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GEOGRAPHIC VARIATION IN *PHRYNOSOMA CORONATUM* (LACERTILIA, PHRYNOSOMATIDAE): FURTHER EVIDENCE FOR A PENINSULAR ARCHIPELAGO

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Abstract: Principal components analysis of 24 morphological and color-pattern characters scored for 634 specimens reveals four distinct, geographic groups within *Phrynosoma coronatum*. The four groups can be diagnosed on the basis of color pattern characters, but there are nearly discrete differences in morphological characters as well. Morphological evidence of hybridization has been detected between two groups. The four morphological groups are likely genetic entities given the close correspondence between the morphological patterns in *Phrynosoma* and genetic units detected in *Urosaurus*. Therefore, the four groups of coast horned lizards are treated as separate species. Latinized names (*blainvillii*, *cerroense*, *coronatum*) are available for three of the four taxa. The subspecies *frontale* and *schmidti* cannot be adequately distinguished by the multivariate analysis and are placed in the synonymy of *P. blainvillii*. In addition, a new species, *Phrynosoma wigginsi*, is described from the eastern side of the Sierra de Guadalupe and Sierra de La Giganta in the central Gulf Coast region of the peninsula of Baja California. Diversification in *Phrynosoma* has occurred via allopatric speciation and the geographic juxtaposition of these morphological groups provides additional evidence for two ancient transpeninsular seaways.

Key words: Baja California; Biogeography; *Phrynosoma*; Phrynosomatidae; Systematics

Phrynosoma coronatum was named and described by H. M. D. de Blainville (1835) based on specimens collected by Paolo Emilio Botta in "California." A few years later, J. E. Gray (1839) described another species, *P. blainvillii*, again from a specimen collected by Botta in California and given to Gray by de Blainville. In the decades that followed, several additional new species were described but were later synonymized or relegated to subspecific rank. Van Denburgh (1922) treated *coronatum* and *blainvillii* as separate species, a concept that was subsequently supported by the studies of Klauber (1936) and Tinkham (1951). Conversely, Linsdale (1932) recognized only one species, *P. coronatum*, with one insular and four mainland races. Tevis (1944), Smith (1946), and Murray (1955) followed the concept of Linsdale, although the number of recognized subspecies varied according to author. In his monograph, Reeve (1952) recognized a single species consisting of five subspecies; the insular *cerroense* was treated as a full species. Jennings (1988*a*) accepted Reeve's taxonomy, but the geographical limits of the subspecies more closely agreed with those of Tevis (1944).

Noting the subjectivity of previous studies and the disagreement among authors, Grismer and Mellink (1994) placed *cerroense* in the synonymy of *P. coronatum* and recommended that the latter species be considered a monotypic taxon exhibiting "smooth," clinal geographic variation. Subsequently, Brattstrom (1997) reexamined variation in six morphological traits used by other authors in the taxonomy of *P. coronatum*. He concluded that the species is highly variable and that there is no taxonomic or biological basis for recognizing subspecies. Grismer (2002*a*) noted that variation in *P. coronatum* is extensive and that it generally corresponds with the phytogeographic regions of the peninsula. He treated the previously recognized subspecies as pattern classes, whose distributional limits closely follow the subspecific boundaries of Reeve (1952).

The potential for morphological clines on the peninsula of Baja California is considerable. The narrow east-west width and broad latitudinal extent of the peninsula favor the establishment of north-south clines along environmental gradients via isolation-by-distance and presumably selection. However, mountain ranges spanning the length of the peninsula may also create elevation and rainfall gradients, as well as potential barriers

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to gene exchange along the east-west axis. These forces are, no doubt, differentially influential with respect to various herpetofaunal elements of the peninsula, depending on their vagility and ecological requirements.

Phrynosoma coronatum occurs from near Kennett, Shasta County, California, southward through central and southern California, reaching the Cape Region of Baja California del Sur (Jennings, 1988*a*). I initiated a multivariate analysis of geographic variation in *P. coronatum* to discover and describe the patterns of variability within this wide-ranging species. An expanded data set containing new, as well as traditional characters, was used to enhance the detection of variation. Both univariate and multivariate statistical approaches were applied to the data set in an effort to better understand the patterns of variation and their underlying causal factors. Although the primary purpose of this investigation was to study geographic variation and its underlying mechanisms in *P. coronatum*, it was anticipated that my analysis would shed light on the taxonomic status of the currently recognized geographic races within this species.

MATERIALS AND METHODS

I examined a total of 671 alcohol-preserved specimens of *P. coronatum*. Of this total, 634 specimens, representing 71 local samples from throughout the range of the taxon, were used for detailed statistical analysis. Sample localities, sample sizes, and museum numbers are given in Appendix I.

Statistical Analysis

The characters recorded from specimens included meristic, morphometric (mensural), and qualitative (color, shape) traits. No left-right asymmetry was detected in characters recorded from both sides; counts are presented here for one side only. Qualitative attributes were coded as binary or multi-state characters. An analysis of variance (ANOVA) was performed to determine which characters showed greater variation among, than within, local samples. Characters that did not display significant differences among samples were discarded. An ANOVA was also used to discover sexually dimorphic characters. Due to statistically significant gender differences for some characters, males and females were treated separately in the multivariate analysis. Principal components (PC) analysis (SAS Institute, 1990) was used to analyze patterns of variation in the male and female data sets. Character observations from individual specimens (rather than sample means) were used as input data for the PC analysis. The original taxonomic identities of the samples were included a posteriori in the multivariate analysis to determine whether resulting clusters corresponded to historically recognized taxa. The mean, range, standard deviation, and standard error were calculated for each meristic and morphometric character for each local sample. The data set for the statistics of dispersion for the 71 local samples is voluminous and is not published here, but it is available from the author upon request. However, statistics of dispersion are tabulated herein for the different population clusters revealed in the PC analysis. Significance of differences among population sample means was tested using the SAS system GLM procedure *t*-tests. One population cluster (labeled BFS; see below) was arbitrarily divided into two geographical groups, the Central Valley and Peninsular Ranges, for comparison.

