL	GUL	PVTL	VL	4TL	4TLD	DOR	DAPVR	PVR
gaigeae	33.5	46.5	4.03	2.2	2.0	3.8	2.54	.5	36.4	11.3	34.3	26.3	11.1	133.5	64.2	51.2
(*20*)	.28	.54	.057	.09	0	.24	.098	.11	.41	.73	.19	.32	.46	1.09	.69	1.08
	32–37	43–50	3.5–4.0	2–3	2	2–6	2.0–3.0	0–1	33–39	6–18	33–36	25–30	7–16	126–142	59–68	44–58
occulor	19.2	22.2	4.44	3.3	1.9	2.1	4.11	0	63.2	16.2	36.1	23.9	6.8	229.7	111.9	56.7
(*9*)	.46	.55	.306	.17	.11	.11	.111	0	1.28	.36	.35	.44	.70	4.09	3.04	2.46
	17–21	20–24	3.0–5.5	3–4	1–2	2–3	4.0–5.0	0	59–71	15–18	35–38	22–25	3–9	213–242	100–122	49–69
micropholis	31.3	30.0	5.58	4.4	2.3	1.5	4.80	.5	60.2	16.0	36.1	26.4	14.1	241.5	123.9	67.9
(*25*)	.47	.33	.157	.13	.11	.16	.071	.12	.73	.16	.13	.28	.46	1.15	1.48	1.64
	28–36	27–35	4.0–7.0	3–5	1–3	0–2	4.0–5.0	0–2	55–68	15–17	35–37	24–29	10–19	231–251	112–140	52–85
sylvaticum	27.6	28.5	4.01	3.2	2.0	2.0	2.78	.6	46.6	18.9	35.7	25.8	14.2	180.0	92.3	51.7
(*98*)	.27	.64	.074	.06	.05	.07	.083	.06	.33	.52	.12	.18	.46	1.36	.77	.70
	23–35	15–38	2.5–5.0	2–5	0–3	0–4	1.0–4.5	0–3	41–56	15–39	33–39	20–31	4–23	150–217	77–113	39–73
tuxtlae	24.6	34.1	4.09	3.7	2.3	5.5	.29	1.6	42.6	39.3	39.6	25.8	16.3	172.0	79.6	45.0
(*81*)	.22	.20	.053	.06	.06	.11	.032	.09	.28	.43	.14	.16	.22	.97	.70	.43
	20–29	30–40	3.0–5.0	3–5	0–3	4–9	0–.9	0–4	37–49	30–47	37–42	23–28	13–20	150–190	69–98	37–55
pajapanensis	33.3	40.5	4.21	3.4	1.8	7.5	.14	.1	38.9	43.8	36.6	28.3	13.8	164.3	69.6	44.0
(*19*)	.35	.40	.088	.12	.10	.31	.037	.07	.53	1.02	.17	.24	.50	1.59	1.22	.84
	30–36	37–43	4.0–5.0	3–4	1–2	6–10	0–.5	0–1	35–43	39–51	35–38	26–30	10–17	152–175	59–82	37–49
flavimaculatum	33.7	28.5	4.45	3.8	2.1	6.8	2.99	.9	47.3	18.6	36.6	27.3	14.7	197.7	90.1	54.3
(*49*)	.56	.26	.084	.08	.05	.20	.119	.09	.41	.41	.13	.25	.34	1.64	1.17	1.00
	27–41	25–32	3.0–5.5	3–5	1–3	4–11	.5–4.0	0–2	40–55	15–27	34–38	23–31	10–22	173–221	75–118	43–69
smithii	23.1	17.5	4.21	3.0	2.1	2.7	3.18	.7	52.4	16.8	35.8	25.2	5.3	194.0	94.2	48.7
(*36*)	.56	.16	.102	.05	.08	.14	.067	.13	.39	.36	.18	.24	.33	1.43	1.15	.73
	18–29	15–19	3.0–5.5	2–4	1–3	2–4	2.0–4.0	0–3	46–57	14–25	33–38	22–28	2–9	178–214	81–110	37–61
tarascae	17.0	16.7	2.67	2.7	2.0	4.0	2.50	.7	42.3	16.0	34.3	22.7	1.7	146.7	75.0	44.3
(*3*)	.58	.33	.333	.33	0	0	0	.33	.67	0	.33	.33	.33	1.67	1.00	1.20
	16–18	16–17	2.0–3.0	2–3	2	4	2.5	0–1	41–43	16	34–35	22–23	1–2	145–150	74–77	42–46

Table 2. Continued.

Group	PVS	PVT1	PVT2	PVT3	RPOL	RPAW	RPFML	RPFL1	RMW	RNL	RML	RAPPSL	RPNH	RSLH
A	36.5	14.6	3.9	0	.208	.407	.491	.405	.094	.199	.127	.052	.744	.745
(*20*)	1.97	1.05	.74	0	.0056	.0168	.0264	.0367	.0400	.0076	.0587	.0323	.0087	.0155
	22–50	8–22	0–11	0	.15–.26	.27–.54	.28–.71	0–.63	0–.62	.15–.26	0–.84	0–.59	.68–.80	.59–.86
B	28.8	29.2	30.8	20.2	.169	.555	.716	.716	0	.148	0	.022	.736	.873
(*5*)	3.34	1.59	.58	.97	.0151	.0281	.0233	.0233	0	.0104	0	.0222	.0314	.0381
	21–39	23–32	30–33	18–23	.13–.22	.50–.66	.67–.78	.67–.78	0	.11–.18	0	0–.11	.61–.78	.76–.96
C	22.0	31.5	30.0	16.0	.145	.629	.709	.709	0	.090	0	0	.776	.805
(*2*)	4.00	.50	0	0	.0251	.0838	.0443	.0443	0	.0059	0	0	.0281	.0216
	18–26	31–32	30	16	.12–.17	.57–.69	.67–.75	.67–.75	0	.08–.10	0	0	.75–.81	.78–.83
D	36.2	31.7	26.0	16.2	.163	.585	.557	.563	0	.147	0	0	.747	1.146
(*25*)	1.99	.72	.96	.32	.0060	.0592	.0175	.0187	0	.0067	0	0	.0133	.0334
	17–56	25–40	17–35	13–20	.12–.24	.27–.85	.42–.76	.42–.76	0	.10–.22	0	0	.66–.95	.94–1.76
E	24.3	30.8	22.6	2.5	.183	.519	.527	.462	.127	.167	.100	.054	.838	1.170
(*33*)	1.50	.70	.84	.53	.0100	.0283	.0193	.0214	.0432	.0088	.0376	.0356	.0202	.0252
	7–42	22–37	16–33	0–13	.07–.32	.30–.75	.27–.82	.19–.81	0–.94	.09–.28	0–.85	0–1.12	.71–1.37	.84–1.55
F	20.0	33.0	22.0	9	.200	.466	1.071	.283	.729	.106	.739	0	.750	1.141
(*1*)	0	0	0	0	0	.0193	0	0	0	0	0	0	0	0
	20	33	22	9.0	.20	.46	1.07	.28	.73	.11	.74	0	.75	1.14
G	23.7	28.4	2.09	12.6	.180	.540	.560	.368	.237	.165	.338	.072	.772	1.171
(*43*)	1.30	.65	.73	.50	.0062	0	.0190	.0309	.0508	.0073	.0746	.0473	.0185	.0181
	12–43	19–35	15–34	4–18	.11–.27	.40–.69	.36–.81	0–.71	0–.84	.07–.29	0–1.32	0–1.65	.64–1.40	.86–1.41
H	14.2	30.3	21.3	15.9	.220	.633	.464	.406	.088	.156	.074	.044	.749	1.073
(*20*)	.78	.50	.87	.18	.0194	.0120	.0311	.0370	.0399	.0121	.0373	.0443	.0368	.0377
	7–20	26–34	15–28	15–17	.14–.56	.39–.82	.11–.70	.11–.65	0–.56	.09–.28	0–.63	0–.89	.65–1.39	.89–1.61

