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BIOSYSTEMATICS OF THE CANYON TREE FROG *HYLA CADAVERINA* COPE (= *HYLA CALIFORNIAE* GORMAN)

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INTRODUCTION

This paper reviews the taxonomy of the canyon tree frog, *Hyla cadaverina*, and describes its geographical variation. Baird and Girard (1852, p. 174) described the Pacific tree frog, *Hyla regilla*, from collections made on the Sacramento River, in Oregon, and in Puget Sound by the U. S. Exploring Expedition under the command of Captain Charles Wilkes. Hallowell described *Hyla scapularis* (1852, p. 183) from Oregon collections and *Hyla scapularis* var. *hypochondriaca* (1854) from Dr. A. L. Heermann's collections from Tejon Pass in southern California. Hallowell (1854) also described a second species from his analysis of Dr. Heermann's Tejon Pass collection as being distinctive from *Hyla scapularis* and used the name *Hyla nebulosa* as the species designation. Baird and Girard (1852, p. 301) referred to *Hyla scapularis* as a synonym of *Hyla regilla* after examining specimens collected by Dr. John L. LeConte in San Francisco. These early collections disclosed the presence on the Pacific Coast of two distinct species, *Hyla regilla* and *Hyla nebulosa*.

Cope (1866, p. 84) substituted *Hyla cadaverina* for the preoccupied *Hyla nebulosa* (Spix, 1824). Yarrow (1882) and Cochran (1961) list the type specimen of *Hyla cadaverina* as USNM 3230. However, Jameson (1966) notes that USNM 3230 is from Fort Vancouver, Washington, and assigned this specimen to *Hyla regilla*. Cope (1889) states that two specimens of *Hyla* collected by Dr. Heermann from Tejon Pass, southern California, are located in the Museum of the Academy of Natural Sciences of Philadelphia.

Test (1898) attempted to rectify the confusion in the general taxonomy of *Hyla regilla*, reviewed the taxonomic history of the species, and lumped *Hyla nebulosa* and *Hyla cadaverina* as synonyms of *Hyla regilla*. Test noted that the specimen of *Hyla nebulosa* which he examined was collected by Dr. A. L. Heermann and that, of the two originally collected by Dr. Heermann, only one (USNM 3230) still existed in the museum collection. Cope (1889) described a specimen of *Hyla nebulosa* (= *Hyla cadaverina*) that was collected from Fort Tejon, California, under the synonymy of *Hyla regilla* var. *regilla* and described the specimen of *Hyla nebulosa* as one of the three color variations. The specimen was in poor condition and was said to be ash gray, with dorsal blotches wanting, and similar to *Hyla squirella*. Cope questioned its synonymy with *Hyla regilla*. The specimens described by Cope and Test are obviously not any of the cotypes originally described by Hallowell as *Hyla nebulosa* (Jameson, et al. 1966). Storer (1925) and Slevin (1928) also place *Hyla nebulosa* and *Hyla cadaverina* in synonymy with *Hyla regilla*.

Baird (1854) described *Hyla affinis* from the northern Sonoran region and Cope (1866), noting the preoccupancy of *Hyla affinis* (Spix, 1824), substituted *Hyla arenicolor* as a synonym. Yarrow (1882) and Cope (1889) refer to two specimens of *Hyla arenicolor* from the collections of H. W. Henshaw in 1875 from southern California. Richardson (1912) described *Hyla arenicolor* and listed specific locales of several collections in southern California in which this species was found. Wright and Wright (1949), Stebbens (1951), and others noted differences between *Hyla arenicolor* collections from east and west of the Mojave and Imperial deserts and Gorman (1960) separated the western populations of *Hyla arenicolor* into a separate species based on morphological and ethological comparisons with the eastern populations. The western populations were designated by Gorman as *Hyla californiae*. The type specimen was an adult female, number 31,773, in the University of California Museum of Vertebrate Zoology collected at Canyon de Llanos, 9 miles (14.5 km.) SSW. of "Alaska" (La Rumorosa), Partido del Norte, Baja California, Mexico.

The historical survey of the literature and the examination of the type specimens reveal that the following names have been used to describe the "canyon tree frog" inhabiting the range from San Luis Obispo County, central California, to approximately latitude 29° north, Baja California, Mexico: *Hyla nebulosa* Hallowell, 1854; *Hyla cadaverina* Cope, 1866; *Hyla regilla* Cope, 1889; *Hyla arenicolor* Yarrow, 1882; *Hyla californiae* Gorman, 1960.

We submit that the first valid name describing the canyon tree frog from the Pacific Coast is *Hyla cadaverina* Cope. Two specimens of *Hyla* both listed as number 3230 in the Museum of the Academy of Natural Sciences of Philadelphia, appear to be the two cotype specimens of *Hyla nebulosa* described by Hallowell.

We have examined the qualitative and quantitative morphological variation of the available specimens and we have studied the nonmorphological and ecological characteristics of the several populations in order to determine whether or not biologically distinguishable races exist.

MATERIALS AND METHODS

MEASUREMENTS. A total of nine individual structural measurements were taken from 225 males representing 26 distinct populations and 72 females representing 10 distinct populations. Vernier calipers were used to measure snout-vent length, head width, forearm length, and shank length. A Bausch and Lomb dissecting microscope with an ocular micrometer insert was used to measure nostril-lip height, finger pad width (third digit), length of the fourth toe, and webbing development (between the fourth and fifth toe). The measurements were recorded in millimeter units. The localities sampled (fig. 1), locality codes, and the number of individuals measured from each population sampled are given in table 1.

An analysis of morphological measurements of *Hyla cadaverina* has shown a highly integrated system of positively correlated characters (Ball and Jameson, 1966). The morphological characters selected for this study reflect total body shape and therefore form a discriminate complex for the differentiation of various localities.

