Brigham Young University
Science Bulletin

A TAXONOMIC STUDY OF CROTAPHYTUS COLLARIS BETWEEN THE RIO GRANDE AND COLORADO RIVERS

by

William Ingram III

and

Wilmer W. Tanner

BIOLOGICAL SERIES—VOLUME XIII, NUMBER 2

April 1971

TABLE OF CONTENTS

A TAXONOMIC STUDY OF CROTAPHYTUS COLLARIS BETWEEN THE RIO GRANDE AND COLORADO RIVERS

by

William Ingram III[1] and Wilmer W. Tanner[2]

INTRODUCTION

The Western Collared Lizard, *Crotaphytus collaris baileyi,* Stejneger, is an attractive lizard of marked variability. Its range, as now recognized, includes the area from the Great Basin south to central Baja California and Sonora; the desert slopes of mountains in southern California, east to the Continental Divide in southwestern Colorado and western New Mexico, and south into Chihuahua, Durango, Coahuila, Nuevo Leon, and San Luis Potosi (Stebbins, 1966; Smith and Taylor, 1950).

The range of *C. c. baileyi* is divided by several natural geographic barriers which have been shown to mark boundary lines for subspecies of other saurian forms. Stebbins (1954) describes patternal differences of *C. collaris* which are both consistent and specific for certain geographic areas. Fitch and Tanner (1951) proposed that at least one geographic area within the range of *C. c. baileyi,* the Upper Colorado River Basin, contains a population of Collared Lizards that is distinguishable on the subspecific level from *C. c. baileyi.* These studies suggest that *C. c. baileyi* may in reality be a heterogeneous taxonomic unit requiring more study.

The first step in the comprehensive study of the populations presently contained in *C. c. baileyi* requires a detailed study of the population represented by the type material. An analysis of the total Western Collared Lizard problem also includes a study of the Collared Lizard populations located in the Chihuahuan Desert and the Upper Colorado River Basin. This includes the three populations' interactions with each other. The analysis of the remaining populations of Collared Lizards now presently contained within *C. c. baileyi* and occurring in areas located primarily west of the Colorado River and Baja, California is the subject of another study currently in progress.

REVIEW OF LITERATURE

In 1890, Dr. Leonhard Stejneger described as new, *Crotaphytus baileyi.* The type locality was listed as "Painted Desert, Little Colorado River, Arizona," and the type specimen designated as U.S. National Museum No. 15281. Other specimens included in the type series were USNM 15282-15287.

Stejneger (1890) distinguished *C. baileyi* from *C. collaris* on the basis of four characters: (1) two rows of interorbitals, (2) smaller supraocular scales, (3) narrower head, and (4) longer snout. At the time of the description, Stejneger indicated that further investigation probably would show *C. baileyi* to intergrade with *C. collaris.* However, he described it as a new species until conclusive evidence of intergradation was provided. The geographic range of *C. baileyi* was set forth as western New Mexico, Arizona, Nevada, and northern Mexico.

E. D. Cope (1900), in his monumental work on North American reptiles, recognized the differences listed by Stejneger. However, he stated that "transitions (of characters between geographic areas) are so numerous that a distinct subspecific name is of doubtful utility." Cope failed to support his conclusions with a clear presentation of data, but merely compared the number of specimens on hand (80) as to the condition of their interorbitals. He failed to recognize *C. baileyi* as either a species or a subspecies because his series contained a large number of specimens intermediate to *C. collaris* or *C. baileyi* with respect to interorbital scalation. However, he states that most of these intermediate specimens came from the central portion of New Mexico and western Texas, the area proposed by Stejneger as the probable region of intergradation. Thus, one wonders why Cope failed to recognize *C. baileyi* and place it as a subspecies of *C. collaris.*

Stone and Rehn (1910) was the first to recognize *C. baileyi* as a subspecies of *C. collaris.* This was based on a series of eleven specimens from Pecos, Texas, in which specimens with characteristics of both *C. baileyi* and *C. collaris* were in the series.

In 1917 Stejneger and Barbour listed *C. c. collaris* and *C. c. baileyi* in their check list using central New Mexico as the dividing line between the two sub-

[1], [2]Department of Zoology and Entomology, Brigham Young University, Provo, Utah 84601

species.

Van Denburgh and Slevin (1921) described as new, *Crotaphytus insularis* from Angel de la Guardia Island, Baja California, Mexico. *Crotaphytus insularis* was separated from *C. c. baileyi* by three characters: (1) longer snout, (2) narrower head, and (3) single incomplete collar (Van Denburgh 1922). Burt (1928) showed definite relationships between the Collared Lizards of Angel de la Guardia Island and those of the mainland of Baja California and southern California. The lizards of this area are also in need of further study as a part of those populations occurring west of the Colorado River.

Crotaphytus dickersonae, was described by Schmidt (1922) from Tiburon Island, Sonora, Mexico. It was said to be distinguishable from *C. c. baileyi* by having "hindleg considerably longer than the body, a longer more distinctly compressed tail and slightly enlarged scales on the middorsal line of the tail." Burt (1928) expressed doubts as to the validity of this species, thus necessitating a further analysis of *C. dickersonae.*

Burt (1928) provided the only complete review of the species to date. He presented a detailed review of the literature and an excellent grasp of the problem of Collared Lizard taxonomy. He recognized the need for further study of the populations of Mexico and southern California and saw trends of variation within the Collared Lizards, but his investigations were not detailed.

Burt's analysis of the data was based on three assumptions, which are not substantiated by our data. He examined a large series (1,252) of lizards for the presence of ten characters, one meristic and nine proportional. His first assumption concerns the method used to assign lizards to either a western or an eastern group. He divided the Collared Lizards into two groups along state lines. The eastern group included Oklahoma, Kansas and Texas; and the western group, New Mexico, Arizona, Utah, Idaho, Oregon, California and Mexico. As was pointed out by Fitch and Tanner (1951), this completely disregards the possibility of the two subspecies' ranges not conforming to state lines. This is especially perplexing since all of the published ranges of *C. c. baileyi* and *C. c. collaris* designate the area of intergradation to be in central New Mexico and western Texas (Stejneger, 1890; Stejneger and Barbour, 1917).

Secondly, within the area Burt assigned to the Western Collared Lizard are the ranges of two forms of Collared Lizards, one form centered in the Great Basin and the other in Baja California and southern California.*

Thirdly, in the comparisons of body size and proportions, it is obvious from Burt's data (79-345 mm. total length for the eastern group) that there was no attempt to group specimens by age class. It is well known that body proportions, as well as length, change significantly from hatchling to adult (Mayr, 1969). The use of different age classes in the analysis of length and proportion characters may bias results proportionally to the percent of the total sample represented by each age class.

Fitch and Tanner (1951) separated the Yellow-headed Collared Lizard, *C. c. auriceps,* from *C. c. baileyi.* It was described as a population from the Upper Colorado River Basin, type locality: three and one-half miles north northeast of Dewey Bridge, Grand Co., Utah. *Crotaphytus c. auriceps* was separated primarily on the characters of coloration and supralabial scalation, thus introducing the factors of coloration and pattern as characters for distinguishing Collared Lizard populations.

The taxonomic history of *C. c. baileyi* and other Collared Lizards, along with their present status, is summarized in the following synonymies.

Crotaphytus collaris baileyi Stejneger

Crotaphytus baileyi Stejneger, 1890, N. Amer. Fauna, 3:103 [Type locality: Painted Desert, Desert of the Little Colorado R., Arizona; U.S. Nat. Mus.]
Crotaphytus collaris baileyi Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus insularis Van Denburgh and Slevin

Crotaphytus insularis Van Denburgh and Slevin, 1921, Proc. Calif. Acad. Sci., ser. 4, vol. 11:96 [Type locality: Angel de la Guardia Island, Baja California, Mexico; Calif. Acad. Sci.].
Crotaphytus collaris baileyi Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus dickersonae Schmidt

Crotaphytus dickersonae Schmidt, 1922, Bull. Amer. Mus. Nat. Hist., 46:638 [Type locality: Tiburon Island, Sonora, Mexico; U.S. Nat. Mus.].
Crotaphytus collaris dickersonae Allen, 1933, Occ. Pap. Mus. Zool. Univ. Mich., 259:7.
Crotaphytus dickersonae Smith and Taylor, 1950, Bull. U.S. Nat. Mus., 199:93
Crotaphytus collaris baileyi Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus collaris auriceps Fitch and Tanner

Crotaphytus collaris auriceps Fitch and Tanner, 1951, Trans. Kans. Acad. Sci., 54(4):553 [Type locality: three and a half miles north northeast of Dewey Bridge, Grand Co., Utah; Kans. Mus. Nat. Hist.].
Crotaphytus collaris baileyi Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

*An analysis of morphological similarity of Collared Lizards demonstrated the difference between forms.

MATERIALS AND METHODS

Selection and Gathering of Material

Specimens of *C. collaris* utilized in this study were from three sources: (1) specimens in the Brigham Young University Herpetological Museum, (2) specimens borrowed from several museums, and (3) live specimens collected in the field. Specimens from the first two sources were used for the measurement of meristic and proportional characters. Those collected in the field were used for pattern and coloration determination.

The museums with specimens on loan are listed below, followed by the abbreviation to be used throughout the remainder of this paper: Brigham Young University, BYU; California Academy of Science, CAS; California State College at Long Beach, CSCLB; University of Colorado Museum, CUM; University of Kansas, KU; Los Angeles County Museum, LACM; San Diego Society of Natural History, SDSNH; University of California, UC; University of Illinois Natural History Museum, UIMNH; United States National Museum, USNM; University of Texas at El Paso, UTEP; University of Utah, UU.

Four collecting trips were made to the area encompassed by this study. In May 1969, one short trip was made to southeastern Utah and a longer trip (two weeks in June) covered western New Mexico to the Nexican border and most of Arizona. During these trips specimens were collected from the Upper Colorado River Basin of Utah and Arizona, and the Chihuahuan Desert of New Mexico. Another extended trip to New Mexico and Arizona in May 1970 resulted in the collection of living specimens from the Upper Colorado River Basin of New Mexico; central New Mexico; Arizona, south of the Mogollon Rim, and additional specimens from the Upper Colorado River Basin of Utah and Arizona. During a final short trip in 1970 to southeastern Utah, we secured specimens from the northernmost extension of the range in Grand County, Utah. All living specimens examined during the course of this study will be deposited in the Brigham Young University Herpetological Museum.

Only those specimens whose snout-vent length was longer than 80 mm. were used in this study for the determination of both meristic-proportional and coloration-patternal characters. This was done to reduce the amount of bias caused by the mixing of age classes on character determination. The cutoff point was reached by determining the lower limit of a 90% confidence interval on the mean of the snout-vent length of adult *C. c. collaris,* using Fitch's data (Fitch, 1956). His data was used rather than data on adult *C. c. baileyi,* because a realistic diagnosis for *C. c. baileyi* has not been determined. Also, Fitch did the only ecological study on the Collared Lizards and is perhaps the most reliable source of adult snout-vent lengths.

The following lizards, listed by county within each state, were examined in the course of this study:

ARIZONA – Apache Co.: BYU 497; LACM 16895; UIMNH 7524; USNM 29184, 38056, 45035, 58610. Cochise Co.: CAS 35128-35135, 48615-48617 80748; USNM 8463, 8466, 8467, 14748, 19704-19706, 24462. Coconino Co.: BYU 506, 11388, 32110, 32109; UIMNH 6543, 35945, 74786-74790; USNM 15821, 15822, 60110-60113, 60115, 60117-60121. Gila Co.: UIMNH 34336, 74797, 74798. Graham Co.: UIMNH 24507, 82348-82353; USNM 5153, 51737, 51739, 54599, 54606. Maricopa Co.: CAS 80681, 80682. Mohave Co.: BYU 32116; UIMNH 74778, 74781-74784. Navajo Co.: BYU 13574; LACM 16894; UIMNH 74794-74796. Pima Co.: LACM 3983; SDSNH 15214; UIMNH 5899. Pinal Co.: UIMNH 74800; USNM 22129, 44681, 44708. Santa Cruz Co.: BYU 32106; LACM 26833; UIMNH 5900; USNM 16807, 17183. Yavapai Co.: BYU 33322; UIMNH 43208, 74767-74777, 82354; USNM 11860, 14814, 15689, 15690, 14710, 15892, 22206, 59750.

COLORADO – Baca Co.: CUM 9678-9680, 11340, 11343, 13666, 21727, 32278-32280. Bent Co.: CUM 19652, 19653. Las Animas Co.: CUM 1292, 2939, 7560-7562, 9675, 9681, 10030-10034, 11345, 32276. Mesa Co.: BYU 11342, 11344. Montezuma Co.: BYU 1577, 32108. Otero Co.: CUM 19654, 19655. Pueblo Co.: CUM 2622. San Miguel Co.: CUM 1333, 4448, 4450, 4451, 4453, 4456, 4458.

KANSAS – Anderson Co.: BYU 898. Montgomery Co.: BYU 22167. Wilson Co.: KU 41, 45, 46, 48-50, 54.

NEW MEXICO – Bernallilo Co.: USNM 58604. Chaves Co.: LACM 3974-3976. Dona Ana Co.: LACM 3971; USNM 22268, 25423; UTEP 54. Eddy Co.: LACM 3973, 16981-16983; UIMNH 8690; USNM 93034. Guadalupe Co.: LACM 16984, 16985, 16987; USNM 32862. Hildago Co.: BYU 32107; LACM 3977. Lea Co.: USNM 94360. Lincoln Co.: LACM 16990. Luna Co.: BYU 31940, 31942, 31944, 32120, 32121; USNM 44955, 80072. McKinley Co.: USNM 27738. Otero Co.: LACM 16975, 16988. Quay Co.: USNM 44940. Rio Arriba Co.: UU 3724-3732. Santa Fe Co.: CUM 7007; LACM 16907, 16908, USNM 8408, 8471. Sierra Co.: LACM 3981, 16992. Socorro Co.: LACM 3979, 3980, 16909, 16910, 16918, 16919, 16923, 16924, 16927-16929, 16931, 16932, 16934, 16935, 16940, 16942, 16944, 16945, 16947-16953, 16957-16962, 16966-16972, 16976, 16977, 16979; USNM 44573. Taos Co.: CUM 7006.

OKLAHOMA – Carter Co.: BYU 500, 1574.

TEXAS – Bexar Co.: BYU 13047, 13050, 13051. Brewster Co.: USNM 32852, 103663. Clay Co.: USNM 32857. El Paso Co.: USNM 59351, 59352; UTEP 52, 55-57; UU 493. Garza Co.: CUM 32277. Llano Co.: USNM 42309. Randall Co.: CUM 13554-13556. Roberts Co.: USNM 32866. Stephans Co.: BYU 13117. Valverde Co.: USNM 32850.

UTAH – Grand Co.: BYU 1625, 1626, 10338, 12854, 12855, 31949, 31950, 31981. San Juan Co.: BYU 1461, 1464, 12619, 13006-13008, 16484, 16801, 16802, 18333-18340, 21706, 31951, 31982, 32088, 32112-32117; UU 1461, 2427.

MEXICO – Chihuahua: BYU 13383-13386, 13410, 13411, 13736, 14211, 14212, 15184, 15186-15188, 15305, 15325, 16969-16976, 17010, 17014; KU3378, 33789, 44127; UC 70704; USNM 14242. Coahuila: UC 24721. Nuevo Leon: USNM 2728. Sonora: CSCLB 2752-2755, 2757, 2759-2764; LACM 8798, 8799, 52882, 52886; UC 10163; USNM 2694.

Statistical Methods

Upon initial examination of both living and preserved specimens, three distinct populations (groups) were postulated: (1) Upper Colorado River Basin, (2) central Arizona, (3) Chihuahuan Desert. An initial analysis consisting of six steps was performed to test the null hypothesis of no difference between groups. Multivariate techniques of data analysis were used extensively in this study for reasons to be discussed later.*

Step (1).

There were 66 meristic and proportional characters chosen to represent all observable areas of phenotypic variation. These characters included scale counts, proportions of body parts, and those patternal aspects that remain even after long periods of preservation. Body parts were measured using a Golgau Vernier Caliper. All scale counts of paired structures (e.g. supralabials) were done on the right side only.