Characters

Twenty-four potentially informative characters as well as the museum number, sex, and snout–vent length (SVL) were taken from each specimen. Morphological terminology follows Klauber (1936), Smith (1946), and Reeve (1952), and, in addition, several new terms are used (Fig. 1). The following morphometric (mm), meristic, and qualitative color characters were used in the analysis.

Tail length (TL) was measured from vent to tail tip and is expressed as a proportion of the SVL. Males and females were analyzed separately due to significant sexual dimorphism in all population samples.

Parietal shelf length (PAR) is the distance from the base of the interoccipital spine to the anterior edge of the parietal eye and was measured with dial calipers to the nearest 0.1 mm and expressed as a proportion of total head length (distance between base of interoccipital to rostral scale).

Interparietal to rostral scale distance (ERD) is the distance from anterior edge of the interparietal scale to the rostral scale and was measured with dial calipers to the nearest 0.1 mm and expressed as a proportion of SVL. Males and females were analyzed separately due to significant sexual dimorphism in some samples.

Postrictal spine length (PST) is the length of the spine (on left side of the head) from base to tip and was measured with dial calipers to the nearest 0.1 mm and expressed as a proportion of ERD.

Parietotemporal scale length (PTM) is a new term describing the scale situated dorsally on the base of the largest temporal horn adjacent to the occipital horn. Length of the scale (on right side of head) was measured with dial calipers to the nearest 0.1 mm and expressed as a proportion of ERD.

Parietotemporal scale shape (PTMS) was subjectively judged as spinous (2), somewhat spinous (1.5) or not spinous (1).

Interoccipital spine length (IOC) is the length of the spine from base to tip, measured with dial calipers to the nearest 0.1 mm and expressed as a proportion of ERD. Males and females were analyzed separately due to significant sexual dimorphism in some samples.

Position of subrictal scale (SUB), on left side of head, was subjectively judged as being in line with (2), slightly above (1.5), or well above (1) the row of chinshields when viewed laterally.

Number of chinshields (CHN) was counted from the first scale in the mental region (on either side of a median scale, if present) to the largest scale anterior to the subrictal; the count did not include "incipient" chinshields (see below). The number was recorded from the left side of the head.

Number of incipient chinshields (INC) is a new term referring to one or more enlarged scales situated between the last chinshield and the anterior edge of the subrictal scale. These modified scales, when present, have apparently incorporated adjacent gulars, including basirictals (see below), and hence may be partly homologous with the latter. The number was recorded from the left side of the head.

Number of basirictals (BAS) is a new term referring to a series of scales along the ventral border of the base of the subrictal scale. Incipient chinshields incorporating a portion of the basirictal series were not counted. The number was recorded from the left side of the head.

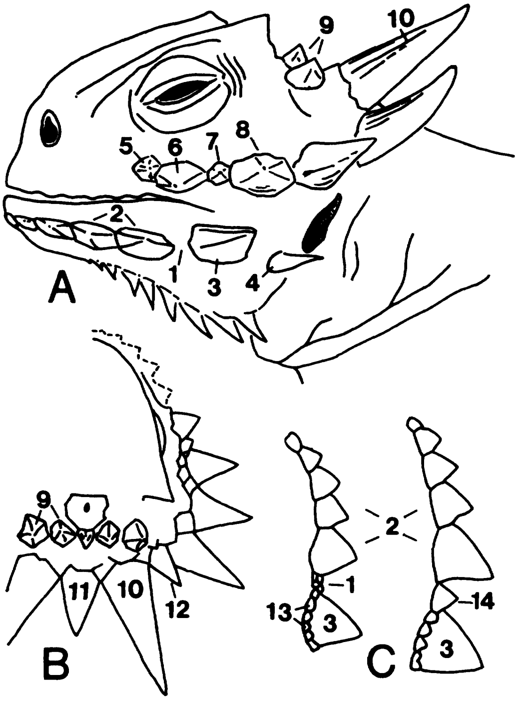

FIG. 1.—Terminology for selected characters used in the study of *Phrynosoma coronatum*. (A) Left lateral aspect of head, (B) dorsal aspect of head, (C) ventral view of left series of chinshields. Terms are: (1) chinshield-subrictal gap, (2) chinshields, (3) subrictal scale, (4) postrictal spine, (5) satellite temporal horn, (6) fifth temporal horn, (7) temporal gap with reduced horn or scale, (8) third temporal horn, (9) preoccipital tubercles, (10) occipital horn, (11) interoccipital spine, (12) parietotemporal scale, (13) basirictals bordering subrictal scale (3), (14) incipient chinshield positioned between last chinshield and subrictal scale (3).

Chinshield-subrictal gap (GAP) is the distance between the last chinshield and the subrictal scale on the left side of the head, measured with dial calipers to the nearest 0.1 mm and expressed as a proportion of ERD. Males and females were analyzed separately due to significant sexual dimorphism in some samples.

Number of gular scales (GUL) is the count of longitudinal rows of gular scales (including the median rows of small scales) at the level of the anterior edge of the subrictal scale.

Length of fourth temporal horn (TMP) is the length of the fourth temporal horn, measured from base to tip with dial calipers to the nearest 0.1 mm and expressed as a proportion of the length of the next anterior (fifth) temporal horn on the right side of the head. Reeve (1952:884) noted that a "gap" in the temporal horn series, observed in some populations, was due to the reduced size of the horn positioned fourth from the rear.

Orientation of third temporal horn (OTH) is the orientation of the third (from the rear) temporal horn on the right side of the head, subjectively recorded as projecting posterolaterally (1) or laterally (2).

Number of preoccipitals (PRE) is a new term referring to a transverse series of enlarged conical scales situated anterior to the occipital horns. The scales vary in shape from bluntly protuberant to spinous. Tinkham (1951) referred to these scales as "postcephalic tubercles."