MATHEMATICAL ANALYSIS. Multivariate statistics, which treats the total variation of (n) characters within and between groups around a grand mean on (n) characteristic vectors, were used to discriminate morphologically between the 26 populations sampled. The biological advantages of the use of multivariate statistical techniques are comprehensively discussed by Jolicoeur (1959), Cooley and Lohnes (1962), and Jameson *et al.* (1966). The variation of characters within the group was calculated by the within group covariance matrix W. The dispersion of group means was determined by the between group covariance matrix B. The characteristic vectors (discriminant functions) are the principal axes of matrix B after the standardization by matrix W.

The standardization of matrix B by matrix W corrects the population positions on the discriminant graphs by adjusting each measurement by the variances of the other measures allowing such variants as age and size to be minimized and the interpopulational differences to be emphasized. The length of the resultant vector from the grand mean expresses the maximum directional displacement of a specific character by specific populations. The data were programmed for and processed by the IBM 1620 computer. The

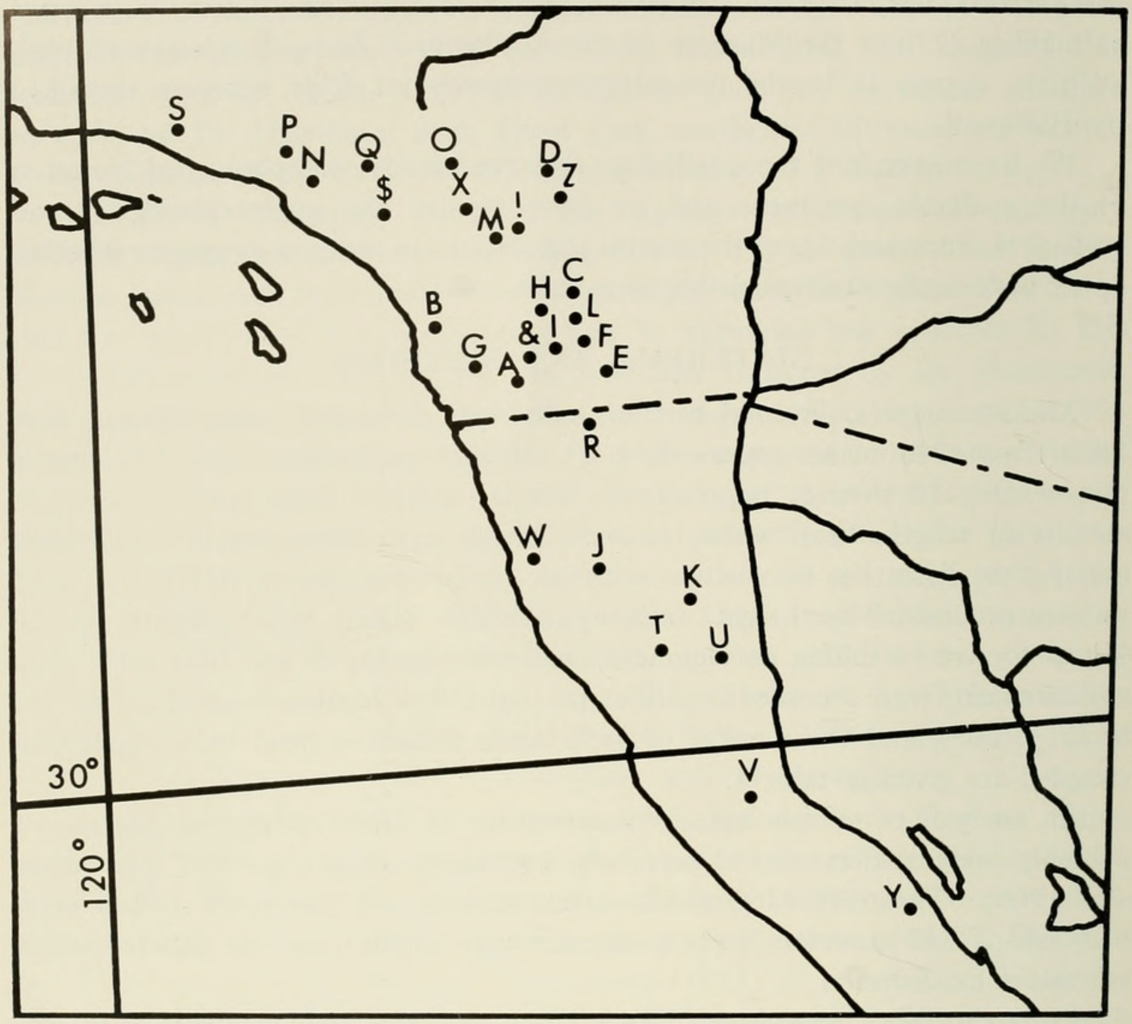

Figure 1. Localities of *Hyla cadaverina* populations sampled. Table 1 gives locality codes.

characteristic vectors are coded as follows on the discriminant graphs: V1, snout-vent length; V2, head width; V3, head length; V4, nostril-lip height; V5, forearm length; V6, finger pad width; V7, shank length; V8, length of fourth toe; V9, degree of webbing between fourth and fifth toe.