Step (2).

A random sample of ten males and ten females from each proposed group was selected from the preserved material on hand. Ostle's random number table and method for entering the table randomly were used to select the random sample (Ostle, 1963). To enable the use of multivariate analysis, only those specimens that possessed some state of each of the 66 characters were used. For example, specimens that were damaged in some aspect were omitted from this part of the study.

Step (3).

The characters were measured on the sample and correlation analysis was performed. This eliminated those characters highly correlated with each other (hence measuring the same source of variation). When two or more characters were found to be highly correlated (0.75 or greater) the character with the greatest variation between groups was selected to represent all the correlates, and the other characters were dropped from the analysis.

Step (4).

A data organizing technique developed and programmed by Wishart (1968) was used to group the lizards in clusters of highest morphological similarity. This technique, known as Ward's Minimum Variance Cluster Analysis, arranges individuals in hierarchal minimum variance clusters, thus grouping together those lizards that are most alike, as defined by the characters measured. Chosen to represent the range of geographic locations available, 80 individuals were used as input (see Fig. 1 for areas represented). The program was halted when four clusters had been formed and the members of each of the clusters were recorded as to which of the proposed groups they represented. A chi-square contingency table was formed (see Table 1). This tested the null hypothesis that the grouping originally proposed was completely independent of a grouping formed by clustering those lizards of closest morphological similarity.

Step (5).

A two-way multivariate analysis of variance following the methods of Anderson (1958) and Morrison (1967) was performed on the data. The following model was used:

$$Y_{ijk} = U + A_i + B_j + e_{ijk}$$

where:

Y_{ijk} = a vector of measurements on an individual
U = a vector of effects on Y due to the mean
A_i = a vector of effects on Y due to location
B_j = a vector of effects on Y due to sex
e_{ijk} = a vector of effects on Y due to experimental error

The U-statistic and Mahalanobis D-square (Anderson, 1958) were used to test the null hypothesis of no difference between groups.

Step (6).

Using Mayr's coefficient of difference as an indicator, 24 characters were chosen that maximized the variation between groups (Mayr, 1969). These characters are listed in a separate section (entitled Taxonomic Characters) which immediately follows this section.

This step was done for three reasons: (1) to eliminate those characters that are relatively invariant from group to group, (2) to reduce the time involved in measuring characters on each lizard, and (3) to keep the matrices used in the analysis within the limits imposed by computer storage space.

Stepwise multiple discriminant analysis was then applied to the data to select the set of functions to be used in placing additional specimens into their proper group (Dixon, 1968).

Living specimens were examined for coloration and patternal characters. All specimens so examined were warmed under 200 watt light bulbs for 15-30 minutes before being analyzed. This was done to approximate the warmth and light the animal receives in nature and to reduce the variability in coloration and pattern that is the result of internal temperature variations of these animals.

Color and pattern characters, chosen to represent all of the observable differences, were combined into

*All statistical techniques which are relatively new or unfamiliar to workers in herpetological taxonomy will be treated in the section, "Statistical Discussion." A brief nontechnical description of each method will be presented.

groups, thus expressing a lizard's color and pattern as a single variable. Aspects of color or pattern that were invariant or so variable as to present no recognizable pattern were discarded from the analysis. (The final list of color-pattern combinations follows the list of proportional and meristic characters.) The combinations were then tested for independence when compared with geographic locations. Where significant, the color-pattern combinations were used to supplement the discriminant functions in identification.

The remaining specimens were then identified to determine the extent of the ranges and intergrading areas of the groups. The probabilities for each individual to be identified as a member of each of the groups were calculated. These probabilities, using a modification of Rao (1952), were used in outlining the areas of intergradation.

Taxonomic Characters

The following is a list of the 24 characters finally selected for measurement on preserved specimens (see Figs. 1 and 2) as well as the pattern and coloration characters selected from live specimens (see Fig. 3). Terms are taken from Smith (1946).

Body measurements.

Snout-vent length, length of second collar, tail length, and hindleg length were measured to the nearest tenth of a millimeter. Hindleg length was measured from the midline to the tip of the fourth toe. The second collar was measured from the insertion, in a straight line, to either its dorsal end or to the dorsal midline if the collar was not disjunct medially. Proportions were then formed from these measurements and used as the actual characters. The proportions were tail/snout-vent, tail/hindleg, and the second collar/snout-vent.

Internasals.

These are the number of scales in a straight line between the middle of each nasal.

Enlarged internasals.

These are the number of scales in the internasal series which were noticeably larger than the rest. These scales invariably formed a median row. If the row began at the anterior or posterior end of the internasal series, it was also recorded.

Fused interorbitals.

These are the number of interorbitals belonging to both supraorbital semicircles.

Frontoparietals.

These are scales in the midline anterior to the interparietal extending anteriorly to the meeting of supraorbital semicircles.

Head dorsal scales.

These are the number of scales lying in the middorsal line between the rostral and interparietal scales.

Loreal-lorilabial series.

These are the number of scales along a straight line perpendicular to the supralabials running through the loreals and lorilabials to the junction of the canthals and suboculars.

Supralabials.

These are the number of scales between the rostral, but not including it, and the point where the scales' shape change from rectangular to pentagonal, with the apex of the pentagon pointing ventrally.

Postmentals in contact with infralabials. These are recorded as 1 or 0 to correspond with yes or no.

Gulars.

These are the number of scales along a transverse line connecting the last infralabial on each side.

Dorsal scales.

Three characters were determined within the dorsals: (1) between the interparietal and the anterior-most projection of the first collar, (2) between the anterior-most projection of the first collar and the posterior border of the second collar, and (3) total dorsals.

Scales between the collar separations.

Two characters were determined from the collar's dorsal separation and one character from the pattern of the first collar: (1) the number of scales along a line connecting the lateral boundaries of the first collar's separation, (2) the number of scales along a line connecting the lateral boundaries of the second collar's separation, and (3) the number of spots, completely isolated from the main portion of the collar, within the first collar's separation.

Ventrals.

These are the number of scales along a midventral line connecting the mental and the anterior edge of the anus.

Subdigital lamellae.

These are the number of lamellae of the second, fourth and fifth toes on the right hind foot. The lamellae were considered to begin with the first scale that was obviously a member of the subdigital lamella series.

Femoral pores.

These are the number of pores in a straight line on the right hindleg.

Color-pattern Combinations

Five combinations of color were chosen. In all cases the color refers to ground color, and variations in hue around the basic color were considered equal. The color combinations, now known as color-pattern types, are (1) body dorsum green, head yellow to second collar, gular patch green, area between infralabials and gular patch yellow, (2) body dorsum green, head yellow to second collar, gular patch green, area between infralabials and gular patch white, (3) body dorsum green, head yellow not past eyes, posterior portion head pale in color, gular patch green, area

between infralabials and gular patch white, (4) center body dorsum brown, sides body dorsum green, head less than half yellow, head posterior cream, gular patch green, area between infralabials and gular patch white, (5) body dorsum brown, head white or cream, gular patch brown, black or intermediate, area between infralabials and gular patch white.

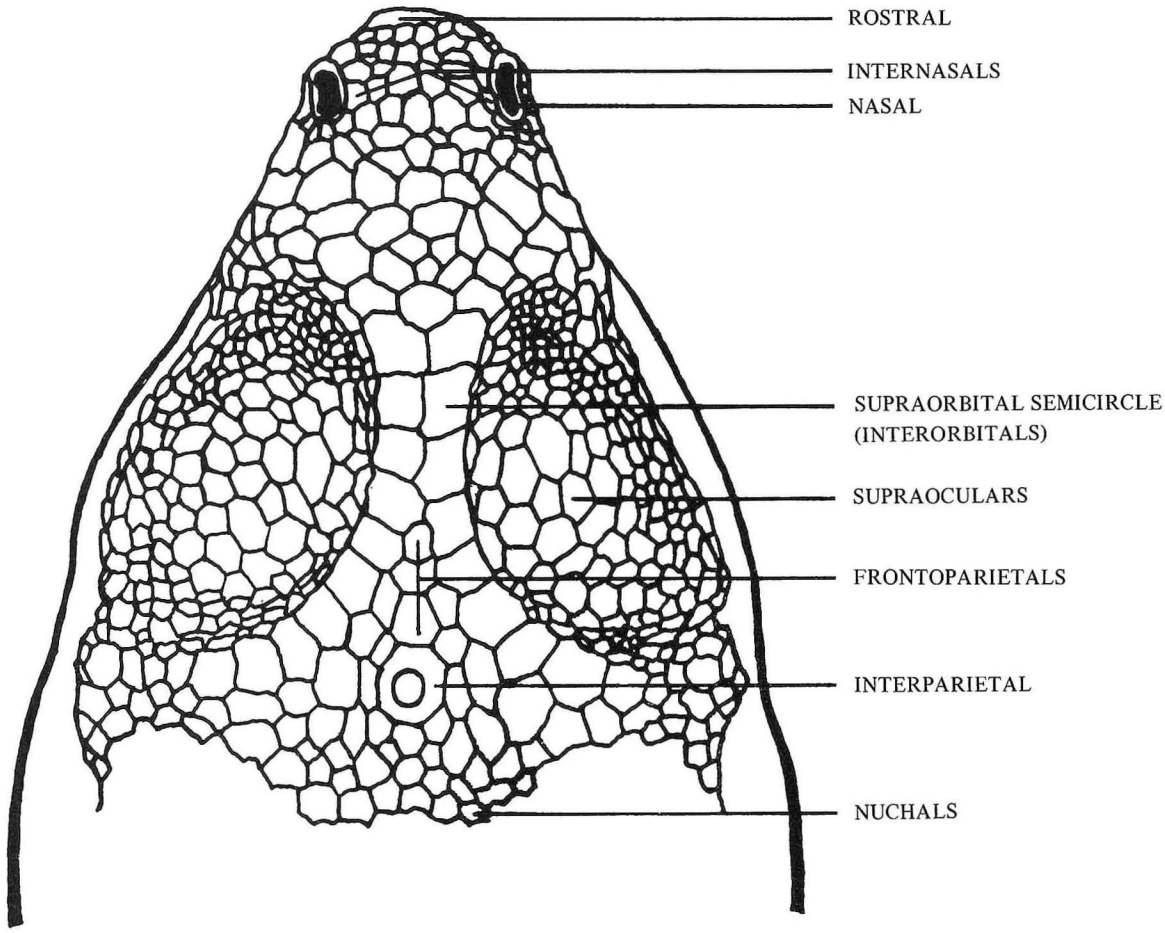


Fig. 1. A dorsal view of head scalation typical for the populations studied. (Drawn from BYU 21705)

RESULTS

Cluster Analysis

The four groupings formed by this method (see Fig. 4) were tested to see if they would support the groupings originally proposed in this study. All individuals from southeastern Utah and southwestern Colorado were considered to be *C. c. auriceps,* Arizonan specimens were labeled as *C. c. baileyi,* southern New Mexican and Mexican specimens were assigned to the Chihuahuan Desert population. Other specimens from Colorado, New Mexico, Texas, and Oklahoma were put in the *C. C. collaris* category.*

A contingency table was prepared comparing the groupings as proposed initially by the study (Upper Colorado River Basin, Central Arizona Plateau, Chihuahuan Desert, and Great Plains) with the four groupings formed by the cluster analysis (see Table 1). The null hypothesis (the two classifications, one by closest morphological resemblance and the other by geographical location, are completely independent of each other) was tested by a chi-square of nine degrees of freedom. The test statistic is significant at the 0.001 level.

*Twenty-five specimens from western Utah, Idaho, Nevada, California, and Baja California were also used in this cluster analysis. These specimens clustered together with no exceptions and remained separate until coefficient of approximately 30.0 was reached. This is taken as evidence that the Collared Lizards found west of the Colorado River are very different from those to the east.

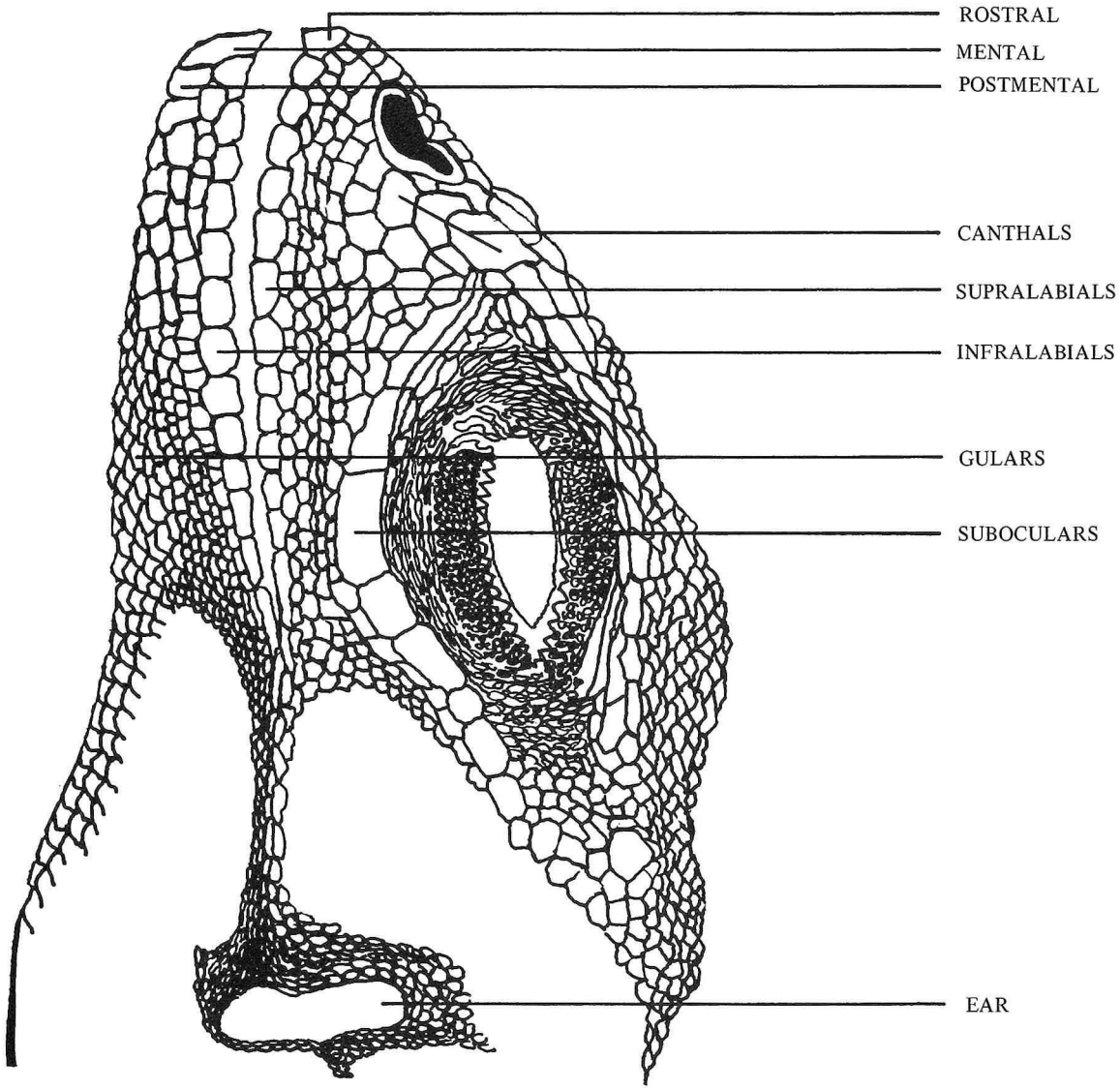


Fig. 2. A lateral view of head scalation typical for the populations studied. (Drawn from BYU 21705)

$$\chi^2_{(1-\alpha,9)} = (0_{iu} - E_{ij})^2/E_{ij}$$

$$\chi^2_{(1-\alpha,9)} = 80.768$$

$$\chi^2_{(0.999,9)} = 29.7$$

Therefore $\chi^2_{(1-\alpha,9)} \geqslant \chi^2_{(0.999.9)}$ and the null hypothesis is rejected. An analysis of the dependence pattern is as follows: The morphological relationships of the lizards examined form essentially the same groupings as those proposed at the onset of this study. (Ostle, 1963).