Number of fringe scales in the lower (second) abdominal row (FRG) was counted from the left side; the counts were somewhat subjective due to variation in scale size and shape.

Cephalic (frontal, supraocular) scale color (CFS) was recorded as tan (1), tan with black rugosities (2), charcoal gray with black rugosities (3), or cephalic area entirely black (4).

Color of cephalic scale borders (CSB) was recorded as no cephalic scale border color (1) or white borders present (2).

Color of temporal horns (CTH) was recorded as the same color as the cephalic scales (1) or paler than the cephalic scales (2).

Surface texture of cephalic scales (TFS) was recorded as scales smooth (0), smooth with rugose edges (0.5), completely rugose (1), rugose with some granulations (1.5), or granular with little or no rugosities (2).

Interparietal to rostral scale number (IRS) was counted in a straight line between the interparietal and the rostral scale.

Subocular scales (SOC) were recorded as not projecting (0) or projecting (1).

Interparietal scale color (ISC) was recorded as tan (1), white (2), or black (3).

RESULTS AND DISCUSSION

Statistical Analyses

Principal components analysis of the 71 local samples of *P. coronatum* reveals four population clusters. Male and female samples are shown in separate multivariate plots (Figs. 2, 3). Character loadings are shown in Table 1. The relative positions of male specimens along PC axis I are attributed primarily to four color characters (CFS, CSB, CTH, ISC) and 10 morphological characters (PAR, PST, PTM, PTMS, IOC, SUB, TMP, OTH, PRE, SOC) that have moderate to high loadings on that axis. In the female samples, PTMS has a slightly lower loading, and PRE has a slightly higher loading than in male samples. Male specimens are separated along PC axis II primarily by 1 color (CTH) and 13 morphological characters (PAR, ERD, PTM, CHN, INC, BAS, GAP, GUL, TMP, OTH, PRE, TFS, IRS), having moderate to high loadings on that axis. In the female samples, ERD is less influential, and FRG is much more influential along PC axis II than in the male samples. None of the color characters used in the multivariate analysis appears to be important in background matching. Otherwise, the four clusters would not have segregated geographically, but would have grouped according to substrates and vegetative associations across regions.

The nominal subspecies *P. c. blainvillii*, *P. c. frontale*, and *P. c. schmidti* comprise a single cluster (denoted hereafter as the BFS cluster; Figs. 2, 3) in which there is considerable overlap among the three nominal subspecies, although some degree of segregation can be seen along PC axis II. The subspecies *blainvillii* is primarily distinguished from *frontale* and *schmidti* by the smooth surfaces of its frontal and supraocular scales (Reeve, 1952). However, cephalic scales with smooth, rugose, and granular surfaces (Fig. 4) are polymorphic within the geographic limits of *P. c. blainvillii* and *P. c. schmidti* (Table 2).

Several subsequent PC analyses (using only samples assignable to *blainvillii*, *frontale*, and *schmidti*) were performed in an attempt to separate these taxa further. The first analysis used the original set of 24 characters; a second analysis used a subset of 16 characters with moderate to high loadings; and a third used six characters having only high loadings on PC I and/or PC II. These further attempts to separate the three subspecies failed (results not presented), apparently because of the polymorphic and polytopic nature of the

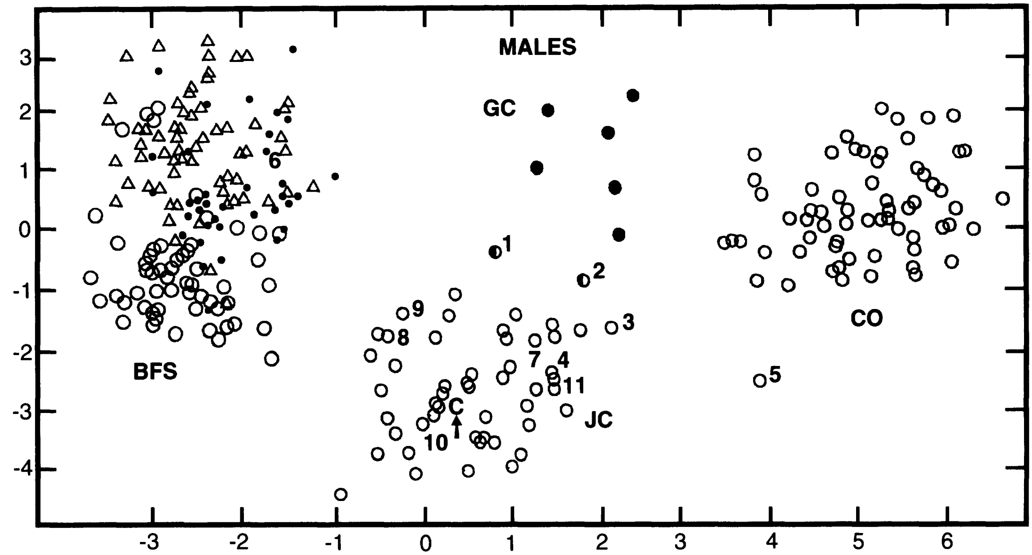

FIG. 2.—Projection of male samples of *Phrynosoma* on the first two principal components (PC I, PC II) of a 24-character correlation matrix. PC I explains 40.6% and PC II explains 11.2% of the total variance. In the BFS cluster, *blainvillii* = triangles, *frontale* = circles, *schmidti* = dots. Other clusters are *jamesi-cerroense* (JC), unnamed Gulf Coast taxon (GC), and *coronatum* (CO). Letter "C" (with arrow) denotes position of male specimen of *cerroense* (SDSNH 17370) in JC cluster. Specimens are designated as follows: 1 and 2, putative hybrids (MVZ 10660 and MVZ 13638, respectively) from San Ignacio; 3, SDSNH 18082 (El Barríl); 4, SDSNH 18085 (Bahía San Francisquito); 5, MVZ 73556 (San José de Gracia); 6, SDSNH 39003 (Bahía de Los Ángeles); 7, CAS 143430; 8, CAS 143431; 9, CAS 143432, all from Miller's Landing; 10, LACM 63479 between Miller's Landing and Rancho Mezquital; 11, CAS 87371 from N of San José de Gracia. See text for further discussion.

variation in the cephalic scale character and the lack of geographic concordance with other characters. If this cluster merits taxonomic recognition, the name *blainvillii* Gray 1839 can be used as it has priority over *frontale* Van Denburgh 1894 and *schmidti* Barbour 1921.