We appreciate the loan of specimens of *Hyla cadaverina* from the following institutions: University of California Museum of Vertebrate Zoology, California Academy of Sciences, Stanford University Natural History Collection, San Diego Museum of Natural History, and the San Diego State College Research Collection. We have examined specimens from and extend our thanks to the appropriate staff members at the Los Angeles County Museum of Natural History, University of Southern California, University of California at Los Angeles, American Museum of Natural History, Academy of Natural Sciences of Philadelphia, Museum of Comparative Zoology, Harvard University, Uni-

TABLE 1. *Geographic localities sampled, locality codes, and the number of specimens measured from each population.*

Locality	Code	Number of individuals measured		Forearm length / Shank length
		Females	Males	Males
Pine Valley, San Diego County	A		5	.406
DeLuz, San Diego County	B		7	.399
Coyote Creek, San Diego County	C		5	.391
Forty-nine Palms Canyon, San Bernardino County	D		10	.424
Agua Caliente Springs, San Diego County	E		5	.416
La Puerta, San Diego County	F	6	15	.406
El Capitan, San Diego County	G	10	5	.410
Tubbs Springs, San Diego County	H	4	9	.404
Sentenac Canyon, San Diego County	I		8	.412
Ojos Negros, Baja California Norte	J		11	.414
Mesquite Springs, Valle Trinidad, Baja California Norte	K	10	11	.418
Borrego Palm Canyon, San Diego County	L	6	11	.416
Little Morongo Canyon, San Bernardino County	M		8	.409
La Crescenta, Los Angeles County	N		9	.383
Mojave River (West Fork), San Bernardino County	O		7	.402
Sespe, Ventura County	P		6	.390
Tujunga River, Los Angeles County	Q		11	.394
Canyon de Llanos, Baja California Norte	R		6	.423
Fillmore, Ventura County	S		11	.389
San Jose, Baja California Norte	T		8	.421
El Cajon Canyon, Baja California Norte	U		9	.445
Aqua Dulce, Baja California Sur	V	8	10	.425
Ensenada, Baja California Norte	W		11	.420
Soboba Springs, Riverside County	X		6	.436
Bahía de los Angeles, Baja California Sur	Y	6	11	.436
Indian Cove, San Bernardino County	Z		10	.428
San Dimas Canyon, Los Angeles County	$	6		
Boulder Creek, San Diego County	&	8		
Whitewater Canyon, Riverside County	!	8		
Totals		72	225	

versity of Michigan Museum of Zoology, Chicago Natural History Museum, and the United States National Museum. E. G. Bauer, D. Bacon, and M. Anderson assisted with the computation at the San Diego State College Computer Center. R. C. Jameson performed the illustrations assisted by the computer. Financial assistance for parts of this study has come from the San Diego State College Foundation, San Diego Natural History Museum, California Academy of Sciences, National Science Foundation (G-15558), and the National Institutes of Health (RG-8489).

Table 2. *Character grand means, standard deviations from the grand mean, and population means of the 26 male populations sampled.*

Characters	V1	V2	V3	V4	V5	V6	V7	V8	V9
				Grand Means					
	31.80	11.98	9.62	2.46	6.89	1.44	16.55	6.54	3.63
		Pooled Standard Deviation from the Grand Mean							
	3.72	0.62	0.30	0.03	0.24	0.29	1.14	0.23	0.15
				Population Means					
Population									
A	30.84	11.52	8.76	2.36	6.68	1.42	16.44	6.16	3.32
B	32.61	12.23	9.30	2.59	6.86	1.67	17.19	6.86	3.70
C	33.96	12.84	9.82	2.60	7.02	1.70	17.94	6.82	3.86
D	33.86	13.07	10.05	2.67	7.18	1.52	16.92	6.81	3.87
E	33.04	12.86	9.78	2.54	7.16	1.78	17.22	6.90	3.64
F	32.29	12.10	9.76	2.54	6.92	1.65	17.05	6.73	3.65
G	34.18	12.54	10.10	2.50	7.28	1.64	17.76	6.86	3.84
H	30.31	10.91	9.02	2.27	6.41	1.46	15.88	6.16	3.50
I	30.71	11.44	9.08	2.31	6.61	1.43	16.01	6.23	3.65
J	31.24	11.78	9.44	2.57	6.93	1.50	16.72	6.47	3.61
K	33.41	11.93	9.79	2.66	7.16	1.66	17.11	6.86	3.90
L	34.42	12.83	10.57	2.67	7.45	1.63	17.91	6.95	3.99
M	30.50	11.00	8.95	2.35	6.44	1.23	15.73	5.80	3.50
N	29.38	11.19	9.02	2.29	6.10	1.32	15.52	6.10	3.66
O	27.94	10.95	8.79	2.29	6.04	1.21	15.03	5.90	3.69
P	29.92	11.18	9.20	2.32	6.32	1.40	16.20	6.52	3.73
Q	28.85	11.08	8.90	2.23	5.88	1.39	14.92	5.86	3.57
R	34.12	12.85	10.52	2.58	7.48	1.52	17.67	7.28	3.77
S	28.83	11.04	9.06	2.16	6.15	1.32	15.80	6.37	3.59
T	28.85	10.89	9.06	2.24	6.29	1.25	14.91	5.76	3.43
U	31.58	12.04	9.94	2.41	7.17	1.32	16.12	6.34	3.80
V	36.41	14.25	11.15	2.76	8.23	1.37	19.38	7.48	4.10
W	31.95	11.89	9.85	2.36	6.99	1.39	16.63	6.71	3.63
X	28.67	11.10	9.08	2.25	6.92	1.30	15.88	6.25	3.72
Y	31.75	12.12	10.15	2.47	6.83	1.10	15.66	6.15	2.28
Z	35.71	13.55	10.38	2.89	7.66	1.57	17.91	7.12	3.91

DESCRIPTION

For gross morphological and ethological descriptions of *Hyla cadaverina*, we refer the reader to Hallowell (1854), Wright and Wright (1949), Stebbins (1951), Gorman (1960), and Ball and Jameson (1966). The tadpole of *Hyla cadaverina* is described by Gaudin (1964, 1965). We deliberately limit our description to new material and to that necessary to document our systematic conclusions.