Analysis of Variance

One of the multivariate generalizations of the analysis of variance tests its hypothesis by means of the U-statistic (Anderson, 1958). The U-statistic was determined to be $U_{(66,3,75)} = 0.0209$. Since most U-statistic tables only go up to p=10, Paul Sampson's

Table 1. A contingency table testing the independence of Ward's clustering method and the proposed groups.

Clusters	Proposed groups			
	Upper Colorado	Central Arizona	Chihuahuan Desert	Great Plains
1	11	4	1	4
2	5	13	0	3
3	1	2	17	1
4	3	1	2	12

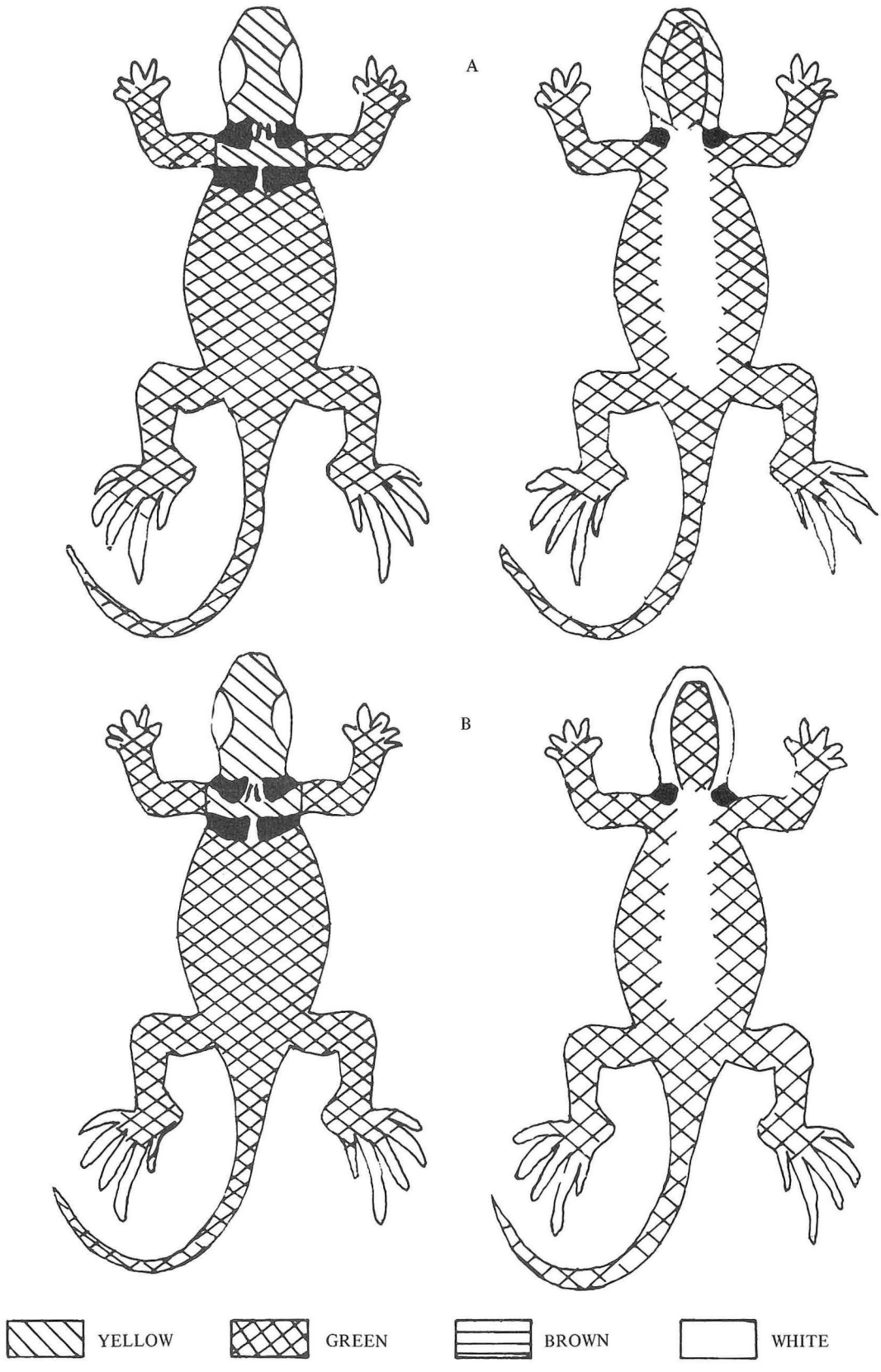
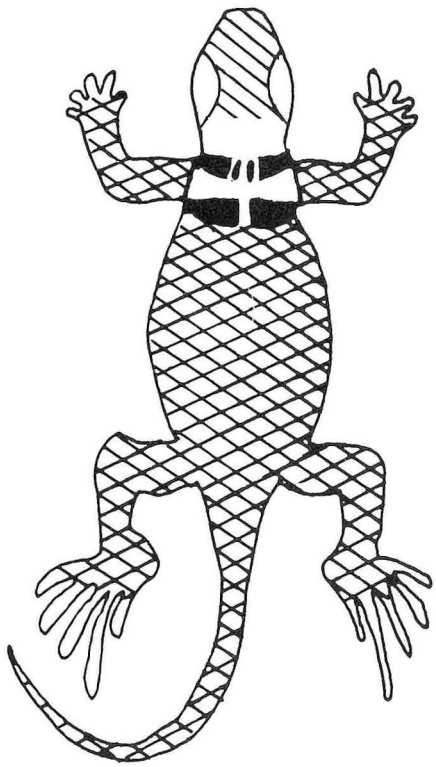
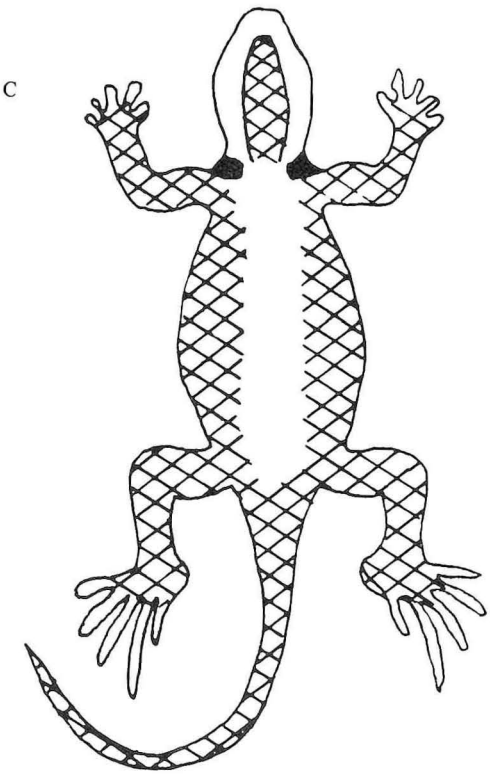


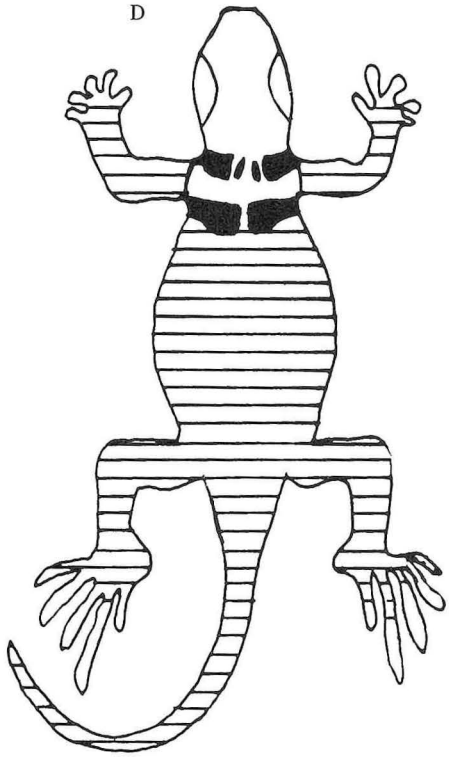
Fig. 3. Color-pattern characters: (A) type one, (B) type two, (C) type three, (D) type five, and (E) type four.



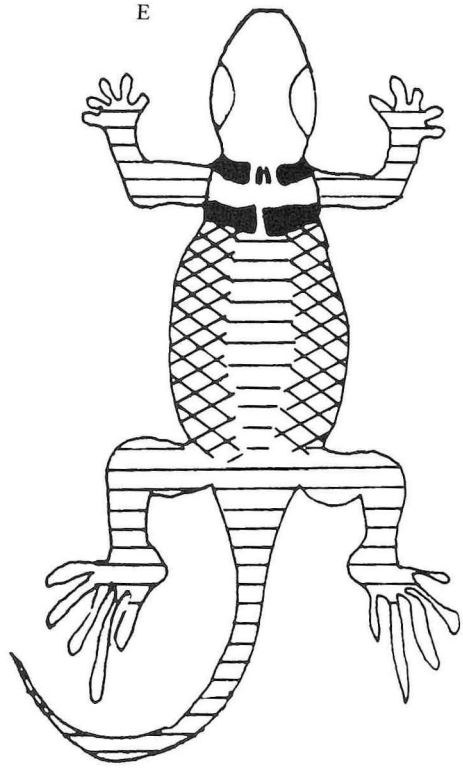
C



D



E



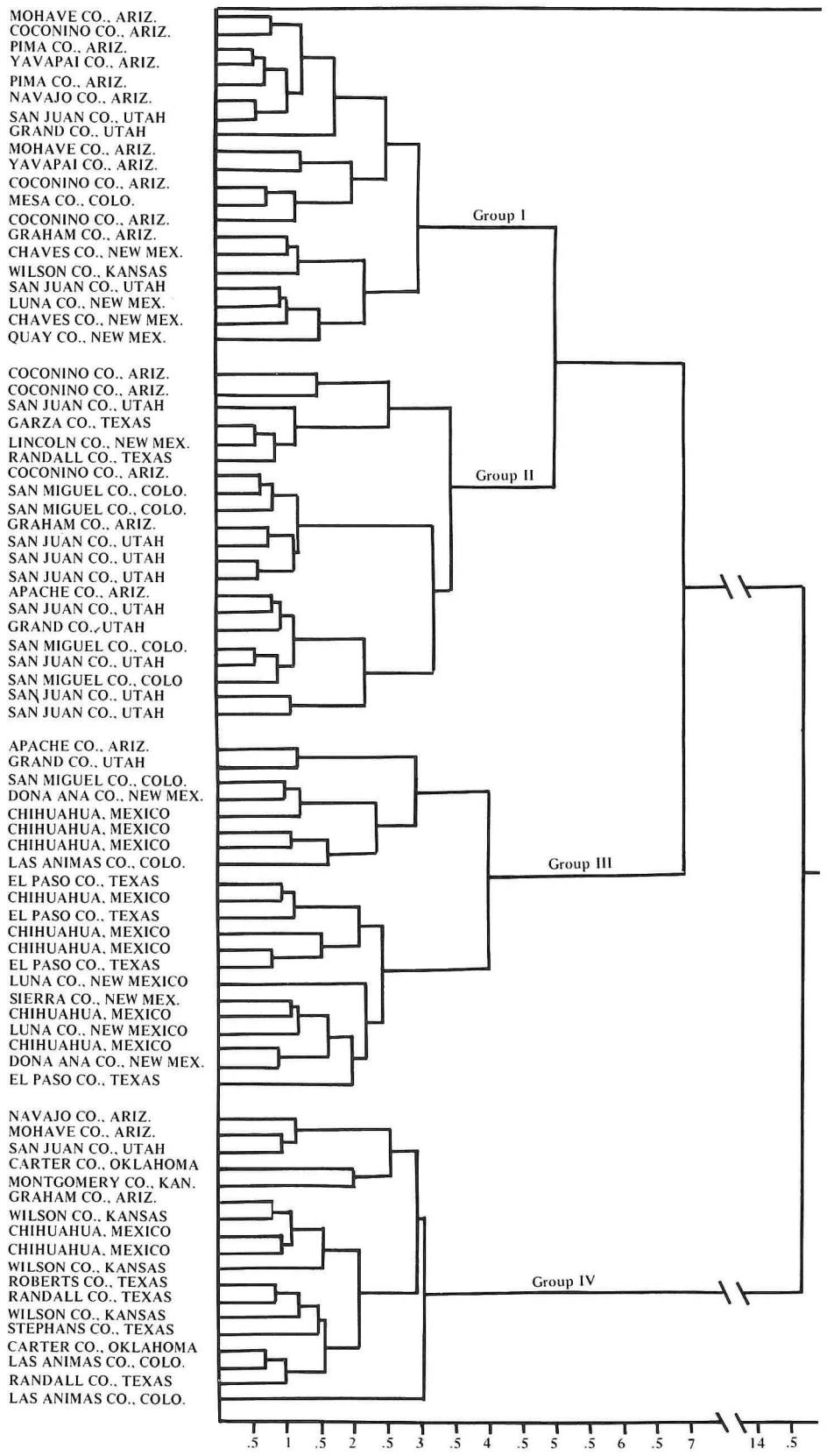


Fig. 4. Results of Ward's clustering method: (I) *auriceps,* (II) *baileyi,* (III) Chihuahua, (IV) *collaris.*

approximate F-value (Dixon, 1968) was used instead of the U-statistic. The approximate F-value is $F_{(1\alpha,72.266.84)} = 80.2955$. The tabular F-value is $F_{(0.999,60,120)} = 2.01$ (Ostle, 1963). Therefore, the approximate F-value is significant at the 0.001 level and the null hypothesis of equal group means is rejected.

The Mahalanobis D-square statistic, which is approximated by the chi-square distribution, also tests the hypothesis of equal group means. This statistic has degrees of freedom equal to the number of variables being measured times the number of groups minus one. The value of the D-square statistic is $D^2_{(1-\alpha,198)} = 571.160$. The tabular chi-square value is $\chi^2_{(0.999,100)} = 153.2$ (Ostle, 1963). The D-square statistic is also significant at the 0.001 level. These statistics give two of the appropriate multivariate methods for determining if the proposed groups are the same or different and therefore distinguishable from each other.

Coloration and Pattern

It was observed that the coloration and pattern groupings did not quite reproduce the groupings first proposed. Therefore, a contingency table, testing for independence of coloration and pattern with regard to geographic location was constructed. The test statistic was found to be significant at the 0.001 level.

$$\chi^2_{(1-\alpha,20)} = (0_{ij} - E_{ij})^2/E_{ij}$$

$$\chi^2_{(1-\alpha,20)} = 148.136$$

$$\chi^2_{(.999,20)} = 47.5 \ldots\ldots\ldots\ldots\ldots$$

Therefore $\chi^2 \geqslant \chi^2_{(.999,20)}$ and the null hypothesis is rejected. It was concluded that there is a definite association between the color-pattern and geographic location (see Table 2).

Discriminate Analysis

The above results were used in altering the proposed groups slightly to see if the population in question could be more closely defined. The UCLA BMOD7 stepwise discriminant analysis program (Dixon, 1968) was run using the following groups as data: (1) Upper Colorado River Basin population, *C. c. auriceps* (N = 10), consisting of those individuals found north of the union of the Colorado and Green rivers at the approximate location of Moab, Grand Co., Utah, (2) the central Arizona plateau population, *C. c. baileyi* (N = 30), containing those individuals found in Coconino and Yavapai counties, Arizona, (3) the Chihuahuan Desert population (N = 45), consisting of those individuals found in El Paso Co., Texas; Luana, Sierra and Hildago counties, New Mexico; and Chihuahua, Mexico, and (4) the Great Plains population, *C. c. collaris* (N = 12), represented by those specimens found in Kansas and Oklahoma.* Only specimens from geographic areas not thought to contain any intergrading populations were used to form the discriminant functions. All other specimens were lumped into an unclassified group to be evaluated by the functions. This is known as model I.

The originally proposed groups were used as data to examine the effect that the change in groups would have upon the program's ability to identify the individuals correctly. The original groups were defined as follows: Upper Colorado River Basin popula-

Table 2. A contingency table testing the independence of coloration-pattern types and geographical locations.