Table 3. Continued.

Species	PVS	PVT1	PVT2	PVT3	RPOL	RPAW	RPFML	RPFL1	RMW	RNL	RML	RAPPSL	RPNH	RSLH
gaigeae	36.5	14.6	3.9	0	.208	.407	.491	.405	.094	.199	.127	.052	.744	.745
(*20*)	1.97	1.05	.74	0	.0056	.0168	.0264	.0367	.0400	.0076	.0587	.0323	.0087	.0155
	22–50	8–22	0–11	0	.15–.26	.27–.54	.28–.71	0–.63	0–1.49	.15–.26	0–.84	0–.59	.68–.80	.59–.86
occulor	26.9	29.9	30.6	19.0	.166	.576	.714	.714	0	.131	0	.016	.748	.854
(*9*)	2.76	1.18	.43	1.02	.0099	.0271	.0188	.0188	0	.0129	0	.0159	.0237	.0295
	18–39	23–32	30–33	16–23	.12–.22	.50–.69	.66–.78	.67–.77	0	.08–.18	0	0–.11	.61–.81	.76–.96
micropholis	36.2	31.7	26.0	16.2	.163	.585	.557	.563	0	.147	0	0	.747	1.146
(*25*)	1.99	.72	.95	.32	.0060	.0283	.0175	.0187	0	.0067	0	0	.0133	.0334
	17–56	25–40	17–35	13–20	.12–.24	.27–.85	.42–.76	.42–.76	0	.09–.22	0	0	.66–.95	.94–1.76
sylvaticum	21.9	29.7	21.0	9.8	.190	.551	.532	.408	.171	.165	.200	.059	.790	1.152
(*98*)	.88	.40	.47	.62	.0062	.0109	.0141	.0172	.0287	.0052	.0373	.0253	.0133	.0144
	7–43	19–37	15–34	0–18	.07–.56	.30–.82	.11–1.07	0–.81	0–.95	.07–.31	0–1.32	0–1.65	.64–1.40	.84–1.61
tuxtlae	5.1	39.9	32.2	1.7	.224	.830	.734	.042	1.024	.108	1.216	.027	.734	.547
(*81*)	.47	.37	.63	.33	.0047	.0128	.0092	.0126	.0243	.0049	.0539	.0159	.0054	.0106
	0–18	31–49	11–42	0–15	.11–.33	.59–1.12	.48–.89	0–.57	0–1.31	.04–.29	0–3.15	0–.99	.63–.83	.32–.77
pajapanensis	2.8	41.2	26.6	.1	.222	.540	.803	.157	1.087	.163	1.656	.002	.764	.485
(*19*)	.56	1.02	1.33	.06	.0081	.0189	.0131	.0246	.0264	.0113	.1192	.0015	.0116	.0349
	0–8	34–49	15–40	0–1	.13–.28	.38–.69	.70–.90	0–.31	.85–1.29	.10–.28	1.00–2.65	0–.03	.69–.86	.32–.88
flavimaculatum	20.1	34.2	25.3	13.7	.204	.411	.699	.175	.834	.145	.978	.061	.736	.557
(*49*)	1.17	.65	.71	.76	.0089	.0199	.0126	.0128	.0447	.0075	.0687	.0356	.0063	.0154
	6–44	24–43	17–35	1–24	.11–.39	.19–.69	.52–.88	0–.73	0–1.31	.07–.28	0–2.43	0–1.66	.58–.83	.36–.89
smithii	17.0	31.1	26.9	16.3	.181	.723	.713	.349	.608	.137	.783	.099	.794	.904
(*36*)	.75	.45	.60	.41	.0065	.0459	.0141	.0414	.0681	.0052	.1050	.0398	.0093	.0106
	8–29	25–39	18–32	13–27	.11–.28	.43–1.35	.54–.89	0–.79	0–1.07	.08–.24	0–2.62	0–1.04	.66–.92	.61–1.22
tarascae	13.7	30.7	25.0	16.0	.299	.591	.361	.361	0	.154	0	0	.982	.756
(*3*)	1.33	.33	1.53	0	.0717	.0923	.0664	.0664	0	.0130	0	0	.0227	.0417
	11–15	30–31	23–28	16	.19–.44	.41–.71	.29–.49	.29–.49	0	.14–.18	0	0	.94–1.02	.69–.83

in PTMP (0–3 in 95/97 EFGH and 4–11 in all J) and RSLH (0.84–1.60 in all EFGH and 0.36–0.79 in 49/50 J) (Table 2). The two specimens of EFGH with a PTMP of 4 are from a population (6) at the northern end of the range (Fig. 1), and the specimen of J with RSLH of 0.89 is from a population in Tabasco (37), that is separated from the southernmost sample (12) of EFGH by 350 km and by intervening populations that are clearly assigned to J. Thus the populations of EFGH and J that are most similar in morphology are not geographically intermediate, and the multivariate and univariate differences between the two population groups are sufficiently constant that they are judged to represent units that are likely reproductively isolated.