TABLE 3. *Character grand means, standard deviations from the grand mean, and population means of the 10 female populations sampled.*

Characters	V1	V2	V3	V4	V5	V6	V7	V8	V9
				Grand Means					
	38.25	14.03	11.16	2.74	8.35	1.76	19.70	7.72	3.41
		Pooled Standard Deviation from the Grand Mean							
	4.71	0.97	0.46	0.04	0.32	0.29	1.60	0.18	0.14
				Population Means					
Population									
G	37.91	13.52	10.75	2.70	8.70	1.75	19.73	7.65	3.44
H	39.60	13.85	11.15	2.70	7.95	2.00	20.27	8.20	3.40
V	42.43	15.90	12.01	3.06	9.49	1.73	21.70	8.10	3.95
F	36.90	14.50	11.16	2.62	8.47	1.68	19.90	7.65	3.42
L	39.83	14.96	11.73	2.75	8.78	1.90	20.66	7.80	3.40
&	34.55	13.02	10.26	2.50	7.73	1.64	18.45	6.96	2.89
K	36.73	13.05	10.29	2.65	7.80	1.67	18.44	7.55	3.23
$	38.23	14.10	11.15	2.85	8.18	1.82	20.05	8.10	3.82
Y	39.78	14.45	12.58	2.93	8.82	1.68	19.66	7.68	3.21
!	36.58	13.02	10.52	2.68	7.60	1.71	18.16	7.50	3.30

The color patterns of *Hyla cadaverina* are highly variable. The mountain forms generally are dark in color and have large melanophore patches which blend into the granite rock patterns along the streams. The coastal and desert forms usually display diffuse melanophore patterns and are generally lighter in color than the montane forms. The diffusion of coloration on the dorsal surface of many of the coastal and desert forms appears to correlate with the prevalent native stone within their habitats.

The character grand means, standard deviations from the grand means, and populations means of the 26 populations of males and 10 populations of females sampled in this study are given in tables 2 and 3. An examination of the grand means of the male and female populations sampled reveals the sexual dimorphic characters of *Hyla cadaverina.* The snout-vent measurement is the best overall measure of size (Ball and Jameson 1966), and the female is 6 to 7 mm. mean larger than the male in snout-vent length. The females are larger in all of the measurements taken except for the degree of webbing.

DISCRIMINATORY ANALYSIS. *Male populations.* The sum of the variance components of the first nine discriminant axes was 1572.98 (X^2 with 225 degrees of freedom), which is highly significant (table 4). The first two discriminant axes contain 59.6 percent (36.9 + 22.7) of the total variation within and between the populations. The multivariate dispersion plots on the

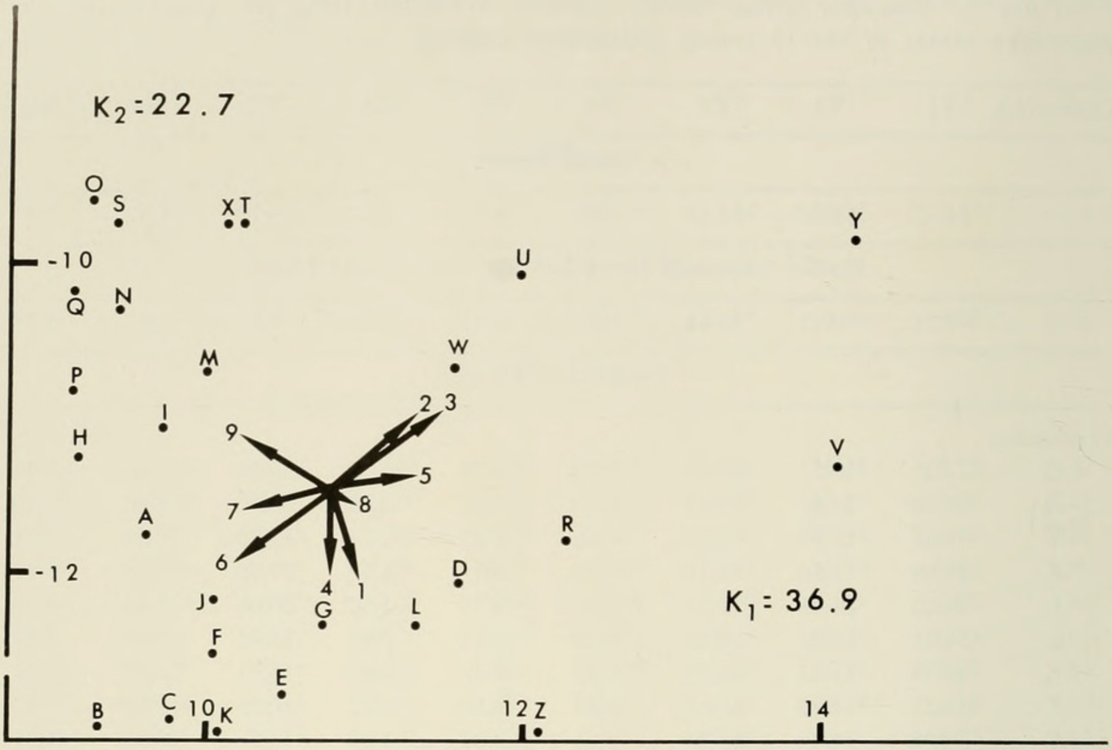

FIGURE 2. Discriminant analysis of 225 male canyon tree frogs. The mean of each sample is shown on the first (K_1 = 36.9%) and second (K_2 = 22.7%) discriminant axes. The original coordinates are represented by the direction of each vector emanating from the grand mean. The length of the vector is representative of one standard deviation of the measurement. The measurements are labeled as indicated in the text. Localities are shown in figure 1.

K_1–K_2 discriminant axes (fig. 2) demonstrates a general north-south (left to right) geographical distribution. The samples from the geographically isolated populations at Agua Dulce (V) and Bahía de los Angeles (Y) appear as isolates, occurring on the right portion of the plot. Both of these populations (V and Y) are among geographical isolates occupying the southern extremes of the distribution of *Hyla cadaverina.*

The populations on the right half of the dispersion plot are separated into a distinct group by generally having larger head dimensions (V2 and V3), longer forearms (V5), and increased length of the fourth toe (V8). Larger finger pad widths (V6), shank lengths (V7), and increased webbing (V9) characterize the populations on the left half of the dispersion plot. Samples from populations at El Capitan (G), Agua Caliente (E), and Borrego Palm Canyon (L) display a larger relative snout-vent length (V1) and nostril-lip height (V4).