Locations	Coloration-pattern types				
	1	2	3	4	5
Upper Colorado River Basin of Utah (north of the union of the Green and Colorado rivers)	7	0	0	0	0
Upper Colorado River Basin of Utah (south of the union of the Green and Colorado rivers)	0	2	0	0	0
Upper Colorado River Basin of New Mexico	1	4	0	0	0
Upper Colorado River Basin of Arizona (east and north of the Little Colorado River)	0	1	3	0	0
Central Arizona (west of the Little Colorado River and north of the Mogollon Rim)	0	0	17	0	0
Southern Arizona (south of the Mogollon Rim)	0	0	2	3	0
Chihuahuan Desert of New Mexico (southern Luna County)	0	0	0	0	7

*The members of Group (4) represent specimens from a close proximity of the type locality for *C. c. collaris*. They were included to demonstrate the presence of a difference between the type population of *C. c. collaris* and the populations of real concern in this study.

tion, *C. c. auriceps;* those individuals found in the Colorado River drainage of Colorado and Utah. All other groups remained the same. This is known as model II.

The classification formed by the first discriminant analysis was chosen as the one that best represented the actual populations of lizards. The determination was made by selecting the model that made fewer wrong classifications of lizards previously defined as *C. c. auriceps.* Model I identified 9 out of 10 correctly or 90%. Model II identified 24 out of 32 correctly or 75%.

The analysis of the output of the stepwise discriminant program reveals two interesting statistics, the U-statistic and the F-statistic. The U-statistic tests equality of means between groups using the variables included in the discriminant function. The U-statistic is 0.06346 with 24,3,93 degrees of freedom. The F-value approximation to the U-statistic was used because of the availability of F-tables. The approximate F-value is 4.42269 with 72,210.06 degrees of freedom. This statistical test determines whether the groups are, or are not statistically separable when given a set of taxonomic characters to be used for classificatory purposes. The tabular F-value is $F(.999,100,120) = 1.82$. Therefore $F(1-\alpha,72,210.06) \geqslant F(.999,100,120)$ and the null hypothesis is rejected.

The F-statistic is used to test the difference between each pair of groups, thus making it possible to determine if all groups are separate from each other. It is measured with 24,70 degrees of freedom, and all groups are separated at the 0.001 level. The F-statistic is summarized in Table 3, and the discriminant functions formed are listed in Table 4.

The taxonomic characters that correspond with the coefficients of the discriminant functions are listed as follows: (1) tail length/hindleg length, (2) tail length/snout-vent length, (3) snout-vent length, (4) internasal scales, (5) number of fused interorbital scales, (6) frontoparietal scales, (7) scales from the union of the posterior canthal and subocular to the supralabial, (8) infralabial contact with postmetal, (9) supralabial scales, (10) gular scale rows, (11) number of enlarged internasals, (12) scales from rostral to interparietal, (13) dorsal scales from interparietal to the anterior edge of the first collar, (14) dorsal scales from the anterior edge of the first collar to the posterior edge of the second collar, (15) total dorsal scales, (16) total ventral scales, (17) dorsal separation of the first collar, (18) dorsal separation of the second collar, (19) number of spots within the dorsal separation of the first collar, (20) second collar length/snout-vent length, (21) subdigital lamellae of the right hind foot, second toe, (22) fourth toe subdigital lamellae, (23) fifth toe subdigital lamellae, (24) femoral pores.

Table 3. A summary of the F-statistics which show differences between individual groups.

Groups	Groups	
	Chihuahua	*baileyi*
auriceps	2.99625	2.29124
baileyi	2.65349	

Table 4. A listing of the coefficients of the discriminant functions.

Variable	Groups		
	auriceps	Chihuahua	*baileyi*
1	51.39813	45.22476	47.94501
2	2.14172	8.31362	5.60604
3	1.27552	1.34056	1.21061
4	10.33790	10.90252	11.58937
5	15.42395	16.15672	15.77870
6	-13.55824	-13.54851	-13.42835
7	7.06088	4.44547	5.51994
8	9.06605	9.79720	9.35053
9	0.56730	-0.59190	0.83744[
10	1.28302	1.24001	1.18661
11	-5.04772	-3.78518	-4.35537
12	1.2393	0.81388	0.85222
13	0.85929	0.99943	0.73786
14	1.63115	1.57809	1.54830
15	0.41538	0.39279	0.56490
16	0.80368	0.81625	0.71332
17	0.70005	0.44894	0.49637
18	0.01570	-0.01466	0.04405
19	1.38450	1.95044	1.19760
20	269.06104	264.62378	294.33545
21	2.11617	2.84886	3.45656
22	1.17804	1.35396	1.12000
23	0.96154	0.98708	1.14926
24	2.53244	2.28217	2.30347
constant	-526.26660	-523.28274	-527.89990

The measurements on each lizard were put into all three functions and a numerical value for that lizard, as evaluated by each of the functions, was obtained. Identification was made by placing the lizard into the group whose function resulted in the largest numerical value. Along with placing each individual into a group, the probability that it belonged in that group as well as the probability of it belonging to each of the other groups was calculated. This probability indicated the assurance with which each individual was classified.

Two aspects of the discriminant analysis' identification were considered. First, the degree of reliability of the identification was examined. Lizards that were

from locations known to be within the ranges of one of the groups, were examined for their reaction to being identified by the discriminant functions. Areas considered definitely to belong to one of the groups are as follows: the Upper Colorado River Basin population, *C. c. auriceps,* Grand Co., Utah and Mesa Co., Colorado; the Central Arizona Plateau population, *C. c. baileyi,* Yavapai and Mohave counties, Arizona; the Chihuahuan Desert population, Hildago, Luna, and Dona Ana counties of New Mexico and Chihuahua, Mexico. In Yavapai and Mohave counties, only those Collared Lizards not resembling the Western form of Collared Lizard were considered. The percentage of individuals classified correctly was determined by dividing the number correctly classified by the total number in the geographic area considered ($N_{s,corr.}/N_{tot.}$). This was summed over all groups to get the total percentage of correctly classified individuals in the sample (see Table 5). Thus, approximately 80% of the sample was identified correctly; which is well within the bounds set by Mayr and others in the 75% rule (Mayr, 1969).

Table 5. Percentage of sample identified correctly using the discriminant analysis.

Group	Sample size	$\frac{N_{corr.}}{N_{tot.}}$	Percentage
auriceps	10	9/10	90.00
baileyi	42	34/42	80.95
Chihuahua	93	75/93	80.64
Total	145	118/145	81.38

Another aspect of the discriminant analysis dealt with using the discriminant functions' identification and the probability for group membership to investigate intergradation between populations. This has always been a problem that made identification of Collared Lizards difficult (Burt, 1928).

The individual, when identified by the discriminant function program as belonging to a group, is labeled with the *a posteriori* probability for its membership in all of the groups. The *a posteriori* probability is the probability of an individual belonging to a group once the group has been defined. This set of probabilities always sums to unity. The probabilities for membership in a group have three options: (1) There will be one large probability and the rest small (e.g., 0.982 and 0.044 and 0.044). In this situation, the individual is placed in the group with the largest probability of membership. Any probability that exceeds 0.70 is considered a large probability of membership. (2) There will be two approximately equal probabilities and the rest small (e.g., 0.5602 and 0.4498). This indicates that the individual is not distinct enough to fit with much assurance into either group. A specimen of this type is considered to represent an intergrade between the groups given the largest probabilities. (3) All the probabilities will be approximately equal. In this case, the individual is assumed to be unidentifiable. This aspect of discriminant analysis is an adaption of Rao's three population discriminant analysis procedure (Rao, 1952). Identification of each specimen used in the study was examined. The percentage of the total sample placed in each group was recorded. This percentage was arranged by geographic area in a north-south line. The results of this analysis are summarized in Figs. 5 and 6.

The characters themselves were examined to establish their effect on the discrimination between groups. This is summarized in Table 6. Table 7 lists the means and standard deviations for the 24 characters of each group. Figure 7 also shows the means and one standard deviation for the characters that give the best individual discrimination between groups.

DISCUSSION

Zoological Discussion

The initial question proposed by a taxonomic study at the subspecific level deals with identification. Specifically, are there any populations that are geographically continuous and also identifiable, following the 75% rule, in respect to other populations?

The multivariate analysis of variance shows that the populations proposed in this study are distinguishable at a high confidence level. This analysis was done using external morphological characters exclusively. The groupings of the cluster analysis, along with its test of independence, lends support to the actual existence of the proposed groups.

Once assured of the existence of these populations, the problem becomes one of identification. Using external morphological characters exclusively, an examination of the means and standard deviations reveals that although their means were different (the statistical tests of population difference showed this), their overlap was such that no one character could be used to identify an unknown specimen with complete accuracy. Discriminant analysis computes a new character, "Z," which is the value of a set of functions or equations. These functions are constructed from linear combinations of the original characters in such a way that as many members as possible from each population have high values for the function that corresponds to their population. In a sense, this is a new taxonomic character that identifies members of each

A key to the abbreviations used in Figs. 5 and 6.

auriceps - The Collared Lizard population of the Upper Collarado River Basin, north of the union of the Colorado and Green Rivers.

baileyi - The Collared Lizard population of central Arizona.

AxB - The intergrade population of *auriceps* and *baileyi*.

chihuahua - The Collared Lizard population of the Chihuahuan Desert.

BxC - The intergrade population of *baileyi* and Chihuahua.

Unident - Individuals not assignable to any of the above groups.

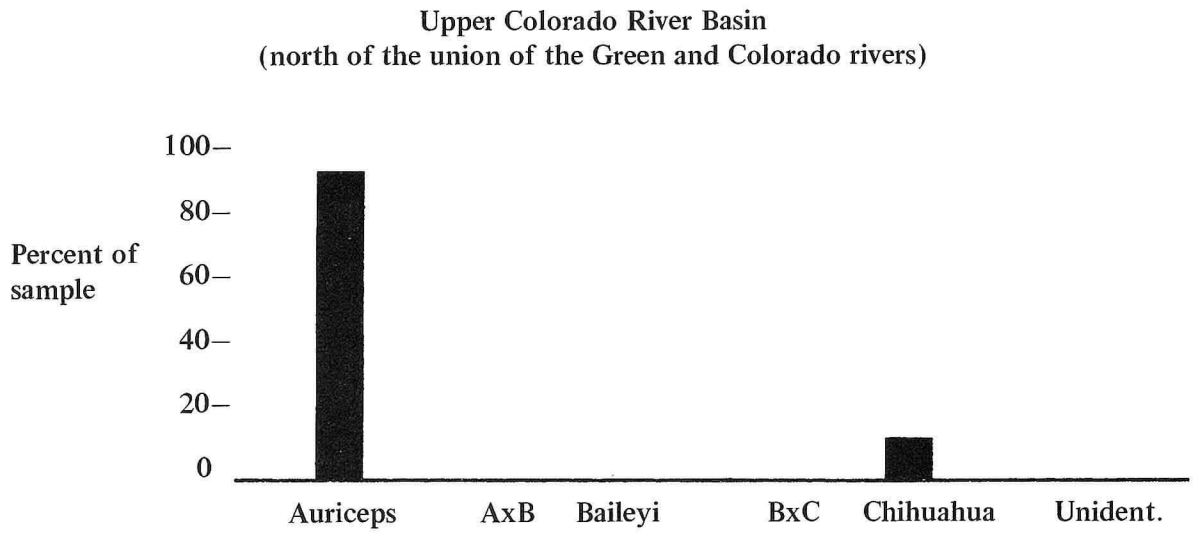


Fig. 5. A comparison of Collared Lizard populations along a line connecting Grand Co., Utah and northern Sonora, Mexico.

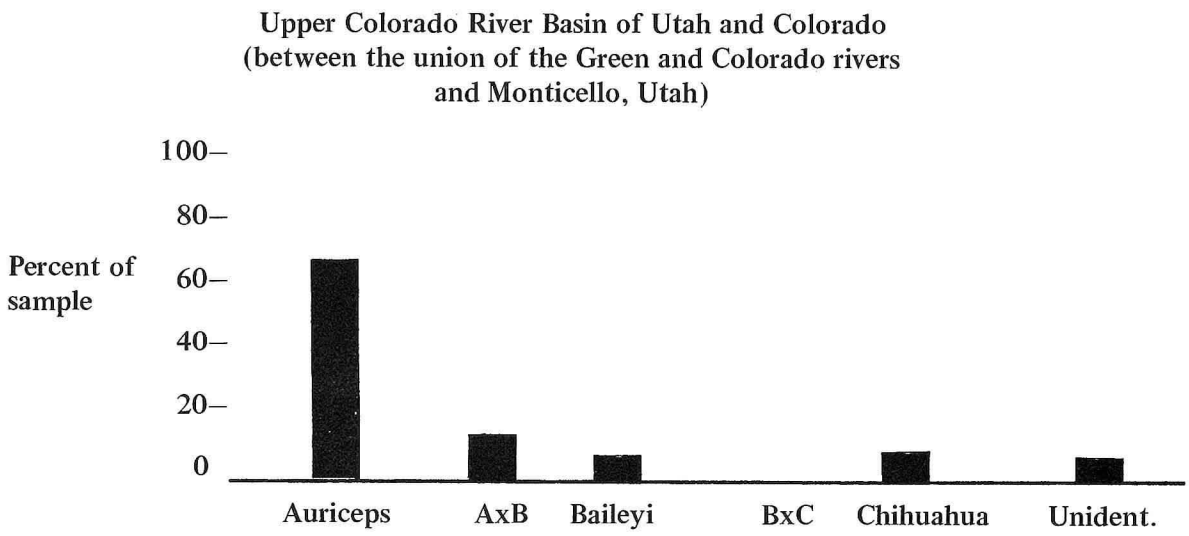
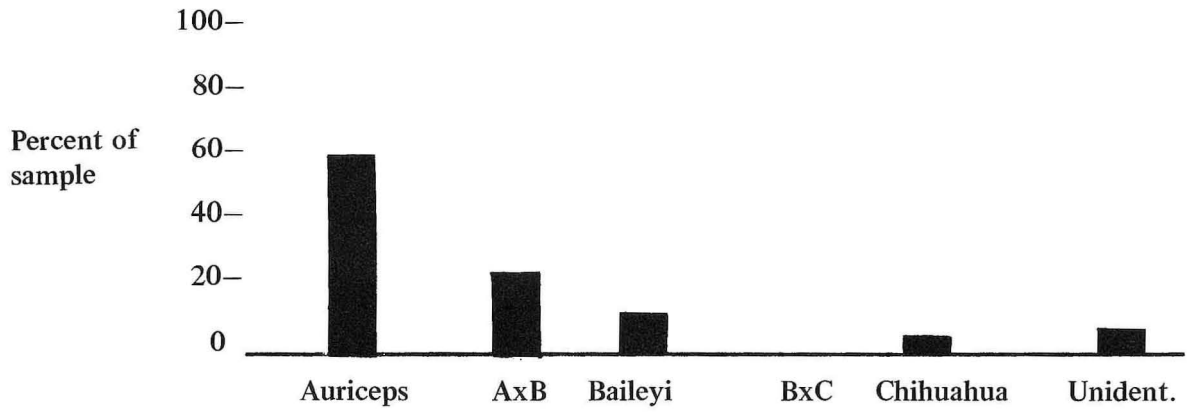
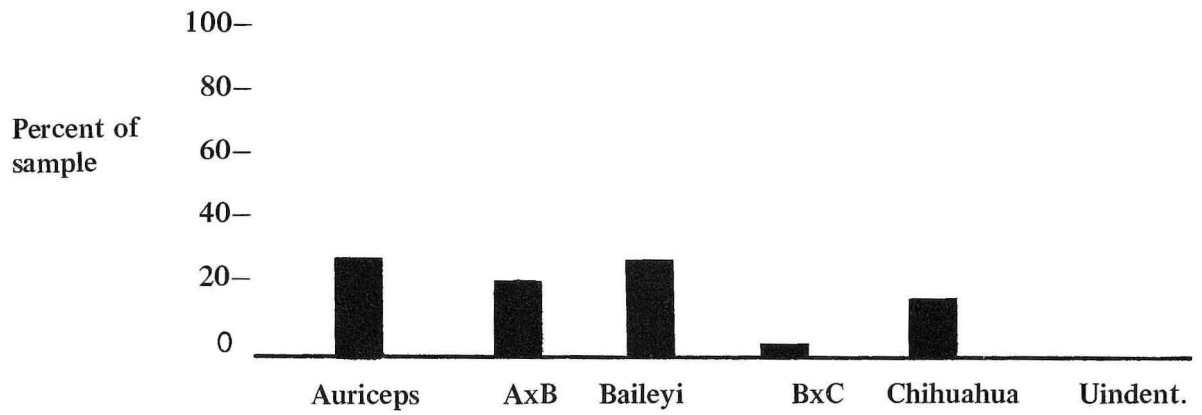