Group D is multivariately closest to G (Fig. 2). The four populations of D are from the Sierra del Abra of Tamaulipas and San Luis Potosí (Fig. 6), and differ in DOR from all populations of group EFGH including those in the Sierra Madre Oriental to the west and Sierra Tamaulipas to the east (Table 2). While two of the three specimens from the Sierra Tamaulipas (sample 7, group G) approach group D in discriminant space, they are not geographically intermediate (Fig. 6) and do not bridge the gap between the two in DOR (Table 2). It is concluded that group D should be considered specifically distinct from EFGH.

Groups B and C are closest to D in discriminant space, but differ in FPT (18–21 vs. 28–36) and LTR (20–24 vs. 27–35). Evaluation of these differences is hampered by small sample sizes of B (N = 4) and C (N = 2). As an estimate of the range of variation that would be expected with larger samples, three standard deviations of D were added to and subtracted from the means of B and C. The estimated ranges of B and C overlap each other for all characters but differ from the observed range of D for FPT (12–27 vs. 28–36) and LTR (17–26 vs. 27–35). The populations of B and C are located in the Jalpan Valley of Querétaro and San Luis Potosí (Fig. 6), and their combined ranges of variation differ in six characters from the populations of E occurring in the Sierra Madre Oriental, 22 km to the east. While larger sample sizes are necessary to fully evaluate the differences between groups B and C, their multivariate juxtaposition and the small univariate differences between them indicate they are probably members of the same species. On the other hand the number and magnitude of the univariate differences between BC and its nearest geographic (E) and discriminant (D) neighbors are such that they are not likely to be bridged by larger samples. Group BC is considered specifically distinct from D and EFGH.

Group A is strongly separated in discriminant space from the populations of all other groups (Figs. 2–3). It is morphologically and geographically closest to group E (Fig. 6), but differs in 6 of the 30 characters (Table 2). The univariate and multivariate differences between A and other population groups clearly qualify it as a distinct morphospecies.

While the combined problems of small sample sizes, disjunct distributions, and discordant variation confound some of the decisions, four unique morphological units of *Lepidophyma* are recognizable in northeastern Mexico: A, BC, D, and EFGH.

ALLOCATION OF NAMES

Several of the groups identified in the discriminant analyses include lizards that are either types or are from or near the type locality of named taxa: Group A: Population 21: *L. gaigeae* Mosauer, 1936; B: 20: *L. smithii occulor* Smith, 1942; D: 14: *L. micropholis* Walker, 1955; E: 11: *L. sylvaticum* Taylor, 1939; G: 6: *L. flavimaculatum tenebrarum* Walker, 1955; I: 51: *L. tuxtlae* Werler and Shannon, 1957, 41: *L. pajapanensis* Werler, 1957, 48: *L. sawini* Smith, 1973, 47: *L. alvarezi* Smith, 1973; J: 28: *L. flavimaculatum* A. Duméril *in* Duméril and Duméril, 1851; K: 44: *L. smithii* Bocourt, 1876; L: 46: *L. tarascae* Bezy, Webb, and Alvarez, 1982.

The oldest available names for the species units recognized in northern Mexico (Fig. 9) from the foregoing discussions are: A, *L. gaigeae*; BC, *L. occulor*; D, *L. micropholis*; and EFGH, *L. sylvaticum*. These are summarized below.

The systematic relationships among populations of *Lepidophyma* in southern Mexico currently are under study (Bezy, in prep.); the southern population groups used in this paper are considered to represent the following species: I = *L. pajapanensis* (Veracruz) and *L. tuxtlae* (Veracruz, Oaxaca, Chiapas); J = *L. flavimaculatum* (Atlantic versant east of the Isthmus of Tehuantepec in Oaxaca, Veracruz, Tabasco, Chiapas, Quintana Roo); K = *L. smithii* (Pacific versant of Guerrero, Oaxaca, Chiapas); and L = *L. tarascae* (coastal Michoacán).

SPECIES ACCOUNTS

Lepidophyma gaigeae Mosauer

Group A; Figures 7, 10

Lepidophyma gaigeae Mosauer, 1936:3. Holotype: MCZ 42145: Durango, State of Hidalgo, Mexico.
Gaigeia gaigeae: Smith, 1939:24.

DIAGNOSTIC CHARACTERS. Differs from other members of the genus except *L. radula* in having 43–50 subequal scales (rather than 15–42 discrete rows of enlarged tubercles) along the side of the body (axilla to groin) (Figs. 7–8) and fewer dorsal scales (126–142 vs. 145–251) (Table 3). It differs from *L. radula* and *L. dontomasi* in having two (rather than one) caudal interwhorls complete ventrally.

DISTRIBUTION. The species is known from Hidalgo (near the type locality) and Querétaro (between El Lobo and Jalpan; Dixon et al., 1972), where it occurs in limestone crevices primarily in pine-oak woodland (Fig. 9).

REMARKS. The high degree of separation of *L. gaigeae* from other populations in the discriminant analyses is consistent with its proposed separate generic (Smith, 1942) or subgeneric (Smith, 1973) status. Geographic variation and relationships of this form to *L. dontomasi* and *L. radula* are currently under study (Bezy, in prep.).

KARYOTYPE. *Lepidophyma gaigeae* has a diploid chromosome number of 38 with nine pairs of macrochromosomes and 10 pairs of microchromosomes. The karyotype is unique in the genus, but closest to those of *L. flavimaculatum*, *L. pajapanensis*, and *L. tuxtlae* (Bezy, 1972).

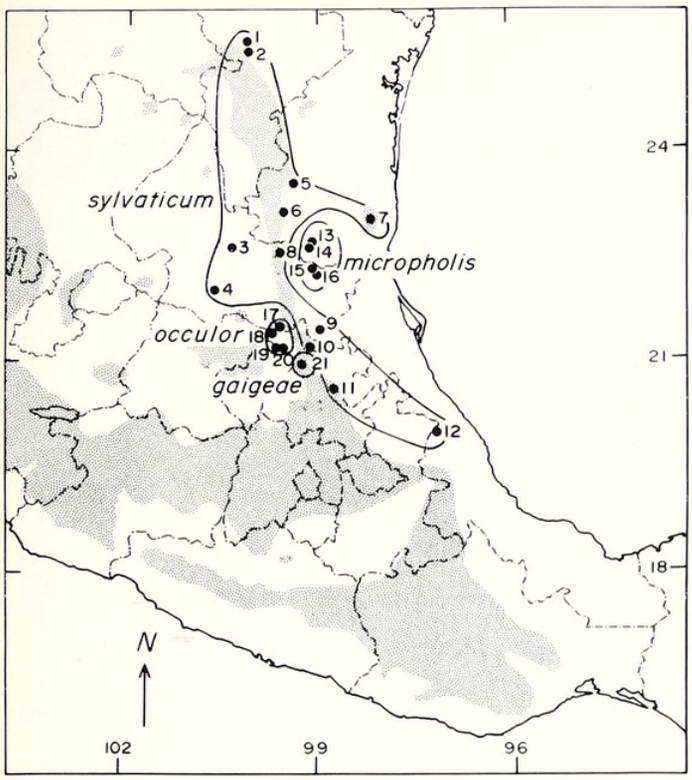

Figure 9. Distribution of the four species of *Lepidophyma* recognized in northeastern Mexico (north of 19°N). Lines enclose the samples included in each species.