The plots of the third and fourth discriminant axes (fig. 3) contain 18.1 percent of the total variation and demonstrate some of the characters by which closely grouped populations on the K_1–K_2 plot differ. A shorter shank length

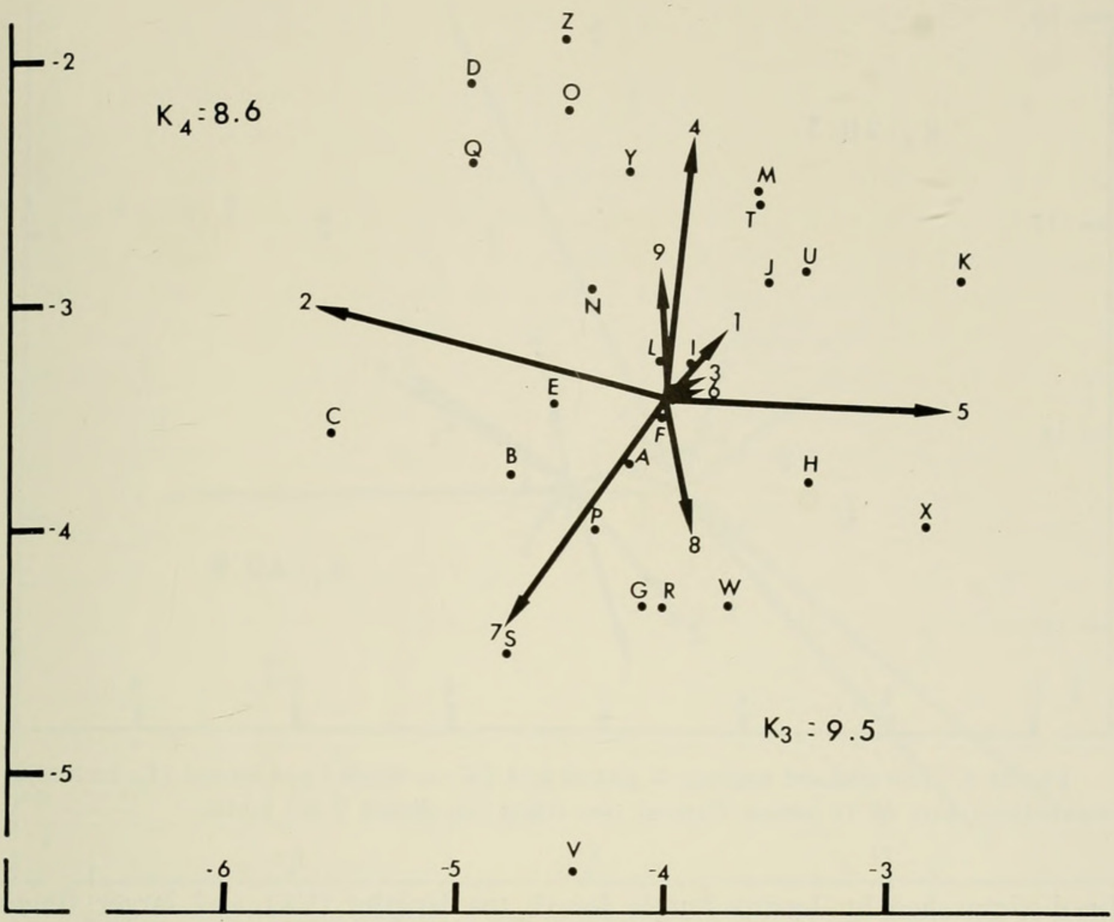

FIGURE 3. Discriminant analysis plot of third ($K_3 = 9.5\%$) and fourth ($K_4 = 8.6\%$) discriminant axes of males. See figure 2 for labels.

(V7) and increased webbing (V9), a longer snout-vent length, (V1) and a higher nostril-lip height (V4) differentiate the population at Bahía de Los Angeles (Y) from that at Agua Dulce (V). Ojos Negros (J) differs from populations Agua Caliente (E) and Coyote Creek (C) by demonstrating a longer snout-vent length (V1), head length (V3) and a small finger pad width (V6).

DISCRIMINANT ANALYSIS. *Female populations.* An examination of the K_1–K_2 discriminant axes of the female populations sampled (fig. 4) displays a population distribution similar to the male K_1–K_2 discriminant plot. The total variance of the female plot is 438.54, significant at the 1 percent level (table 5). The plots of the first (variance 178.99, 40.8 percent) and the second axes (variance 90.13, 20.5 percent) again demonstrate that the southern isolates Agua Dulce (V) and Bahía de los Angeles (Y) are isolated on the plot. The sample from Tubbs Springs (H) appears along with Whitewater Canyon (!) Mesquite Springs (K) and San Dimas Canyon ($). These populations can