Fig. 5. (continued)

Upper Colorado River Basin of Utah and Colorado
(south of Monticello, the San Juan River drainage)



Upper Colorado River Basin of Arizona
(east of the Little Colorado River)



Central Arizona
(between the Little Colorado River and the Mogollon Rim)

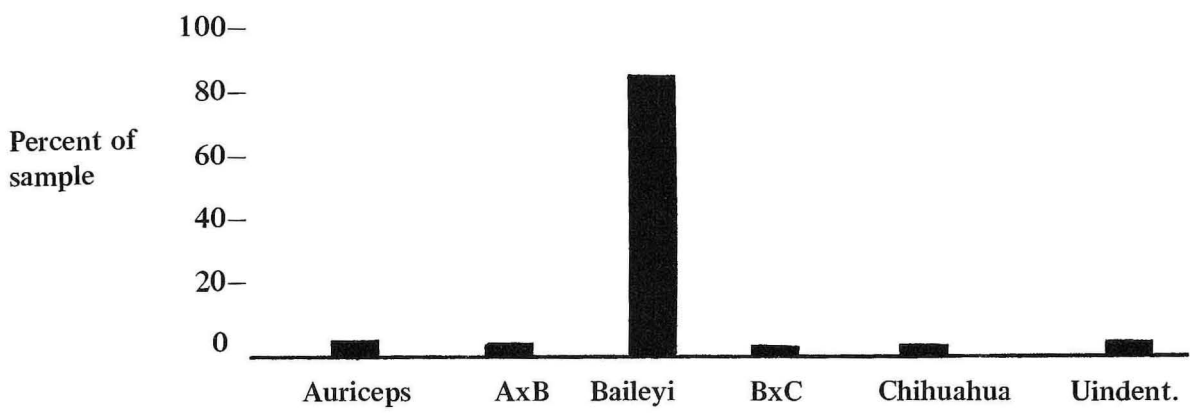
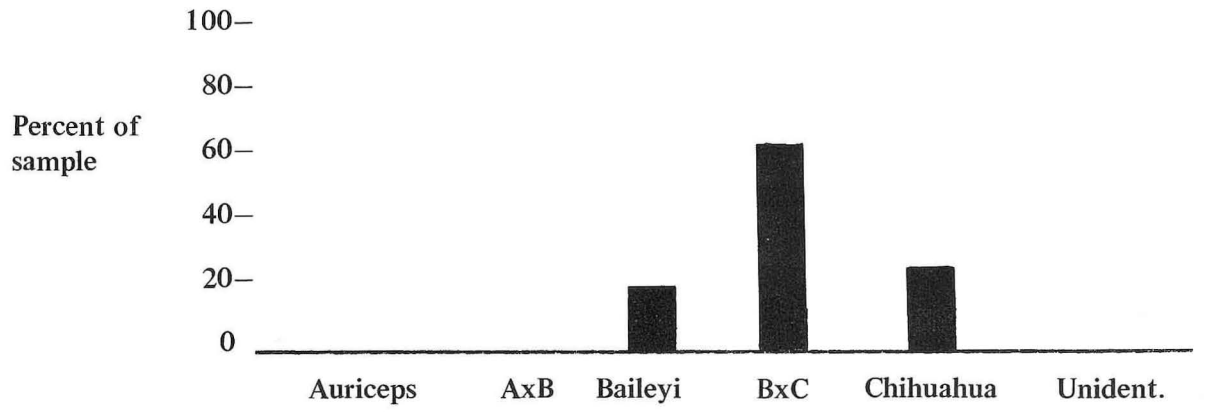
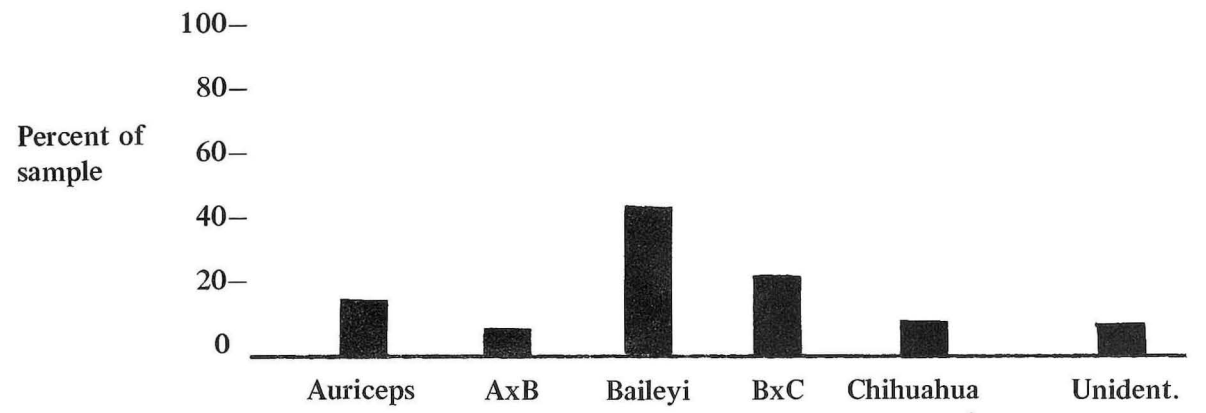


Fig. 5 continued

Gila County, Arizona
(the base of the Mogollon Rim)



Pinal and Graham Counties, Arizona
(mountains south of the Mogollon Rim)



Sonoran Desert of Arizona and Mexico
(Cochise, Pima, and Santa Cruz counties and Sonora, Mexico)

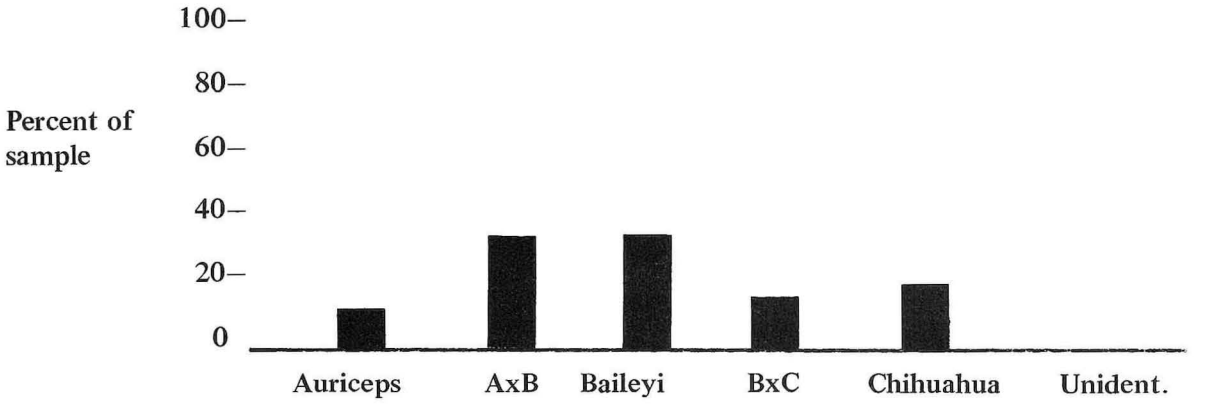


fig. 5 continued

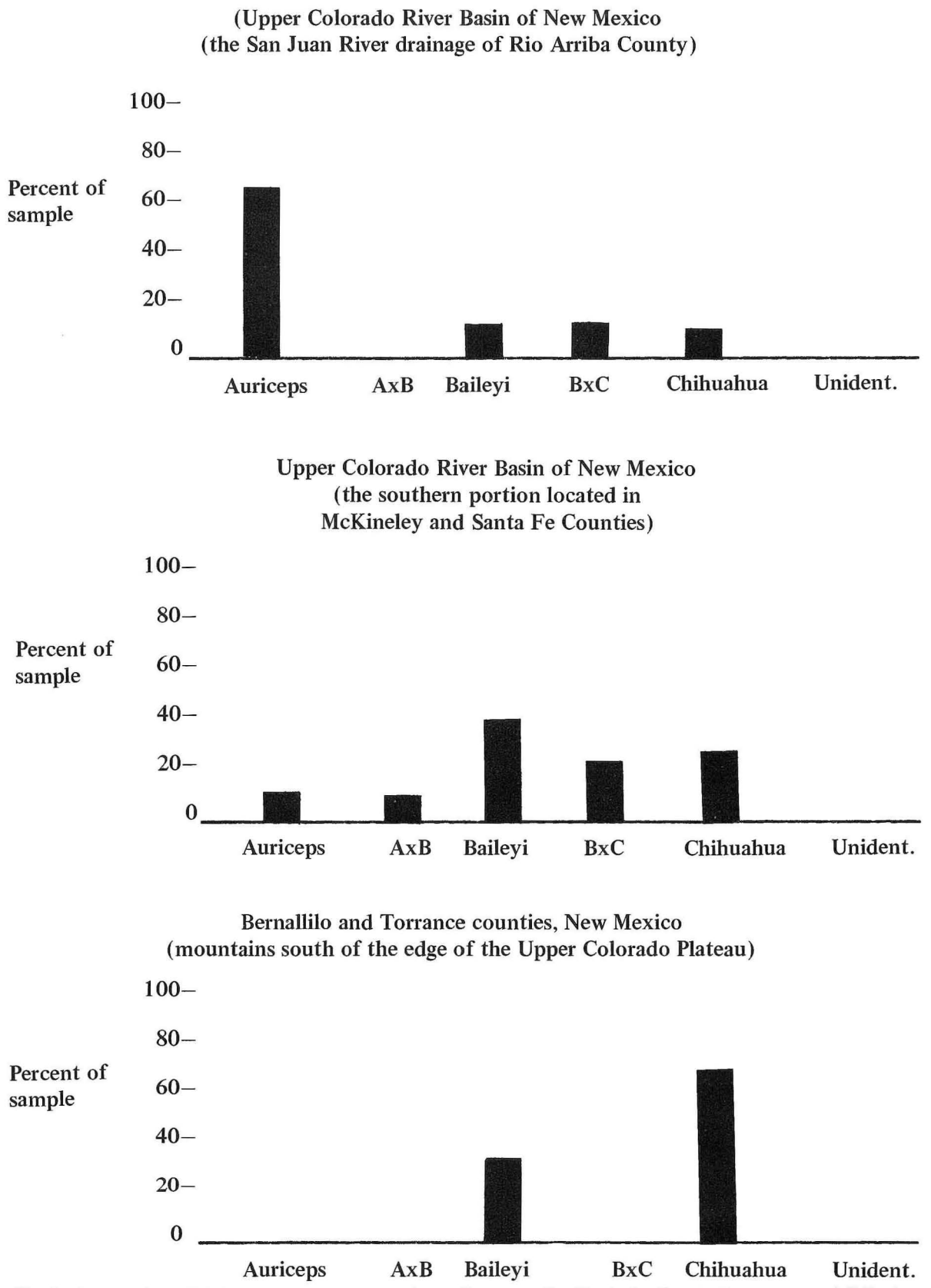


Fig. 6. A comparison of Collared Lizard populations along a line connecting Rio Arriba County, New Mexico and Chihuahua, Mexico.

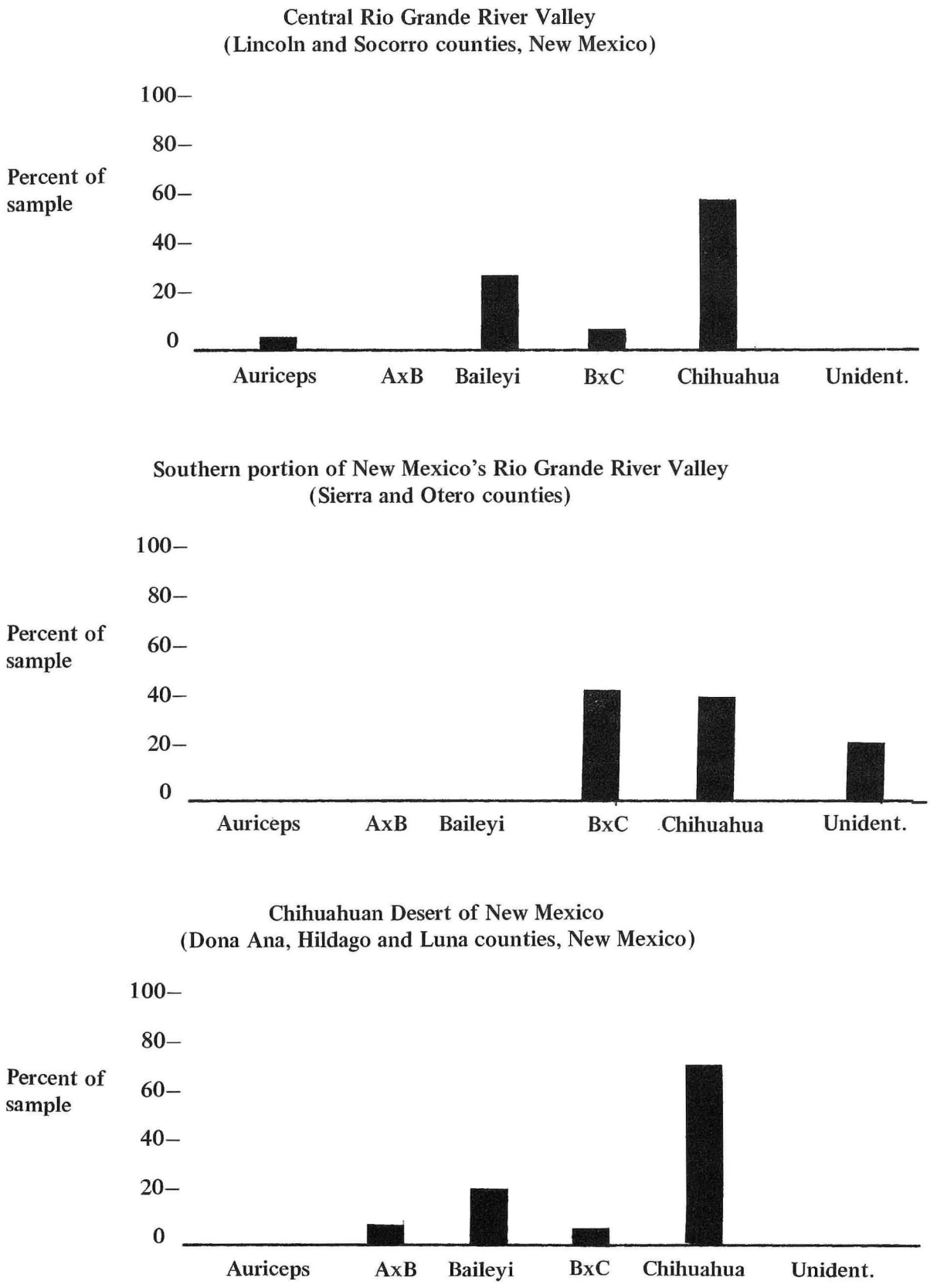
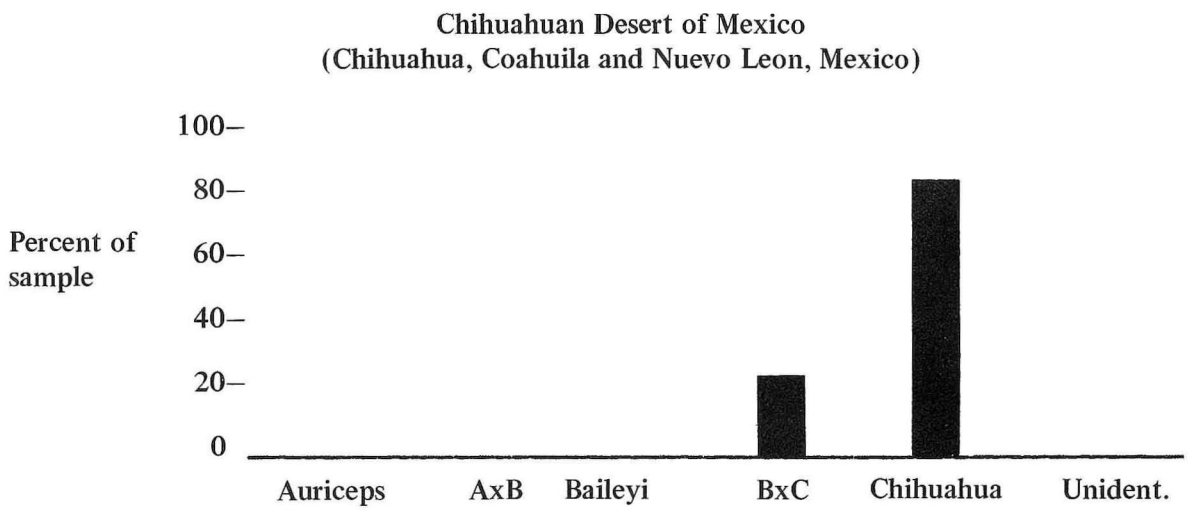


Fig. 6. (continued)



group with a high degree of reliability. This reliability is expressed in the form of a probability for joining each group (Sokal and Rohlf, 1969). The discriminant functions have demonstrated their ability to identify the three populations accurately.

