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Morphological and Biochemical Differentiation in Spanish and Moroccan Populations of the Lizard, *Lacerta lepida*

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ABSTRACT. — **Morphological and biochemical divergence between Spanish and Moroccan populations of *Lacerta lepida* demonstrate that these populations are not conspecific; Iberian populations are referred to *Lacerta lepida*, Moroccan populations to *L. pater*. An evolutionary scenario, consistent with the biochemical and morphological data, is inferred from the physiographic history of the region.**

Lacerta lepida inhabits the Iberian peninsula, France, N.W. Italy, and North Africa; the subspecies *L. l. lepida* is restricted to Europe, *L. l. pater* to North Africa (Boulenger, 1887; Bischoff et al., 1984). Artificially hybridized specimens drawn from Spanish and Tunisian populations have been shown to exhibit reduced fertility, however, and it has been suggested that North African and European populations be considered separate species (Bischoff, 1982). I was curious to know to what degree, if at all, this indication of genetic independence between European and North African populations might be confirmed through data gathered by standard systematic methods.

Electrophoretic, micro-complement fixation, and morphological analysis revealed substantial differentiation between Spanish and Moroccan populations and confirmed that European and North African populations are not conspecific. The data supporting this conclusion are presented in the following pages, along with an inferred reconstruction of the evoutionary history of Iberian and Moroccan populations.

MATERIALS AND METHODS

Electrophoresis.—Eleven individuals were collected from near Alcalá de los Gazules (36°28'N, 5°44'W; 1 specimen), Benalup de Sidonia (36°20'N, 5°49'W; 5 specimens), and Facinas (36°08'N, 5°42'W; 5 specimens), Cádiz Province, Spain. Specimens collected in Tétouan Prefecture at Dar Chaoui (35°34'N, 5°44'W; 2 specimens) and Ksar es Srhir (35°51'N, 5°34'W; 1 specimen), and one specimen from the vicinity of Ouezzane (34°48'N, 5°36'W) in Kenitra Prefecture represent populations from Morocco.

Specimens were sacrificed in the field and samples of blood plasma, heart, and liver were removed, frozen, and stored in liquid nitrogen (−196°C). In the laboratory, tissues were transferred to a freezer (−76°C) until used in electrophoresis (heart and liver) two to 12 months later, or in micro-complement fixation analysis (blood plasma) 24 months later.

Proteins were separated electrophoretically in horizontal starch gels (11.5% hydrolyzed starch, Sigma Chemical Co.) and localized by standard histochemical staining procedures (Selander et al., 1971; Ayala et al., 1972; Harris and Hopkinson, 1976; Table 1). Genetic interpretations of allozymic data were based on criteria developed by Selander et al. (1971). Multiple loci within a protein system were numbered with "1" designating the most anodally migrating set of allelic products. Alleles of a locus were lettered, with "a" representing the most anodally migrating product. Allele frequency data (Table 2) were used directly for the computation of unbiased genetic distances and associated standard errors ($\hat{D}$; Nei, 1978, 1971, respectively) between *Lacerta* populations.

Micro-complement Fixation.—Antiserum was prepared to albumin purified from plasma samples of *Lacerta l. lepida* by L. R. Maxson at the University of Illinois; micro-

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TABLE 1. Protein systems examined by electrophoresis; enzymes are arranged by Enzyme Commission number.