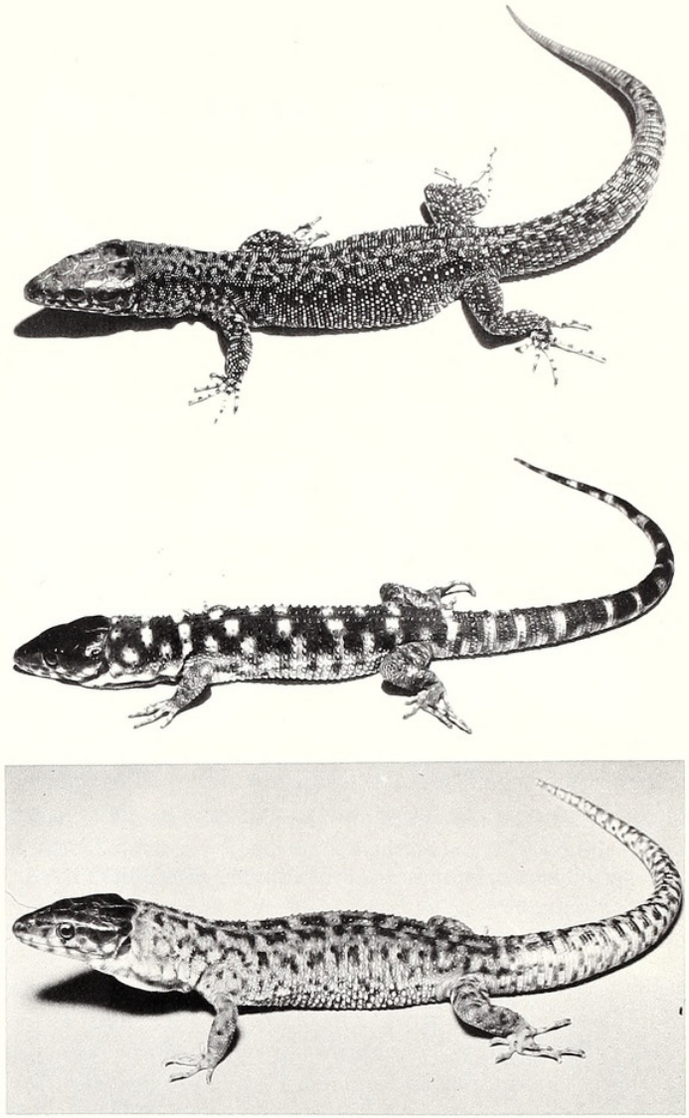

Figure 10. Living individuals of *Lepidophyma gaigeae* (*upper*, LACM 127170), *L. occulor* (*middle*, sample 18, TCWC 35605), and *L. micropholis* (*lower*, sample 16, TCWC 60767).

Lepidophyma occulor Smith

Group BC; Figure 10

Lepidophyma smithii occulor Smith, 1942:378. Holotype: USNM 47133: Jalpan, Querétaro.
Lepidophyma flavimaculatum occulor: Walker, 1955:5.
Lepidophyma occulor: Bezy, 1972:15.

DIAGNOSTIC CHARACTERS. Differs from all other species of *Lepidophyma* except *L. micropholis* in having more gulars (59–71 vs. 33–57), and from *L. micropholis* in having fewer femoral pores (17–21 vs. 28–36), fewer lateral tubercle rows (20–24 vs. 27–35), and fewer divided fourth toe lamellae (3–9 vs. 10–19) (Table 3).

DISTRIBUTION. *Lepidophyma occulor* is known from four localities in the Jalpan Valley of Querétaro and San Luis Potosí (Fig. 9), where it has been found beneath stones in arid tropical scrub (Dixon et al., 1972).

REMARKS. The species alternatively has been considered a subspecies of either *L. smithii* (Smith, 1942) or *L. flavimaculatum* (Walker, 1955) from both of which it is well separated multivariately (Fig. 3), differing from the former in lateral tubercle rows and gulars and from the latter in femoral pores, lateral tubercle rows, pretympanics, gulars, and divided fourth toe lamellae. It is multivariately closest to *L. micropholis* from which it differs in femoral pores, lateral tubercle rows, and divided fourth toe lamellae (Table 3).

KARYOTYPE. *Lepidophyma occulor* has a diploid chromosome number of 36, with the lowest number of microchromosomes (18) known in the family Xantusiidae (Bezy, 1972).

Lepidophyma micropholis Walker

Group D; Figure 10

Lepidophyma micropholis Walker, 1955:6. Holotype: UMMZ 101298: cave at El Pachon, about 5 miles NNE of Antigua Morelos, Tamaulipas.

DIAGNOSTIC CHARACTERS. Differs from all other species in the genus (except *L. occulor*) in having more dorsal