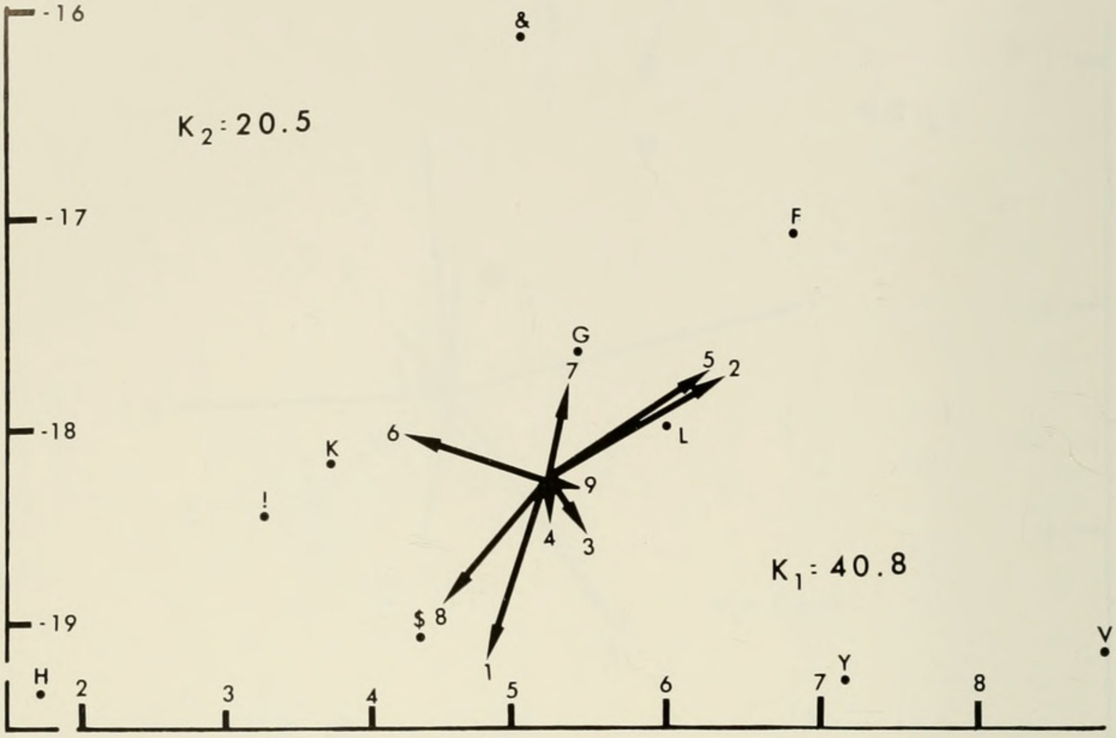

Figure 4. Discriminant analysis of plot of first ($K_1 = 40.8\%$) and second ($K_2 = 20.5\%$) discriminant axes of 72 female Canyon tree frogs. See figure 2 for labels.

be distinguished by having longer fourth toe lengths (V8) and larger finger pad widths (V6).

Longer shank lengths (V7) and shorter nostril-lip height (V4) discriminate frogs from El Capitan (G) and Boulder Creek (&) from the other populations. Animals from Bahía de los Angeles (Y) Aqua Dulce (V) and La Puerta (F) are characterized by having larger facial dimensions (V2 and V3), increased webbing (V9), and longer forearms (V5).

Table 4. *The percent of significant information and the characteristic roots (variance component) of the nine morphological measurements taken from 26 male populations.*

Discriminant Axis	*Variance Component*	*Percent of Total*	*Degrees of Freedom*	*Probability*
1	581.26	36.9	33	< 0.01
2	357.19	22.7	31	< 0.01
3	150.28	9.5	29	< 0.01
4	136.90	8.6	27	< 0.01
5	110.71	7.1	25	< 0.01
6	79.41	5.0	23	< 0.01
7	76.67	4.8	21	< 0.01
8	53.71	3.3	19	< 0.01
9	26.85	1.6	17	> 0.05

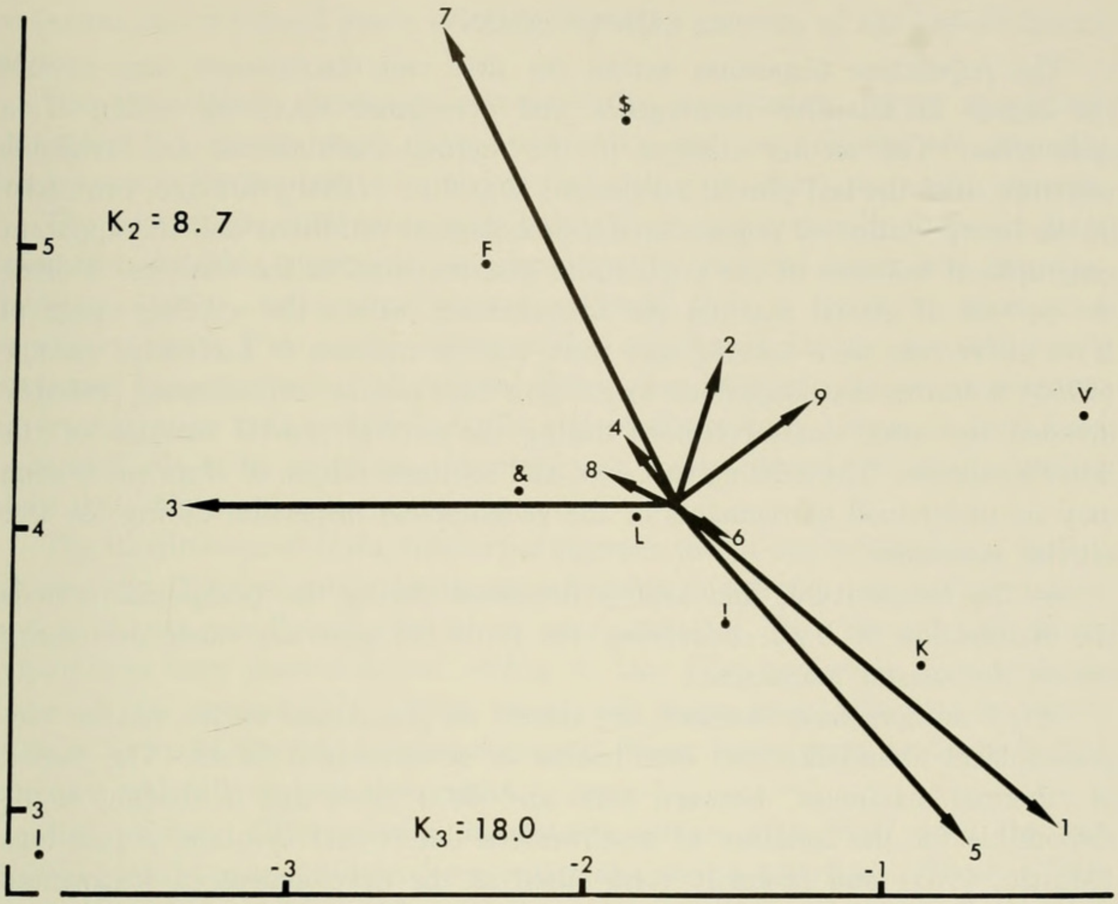

FIGURE 5. Discriminant analysis of plot of third (K_3 = 18.0%) and fourth (K_4 = 8.7%) discriminant axes of females. See figure 2 for labels.