Protein (abbreviation)	Enzyme Commission number	Electrophoretic conditions
Albumin (Ab)	—	B
Hemoglobin (Hb)	—	B
(Oxidoreductases)		
Alcohol dehydrogenase (Adh)	1.1.1.1	A
Glycerol-3-phosphate dehydrogenase (Gpd)	1.1.1.8	D
L-Iditol dehydrogenase (Sordh)	1.1.1.14	D
L-Lactate dehydrogenase (Ldh)	1.1.1.27	F
Malate dehydrogenase (Mdh)	1.1.1.37	F
Malate dehydrogenase (Me)	1.1.1.40	F
Isocitrate dehydrogenase (Icd)	1.1.1.42	G
Phosphogluconate dehydrogenase (Pgd)	1.1.1.44	E
Glucose-6-phosphate dehydrogenase (Gd)	1.1.1.49	D
Aldehyde dehydrogenase (Aldh)	1.2.1.3	F
Glyceraldehyde-3-phosphate dehydrogenase (Gapdh)	1.2.1.12	H
Glutamate dehydrogenase (Glud)	1.4.1.3	D
Superoxide dismutase (Sod)	1.15.1.1	A
(Transferases)		
Aspartate aminotransferase (Aat)	2.6.1.1	D
Hexokinase (Hk)	2.7.1.1	G
Creatine kinase (Ck)	2.7.3.2	G
Adenylate kinase (Ak)	2.7.4.3	G
(Hydrolases)		
Carboxylesterase (Est)	3.1.1.1	B
Carboxylesterase-D (Est-D)	3.1.1.1	B
Acid phosphatase (Acp)	3.1.3.2	G
Fructose-bisphosphatase (Hdp)	3.1.3.11	H
N-Acetyl-beta-glucosaminidase (Hex)	3.2.1.30	G
Dipeptidase I, L-Leucyl-L-alanine (La)	3.4.11	B
Dipeptidase III, L-Leucylglycylglycine (Lgg)	3.4.11	C
Proline dipeptidase (Pap)	3.4.13.9	B
Adenosine deaminase (Ada)	3.5.4.4	A
(Lyases)		
Fructose-bisphosphate-aldolase (Ald)	4.1.2.13	H
Aconitate hydratase (Acon)	4.2.1.3	E
(Isomerases)		
Mannose-6-phosphate isomerase (Mpi)	5.3.1.8	E
Glucose-6-phosphate isomerase (Gpi)	5.3.1.9	F
Phosphoglucomutase (Pgm)	5.4.2.2	E

A. Histidine, pH 7.8 gel and electrode buffer (Harris and Hopkinson, 1976), 150v/3h.

complement fixation (MC'F) analysis was performed according to methods described by Champion et al. (1974). Data are reported as immunological distance (ID) units where one unit of ID is roughly equivalent to one amino acid substitution between compared albumins (Maxson and Wilson, 1974) and to between 0.55 and 0.60 million years of lineage independence.

Morphology.—Specimens included those used for electrophoresis and MC'F as well as additional material from Cádiz Province, Spain, and from throughout the range of the species in Morocco. Frontoparietal, occipital, and frontal widths, and occipital and frontal lengths (Fig. 1) were taken to 0.1 mm with dial calipers; snout–vent length (SVL) was taken to the nearest mm with a steel ruler. In addition, numbers of femoral pores and mid-body dorsal scale rows were tabulated.

Lizards are sexually dimorphic and continuous variables were analyzed separately within and between sexes; meristic variables are used to distinguish between species within the Lacertidae and are treated without regard to the sex of the individual. The effect of having limited numbers of individuals of each size representing each sex of each population was minimized by converting each character measurement to its natural logarithm; the variance of ln-transformed data estimates intrinsic variability and is unaffected by size (Lewontin, 1966; Moriarty, 1977). Sexual differences in allometry within populations and differences in allometric coefficients between Spanish and Moroccan populations were identified when ln-transformed data rep-

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B. LiOH A + B, pH 8.2 gel and LiOH A, pH 8.1 electrode buffer (Selander et al., 1971), 300v/3h.

C. Poulik, pH 8.7 gel and borate, pH 8.2 electrode buffer (Selander et al., 1971), 250v/3h.

D. Tris citrate II, pH 8.0 gel and electrode buffer (Selander et al., 1971), 130v/4h.

E. Tris citrate II, pH 8.0 + NADP gel and tris citrate II, pH 8.0 electrode buffer (Selander et al., 1971), 130v/4h.

F. Tris citrate III, pH 7.0 gel and electrode buffer (Ayala et al., 1972), 180v/3h.

G. Tris citrate III, pH 7.0 + 15% glycerine gel and tris citrate III, pH 7.0 electrode buffer (Ayala et al., 1972), 180v/3h.

H. Tris citrate III, pH 7.0 + NAD + 2-mercaptoethanol gel and tris citrate III, pH 7.0 electrode buffer (Ayala et al., 1972), 180v/3h.

TABLE 2. Genic variation between samples of *Lacerta lepida*.