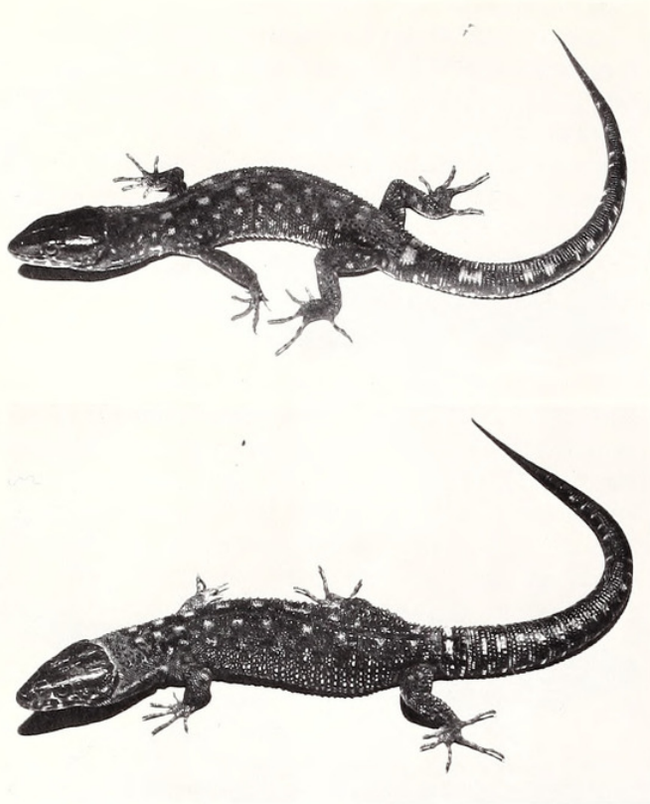

Figure 11. Living individuals of southern Madrean (*upper*, sample 11, LACM 106752) and northern Madrean (*lower*, sample 8, LACM 131146) population groups of *Lepidophyma sylvaticum*.

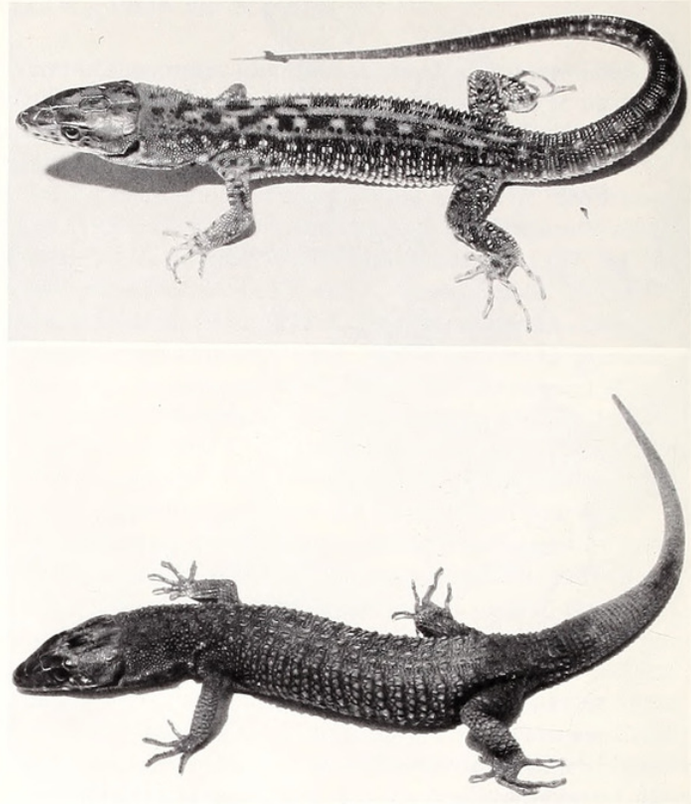

Figure 12. Living individuals of northern Madrean (*upper*, sample 6, LACM 106752) and western (*lower*, sample 1, LACM 106781) population groups of *Lepidophyma sylvaticum*.

scales (231–251 vs. 126–222) and from *L. occulor* in having more lateral tubercle rows (27–35 vs. 20–24) (Table 3).

DISTRIBUTION. *Lepidophyma micropholis* occurs in southern Tamaulipas and northern San Luis Potosí at four localities situated along the Sierra del Abra (Fig. 9). This caverniferous, low-lying range constitutes the easternmost front of the Sierra Madre Oriental in the highly dissected region between the Rio Guayalejo and the Rio Tamuin (Mitchell et al., 1977). The lizards have been found primarily in limestone caves (El Pachon and Quintero) and fissures.

REMARKS. This extensively cavernicolous species is closest in scalation to *L. occulor* and *L. sylvaticum*, and future work may demonstrate the existence of morphologically and biochemically intermediate populations, similar to those occurring between the epigean and troglodytic *Astyanax mexicanus* of the Sierra del Abra (Avise and Selander, 1972; Mitchell et al., 1977).

KARYOTYPE. *Lepidophyma micropholis* has a diploid chromosome number of 36 with 16 macrochromosomes and 20 microchromosomes (Bezy, 1972).

Lepidophyma sylvaticum Taylor

Group EFGH; Figures 7–8, 11–12

Lepidophyma sylvatica Taylor, 1939:131. Holotype: FMNH 100102: 7 mi. north of Zacaultipan, Hidalgo.

Gaigeia sylvatica: Smith, 1942:380.

Lepidophyma sylvaticum: Walker, 1955:9.

Lepidophyma flavimaculatum tenebrarum Walker, 1955:1. NEW SYNONYMY. Holotype: UMMZ 101374: ±5 miles NW (by road) of Gomez Farias in the Sierra Madre Oriental at "Rancho del Cielo."

DIAGNOSTIC CHARACTERS. Differs from *L. gaigeae* and *L. occulor* in numbers of gulars (41–56 vs. 33–39 and 59–71, respectively), from *L. micropholis* in numbers of dorsals (150–217 vs. 231–251), from *L. tarascae* in numbers of femoral pores (23–35 vs. 16–18), from *L. smithii* in having a parietal foramen, from *L. flavimaculatum* in numbers of pretympanics (0–3 vs. 4–11, 99%) and ratio of supralabial height (0.84–1.61 vs. 0.36–0.79, 99%), from *L. tuxtlae* in ratio of supralabial height (0.84–1.61 vs. 0.32–0.77), and from *L. pajapanensis* in numbers of pretympanics (0–4 vs. 6–10) (Table 3).

DISTRIBUTION. The 12 populations occur from Veracruz to Nuevo León along the Sierra Madre Oriental and adjacent Mesa Central and Sierra Tamaulipas (Fig. 9).

REMARKS. The four population groups included in *L. sylvaticum* are moderately divergent from one another and further work may indicate that one or more of them should be given separate taxonomic recognition (i.e., subspecies).