Cluster JC (Figs. 2, 3) consists of the nominal subspecies *P. c. jamesi* from the Vizcaíno Desert and a small sample of *P. cerroense* from Isla de Cedros. Schmidt (1922:669) first commented on the close relationship between *cerroense* and *jamesi* when he described the latter, suggesting that *cerroense* was derived from a *jamesi*-like stock. The two forms occupy geographically proximate areas, and Grismer and Mellink (1994) and Grismer et al. (1994) point out that Isla de Cedros is part of a submerged, westward extension of the Vizcaíno Peninsula. The taxonomic status of *cerroense* has remained largely unchallenged, except by Linsdale (1932), who reduced it to subspecific rank. Both Reeve (1952) and Presch (1969) treated it as a full species. Jennings (1988*b*) followed these two workers, alluding to previously noted differences between insular and mainland forms in scalation and osteology. Presch (1969) stated that *P. cerroense* shows a reduction in caudal vertebrae compared with *P. coronatum*, but his table 1 contradicts that claim, prompting Grismer and Mellink (1994) to relegate *cerroense* to the synonymy of *P. coronatum*. In my multivariate analysis, specimens of *cerroense* fall within the *jamesi* cluster for both males and females, although one of the females is located near the cluster's edge. If the JC cluster merits taxonomic recognition, the name *cerroense* Stejneger 1893 has priority over *jamesi* Schmidt 1922 and can be applied to this group.

A small sample of horned lizards from the Gulf of California side of the peninsula, east of the Sierra de Guadalupe and Sierra de La Giganta, comprises cluster GC (Figs. 2, 3). Heretofore, lizards from the Gulf Coast side of the central peninsula were classified as *P. c. jamesi* (Jennings, 1988*a*; Reeve, 1952), but, on the basis of my multivariate analysis, they are shown to differ morphologically from populations inhabiting the Vizcaíno Desert of the Pacific Coast.

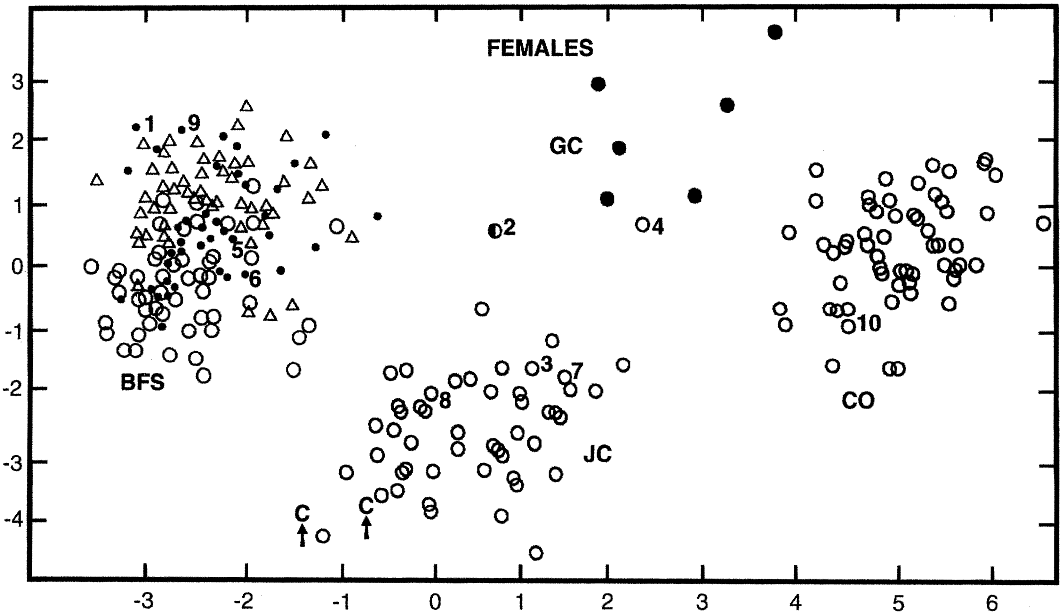

FIG. 3.—Projection of female samples of *Phrynosoma* on the first two principal components (PC I, PC II) of a 24-character correlation matrix. PC I explains 38.9% and PC II explains 12.4% of the total variance. In the BFS cluster, *blainvillii* = triangles, *frontale* = circles, *schmidti* = dots. Other clusters are *jamesi-cerroense* (JC), unnamed Gulf Coast taxon (GC), and *coronatum* (CO). Specimens designated as follows: 1, LACM 4333 (Arroyo San Javier); 2, MVZ 13639, a putative hybrid from near San Ignacio; 3, SDSNH 18084; 4, SDSNH 18083 (both from El Barríl); 5, MVZ 161207 (WNW of Bahía de Los Ángeles); 6, SDSNH 47841 (Bahía de Los Ángeles); 7, MVZ 37331; 8, MVZ 37332 (both from Miller's Landing); 9, MVZ 37329 (near Punta Prieta); 10, MVZ 73555 (from Médaño Blanco). Letter "C" (with arrow) denotes positions of two female specimens of *cerroense* (SDSNH 17369 and 24357). See text for further discussion.

Cluster CO (Figs. 2, 3) consists of samples classified as *P. c. coronatum* from the southern portion of the peninsula. In the PC analysis, there were no misclassifications of specimens assigned, a posteriori, to this nominal subspecies.