		Spain	Morocco
Number of specimens:		11	4
Mean heterozygosity per locus:		0.12	0.11
Percentage of loci polymorphic:		38.5	23.1
Locus and alleles:			
Ab	a	0.00	1.00
	b	1.00	0.00
Acon2	a	0.91	1.00
	b	0.09	0.00
Ada	a	0.00	0.25
	b	0.91	0.75
	c	0.09	0.00
Ak	a	0.91	1.00
	b	0.09	0.00
Ald	a	0.91	0.75
	b	0.09	0.00
	c	0.00	0.25
Est	a	0.09	0.12
	b	0.00	0.12
	c	0.91	0.75
Gapdh	a	0.09	0.00
	b	0.82	0.75
	c	0.09	0.00
	d	0.00	0.25
Gd	a	0.36	0.00
	b	0.27	0.00
	c	0.36	1.00
Glud	a	0.64	0.50
	b	0.36	0.50
Gpi	a	0.96	1.00
	b	0.04	0.00
Hex	a	0.00	0.25
	b	0.18	0.50
	c	0.82	0.25
Hk	a	0.91	1.00
	b	0.09	0.00
Icd1	a	1.00	0.25
	b	0.00	0.75
Icd2	a	0.91	0.50
	b	0.09	0.50
Lgg	a	0.36	0.00
	b	0.64	1.00
Me	a	0.18	0.25
	b	0.82	0.75
Pap	a	0.00	1.00
	b	1.00	0.00
Sod2	a	0.36	0.00
	b	0.54	0.00
	c	0.09	1.00
Sordh	a	1.00	0.00
	b	0.00	1.00

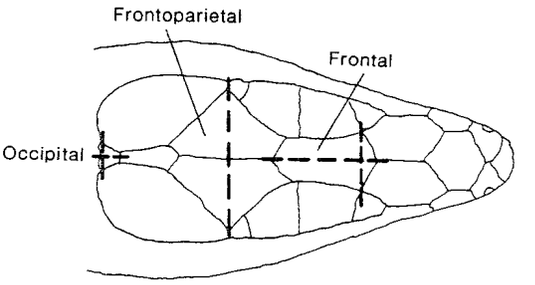

FIG. 1. Diagrammatic representation of the head of *L. lepida*. Linear dimensions were determined by measuring along heavy dotted lines.

resenting continuous variables were subjected to an Analysis of Covariance in which SVL was selected as the independent variable. Although allometry is correctly assessed only from the study of growth of an individual, I used individuals of different sizes from a population to obtain estimates of allometric coefficients. Identification of dissimilarities in allometric growth through analysis of transformed data is acceptable for comparing populations (Thorpe, 1976). Differences in trends of meristic variables between Spanish and Moroccan populations were assessed by Analysis of Variance in which variables were also represented by ln-transformed data.

Linear regression analysis, in which measurement data were left untransformed, was also performed for variables demonstrating significant differences in allometric growth. For ease of presentation and interpretation, only resulting slope and intercept values are reported for these analyses (Table 4).

I selected $\alpha = 0.05$ as the level for significance of all statistical tests. All reported probabilities are those of committing a Type I error in a two-tailed test.

RESULTS

Electrophoretic Comparisons

In total, the products of 39 presumptive gene loci were resolved. Aat1, Aat2, Acon1, Acp, Adh, Aldh1, Aldh2, Ck, Est-D, Gpd, Hb, Hdp, La, Ldh1, Ldh2, Mdh, Mpi, Pgd, Pgm, and Sod1 were monomorphic within and between Moroccan and Spanish *L. lepida*. Moroccan populations, however, have

TABLE 3. Range of variation, mean value (±1 SE), and statistical comparison (Analysis of Variance; *F* value and probablity [*P*]) of continuous variables between sexes within samples representing Spanish and Moroccan populations, and between meristic variables representing either Spanish or Moroccan samples.