The northern Madrean group (G) includes four populations in southern Tamaulipas and northern San Luis Potosí, three from along the main axis of the Sierra Madre Oriental and

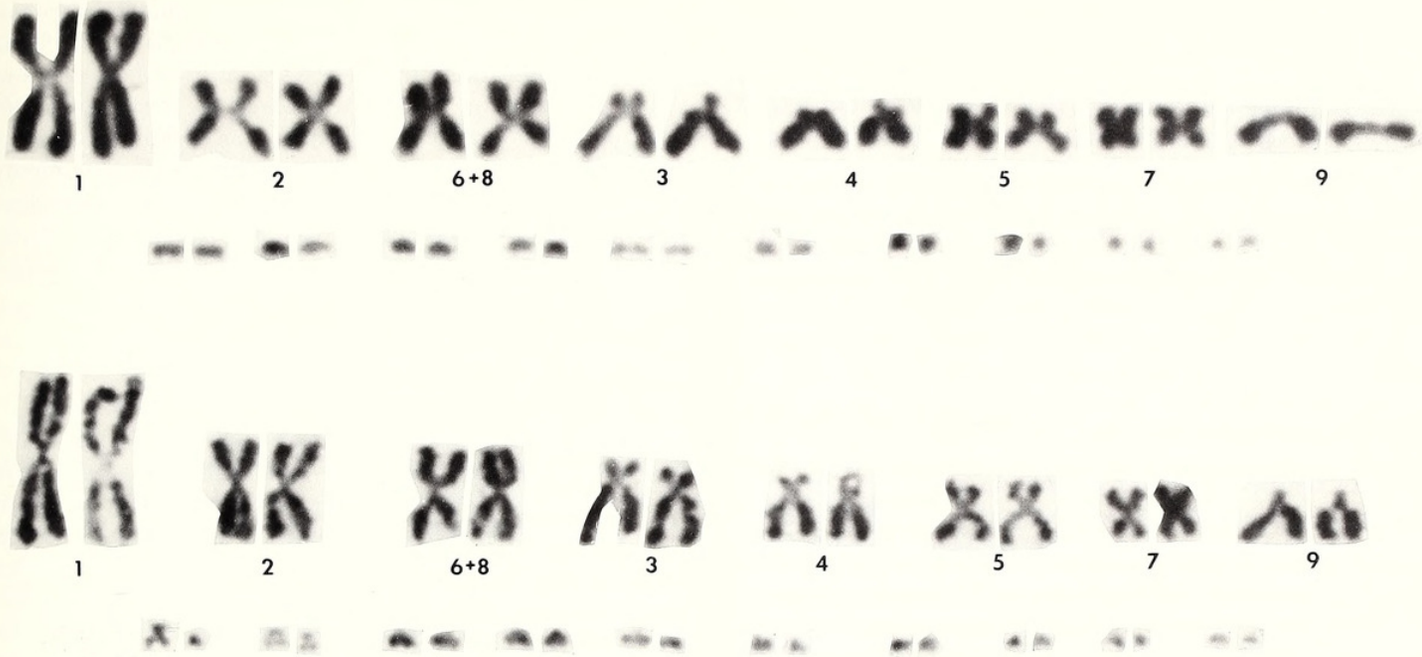

Figure 13. Karyotypes of *Lepidophyma sylvaticum* (sample 6; *upper*, LACM 106758, ♂; *lower*, LACM 106763, ♀).

one in the Sierra Tamaulipas. They differ from the three populations (group E) of southern San Luis Potosí, Querétaro, and Hidalgo in lateral tubercle rows (34/39 northern Madrean with 31 or less, 30/33 southern Madrean with 32 or more) (Table 2). The hiatus between the ranges of the two corresponds roughly to the Rio Panuco gap in the Sierra Madre Oriental. Should further work demonstrate a need to accord them separate nomenclatural status, *L. sylvaticum* Taylor, 1939 is applicable to the southern group, and *L. f. tenebrarum* Walker, 1955 is available for the northern group.

The southernmost specimen (group F) assigned to *L. sylvaticum* is from ca. 170 km SE of the type locality and occurs at the northern base of the Cordillera Volcanica in central Veracruz (Fig. 6). It has similarities to both southern and northern Madrean *L. sylvaticum*, being closest to the former in lateral tubercle rows and femoral pores, and to the latter in dorsals. No other *Lepidophyma* are known from the Cordillera Volcanica. The nearest populations to the south are *L. tuxtlae* and *L. pajapanensis* of the Tuxtlas region (which differ from *L. sylvaticum* in numbers of large paravertebrals, pretympanics, and dorsals, and in ratio of supralabial height), and *L. flavimaculatum* of the northern Isthmus of Tehuantepec (which differ in pretympanics, lateral tubercle rows, and ratio of supralabial height) (Tables 2–3).

The western group of *L. sylvaticum* (H, Figs. 6, 8, 12) includes one population in the Sierra Alvarez on the Mesa Central of southeastern San Luis Potosí and two in canyons around the northern base of the Sierra Madre Oriental below the Cumbres de Monterey of Nuevo León. A fourth locality (sample 3) is represented by a fragmentary specimen, but the limited data obtainable from it suggests it is a member of the western group. The group differs from all other *L. sylvaticum* in lateral tubercle rows, and from southern Madrean samples of *L. sylvaticum* in numbers of fourth toe lamellae and numbers of paravertebrals larger than three dorsal scales (Table 2).

KARYOTYPE. Chromosomal information was obtained from 16 specimens (6♂, 9♀, 1 juv.) of *L. sylvaticum*: three from sample 11, one from 10, eight from 6, and four from 1. A total of 271 metaphase spreads were studied.

In all four populations the karyotype was found to consist of a diploid number of 36 with 16 macrochromosomes and 20 microchromosomes (Fig. 13). There are five metacentric to submetacentric (Nos. 1, 2, 2A, 5, 7), two subtelocentric (3, 4), and one acrocentric (9) pairs of macrochromosomes (pair numbering after Bezy, 1972). No secondary constrictions were observed. The cells of six specimens (5♀, 1 juv.) of sample 6 were found consistently to have a pair of heteromorphic chromosomes involving the largest pair of microchromosomes, with a metacentric member, ca. 1.5 times the size of the next largest micro (Fig. 13).

The karyotype of *L. sylvaticum* appears identical in all respects (except the heteromorphism) to that of *L. micropholis* (Bezy, 1972). It differs from that of *L. flavimaculatum*, *L. tuxtlae*, and *L. pajapanensis* in having one less pair of macrochromosomes (the large metacentric 2A presumably was formed from centric fusions involving pairs 6 and 7), a pair 3 that lacks terminal satellites, and a submetacentric rather than subtelocentric pair 7; from that of *L. smithii* in that pair 2A is more metacentric (rather than submetacentric), pair 3 lacks satellites, and the smallest macro pair is acrocentric rather than subtelocentric; and from that of *L. occulor* in having one more pair of macrochromosomes, one less pair of microchromosomes, and an acrocentric (rather than submetacentric) pair 9.