Coloration was studied separately from the morphological characters. This aspect of a lizard's phenotype consistently demonstrated differences between populations. There may be some questions as to the validity of coloration when used as a taxonomic character due to a possible relationship between coloration and diet. However, the similarity of classifications of Collared Lizards by color patterns and by morphological characters tends to dispute this idea. In an animal such as the Collared Lizard, that is active, diurnal, highly territorial, and uses sight to recognize both territorial intruders and potential mates (Fitch, 1956), it is difficult to imagine a character more important than color pattern. Since coloration fades rapidly on preserved specimens, this method of identification works on live specimens only. The population of *C. c. auriceps* is characterized by coloration-patternal type 1; *C. c. baileyi,* by type 3; intergrades between the two, by type 2; the Chihuahuan Desert population, by type 5; and intergrades between the Chihuahuan Desert population and *C. c. baileyi,* by type 4.

By combining the information obtained from both coloration-patternal and morphological characters, it is possible to explain the structure of the Collared Lizard populations between the Rio Grande and Colorado Rivers (see Fig. 8). Located in the northern extension of the Upper Colorado River Basin is *C. c. auriceps.* Its range should now be restricted on the south, to the region of the union of the Green and Colorado rivers in the vicinity of Moab, Grand County, Utah. Northward, they extend at least to the Book Cliffs area and possibly further. South of the union of the Green and Colorado rivers, an increasing number of individuals is identified by the discriminant functions as *C. c. auriceps* X *C. c. baileyi* intergrades. This corresponds with a decreasing number identified as *C. c. auriceps,* which is also supported by the color patterns observed. In this region, numerous lizards are found of color type 2, which is intermediate to color type 1, *C. c. auriceps;* and color type 3, *C. c. baileyi.* The area of intergradation is limited to the region somewhat south of Moab, Utah, and extending to the vicinity of the Little Colorado River of Arizona.

Crotaphytus collaris baileyi is now restricted to the region south of the Painted Desert, across the center of Arizona. It is also expected to occur in the

Table 6. A comparison of the percent of correctly identified individuals within groups as new variables are added to the discriminant functions.

Step	Variable added	Groups			
		auriceps	*baileyi*	Chihuahua	*collaris*
1	5	0	90	16	75
2	8	40	43	47	92
3	7	80	50	60	83
4	21	80	60	69	92
5	10	80	63	69	92
6	14	80	67	73	92
7	4	80	60	73	100
8	17	80	70	73	100
9	18	80	67	71	100
10	3	80	73	73	100
12	19	80	73	78	100
13	20	80	80	84	100
14	13	80	77	89	92
15	15	80	70	88	100
16	12	80	70	88	100
17	22	80	73	88	100
18	23	80	77	89	92
19	11	90	77	89	92
20	2	90	77	92	92
24	6	90	77	92	100

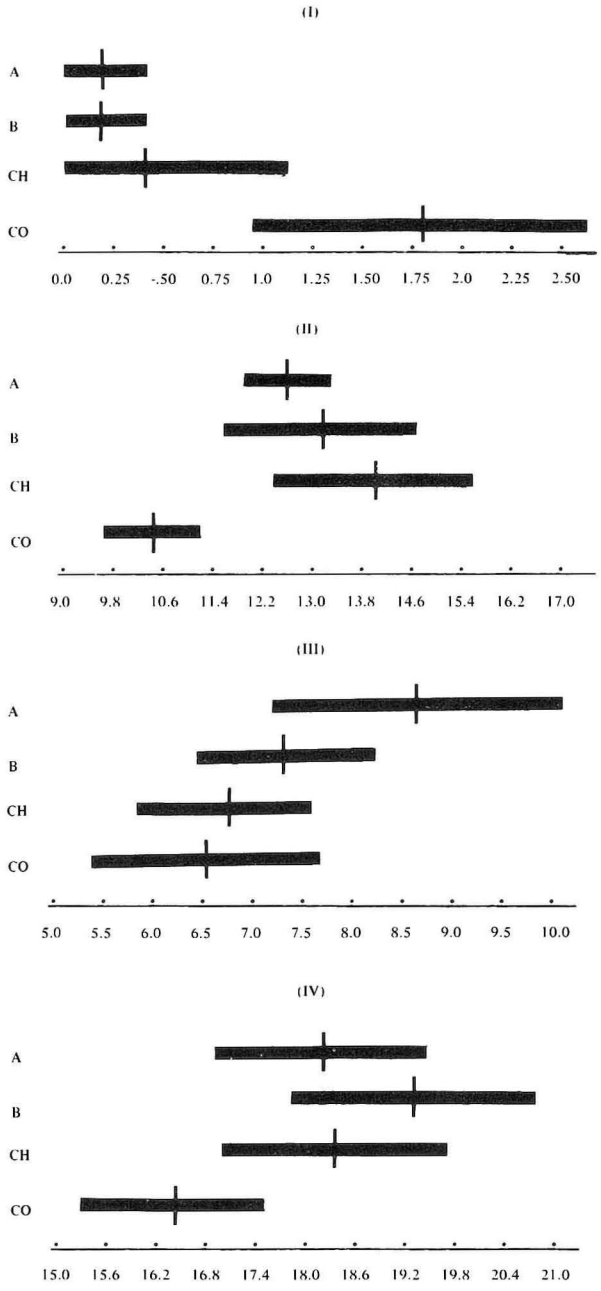


Fig. 7. Means and standard deviations plotted for the four characters that contribute the most to population discrimination: (I) fused interorbitals, (II) supralabials, (III) loreallorilabial series, (IV) subdigital lamellae of second toe on hind foot, (CO) Great Plains population, (CH) Chihuahuan Desert population, (B) central Arizona population, (A) Upper Colorado River Basin population.

western central mountains of New Mexico; however, specimens from this area were too few to state this with assurance. *C. c. baileyi* seems to be centered in Mohave, Yavapai, and southern Coconino counties of Arizona and follows the Mogollon Rim and adjacent mountains to the east. In the south, the picture becomes more confused. Isolated populations of *C. c. baileyi* are found on the mountain tops, and, in the lower elevations, intergrades between *C. c. baileyi* and the Chihuahuan population are found. In general, this area is populated by *C. c. baileyi* X Chihuahuan intergrades; however, the exact relationships are in need of further study.

The exact type locality of *C. c. baileyi* is unknown. Stejneger describes it as the Painted Desert of the Little Colorado River. In his original description of *baileyi,* two facts become apparent. First, the red spots described on the neck of the type (which is a male), and the time of collection (late August, when generally only juveniles and hatchlings are active) indicate the type to be a juvenile. Secondly, the type locality is somewhere between Cameron and Wupatki National Monument in Coconino County, Arizona. Stejneger describes the locality for collection of the type as in the vicinity of the Little Colorado River. The type was collected on the second excursion to the desert, which took him north from Flagstaff to Tuba City on a route that is followed by U.S. Highway 89 (Stejneger, 1890). Locating the type locality as south and west of the Little Colorado River places it within the range of *C. c. baileyi* as determined by this study.

The population centered in Chihuahua should now be recognized as a subspecies and separate from *C. c. baileyi* and *C. c. auriceps.* This is done on the basis of its overall morphological distinctiveness as expressed by the discriminant functions and also by its strikingly different coloration. The brown of its doral coloration is easily distinguished from the green of either *C. c. baileyi* or *C. c. auriceps.* The new population, centered in Chihuahua, Mexico, extends northward to Socorro County, New Mexico, dispersing up the lowlands of the Rio Grande River Valley. The eastern and southern extents of its range are in need of further study. To the west is an area where isolated populations of *C. c. baileyi* occur on the higher mountain ranges (e.g., Tanque Verde Mountains near Tucson). This provides for intergradation to occur and for the coloration-pattern type 4 to become common. The overall ranges are shown for the three populations in Fig. 8.

Twelve individuals from the area of the type locality of *C. c. collaris* were included in the discriminant analysis. This was done to obtain an idea as to the relationship of *C. c. collaris* to the populations studied. Also included in the analysis were a number of individuals from eastern New Mexico, Texas, and eastern Colorado. All are within the presently determined range of *C. c. collaris.* Two facts resulted from this analysis: (1) the lizards from the type locality were identified with 100% assurance, and (2) no meaningful pattern could be discerned for the remaining supposed *C. c. collaris.* This suggests that the subspecies, *C. c. collaris,* is also a heterogeneous grouping

Table 7. A listing of the means and standard deviations for the 24 characters measured on the individuals used in forming the discriminant functions.

Character	Groups							
	auriceps		*baileyi*		Chihuahua		*collaris*	
	Mean	Stand. dev.	Mean	Stand. dev.	Mean	Stand. dev.	Mean	Stand. dev.
1	2.2	0.3	2.2	0.2	2.2	0.2	2.1	0.1
2	1.8	0.2	1.9	0.1	1.9	0.2	1.8	0.1
3	94.3	7.2	93.1	6.2	95.3	7.8	91.8	7.8
4	5.8	0.8	6.0	0.7	6.0	0.7	4.8	0.8
5	0.1	0.3	0.1	0.3	0.4	0.7	1.8	0.8
6	2.3	0.8	2.0	0.7	2.0	0.9	1.2	0.4
7	8.6	1.5	7.3	0.9	6.7	0.9	7.4	1.2
8	12.5	0.7	13.2	1.6	13.9	1.6	10.5	0.8
9	0.9	0.3	1.0	0.2	0.9	0.2	0.8	0.4
10	66.1	4.5	61.0	6.2	62.8	6.0	52.8	6.1
11	0.1	0.3	0.5	0.7	0.6	0.7	0.1	0.3
12	15.7	1.2	14.7	1.7	14.4	2.7	14.7	1.0
13	24.5	6.1	25.4	7.3	28.6	3.9	26.2	2.6
14	33.7	6.5	33.1	5.8	28.4	4.3	24.5	3.9
15	158.1	7.9	163.5	11.7	155.8	10.4	142.1	9.5
16	195.4	9.8	187.5	11.5	187.7	10.9	170.2	6.2
17	28.9	4.7	24.2	7.8	23.3	5.8	24.2	10.3
18	1.4	1.8	4.3	3.8	5.4	4.3	7.8	6.1
19	1.9	0.3	1.7	0.6	1.9	0.4	1.0	0.3
20	0.2	0.0	0.2	0.0	0.2	0.0	0.1	0.0
21	17.3	1.3	19.5	1.5	18.7	1.4	16.4	1.2
22	33.0	3.9	34.7	3.0	34.4	3.0	28.8	2.1
23	15.0	1.7	15.5	1.5	15.0	1.8	13.9	1.5
24	18.6	1.6	17.8	1.4	18.2	1.9	17.6	1.3

and should be studied. The ease of separation of the specimens from the area of the type for *C. c. collaris* supports the present separation of three western populations from an eastern Great Plains group now designated as *C. c. collaris*. This was also supported by the grouping of the cluster analysis. Following Rao's technique (1952), a graph of the first two canonical variables was plotted (see Statistical Discussion). This provides a two-dimensional representation of the interrelationship of the populations (see Fig. 9).

A diagnosis of the three populations' characteristics and their comparison with the material representing the type population of *C. c. collaris* is as follows:

Crotaphytus collaris auriceps is separated, as are the other groups, primarily on coloration and pattern. It has a light green body with a bright yellow head. The yellow on the head extends posteriorly to or just past the second collar and ventrally onto the throat. In males, the yellow on the throat meets the green of the gular patch. Morphologically *C. c. auriceps* is separated from *C. c. collaris* by a fewer number of specimens with fused interorbitals. It is separated from *C. c. baileyi* primarily by a smaller number of supralabials, as indicated by Fitch and Tanner (1951), and a greater number in the loreal-lorilabial series. *C. c. auriceps* is also distinguishable from the Chihuahuan Desert population by the above characters and is further separated by possessing fewer subdigital lamellae on the second toe of the hind foot.

Crotaphytus collaris baileyi has a dark green body, and, if yellow is present on the head, it does not extend posteriorly beyond a line drawn between the rear of the supraorbital semicircles. Yellow is never found on the throat. Using morphological characters exclusively, *C. c. baileyi* is separated from *C. c. collaris* by a smaller number of specimens with fused interoribitals, a greater number of supralabials, and a greater number in the loreal-lorilabial series. *C. c. baileyi* was not separated with much assurance from the Chihuahuan Desert population until 14 characters had been added to the discriminant function. This suggests the differences between the populations are expressed as a function of many variables (a sum of many small differences) rather than just one.

The Chihuahuan Desert population differs from *C. c. collaris* morphologically mainly by having fewer individuals with fused interorbitals and having more supralabials. Color and patterns of *C. c. collaris* were not analyzed. The Chihuahuan Desert population has been demonstrated to be sufficiently different from all presently recognized populations to merit designation at the subspecific level. It is therefore named as

A key to the sumbols used in Fig. 8.

Range of the Upper Colorado River Basin population, *C. c. auriceps.*

Range of the central Arizona population, *C. c. baileyi.*

Range of *C. c. baileyi* x *C. c. auriceps* intergrades.

Range of the Chihuahua Desert population, *C. c. fuscus.*

Range of *C. c. fuscus* x *C. c. baileyi* intergrades.