	Spanish populations		Moroccan populations	
Variable	Males	Females	Males	Females
Snout-vent length				
Range	47–229	54–211	46–170	59–165
$\bar{x} \pm$ SE	145.5 ± 7.4	130.7 ± 6.2	114.6 ± 6.5	120.8 ± 5.6
N	43	45	39	27
F	1.1		1.05	
P	>0.50		>0.60	
Frontoparietal width				
Range	4.9–17.9	5.1–14.9	4.5–14.4	5.5–10.9
$\bar{x} \pm$ SE	10.7 ± 0.6	9.1 ± 0.4	9.2 ± 0.5	8.8 ± 0.3
N	42	44	38	27
F	4.2		<0.1	
P	>0.05		>0.90	
Occipital width				
Range	2.9–16.2	3.0–11.2	2.0–8.1	2.8–6.9
$\bar{x} \pm$ SE	8.8 ± 0.6	6.6 ± 0.3	4.9 ± 0.3	4.8 ± 0.2
N	39	43	39	27
F	8.7		0.2	
P	<0.01		>0.90	
Occipital length				
Range	1.0–11.0	1.0-6.2	0.8–6.9	1.4–5.5
$\bar{x} \pm$ SE	5.6 ± 0.5	3.9 ± 0.2	3.7 ± 0.3	3.6 ± 0.2
N	40	42	39	27
F	5.1		0.5	
P	>0.05		>0.90	
Frontal length				
Range	4.4–15.7	5.1–12.0	4.5–11.3	5.0–9.6
$\bar{x} \pm$ SE	9.1 ± 0.4	8.0 ± 0.3	8.0 ± 0.4	7.5 ± 0.2
N	41	44	37	27
F	4.1		0.2	
P	>0.05		>0.90	
Frontal width				
Range	2.6–11.1	2.7–7.7	2.1–7.4	3.0–6.4
$\bar{x} \pm$ SE	6.3 ± 0.3	5.2 ± 0.2	5.0 ± 0.3	5.0 ± 0.2
N	42	45	37	27
F	6.5		0.3	
P	<0.05		>0.90	
Dorsal scale rows				
Range	55–80		67–93	
$\bar{x} \pm$ SE	63.9 ± 0.4		81.0 ± 0.7	
N	88		64	
F	445.8			
P	≪0.01			
Femoral pores				
Range	22–30		27–44	
$\bar{x} \pm$ SE	25.5 ± 0.2		36.4 ± 0.4	
N	88		66	
F	816.2			
P	≪0.01			

TABLE 4. Estimates of slope (b) and intercept (a) obtained when measurements derived from various morphological features (y) were regressed against snout-vent length (x) in male and female *Lacerta lepida* from Spain and Morocco. Linear regression results are reported only for those allometric growth characteristics which were found to be significantly different in an analysis of covariance (see text); an Analysis of Variance technique (Sokal and Rohlf, 1981:471) was used to assess the hypothesis that each linear regression was significant (values of F_s and associated significance levels [P] for this statistical test are provided).

	Spain		Morocco	
	Males	Females	Males	Females
		Frontoparietal width		
b ± SE	$0.07 \pm 4.9 \times 10^{-3}$	$0.05 \pm 2.0 \times 10^{-3}$	$0.07 \pm 3.7 \times 10^{-3}$	$0.05 \pm 4.6 \times 10^{-3}$
a ± SE	1.26 ± 0.76	2.00 ± 0.28	0.95 ± 0.46	3.36 ± 0.58
F_s, P	175.4, $\ll$0.001	729.0, $\ll$0.001	366.8, $\ll$0.001	94.2, $\ll$0.001
		Occipital width		
b ± SE	$0.07 \pm 3.9 \times 10^{-3}$	$0.04 \pm 2.9 \times 10^{-3}$	$0.04 \pm 2.2 \times 10^{-3}$	—
a ± SE	−0.80 ± 0.60	1.16 ± 0.40	0.25 ± 0.26	—
F_s, P	294.1, $\ll$0.001	203.3, $\ll$0.001	356.3, $\ll$0.001	—
		Frontal length		
b ± SE	$0.05 \pm 2.7 \times 10^{-3}$	$0.04 \pm 1.9 \times 10^{-3}$	$0.05 \pm 2.0 \times 10^{-3}$	$0.04 \pm 4.4 \times 10^{-3}$
a ± SE	2.05 ± 0.41	2.67 ± 0.26	1.90 ± 0.24	3.01 ± 0.55
F_s, P	330.8, $\ll$0.001	468.5, $\ll$0.001	699.6, $\ll$0.001	69.9, $\ll$0.001
		Frontal width		
b ± SE	$0.04 \pm 1.6 \times 10^{-3}$	$0.03 \pm 1.29 \times 10^{-3}$	—	—
a ± SE	0.25 ± 0.25	1.11 ± 0.18	—	—
F_s, P	651.3, $\ll$0.001	586.9, $\ll$0.001	—	—
		Occipital length		
b ± SE	$0.06 \pm 3.1 \times 10^{-3}$	$0.03 \pm 1.4 \times 10^{-3}$	—	—
a ± SE	−2.30 ± 0.48	−0.52 ± 0.19	—	—
F_s, P	309.8, $\ll$0.001	599.2, $\ll$0.001	—	—

at least 9 alleles that are not found in Spain and Spanish populations may have as many as 16 alleles not found in Morocco. Fixed differences identified at three loci (Ab, Pap, Sordh) contribute to a genetic distance ($\hat{D} \pm$ SE) of 0.15 ± 0.6 between Spanish and Moroccan populations. Table 2 summarizes the distribution of alleles at the 19 polymorphic loci.