Lepidophyma sylvaticum thus differs karyotypically from

the species that are closest to it in scalation (*L. flavimaculatum, L. smithii,* and *L. occulor*) except *L. micropholis.* Such chromosomal differences in themselves would not be expected to present reproductive barriers, and some cases of extraordinary geographic variation in karyotypes have been documented in species of other lizard families (e.g., Hall and Selander, 1973; Sites, 1983). However, among lizards chromosomal divergence most often is associated with differentiation at or above the species level. The karyotypic identity of *L. micropholis* and *L. sylvaticum* serves to underscore the morphologic and biogeographic relationships which suggest that the former may be a troglodytic derivative of the latter, and that future work might demonstrate a morphologic and genetic continuum between the two.

The microchromosomal heteromorphism found in the females of sample 6 was not detected in samples 1, 10, and 11. It occurs in all females (five; plus one juvenile) of sample 6, but is absent in the two females of sample 1 and in all males studied (two each from samples 1, 6, and 11, and one from 10). It may constitute a sex chromosomal heteromorphism (ZW) present in population 6, absent in population 1, and of unknown occurrence in populations 10 and 11 (no preparations from females available). On the other hand, it may represent a heterozygous condition where unsampled homozygous individuals (for the large macrochromosome) occur in the population, or in adjacent populations. Until additional material is obtained, all that can be said is that it is a heteromorphic condition which has been found only in females of population 6, and not detected in any other population in the family.

SEX RATIO. Two samples of *L. sylvaticum* have sex ratios (♀/♂ + ♀) that differ significantly (0.05 level, Fisher exact test, Yates correction) from 0.50: sample 6 with 0.89 (25/28) and sample 10 with 0.85 (11/13). The skewed sex ratios of these samples have been discussed earlier in relationship to the unisexual populations of *L. flavimaculatum* occurring in Panama and Costa Rica (Bezy, 1972). Although the sample sizes of populations 6 and 10 of *L. sylvaticum* remain smaller than desirable, both are now sufficiently large to conclude that the sex ratios differ significantly (0.05 level) from those of other *Lepidophyma* populations in eastern Mexico: *L. tuxtlae* (30/59) and *L. gaigeae* (150/260).

In addition to previously discussed factors that may be responsible for the observed skewed sex ratios (Bezy, 1972), temperature-dependent sex determination has now been documented for lizards (Bull, 1980), and comparable effects could be operative in *Lepidophyma.* Theoretical considerations would predict that this may not be the case in that temperature-dependent sex determination is thought to interfere with the evolution of both viviparity (ovoviviparity) and sex chromosomes (Bull, 1980). Viviparity appears to be universal among xantusiids (Blackburn, 1982), and the population (6) of *L. sylvaticum* with the most aberrant sex ratio is the only one in the family with heteromorphism, possibly indicating the presence of sex chromosomes. Experimental data are needed to evaluate the role of environmental factors, particularly temperature, in determining sex ratio in xantusiids.

The aberrant sex ratios and the heteromorphic chromosomes of populations of *L. sylvaticum* could be a consequence of hybridization. Both conditions frequently are found in hybrid populations, the skewed sex ratios perhaps resulting from a disruption in the balance of the sex-determining mechanism or an increased expression of lethals in one of the sexes (Darevsky et al., 1978; White, 1973). The identification of populations homozygous for the large microchromosome and additional data (e.g., allozymes) would be required to establish the existence of and possible participants in such a hybridization.

KEY TO THE SPECIES OF *LEPIDOPHYMA* OF NORTHEASTERN MEXICO

1a. Side of body lacking vertical rows of enlarged keeled tubercles (Fig. 7), but with 43–50 subequal scales (axilla to groin); less than 145 dorsal scales (occiput to rump); tail with two interwhorls complete dorsally and ventrally ..... *L. gaigeae*

1b. Side of body with enlarged, keeled tubercles arranged in 15–42 vertical rows (A–G) separated by smaller granular scales (Figs. 7–8); 145 or more dorsal scales (O–R); tail usually with more than 2 interwhorls complete dorsally 2

2a. Total femoral pores 21 or less (gulars 59 or more; divided 4th toe lamellae 9 or less; lateral tubercle rows 24 or less) ..... *L. occulor*

2b. Total femoral pores 23 or more 3

3a. Dorsal scales (O–R) 231 or more (gulars 55 or more; divided 4th toe lamellae 10 or more; lateral tubercle rows 27 or more) ..... *L. micropholis*

3b. Dorsal scales (O–R) 217 or less (gulars 56 or less; divided 4th toe lamellae 4–23; lateral tubercle rows 15–38) ..... *L. sylvaticum*

SPECIMENS EXAMINED

The 351 specimens and 52 population samples studied from Mexico are listed below. Sample numbers are in parentheses preceding localities.

L. gaigeae

HIDALGO: (21): La Placita, 8 km S Jacala (UIMNH 26180–86, 26191–99, 26204, 26207–09).

L. micropholis

SAN LUIS POTOSÍ: (15): 6 mi. E Valles (BCB 13837–42); (16): 5.5 mi. S, 1.4 mi. E Valles (TCWC 60621, 60766–67). TAMAULIPAS: (13): Gruta de Quintero, 1.5 mi. S Quintero (AMNH 93409, LACM 66662, SAM 885); (14): cave at El Pachon, ca. 5 mi. (by rd) NNE Antigua Morelos (LACM 106767–68, UAZ 28762, 28767–69, UMMZ 101299, 102886–88); 11.3 mi. S Ciudad Mante, Hwy 85 (TCWC 57256).

L. occulor

QUERÉTARO: (18): 2.5 mi. S Conca, Hda. Conca (TCWC 35605–06, 48499); (19): Jalpan (USNM 47134–35); (20): 1.2 mi. E Landa de Matamoros (TCWC 29691); 1.5 mi. E Landa

(TCWC 33063). SAN LUIS POTOSÍ: (17): Boa Capulin (LSUMZ 2379–80).