In the following discussions, I informally use the names *blainvillii*, *cerroense*, *coronatum*, and "Gulf Coast" to denote the four clusters revealed by the PC analysis pending formal justification of taxonomic rank (see Taxonomic Assessment). Several intermediate specimens and outliers associated with the four clusters require further discussion. Three specimens (1–2 in Fig. 2; 2 in Fig. 3) from near San Ignacio (MVZ 10660, 13638–39) fall generally between the *cerroense* cluster of the Vizcaíno Desert and that of the unnamed population from the Gulf Coast of the peninsula. These specimens appear to be morphological intermediates based on the multivariate analysis and the univariate assessment of their characters. A zone of contact and gene exchange apparently occurs along low foothills (just south of Volcan de Las Tres Virgenes), separating the Pacific slope near San Ignacio from the Gulf Coast desert near Santa Rosalía.

Reeve (1952:885) commented that horned lizards from El Barríl (SDSNH 18082–84) and Bahía San Francisquito (SDSNH 18085), both localities on the Gulf Coast of the peninsula, appear to be distinct and could represent a new taxon. However, in my multivariate analysis, three of the four specimens fall more or less within the *cerroense* cluster and one falls marginally within the un-named Gulf Coast cluster of specimens (3–4 in Fig. 2; 3–4 in Fig. 3). The apparently wide range of morphological variation in the El Barríl sample suggests genetic influences from both the Vizcaíno Desert (*cerroense*) and the unnamed Gulf Coast horned lizard. This hypothesis is tenable, considering the geographic location of El Barríl, but horned lizard populations in this area warrant further study.

Specimens from near Bahía de Los Ángeles were first classified as *P. c. frontale* by Tevis (1944), and later as *P. c. jamesi* by Reeve

(1952:885) and Jennings (1988*a*). Two specimens from this locality (SDSNH 39003, 47841), as well as one specimen from 21 km WNW of Bahía de Los Ángeles (MVZ 161207), fall within the BFS cluster (6 in Fig. 2; 5–6 in Fig. 3) of the PC analysis and can be assigned to *blainvillii*. Likewise, two specimens (not used in the PC analysis), a juvenile from Bahía de Los Ángeles (LACM 4308) and a road-kill adult (MVZ 182262) taken 23–32 km WNW of the bay, also agree with *blainvillii* on the basis of morphology. The southern limit of *blainvillii* includes the Sierra de San Borja and the Sierra de Calmallí. It needs to be determined whether or not isolated, montane populations occur farther south.

A series of horned lizards from near Miller's Landing (28° 32′ N) on the Pacific Coast (MVZ 37331–32, CAS 143430–32) and between Miller's Landing and Rancho Mezquital (LACM 63479) falls within the *cerroense* cluster of the PC analysis (7–10 in Fig. 2; 7–8 in Fig. 3). However, another specimen (LACM 4333) from San Xavier falls within the BFS cluster (1 in Fig. 3) and is assignable to *blainvillii*. San Xavier (= Arroyo San Javier, approximately 28° 32′ N; Bostic, 1971) is located NE of Miller's Landing, along the lower western slopes of the Sierra de Calmallí. The exact collection locality of the Arroyo San Javier specimen is unknown, but the apparent proximity (about <16 km) of the two forms of horned lizards in this area suggests that they are narrowly allopatric or parapatrically associated, perhaps along an elevation gradient. There is no morphological evidence from the PC analysis to suggest that the two forms are hybridizing (sensu Zweifel, 1962). Interestingly, the Arroyo San Javier specimen (1 in Fig. 3) falls along the margin of the BFS cluster farthest in multivariate space from the *cerroense* cluster, evidence, perhaps, of morphological character displacement. North of Arroyo San Javier, the nearest known population of *blainvillii* is from 3.2 km NW of Punta Prieta (MVZ 37329; 9 in Fig. 3).

TABLE 1.—Character loadings from correlation matrices onto the first and second principal components of the multivariate analysis.

	Males		Females	
Character	PCI	PCII	PCI	PCII
TL	0.124331	0.044001	0.115790	−0.052371
PAR	0.241149	0.172103	0.255159	0.147456
ERD	−0.036155	0.214562	−0.032771	0.156481
PST	−0.275355	−0.063658	−0.282964	−0.061103
PTM	0.198633	0.248898	0.178412	0.292587
PTMS	0.210982	0.125025	0.191211	0.180307
IOC	0.269663	0.120099	0.280405	0.138010
SUB	0.232229	−0.063961	0.231777	−0.052460
CHN	−0.086719	0.378479	−0.069604	0.349890
INC	−0.019779	0.222856	−0.038996	0.225883
BAS	0.022320	−0.348197	−0.013756	−0.285043
GAP	−0.006687	−0.324404	−0.025922	−0.367999
GUL	0.155818	0.292527	0.116041	0.289988
TMP	−0.227148	0.230669	−0.212845	0.228059
OTH	0.251785	−0.245848	0.251450	−0.222998
PRE	0.195965	0.188771	0.210874	0.168900
FRG	0.145110	0.016537	0.125881	0.215768
CFS	0.304398	−0.103885	0.307579	−0.146185
CSB	0.287507	0.086510	0.298202	0.035603
CTH	0.271106	−0.227260	0.268276	−0.266292
TFS	0.084994	−0.233333	0.091545	−0.179994
IRS	−0.114072	−0.196098	−0.149583	−0.135955
SOC	0.265197	0.027929	0.262467	0.022114
ISC	0.303443	−0.064332	0.308093	−0.106881