Micro-complement Fixation

The 22 h titer was 2300 for *L. l. lepida* antiserum. The average slope of the antiserum was 400 and the antiserum was directed solely to serum albumin. MC'F tests using either purified albumin or whole plasma were indistinguishable. Eight ID units were recorded in a one-way test between the antiserum to *L. l. lepida* from southern Spain and plasma from *L. l. pater* from northern Morocco.

Morphological Comparisons

Between Sexes.—*Lacerta lepida* from southern Spain are sexually dimorphic. Widths of frontal and occipital scales of males are significantly greater than those of females (Table 3). Allometric growth relationships between SVL and frontoparietal width ($F = 9.05$, $P < 0.01$), SVL and occipital width ($F = 36.94$, $P \ll 0.01$), SVL and frontal width ($F = 25.32$, $P \ll 0.01$), SVL and occipital length ($F = 32.10$, $P \ll 0.01$), and between SVL and frontal length ($F = 13.52$, $P \ll 0.01$) are also significantly different between males and females of southern Spain (Table 4).

Sexual dimorphism, while present, is less marked in Moroccan *L. lepida*. Only the allometric growth relationships between SVL and frontoparietal width ($F = 7.32$, $P = 0.02$) and between SVL and frontal length

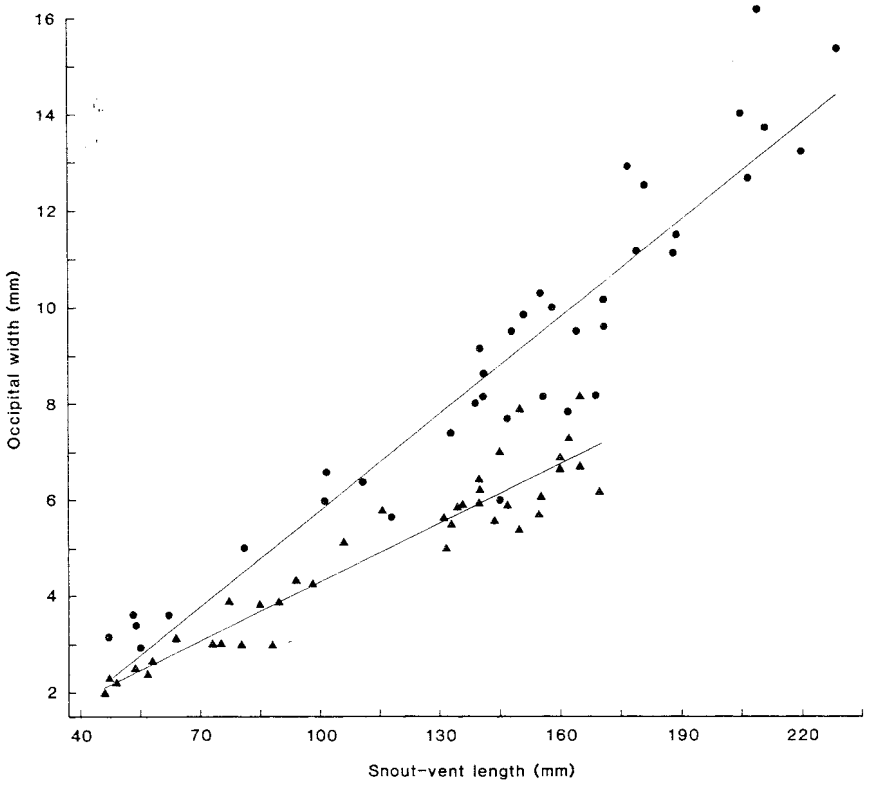

FIG. 2. Snout-vent length regressed on occipital width in male *Lacerta lepida* from Spain (circles, upper solid line) and Morocco (triangles, lower solid line). See Table 4 for regression coefficients.

($F = 24.28$, $P \ll 0.01$) are significantly different between males and females representing this population (Table 4).