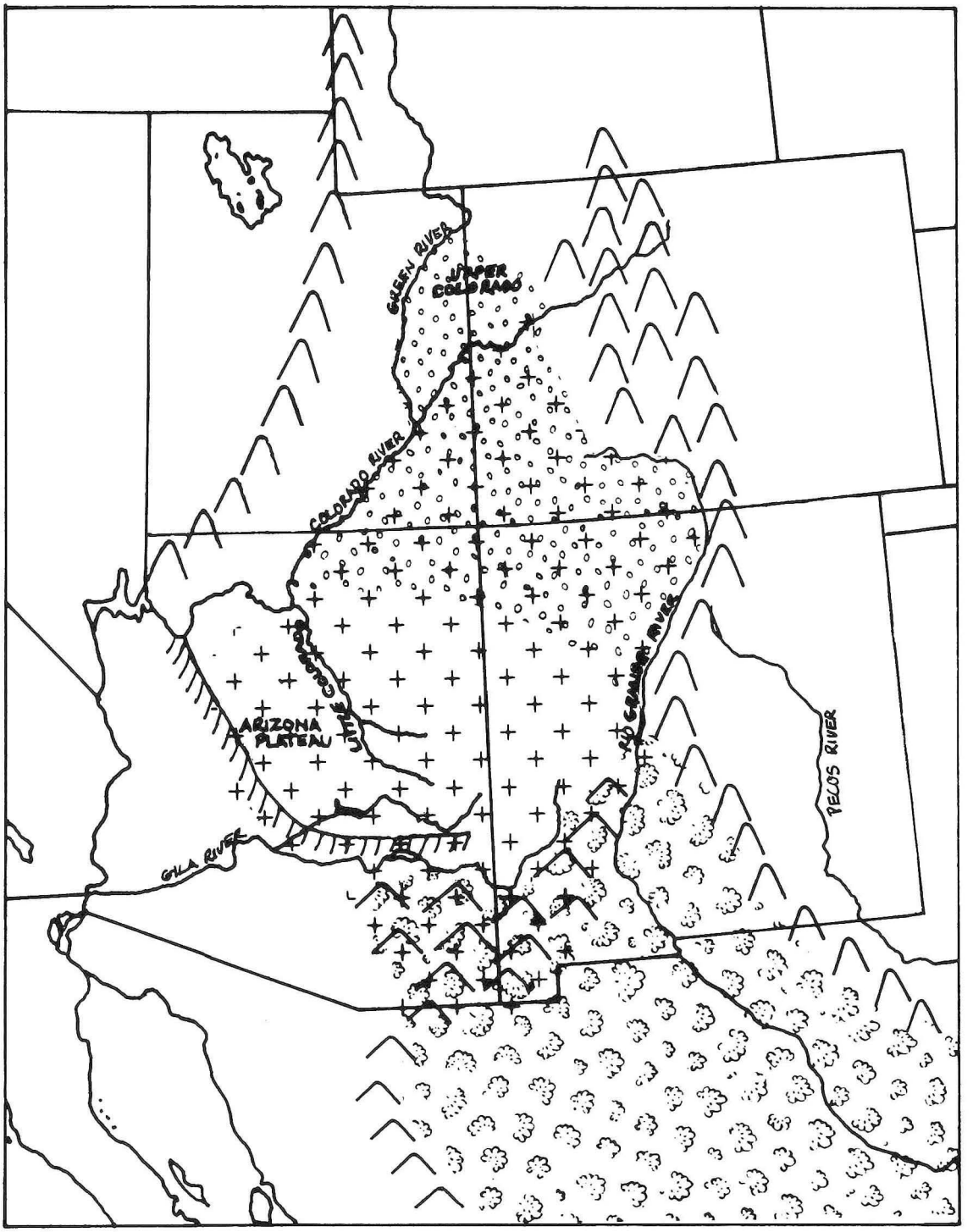


Fig. 8. A range map for the populations studied.

A key to the symbols used

A - The upper Colorado River Basin population.
B - The central Arizona population.
F - The Chihuahuan Desert population.
C - The Great Plains population.

& - Misidentified A.
O - Misidentified B.
$ - Misidentified F.

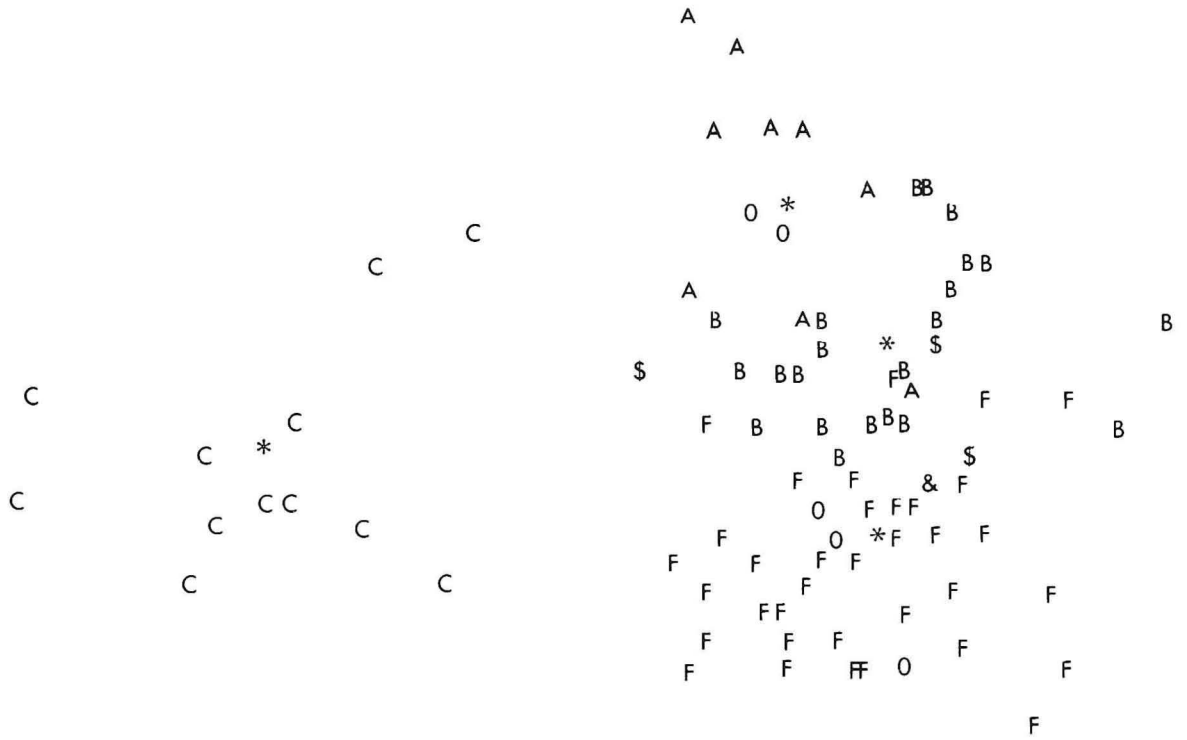


Fig. 9. A two-dimensional representation of the interpopulation morphological relationships formed from the canonical variates.

Crotaphytus collaris fuscus subsp. nov.

Type. – Adult male, Brigham Young University No. 16970, collected 6.5 mi. N. and 1.5 mi. W. of Chihuahua City, Chihuahua, Mexico, by Wilmer W. Tanner on July 21, 1960.

Paratypes. – Chihuahua: topotypes, BYU 14211, 14212, 15305, 15325-15331, 15817-15822, 16969, 16971-16977, 17010; Chihuahua City: UC 70704; Colonia Juarez: BYU 3736, 15185-15188; Hechichero: KU 33789; Nuevo Casas Grandes: BYU 15184; palomas: BYU 17014; Ricardo Magon: BYU 13382-13386, 13410, 13411; Victoria: KU 33788.

Diagnosis. – It differs from *C. c. baileyi*, *C. c. auriceps* and *C. c. collaris* in having a brown dorsal color with no trace of green and a light to cream colored head with no trace of yellow. The morphological differences, no one of which is conclusive, are many and add up to a general difference from the recognized populations that is best expressed by the previously mentioned discriminant functions.

Description of the type. – Head and body length 106 mm, tail length 222 mm, width of head at angle of jaw 28 mm, hindleg length from midline to tip of fourth toe 89 mm, femoral pores 20-20, supralabials 14-14, infralabials 12-11, fused interorbitals 0, internasals 6, frontoparietals 2, loreal-lorilabial series 7, postmentals in contact with infralabials, gular scale rows at angle of jaw 69, scales from rostral to interparietal 15, scales from interparietal to anterior edge of first collar 25, scales from anterior edge of first collar to posterior edge of second collar 28, total dorsals 140, total ventrals 181, scales within dorsal separation of first collar 26, scales within dorsal separation of second collar 5, number of spots within dorsal separation of first collar 2, subdigital lamellae of second toe of right hind foot 17, subdigital lamellae of fourth toe 31, subdigital lamellae of fifth toe 16.

Type described from preserved specimen and natural coloration not apparent. General pattern and coloration as described from living specimens. Head pale (white or cream) with a few small dark spots distributed randomly across back of head, gular patch black, bluish black or dark brown, never green, reticulation present on lateral edges of gular patch, reticulations to infralabials, first collar widely disjunct dorsally

with two small spots in disjunction, second collar narrowly disjunct dorsally, second collar on forearm, body dorsum of varying shades of brown, never green; small white spots, rarely any yellow, scattered profusely; front legs same color as body dorsum but patternless; hindlegs same as body dorsum with spotting of body continued to thigh; feet pale; body venter white or cream; body dorsum ground color, fades into venter in region of midbody; no dark axillary or groin patches present.

The populations represented by *C. c. collaris, C. c. baileyi, C. c. auriceps,* and *C. c. fuscus* should be considered as an evolutionary group because of their greater morphological and patternal similarity when compared with the Collared Lizards west of the Colorado River. This group will be referred to as the *collaris*-complex.

The following phylogeny is based on morphological and patternal evidence. The population ancestral to the *collaris*-complex originated in east central Mexico, probably Chihuahua or Coahuila, from which they established themselves in the border states of Mexico and the United States. With improving climatic conditions, following the Pleistocene, they advanced northward. The population followed three corridors of dispersal: (1) along the low mountains of southwestern New Mexico and southeastern Arizona, (2) up the Rio Grande River Valley, and (3) east of the central mountains of New Mexico.

The first corridor led to the high plateaus of central Arizona and the Upper Colorado River Basin. Upon reaching the elevation barrier presented by the southern edge of the plateaus, a segment of the ancestral population, which invaded the higher elevations, was isolated and continued to disperse along the drainages of the Colorado River and its tributaries. This population, *C. c. baileyi,* moved northeast into Utah and Colorado following the mountain ranges that skirt the relatively uninhabitable Painted Desert and Monument Valley region of Arizona. This resulted in a large population centered in the Upper Colorado River Basin of Utah and Colorado, loosely associated with the main population of central Arizona. The length of the connection, coupled with the spotty distribution in northeastern Arizona, reduced the amount of genetic exchange possible between the two main populations. This allowed a distinct population, *C. c. auriceps,* to form at the northern boundary of the Upper Colorado River Basin.

Crotaphytus collaris auriceps is probably the youngest population of the *collaris*-complex. Three facts support this idea: (1) *C. c. auriceps* is located in the area most recently open to expansion by reptilian forms, the central portion of the Upper Colorado River Basin. (2) *C. c. auriceps* presents the smallest change in color and pattern from *C. c. baileyi,* thus suggesting recent evolution from that form, and the greatest change from the population closest to ancestral stock (the Chihuahuan Desert population, *C. c. fuscus*). (3) *C. c. auriceps* still possesses a wide intergrade zone with *C. c. baileyi,* suggesting that they have had little time to separate.

Crotaphytus collaris fuscus has probably changed little from the ancestral form, as it occupies essentially the same range. As conditions improved, following the Pleistocene, *C. c. fuscus* dispersed northward following the Rio Grande River along the low mountain ranges and river basins. It appears to be contained by the higher elevations encountered to the north and west. The range of *C. c. fuscus* may be outlined by constructing a line following the 5,000 foot elevation level in southern Arizona and New Mexico.

The population that dispersed eastward presently inhabits the Great Plains region. It became isolated from the western segment of the *collaris*-complex by the Rocky Mountains and differentiated into a distinct population now considered to be *C. c. collaris* (see Fig. 10).

Statistical Discussion

One of the major difficulties in using statistics in the zoological sciences is the lack of descriptions of the techniques phrased in the language of a zoologist. The purpose of this section is twofold: (1) to explain the necessity of using multivariate statistics in the taxonomy of subspecies, and (2) to explain in understandable terms the statistical methods used in this paper.

One of the more important discoveries of this study has been in the realm of methodology. Univariate methods are those techniques of data analysis and statistical decision-making where only one variable is measured on each experimental unit. Examples of this type of analysis are T-test of means, Chi-square, and Analysis of Variance. In recent years, a new statistical technique has grown out of classical univariate analysis. This form of statistics, the multivariate or generalized analysis, should be recognized as the proper form to use in taxonomic studies where more than one character is being analyzed. Multivariate analysis is designed to perform analyses that are analogous to those of univariate methods for cases where more than one measurement, or variate, is being determined on each experimental unit or specimen (Anderson, 1958).

There are definite hazards to using univariate methods where multiple measurements are being made on a single experimental unit. These hazards are centered in the inability of knowing the exact alpha-level of a statistical test, unless the assumptions of that test are complied with. The alpha-level of a test is the probability that the difference observed in the data is due to chance.

In most herpetological taxonomic studies, more than one variate or taxonomic character is measured

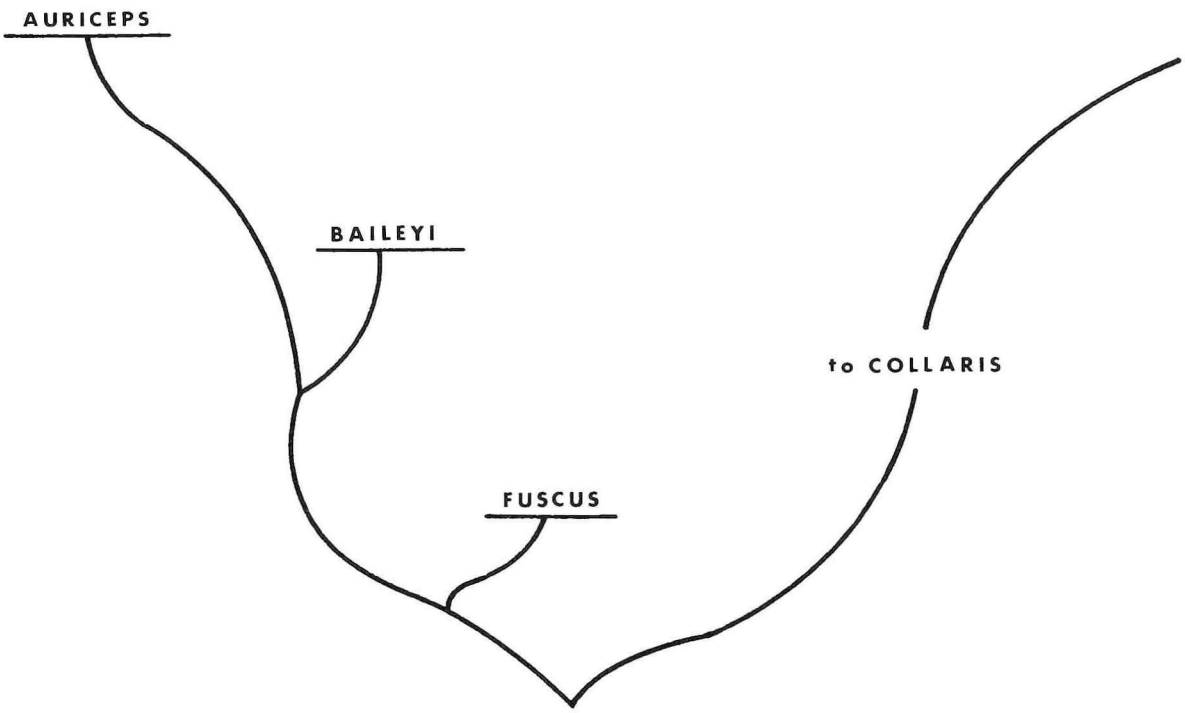


Fig. 10. Proposed phylogenetic relationship of the populations of the *collaris*-complex.

on each individual. These variates usually are then analyzed separately with a univariate method, and the results are combined to support a conclusion.

If such multiple measurements are analyzed on the basis of separate univariate treatments of the variables, the combination of the results of the univariate tests and the assignment of a level of confidence to any inference drawn from these tests present a problem. If all the variables are perfectly correlated, the same conclusion is drawn from each variable, and univariate methods are acceptable. Perfect correlation means that all the variables change values in the same relationship to each other (e.g., for each five scale increase of the dorsals, the femoral pores increased one). However, variables that are perfectly correlated are each measuring the same source of variation. To prevent heavy weighting of that source of variation, only one of the correlates should be measured. If the variables are completely independent and significance at the 0.10 level is claimed (when at least one variable shows significance), the true level of significance is $1-(.90^n)$ with ^{n} equal to the number of variables measured (Steel, 1955). Suppose four different variables are measured and tested at an alpha-level of 0.10. Using the above formula, it can be seen that the true alpha-level of any conclusion drawn from the combination of the four tests is actually $1-(.90^4) = 1-(.66) = 0.34$. This differs greatly from the alpha-level of 0.10 that would normally be assumed. If the rule would be to claim significance when all the variables show significance, the alpha-level would become $(0.10)^n$, with ^{n} equal to the number of variables measured. Using the previous example, the true alpha-level becomes 0.0001. This makes it practically impossible ever to detect a difference. Often independence of variables is assumed without proof. For a variable to be considered completely independent, its value must not be influenced by the value of any other of the measured variables. In taxonomy, which deals with characters controlled by an unknown arrangement of the genotype, the assumption of independence of variables without prior verification seems untenable.