The Cape Region is occupied by the nominal subspecies *coronatum*, which was previously known from as far north as Santo Domingo on the Plain of Magdalena (Jennings, 1988*a*). Additional specimens (MVZ 73555; LACM 4304) have been collected near Médaño Blanco (approximately 25° 36′ N latitude). Only MVZ 73555 (an adult) was used in the multivariate analysis, and it falls well within the *coronatum* cluster (10 in Fig. 3). It appears that *coronatum* and *cerroense* are allopatric, but this is probably due to the lack of collecting effort from a critical region of the peninsula between 25° 36′ N, 26° 35′ N latitude. Contact is anticipated along the Pacific side of the peninsula because of the absence of any obvious physical barriers between the Vizcaíno Desert and Plain of Magdalena. The southern distributional limit of *cerroense* is poorly known. A specimen (MVZ 73556) collected at San José de Gracia (approximately 26° 35′ N) is a morphological outlier in the PC analysis (5 in Fig. 2), and its position on the plot may suggest genetic influence from *coronatum*. However, the specimen does not approach the *coronatum* cluster along PC axis II and does not exhibit any coloration features of *coronatum*. Also, another specimen (CAS 87371) from 6.4 km N of San José de Gracia (112 km by road S of San Ignacio) is typical in morphology and color pattern, falling well within the *cerroense* cluster (11 in Fig. 2). The map of Reeve

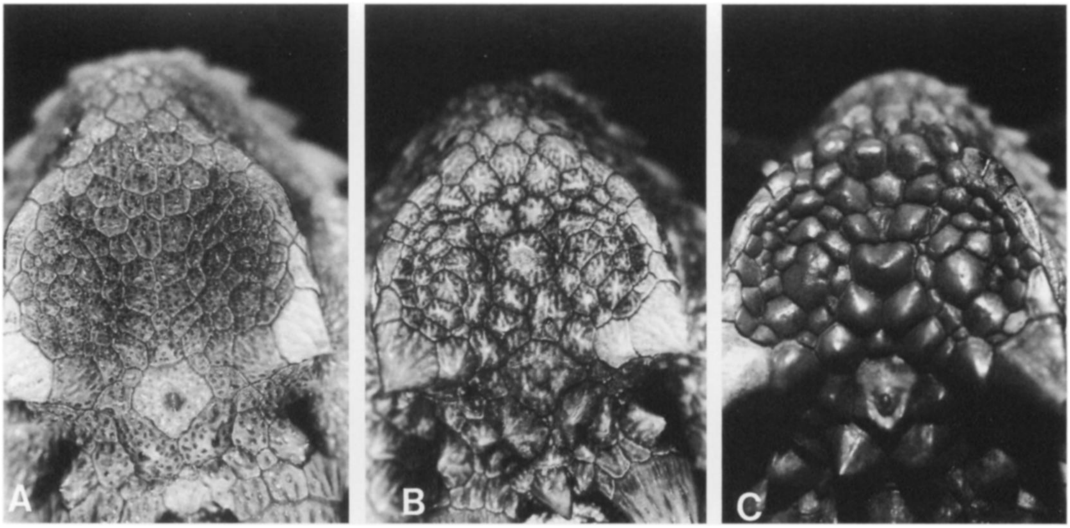

FIG. 4.—Variation in surface texture of cephalic scales among and within populations classified as subspecies *Phrynosoma coronatum blainvillii*, *frontale*, and *schmidti*. (A) granular surface, MVZ 36424, San Benito County, CA. (B) rugose surface, MVZ 2412, Los Ángeles County, CA. (C) smooth surface, MVZ 43489, San Diego County, CA.

(1952) shows a locality record in the critical area near Punta San Juanico (26° 05′ N latitude), but I believe this is erroneous (see below, in Misidentified specimens).

The broad latitudinal extent (1300 km) of the peninsula of Baja California is theoretically conducive to clinal patterns of variation. *Phrynosoma coronatum*, as presently defined, has an extensive latitudinal range from northern California (near latitude 41° N) to the Cape Region (near latitude 23° N). Hence, this taxon is ideal for searching for north-south character clines correlated with environmental gradients. Ten continuous variables (mensural and meristic) with moderate to high loadings on PC axis I (TL, PTM, PAR, IOC, GUL, PRE, FRG, IRS, TMP, PST) were examined for possible clinal variation. Sample means for these variables were arranged in a north to south sequence (Fig. 5); samples 1–16 represent the *blainvillii* cluster, 17–19 the *cerroense* cluster, and 20–22 the *coronatum* cluster. Samples 1–16 show non-clinal or weakly clinal patterns of variation between 37° 49′ and 30° 30′ N latitude, about 834 km of California and northern Baja California. However, large gaps exist between samples 16 and 17 (*blainvillii* and *cerroense*; about 2° 32′ latitude or 289 km) and samples 19 and 20 (*cerroense* and *coronatum*; about 3° 10′ latitude or 361 km), and little can be said about any character trends within these gaps. In the case of samples 16 and 17, univariate examination of five smaller samples from intervening localities, as well as the positions of these specimens on the PC plots, suggests that abrupt character shifts should be expected.

Taxonomic Assessment

The fundamental criterion for species recognition in empirically based systematic studies is the presence of one or more fixed or non-overlapping differences between species, regardless of which underlying species concept is employed (Nixon and Wheeler, 1990). The name *Phrynosoma coronatum*, as currently applied, encompasses at least four distinct groups of populations. These forms differ discretely from one another by several color pattern characters (Table 3). They also show statistically significant differences in sample means for a number of morphological characters (Tables 4, 5), the most useful of which are PAR, PST, TMP, OTH, SUB, and IRS because they display limited overlap between groups. The multivariate assessment of the differential characters reveals that these four groups form discrete clusters, with few intermediates, which strongly suggests that they represent independent evolutionary lineages.

TABLE 2.—Variation in cephalic scale texture within and among selected population samples of *Phrynosoma coronatum*. Sample sizes are in parentheses. Abbreviations are: gran = granular, rug = rugose, smo = smooth, or various combinations (e.g., smo + rug = smooth with rugose edges).