The plots of the third and fourth discriminant axes (fig. 5) contain 26 percent of the total variation. A longer head length (V3) along with reduced webbing (V9) differentiates frogs from Bahía de los Angeles (Y) from those from Agua Dulce (V). Populations at Tubbs Springs (H) and San Dimas Canyon ($) differ from those at Mesquite Springs (K) and Whitewater Canyon (!) by having larger head widths (V2).

TABLE 5. *The percent of significant information and the characteristic roots (variance component) of the nine morphological measurements taken from 10 female populations.*

Discriminant Axis	*Variance Component*	*Percent of Total*	*Degrees of Freedom*	*Probability*
1	178.99	40.8	17	< 0.01
2	90.13	20.5	15	< 0.01
3	79.31	18.0	13	< 0.01
4	38.51	8.7	11	< 0.01
5	32.21	7.3	4	< 0.01
6	14.62	3.2	7	< 0.01
7	4.77	1.0	5	> 0.05

DISCUSSION

The population dispersion within the first two discriminant axes reveals the degree of adaptive convergence and divergence occurring within *Hyla cadaverina.* The secular changes in the thermal environment and available moisture since the last pluvial maximum, 10,000 to 11,000 years ago, can assist in the interpretation of populational morphological variations and the apparent geographical isolation of the populations discriminated in the analysis. During the periods of glacial maxima the temperatures within the existing range of *Hyla cadaverina* were lowered and there was an increase in humidity. Savage (1960) indicates that amphibian forms with high rainfall requirements probably invaded the moist coastal regions during the several pluvial maxima of the late Pleistocene. The existing east-west and southern ranges of *Hyla cadaverina* may be understood as remnants of the geographical dispersion during the last pluvial maximum.

As the temperatures and aridity increased during the postglacial periods the distribution of *Hyla cadaverina* was restricted generally north and south within the coastal mountains.

Many authors have stressed the effects of postglacial cycles on the biogeographical abundance and distribution of southwestern forms. The period of "thermal maximum" between 4000 and 8000 years ago is thought to be responsible for the isolation of southwestern desert and montane populations (Martin, 1963) and probably contributed to the development of fragmented populations of *Hyla cadaverina* to the east (desert) and in the high desert of the northern Baja California peninsula. Amphibians such as *Bufo microscaphus, Scaphiopus hammondii,* and *Hyla regilla deserticola* share similar geographic ranges with *Hyla cadaverina* and may have undergone similar evolutionary patterns. As the temperature and aridity increased postglacially, amphibian populations became isolated in the south and eastern limits of their distribution to desert springs and cismontane within stream habitats. Eastern isolates of *Hyla cadaverina* (Forty-nine Palms Canyon and Indian Cove) and southern isolates sampled (Agua Dulce and Bahía de los Angeles) are limited to spring-fed oases. The southern populations have probably been isolated from the intact species population the longest since the last altithermal period and this is reflected by the discriminant separation of these populations (fig. 2). Martin (1963), using pollen records, indicates that post pluvial droughts were probably limited to the winter months and that the interglacial period was relatively wet from summer rains.

The coefficients derived using populations means of forearm length/shank length suggests appendage adaptations accompanying aquatic habitat differences and isolation in desert springs areas (see table 1). The populations with relatively shorter shank lengths and larger forearm lengths (larger coefficients in table 1) are characteristically found in isolated springs within the southern or eastern distributional limits or along the steep canyons of the eastern Sierra slopes.

The populations displaying proportionally significantly larger appendage characters, i.e., shank length, finger pad width, and toe webbing, are generally from aquatic environments requiring the ability to adapt to swift currents.

The populations from more xeric habitats are proportionally larger in their snout-vent lengths, suggesting an adaptation for reduced water loss capacity. Jameson (1966), using experimental evidence from a series of desiccation experiments with *Hyla regilla,* indicated that organismal size was not sufficiently explained by latitudinal or elevational distribution. Genetic characters adapting *Hyla cadaverina* both morphologically and physiologically appear to have been playing a role in its evolution. Montane and coastal forms are usually smaller than their more xeric counterparts.

The distribution of *Hyla cadaverina* suggests that it has adapted to a variety of weathers. The mountain forms are subjected to extreme temperature ranges and have been vocally recorded at air tempratures of 7°C. Several high desert populations have been observed calling in late June and early July with air temperatures around 30°C. High elevational forms must hibernate in winter months to avoid freezing temperatures and desert forms must aestivate in late summer and fall or face desiccation.

The primary differentiation in western canyon tree frogs since the last pluvial period appears to have been within the xeric populations. There is little doubt that many of the populations of the desert regions are genetically isolated from those in the mountains. Obviously animals in one mountain range are spatially isolated from those in other ranges. While we can generally recognize that a given collection is from the desert or from a particular mountain range, the translation of the cues to a key or to a workable description has been intractable. Additionally, we have not discerned significant differences in the life history of the animals from the several habitats. We conclude that the isolated populations are continuing to evolve in parallel paths as a result of the common genetic background and the restriction to a relatively narrow ecological niche. We refrain from describing subspecies of *Hyla cadavenia* for we feel that to do so at this stage of knowledge would merely obscure biological truths. (Jameson, et al., 1966, p. 552.)