If either complete dependence or independence of variables were known to be the case, rules could be formulated to allow inferences from a combination of univariate analyses of the data. However, the true situation invariably lies somewhere between the two extremes. Thus, one would not know the true level of significance of the inferences on the combined results of univariate analyses. By using the multivariate generalizations of univariate methods, this problem of indeterminant alpha-level is controlled (Steel, 1955).

Mayr (1969) has advocated the use of multivariate methods wherever multiple measurements are used. He states also that often the calculations (e.g., the determinant of a 100 X 100 matrix) are prohibitive. With the advent of fast digital computers and packaged programs, this is no longer true.

Another more compelling reason for using multivariate analysis of data concerns what is actually being analyzed. Taxonomists are classifying whole organisms, not any one scale count (Mayr, 1969; Sokal and Sneath, 1963). Univariate methods con-

sider only one variable at a time as completely unrelated to all other variables. Multivariate methods consider groups of characters, as a unit, and their relationships with each other. This is a better approximation of the organisms with which taxonomists are concerned. The following is a description of the multivariate techniques used:

Multivariate analysis of variance. A method to test the difference of group means for those cases where more than one variable is recorded for each individual. This is the multivariate extension of the familiar analysis of variance and F-Test. It is appropriate for testing hypothesis concerning differences between populations.

Cluster analysis. When a taxonomic study is made taking two measurements on each individual, the specimens studied could be represented as points on a two-dimensional space. The resulting graph would illustrate the phenotypic interrelations of the individuals. Expanding this to 90 measurements on each individual, the specimens could be represented as points in a hypothetical 90 (or p)-dimensional hyperspace. The representation of individuals on a 90-dimensional graph is best grasped by visualizing many points in space grouped in clusters of varying size. The number of dimensions in the hyperspace is equal to the number of variables measured. This concept of individuals being represented as points in a p-dimensional space is essential to cluster and discriminant analyses.

Ward's method of cluster analysis forms spherical clusters of individuals in the hyperspace. New clusters are formed by measuring the distance from each individual in the original cluster to the center of the cluster, called the centroid. These distances are summed to form the error sum of squares for the cluster. The individuals to be added to the cluster are conditionally added, and the new centroid formed. An error sum of squares for the newly formed cluster is calculated. This procedure is done for all possible entries to the original cluster (possible entries include other clusters as well as individuals). The entry that causes the least increase in the error sum of squares is joined to the original cluster. Each new cluster is formed by joining those individuals that move the centroid the smallest distance. In other words, each cluster is composed of those individuals located closest to each other in the hyperspace. Thus, it is seen that this method unites individuals of the highest morphological similarity first (Wishart, 1969). The main assumption that must be valid for this procedure to give meaningful results is that the characters chosen represent the phenotype of the animal as well as possible.

Canonical analysis. This method allows the examination of the relationship of two sets of variables. The two sets used in this study were (1) groups and (2) variables measured on the individuals. This resulted in two variables, evaluated for each individual, formed from a linear function of all the variables measured. These two new variables maximized the correlation between groups and originally measured variables. When plotted on an x and y axis, the variables form a two-dimensional graph of the relationships of the groups to each other (Dixon, 1968; Rao, 1952).

Discriminate analysis. This technique theoretically constructs p-dimensional planes in the hyperspace, which separate the clusters of individuals. In practice, it builds a single variable from all the variables measured and maximizes the difference between groups (Anderson, 1958; Sokal and Rohlf, 1969).

Rao (1952) describes a "gray" area located between two clusters, in which a few individuals may occur. In this area the individual's probability of belonging to either cluster is not great enough to grant membership with assurance. Rao states the possible conclusions in a system consisting of three clusters. The individuals either belong to (1) one of the three clusters, (2) one of two clusters, or (3) all three clusters and no conclusion may be drawn.

The procedure for using discriminant analysis in a subspecific problem, as developed in this study, parallels Rao's concept. The major distinction is because of the ability of members of two distinct clusters (subspecific population) to interbreed and produce individuals with characteristics intermediate to either of the clusters. Thus, Rao's "gray" area becomes a region occupied by intergrades between the two clusters. As in Rao, an individual with an equal probability of joining all of the groups is considered unidentifiable (see Fig. 11). This procedure, like so many procedures in taxonomy, is based on certain subjective decisions. Therefore, the validity of its results is dependent upon the validity of the assumption made. The assumptions are as follows below:

(1) Among the individuals to be classified, at least two distinct populations must be represented. Prior to using discriminant analysis, an appropriate method must be employed to determine the number of populations present. A test of the population difference is also advisable.

(2) The most crucial assumption concerns the selection of members used in forming the discriminant functions. In order to identify intergrade populations correctly, the individuals used to form the functions must be selected so that only "pure stock" of the populations being investigated is represented. The sample used to form the discriminant functions define, as far as the analysis is concerned, the parameters of that population. Thus, as more intergrades are included in the sample, a less precise definition of the population and its parameters results; and the identification of individuals by the discriminant analysis declines in reliability.

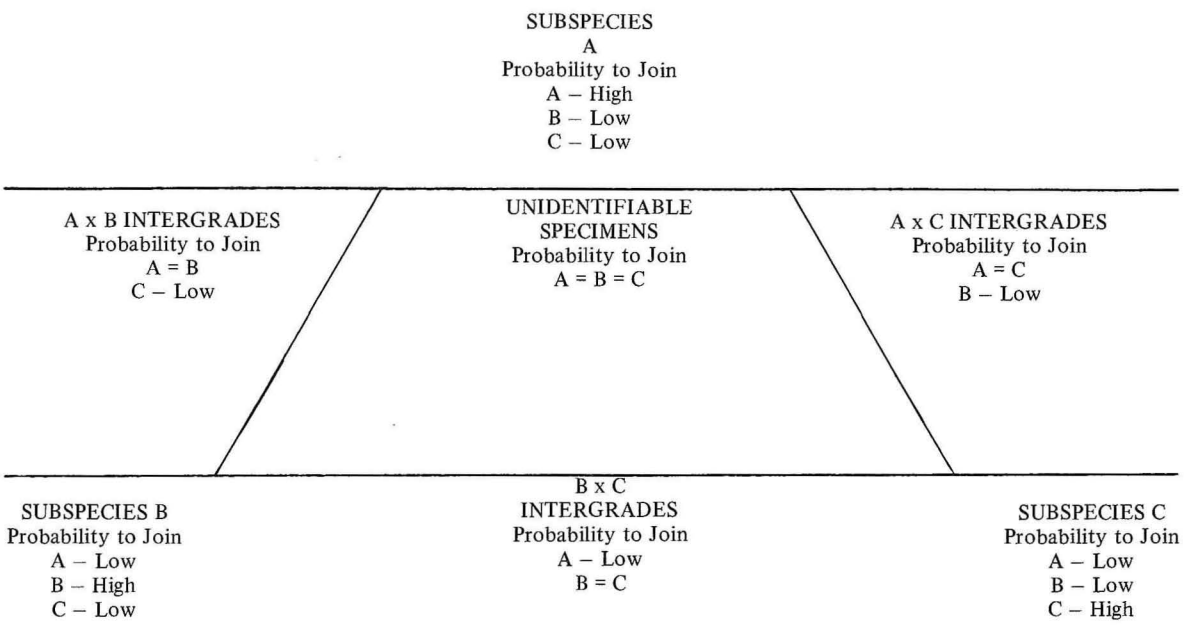


Fig. 11. The subspecific identification problem as viewed by discriminant analysis (modified after Rao, 1952).

(3) Any one individual to be identified, must be considered to have an equal prior probability of belonging to any of the populations. This can be assured by placing an equal number in each of the groups used to form the discriminant functions. It is acceptable to use unequal numbers if specimen availability or some other factor necessitates. In this study, availability of pure *C. c. auriceps* and *C. c. collaris* limited those samples and a decision was made to sacrifice equality of *a priori* probabilities to gain a better definition of the population parameters of the other two subspecies.

(4) Discriminant analysis is a statistical method, and, as such, its reliability hinges on the amount of information put into it. As the number of individuals and variables used in forming the functions increases, so does the reliability of the results. This is also true of the reliability of identification of new specimens. The results of statistics are always phrased in probabilities and the higher the probability, the more sure the conclusion. It is possible, especially in a subspecific problem, to have any one individual wrongly identified as belonging to a population. This becomes more likely, the closer the populations resemble each other. Therefore, conclusions about which population is present in a certain area should be made on a basis of the population most frequently identified from that area. One specimen (or perhaps a few) is not enough to make a valid conclusion about the population structure of an entire area.

SUMMARY AND CONCLUSIONS

Little work has been done previously on the taxonomy of *Crotaphytus collaris baileyi.* This and the demonstration by Fitch and Tanner that *C. c. baileyi* is a heterogeneous grouping prompted the present study. Only the populations of the type material, the Upper Colorado River Basin, and the Chihuahuan Desert were studied. Multivariate, variance, canonical and discriminant analyses of external characters were performed, and pattern-coloration characters were examined on living specimens.

The results of the analyses show significance between all three populations. The discriminant functions distinguished between the populations with 80% reliability and patternal characters were discriminatory with near 100% reliability. Therefore, a new subspecific name, *C. c fuscus,* was applied to the Chihuahuan population.

The *collaris*-complex was shown to consist of at least four subspecies: *C. c. auriceps, C. c. baileyi, C. c. collaris* and the new subspecies, *C. c. fuscus* from the Chihuahuan Desert. *C. c. auriceps'* range was restricted to the area near Moab, Utah, and north of the union of the Green and Colorado rivers. A broad intergrade zone south into the Painted Desert was established between *C. c. auriceps* and *C. c. baileyi.* The range of *C. c. baileyi* was established as central Arizona. Southern and central New Mexico and most of Mexico east of central Sonora were established as the range for *C. c. fuscus.* Further study of the populations presently recognized as *C. c. collaris* was ad-

vised.

While all the populations were separable on the basis of morphology, the best characters for identification were color and pattern. *C. c. auriceps* has a light green body and the yellow of the head extends onto the side of the throat. *C. c. baileyi* has a darker green body with reduced yellow on the head. The area of the throat between the infralabials and the gular patch is always white. *C. c. fuscus* has a brown body and a white to cream head.

Important discoveries were also made in methodology. The necessity for using multivariate statistics in taxonomic studies which investigate more than one character was demonstrated. The use of *a posteriori* probabilities was presented as a new technique for investigation of taxonomic problems involving intergradation.

ACKNOWLEDGMENTS

We wish to extend our gratitude to Dr. Melvin W. Carter and Mr. Vernon Crandall for their suggestions and aid in the preparation of the statistical material and to Dr. Clive D. Jorgensen for introducing to us Cluster analysis.

The manuscript was read by Drs. Ferron L. Anderson, August W. Jaussi, H. Duane Smith and Stephen L. Wood of Brigham Young University and by Dr. Henry S. Fitch of Kansas University. We appreciate their helpful suggestions.

Materials were supplied by the following institutions. Brigham Young University (BYU), California Academy of Science (CAS), California State College at Long Beach (CSCLB), Los Angeles County Museum (LACM), Museum of Vertebrate Zoology (MVZ), United States National Museum (USNM), University of Colorado (UC), University of Illinois Natural History Museum (UIMNH), University of Kansas (KU), and University of Texas at El Paso (UTEP). For the loan of specimens and courtesies shown us by the personnel of these institutions, we are most grateful.

We also express our appreciation to Mr. Nathan M. Smith and Mr. J. Robert McMorris for their help with specimens in the laboratory and in the field. Mr. Michael Andelin prepared the art work, and Mrs. Janice Ingram assisted in editing and typing the rough draft of this manuscript. We appreciate their assistance and the assistance of all those involved in this study.

LITERATURE CITED

Allen, M. J. 1933. Report on a collection of amphibians and reptiles from Sonora, Mexico, with description of a new lizard. Occ. Pap. Mus. Zool. Univ. Mich., 259:1-15.

Anderson, T. W. 1958. An introduction to multivariate statistics. John Wiley and Sons, Inc., London. p. 126-307.

Burt, C. E. 1928. The synonymy, variation and distribution of the Collared Lizard, *Crotaphytus collaris,* (Say). Occ. Pap. Mus. Zool. Univ. Mich., 196:1-19.

Cope, E. D. 1900. The crocadilians, lizards, and snakes of North America. Ann. Rep. U.S. Nat. Mus. for 1898, p.153-1270.

Dixon, W. J. 1968. Biomedical computer programs. Univ. of Calif. Press, Los Angeles. p. 214a-215.

Fitch, H. S. and W. W. Tanner. 1951. Remarks concerning the systematics of the Collared Lizard (*Crotaphytus collaris*). Trans Kans. Acad. Sci., 54(4):548-559.

Fitch, H. S. 1956. An ecological study of the Collared Lizard (*Crotaphytus collaris*). Univ. Kans. Mus. Nat. Hist. Publ., 8:213-274.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York. p. 181-197.

Morrison, D. F. 1967. Multivariate statistical methods. McGraw-Hill Book Co., New York. p. 159-207.

Ostle, B. 1966. Statistics in research. Iowa State Univ. Press, Ames, Iowa. p. 129, 512-564.

Pack, L. C. and W. W. Tanner. 1970. A taxonomic comparison of *Uta stansburiana* of the Great Basin and the Upper Colorado River Basin in Utah, with a description of new subspecies. Gt. Basin Nat., 30(2):71-90.

Rao, C. R. 1952. Advanced statistical methods in biometric research. John Wiley and Sons, Inc., New York. p. 273-370.

Schmidt, K. P. 1922. The amphibians and reptiles of Lower California and the neighboring islands. Bull. Amer. Mus. Nat. Hist., 46:607-707.

Smith, H. M. 1946. Handbook of lizards: lizards of the United States and Canada. Comstock Publishing Co., Ithaca, New York. p. 166-172.

Smith, H. M. and E. H. Taylor. 1950. An annotated checklist and key to the reptiles of Mexico, exclusive of the snakes. Bull. U.S. Nat. Mus. p. 199.

Sokal, R. R. and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco. p. 1-357.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry: the principles and practices of statistics in biological research. W. H. Freeman and Co., San Francisco. p. 1-776.

Stebbins, R. C. 1954. Reptiles and amphibians of western North America. Univ. of Calif. Press, Berkeley, California. p. 227-229.

Stebbins, R. C. 1966. A field guide to the western reptiles and amphibians. Houghton Mifflin Co., Boston. p. 99-100.

Steel, R. G. D. 1955. An analysis of perennial crop data. Biometrics, 11(2):201-212.

Stejneger, L. 1890. An annotated list of reptiles and batrachians collected by Dr. C. Hart Merriam and Vernon Bailey on the San Francisco Mountain Plateau and Desert of the Little Colorado River, Arizona, with descriptions of new species. N. Amer. Fauna, 3:103-118.

Stejneger, L. and T. Barbour. 1917. A checklist of North American amphibians and reptiles. Harvard Univ. Press, Cambridge, Massachusetts. p. 45.

Stone, W. and A. G. Rehn. 1910. On the terrestrial vertebrates of portions of southern New Mexico and western Texas. Proc. Acad. Nat. Sci. Phila., 40:16-34.

Van Denburgh, J. and J. R. Slevin. 1921. Preliminary diagnosis of new species of reptiles from islands in the Gulf of California, Mexico. Proc. Calif. Acad. Sci. Ser. 4, 11:95-98.

Van Denburgh, J. 1922. The reptiles of western North America. Vol. 1, "Lizards", Occ. Pap. Calif. Acad. Sci., 10:95-98.

Wishart, D. 1968. A fortran II programme (CLUSTAN) for numerical classification. Computing Laboratory, St. Andrews, Fife, Scotland. p. 1-50.

Wishart, D. 1969. Mode analysis: a generalisation of nearest neighbour which reduces chaining effects, pp. 282-308. *In* A. J. Cole (ed.) Numerical taxonomy. Academic Press, London.