CA: San Benito County: Pinnacles National Monument (12)
gran (4); gran + rug (8)

CA: San Joaquin County: Lathrop (18)
gran (7); gran + rug (9); rug (2)

CA: Fresno County: E of Mendota (15)
gran (1); gran + rug (6); rug (8)

CA: Tulare County: Earlimart (32)
gran (5); gran + rug (20); rug (7)

CA: Kern County: San Emigdio Plain (16)
gran (3); gran + rug (5); rug (8)

CA: Kern County: near Bakersfield (15)
gran (5); gran + rug (3); rug (7)

CA: Kern County: 6 mi. N of Weldon (7)
gran (7)

CA: Los Angeles County: Pasadena (16)
gran (1); gran + rug (8); rug (7)

CA: Riverside Co: San Jacinto Mountains (26)
rug (1); smo + rug (7); smo (18)

CA: San Diego County: near San Diego (23)
gran + rug (2); rug (12); smo + rug (6); smo (2); smo + rug + gran (1)

CA: San Diego County: National City–Tijuana River (12)
gran + rug (2); rug (9); smo (1)

CA: San Diego County: La Mesa (5)
gran + rug (1); rug (1); smo + rug (3)

CA: San Diego County: near Campo (9)
rug (1); smo + rug (3); smo (5)

CA: San Diego County: near Jacumba Hot Springs (13)
smo + rug (3); smo (10)

CA: San Diego County: near Jamul Creek (4)
gran + rug (1); rug (3)

CA: San Diego County: near Lakeside (4)
smo + rug (3); smo (1)

CA: San Diego County: near Escondido (10)
rug (2); smo + rug (4); smo (4)

CA: San Diego County: Mount Palomar (10)
rug (2); smo + rug (6); smo (2)

CA: San Diego County: La Jolla (5)
smo + rug (1); smo (4)

BC: near Ensenada (16)
rug (9); smo + rug (7)

BC: Rancho Agua Blanca (1)
smo + rug (1)

BC: Mision Santa Catarina (1)
rug (1)

BC: Las Cabras (1)
rug (1)

TABLE 2.—Continued.

BC: 5 km W of San Vicente (1)
rug (1)

BC: Mike's Sky Ranch (2)
smo (2)

BC: Meling Ranch (6)
rug (4); smo + rug (1); smo (1)

BC; near San Telmo (4)
rug + gran (1); rug (3)

BC: near Valladares (9)
rug (9)

BC: Colonia Guerrero (25)
rug (25)

BC: near Bahia San Quintin (20)
rug (20)

BC: El Rosario (2)
rug (2)

BC: near El Arenoso (4)
rug (4)

BC: near El Marmol (3)
gran (2); rug (1)

BC: near Catavina (4)
rug (4)

BC: 16 km S of Laguna Seca Chapala (4)
rug (4)

BC: Arroyo San Javier (1)
rug (1)

BC: near Punta Prieta (3)
rug (3)

BC: near Bahia de Los Angeles (5)
gran (1); rug (4)

BC: Rancho El Barril (4)
rug + gran (3); smo + rug (1)

Klauber (1936:105) emphasized two morphological features that distinguish *blainvillii* from *coronatum*. He drew attention to the orientation of the temporal horns and whether or not the temporal horn series is continuous or interrupted by a reduced fourth temporal horn. The temporal horns are directed posterolaterally in a large percentage (81.6–94.2%) of *blainvillii*, whereas, in the other three taxa, 98.2–100% exhibit lateral orientation (OTH; Table 4). Presence of a "temporal gap" is determined by the relative size of the fourth and fifth temporal horns. The absence of a "gap" (fourth horn as large or larger than the fifth) is indicated by values of 1.00 or