L. sylvaticum

HIDALGO: (11): 5.8 mi. (by Hwy 105) S Tianquistengo (LACM 106741–48); 4.0 mi. (by Hwy 105) S Tianquistengo (LACM 106721); 3 mi. S Tianquistengo (UIMNH 26230). NUEVO LEÓN: (1): La Boca (KU 92612–13); ca. 7 km NE Santiago, Presa La Boca (LACM 106781–792); (2): 5 mi. N Las Ajuntas (EAL 4644). QUERÉTARO: (10): El Madroño, 3.5 mi. W (rd) El Lobo [and vic] (LACM 109771, SAM 1104, TCWC 29692–29707, 32291, 33064, 35607, UMMZ 129749). SAN LUIS POTOSÍ: (3): Buenavista (ca. 20 mi. NE Cerritos) (AMNH 64025); (4): Alvarez (58 kilo) (MCZ 24507–08); between San Francisco and Alvarez (MCZ 157826); Valle de los Fantasmos (SDNHM 60482); (8): 27 km (by Mex 80) W El Naranjo (LACM 131145–48); 3.8 mi. (by Hwy 80) NNE Ciudad del Maiz (LACM 131144); 5 mi. NE Ciudad del Maiz (TCWC 35582); (9): Huichihuagan (FMNH 39631). TAMAULIPAS: (5): 8 mi. S, 6 mi. W Victorio, Sierra Madre Oriental (KU 33992); (6): Rancho del Cielo [and vic] (AMNH 107273, LACM 106751–60, 106762–65, LSUMZ 10989, UMMZ 101301, 101375, 102977–81, 109763–67); (7): Sierra de Tamaulipas, Santa Maria (UMMZ 102889–90); 10 mi. W, 2 mi. S Piedra (KU 33993–94). VERACRUZ: (12): 4 km W Tlapacoyan (KU 26909).

L. flavimaculatum

CHIAPAS: (22): Palenque (LACM 65117–19); Ruinas de Palenque (EAL 3030–31, FSM 32915–16, KU 94104–05); San Juanito, Palenque (USNM 111486–87); (23): 4.5 km S Pichucalco (KU 94106); (24): El Estoracan, ca. 50 km N Cintalapa (AMNH 73468); (25): Chiapa, 1 mi. W (TNHC 27517–18); (26): Ocozocoautla Selvas El Ocote (MCZ 54321–22); 16.1 mi. NW Ocozocoautla (LACM 61259); 26 km N Ocozocoautla (UTEP 5367–68); 32 km NW Ocozocoautla, Selva del Ocote (JFC); 25 mi. (by rd to Malpaso) NW Ocozocoautla (UAZ 28764, 28805–07); 12 km N Berriozabal (UTEP 5365–66); (27): ca. 5 km S Solusuchiapa (UAZ 31635); (28): Lago Miramar, near San Quintin (JFC); (29): Lacanja (LACM 114244). OAXACA: (30): 2.8 mi. N Rio Sarabia (UMMZ 115096); (31): 2 km S Tolosita (KU 39676); (32): Rio Mono Blanco, Juchitan (UIMNH 36832); (33): La Gloria (UIMNH 35515); (34): Mogoñe (UIMNH 40811); (35): 50.5 mi. S Acayucan, Hwy 185 (TNHC 25182). QUINTANA ROO: (36): 4.1 km NE Felipe Carrillo Puerto (UMRC 79-252). TABASCO: (37): Teapa (LACM 61260–61, LSUMZ 6878–79, UIMNH 47883, UMMZ 113777); (38): Soledad (UIMNH 47884). VERACRUZ: (39): 20 km E Jesus Carranza (KU 24453); 25 km SE Jesus Carranza (KU 26920–21); 35 km SW Jesus Carranza (KU 26919); (40): Rio de las Playas (USNM 118638).

L. pajapanensis

VERACRUZ; (41): Sontecomapan, Los Tuxtlas [and vic] (TCWC 21365, UAZ 28765, 28808–11, UTAR 3107, 3110, 3116, TCWC 21365); Coyame, 9 mi. (by rd) SE Catemaco (UAZ 28804); Univ. Mex. Biol. Exp. Sta., ca. 33 km ENE Catemaco (TCWC 53351); Colonia de Bastonal, above Quezalapam (TCWC 19133); Laguna Catemaco, nr Cuezalapan (UMMZ 126363–64); 4 mi. SE Tebanca, Los Tuxtlas (TCWC 21364); S slope Volcan San Martin (KU 97290, UMMZ 118220, 126362); (42): 35 km SE Jesus Carranza (KU 26913).

L. smithii

CHIAPAS: (43): La Esperanza (UIMNH 10952–56, 10958–59, 10963, 10965, 10968–69, 10970–71, 10975–79, 10997–98); (44): Tonala (UIMNH 26227–29). GUERRERO: (45): 2 km W Puerto Marquez (CU 9676–79, 9692–93, 9772, LACM 128590, 130027–29).

L. tarascae

MICHOACÁN: (46): near Mexiquillo, Aquila District (ENCB 9221–22, LACM 134226).

L. tuxtlae

CHIAPAS: (47): 25 mi. (by rd to Malpaso) NW Ocozocoautla (UAZ 28780–82). OAXACA: (48): Vista Hermosa (KU 87396–98); 30 mi. (by rd) NE Llano de las Flores (UMMZ 125870); (49): Mts nr La Gloria (UIMNH 37236); (50): Finca San Carlos, Matias Romero Oaxaca (FSM 32918). VERACRUZ: (51): Volcan San Martin (TCWC 22102–03, TNHC 29792–93, UIMNH 80695–99, UMMZ 118219, 121165, 122112, 126360–61); S slope Volcan San Martin Tuxtla (KU 59560); Rancho El Tular, 15 mi. N San Andres Tuxtla (USNM 139731); Rio Tecolapan, 2.4 mi. NNW Tapalapan (UMMZ 115098–99); Salto de Eyipantla (TCWC 19134); Montepio (FSM 32917); Sontecomapan [and vic] (CM 41470, FSM 32914, TCWC 19135, 26717, UAZ 28770–79, UTAR 3101, 3103–04, 3108–09, 3111–13, 3115, 3127); 7.7 mi. NW Sontecomapan (UTAR 3728–30, 3733–34); E of Lago Catemaco, 12.7 mi. from Catemaco by rd (LACM 106795); 18 mi. NNE Catemaco (JCL 67); Univ. Mex. Bio. Exp. Sta., ca. 33 km ENE Catemaco (TCWC 53352–53); between Laguna Catemaco and Volcan Martin (UMMZ 121166); Coyame (UAZ 28763); midway between Coyame and Tebanca (UMMZ 121164); 4 mi. SE Tebanca (TCWC 21366); 5.6 mi. ESE Tebanca (UTAR 3156); Rio Quetzalapan [and vic] (TCWC 19136, 21367–69, UTAR 3133, 3139–40); Colonia de Bastonal (TCWC 19137); Dos Arroyos, 5 mi. E Zapoapan (TCWC 21370–71); (52): 25 km SE Jesus Carranza (KU 26912).

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