The evolutionary relationship of *Hyla cadaverina* to the other southwestern species of tree frogs has not been firmly established. Gorman (1960) suggests *Hyla arenicolor* as the probable sibling or parent species of *Hyla cadaverina.* The present distribution of *Hyla arenicolor* is from Texas to middle Arizona and including northern Mexico. Contact between *Hyla cadaverina* and *Hyla arenicolor* could have been established during the last pluvial period. The adult morphology of both *Hyla cadaverina* and *Hyla arenicolor* is very similar to *Hyla regilla.* Gaudin (1965) states that larval characters, especially larval mouth parts, of *Hyla regilla* and *Hyla cadaverina* more closely resemble each other than either does *Hyla arenicolor*. The calls suggest that *Hyla cadaverina* and *H. regilla* are closely related. Discriminant analysis of the relationships of North American *Hyla* reveals a closer morphological relationship between *Hyla arenicolor* and *Hyla cadaverina* that either have to *Hyla regilla*. Hybridization experiments using *H. regilla, H. cadaverina,* and *H. arenicolor* fail at very early stages. Conclusive assumptions of the evolutionary relations of southwestern species of *Hyla* await further study.

SYNONYMY

Hyla cadaverina, (Cope).

Hyla nebulosa, Hallowell, 1854. Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 7, p. 96; type description; type locality, Tejon Pass (California).

Hyla cadaverina, Cope, 1866. Journal of the Academy of Natural Sciences of Philadelphia, second series, vol. 6, p. 84. Substitute name for preoccupied *H. nebulosa* Spix, 1824.

Hyla regilla, Baird and Girard. Cope, 1889. Bulletin U. S. National Museum, vol. 34, p. 359.

Hyla arenicolor, Cope. Yarrow, 1882. Bulletin U. S. National Museum, vol. 24, pp. 1–249.

Hyla californiae, Gorman. 1960. Herpetologica, vol. 16, pp. 214–222.

Holotype. Number 3230. Museum of the Academy of Natural Sciences of Philadelphia. Collected by Dr. Heermann.

TYPE SPECIMENS

The following type specimens were examined: United States National Museum: 3230 (*Hyla nebulosa* by error), 3235 (*Hyla scapularis hypochordriaca*), 9182 (*Hyla regilla*, Puget Sound), 15409 (*Hyla regilla*, Sacramento River). Academy of Natural Sciences of Philadelphia: 1978 (*Hyla scapularis*), 3230 (*Hyla nebulosa*). Museum of Vertebrate Zoology of the University of California: 31773 (*Hyla californiae*).

TEJON PASS SAMPLE

The description of a male-specimen sample from Tejon Pass, Los Angeles County, California (Los Angeles County Museum No. 26340-26348) follows:

A moderate to small population typical of the northern montane and coastal forms attaining an average snout-vent size of approximately 30.4 mm.; dorsal skin moderately pustulate; volmerine teeth distinct; moderate pectoral granulation becoming fine anteriorly and posteriorly. A small vestige of webbing exists between the first three fingers; finger pads large; first finger of males possessing nuptial callosities; toes at least three quarters webbed; tibiotarsal articulation to mid or anterior portion of the eye. The specimens color in alcohol a dark grayish brown with small diffuse melanophore patches closely dorsolaterally associated; abdomen a dark cream color; the vocal sac of the male not heavily pigmented with melanin; back of the thighs usually containing three melanin patches. The average morphological measures in mm. are as follows: snout-vent length 30.4, head width 11.3, head length 9.0, nostril to lip 2.4, forearm length 6.8, finger pad width (third digit) 1.4, shank length 15.6, length of fourth toe 6.3, and the webbing between the fourth and fifth toe 3.0.

SPECIMENS ANALYZED

Ventura County. California Academy of Sciences: 50309, 50311–15, 50396, 50399, 50409–10, 50418, 50440, 50446, 50453, 50455, 50467–68.

Los Angeles County. California Academy of Sciences: 39887–88, 39891, 39906, 39913, 39915, 39923, 39944, 39948, 39954–55, 40009, 40012, 40016, 40019–20, 40023–26. Los Angeles County Museum: 26340–48. San Diego Natural History Museum: 19251–52, 19255–57, 19259.

Riverside County. California Academy of Sciences: 43563–65, 43567, 43569–70. San Diego State College: 725–26, 734, 1033–34, 1116, 1143, 1164.

San Bernardino County. University of California, Museum of Vertebrate Zoology: 14061, 14064, 28245–46, 28250, 28252–55, 41052–59, 52455–60, 52462–63, 52470, 52480–81, 58434–36, 58438–39, 58440, 58442.

San Diego County. San Diego Natural History Museum: 342, 956, 958–59, 961, 963–66, 971, 973, 1112, 1114, 7517–19, 7522–25, 11521–24, 11527–31, 11536–43, 11592, 11987–89, 12008, 12499, 13256–59, 13331–32, 13334–38, 14256–58, 14260–65, 14267, 14272, 14274–75, 14497–98, 17134, 21302–03, 21306, 21308–09, 21311–14, 21316–17, 25177–80, 31359–66, 37250–52, 37254–56, 37258–60, 37263–64.

Baja California del Norte. San Diego Natural History Museum: 1041, 1044, 1049–54, 16955–62, 16964–65, 16967–74, 16976, 16978–79, 23463–64, 23466–67, 23469, 23472, 23474–77, 23479. University of California, Museum of Vertebrate Zoology: 9572, 9574–80, 9582, 31766–68, 31772, 31774, 31777. California Academy of Sciences: 13424, 13428–30, 13432–35, 13437–38, 13442, 57460–64, 57468, 57518–19. San Diego State College: B10–13, 682, 687–88, 694, 697, 719–20, 724, 727–29, 732–33, 735, 1038–40, 1042–43, 1046–48.

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