Between Populations.—Male *L. lepida* from Spain differ from male *L. lepida* from Morocco in SVL ($F = 6.54$, $P < 0.05$), occipital width ($F = 35.43$, $P \ll 0.01$), and frontal width ($F = 8.72$, $P < 0.01$), and in the allometric growth relationship between SVL and occipital width ($F = 156.98$, $P \ll 0.01$; Fig. 2). Female specimens sampled from these populations also differ in occipital width ($F = 18.63$, $P \ll 0.01$) and in the allometric relationship between SVL and occipital width ($F = 63.66$, $P \ll 0.01$). In addition, Spanish specimens have significantly higher numbers of dorsal scale rows and lower numbers of femoral pores than Moroccan specimens (Table 3).

SYSTEMATIC CONSIDERATIONS

Electrophoretic, immunological, and morphological comparisons of Moroccan and Iberian samples of *L. lepida* confirm that these populations are morphologically and genetically different (Tables 2, 3, and 4). While it is possible that not all populations within a single continent are conspecific, at this time it is zoogeographically and systematically conservative to consider European populations *L. lepida* and, in concurrence with Bischoff (1982), African populations *L. pater* Lataste, 1880.

DISCUSSION

The degree of morphological differentiation between Spanish and Moroccan populations of these lacertid lizards is subtle (Results, Tables) but the biochemical data indicate that these populations are well differentiated. Interspecific genic differentiation has been surveyed in the genus *Lacerta*, and electrophoretically determined estimates of genetic distance within the genus range from 0.13 (between *L. oxycephala* and *L. graeca*) to 1.70 (between *L.*

bedriagae and *L. viridis*; Mayer and Tiedemann, 1982). While genetic distances computed from different, and differing numbers, of loci among representatives of different taxa may not be directly comparable (Busack, 1986), these data do provide an indication of the range in values expected between biological species within the genus *Lacerta*. Allelic independence at three electrophoretic loci confirms the genetic independence of *L. lepida* from *L. pater* (Table 2) and the unbiased genetic distance ($\hat{D}$) between these two populations is within the range obtained from comparisons between other biological species of the genus.

If the ancestral stock representing *L. lepida-L. pater* inhabited Iberia and North Africa prior to the formation of the Strait of Gibraltar (Pliocene), the physiographic change associated with the formation of the Strait may have precipitated its evolution into two species. As Atlantic waters eroded a channel to the Mediterranean during Miocene-Pliocene (Hsü, 1983), the forming Strait may have partitioned the *L. lepida-L. pater* gene pool into two pools that evolved to become *L. pater* and *L. lepida*. The electrophoretic, immunological, and morphological data coincide fairly well with this evolutionary scenario, and correlations from the albumin immunological clock place the initiation of genetic independence between these taxa at Pliocene (4–5 mybp).

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Specimens Examined

L. lepida—(Electrophoretic Analysis): SDB 1537, 1572, and 1672 at the Universidad de León, Spain; Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), 186055–57, 186061–64, and 186070. (Immunological Analysis): L. R. Maxson (LM) 867 at the University of Illinois, Urbana, and SDB 1672 (=LM 918) at the Universidad de León, Spain. (Morphological Analysis): Carnegie Museum of Natural History (CM) 50948, 51043–44, 51082, 51085, 51103–04, 51918, 51946, 52021, 52180–81, 52621, 53060, 53133, 53136–38, 53176–77, 53185, 53201–12, 53218, 53224, 53298, 53316, 53360, 53365–66, 53370, 53418, 53905, 53917–19, 54214, 54235, 54268, 54570, 54595, 54689, 54797–99, 54865, 54870, 54877, 54879, 55332, 55349, 55439–40, 55449, 55469, 55493, 55497, and 55669–73; MVZ 186055–71.

L. pater—(Electrophoretic Analysis): MVZ 178290 and 186203–05. (Immunological Analysis): MVZ 186203 (=LM 735). (Morphological Analysis): CM 55216–18; Museum of Comparative Zoology, Harvard 29972–73, 29976, 29978–79, and 29974–75; MVZ 162584, 178279–90, and 186203–05; California Academy of Sciences 92417–19 and 153730; Field Museum of Natural History 66607, 199774, and 199803–06; Naturhistorisches Museum Wien 10938:14, 10939:1–39:3, 10940, and 10945; Muséum National d'Histoire naturelle, Paris 1912-470, 1916-48, and 1925-150; Muséum d'Histoire naturelle, Genève 663.87, 915.45–.46, 1361.58, and 1510.19; Museum A. Koenig, Bonn 6386, 17837, 18653, 18676, 20401–02, 26233–35, 27353–54, 34558–59, and 44105; National Museum of Natural History, Washington 196435 and 196436.

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