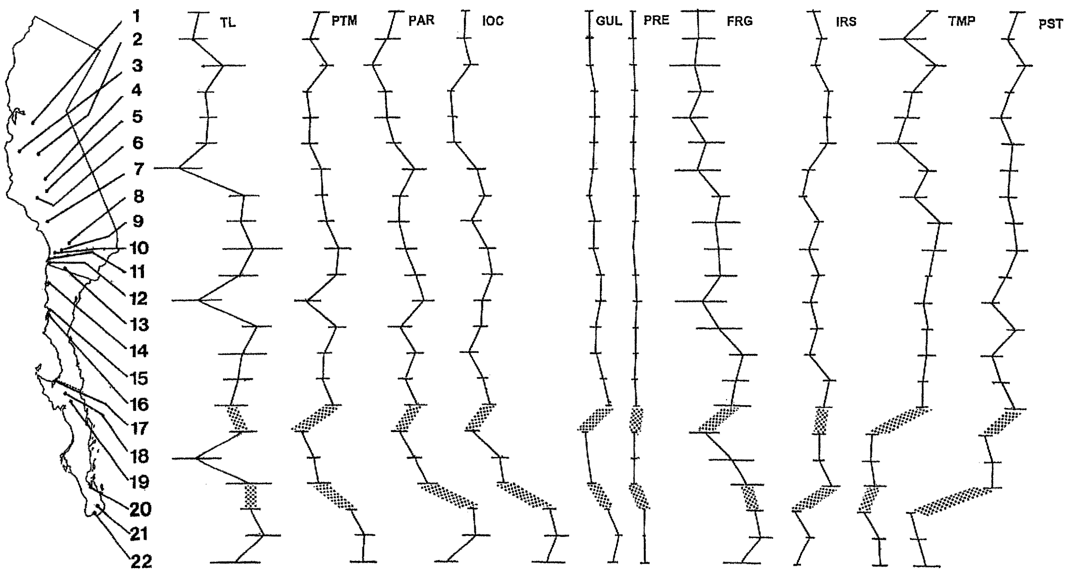

FIG. 5.—Patterns of 10 continuous variables (meristic and mensural) for 22 *Phrynosoma* population samples arranged from north to south. Horizontal bars are 2 SE of the sample mean (line intersecting bar) of the variable. Stippled zones indicate large geographic gaps between samples. X axis not shown. Localities are as follows: CA, 1, Lathrop (37° 49′ N); 2, Mendota (36° 43′ N); 3, Pinnacles (36° 29′ N); 4, Earlimart (35° 52′ N); 5, Bakersfield (35° 22′ N); 6, San Emigdio Plain (34° 59′ N); 7, Pasadena (34° 07′ N); 8, San Jacinto Mountains (33° 45′ N); 9, Mount Palomar (33° 20′ N); 10, Twin Oaks (33° 11′ N); 11, San Diego (32° 44′ N); 12, National City (32° 40′ N); 13, Jacumba (32° 36′ N); BC, 14, Ensenada (31° 54′ N); 15, Colonia Vicente Guerrero (30° 42′ N); 16, San Quintin (30° 30′ N); BCS, 17, Guerrero Negro (27° 58′ N); 18, El Vizcaíno (27° 34′ N); 19, NW of San Ignacio (27° 20′ N); 20, La Paz (24° 10′ N); 21, Eureka (23° 25′ N); 22, San José del Cabo (23° 04′ N). See text for further discussion.

greater, whereas a "gap" is created by a reduced or rudimentary fourth horn (values <1.00). Collectively, the southern forms (*cerroense*, *coronatum*, and the unnamed Gulf Coast population) have a distinct temporal gap in contrast to *blainvillii*, in which the temporal horn series is usually continuous. However, 28 out of 82 specimens (34%) of *blainvillii* from the Central Valley of California and 19 out of 198 specimens (9.6%) of *blainvillii* from the peninsular ranges of southern California and northern Baja California have a slightly reduced fourth temporal horn. Thus, the range of variation in *blainvillii* overlaps to a limited extent with that of *cerroense* and *coronatum*, but essentially not with the Gulf Coast population sample (TMP; Table 4). About 20% of the specimens of *coronatum* from La Paz have a continuous series of four temporal horns. However, this difference is apparently due to extreme reduction and loss of the fourth horn such that the "fifth" horn completely occupies its place. This inference is drawn from specimens exhibiting transitional stages in the loss of the fourth horn.

The form *blainvillii* differs discretely from *cerroense* in the color characters CFS, CTH, and ISC (Table 3) and the nearly discrete differences in two morphological characters (TMP, OTH; Table 4). Furthermore, populations of *cerroense* and *blainvillii* are closely juxtaposed (possibly as close as 16 km), between Miller's Landing and Arroyo San Javier. As discussed previously, there is no morphological evidence of hybridization in the specimens examined from these two proximate localities. However, even if hybridization were detected, gene flow would likely be quite restricted in comparison to the extensive geographic ranges of the two forms (especially *blainvillii*) and could not be considered to have any significant influence on the evolutionary trajectories of either taxon. Thus, it appears that *blainvillii* and *cerroense* essentially meet the criteria of good phylogenetic species (sensu Cracraft, 1983).

The taxonomic treatment of hybridizing forms can be problematic. In cases of stable hybrid zones, the interacting populations have often been regarded as distinct species (Bigelow, 1965; Dobzhansky, 1940:354; Mayr, 1942:285; Wright, 1978:5). The rationale is that, despite gene exchange, the interacting groups represent different coadapted gene complexes, and, due to the elimination of recombinant genotypes by selection, they seem to be little affected by introgression. Barton and Hewitt (1985) give an opposing view.

The unnamed Gulf Coast horned lizard and *cerroense* differ discretely by several color characters (CFS, CTH, ISC; Table 3) and show nearly non-overlapping variation in the development of the parietal shelf (PAR; Table 4). Only 2 of 108 *cerroense* (1.9%) and 2 of 14 Gulf Coast horned lizards (14%) fall within the limits of overlap. Also, only 7.4% of the *cerroense* specimens overlap with the Gulf Coast form in the position of the subrictal scale (SUB; Table 4).

The detection of several morphological intermediates between the unnamed Gulf Coast horned lizard population and *cerroense* suggests that they may be hybridizing, but little is presently known about the zone of potential gene exchange. The straight-line distance between San Ignacio (the collection site for several putative hybrid specimens) and Santa Rosalía, where typical Gulf Coast specimens have been collected, is about 62 km. The low foothills between the Sierra Guadalupe and Volcan de Las Tres Virgenes may provide a corridor for contact between the two forms. Otherwise, the Sierra Guadalupe separates the Gulf Coast horned lizard population from *cerroense*.

The Vizcaíno Desert inhabited by *cerroense* comprises the southern portion of the Vizcaíno Division of the Sonoran Desert (Crosswhite and Crosswhite, 1982). This span is cooler than other desert areas of the peninsula due to maritime influence from the Pacific Ocean, which often produces cool, breezy, and cloudy days. Precipitation is highly variable from year to year, but moisture in the form of condensed fog can penetrate several kilometers inland from the coast (Crosswhite and Crosswhite, 1982; Meigs, 1966). By comparison, the low desert on the Gulf side of the peninsula is very hot and arid and receives virtually no winter rainfall. This

TABLE 3.—Summary of color pattern characters among the four taxa belonging to the *Phrynosoma coronatum* group.

Character	*blainvillii* (n = 357)	*cerroense* (n = 108)	*coronatum* (n = 141)	Gulf Coast (n = 14)
Cephalic scale color (CFS) (frontals; supraoculars)	Pale to medium tan (100%)	Charcoal gray with black rugosities, to entirely black (100%)	Black (100%)	Medium tan with crests of rugosities dark brown to black (100%)
White borders between cephalic scales (CSB)	Absent (100%)	Absent (77%) Faint borders (23%)	Distinct borders (100%)	Absent (100%)
Temporal horn color (CTH)	Similar to cephalic scales (100%)	Paler than cephalic scales (100%)	Paler than cephalic scales (100%)	Similar to cephalic scales (100%)
Interparietal scale color (ISC)	Pale to medium tan, like cephalic scales (100%)	White, in contrast to dark cephalic scales (100%)	Black, like cephalic scales (100%)	Medium tan, like cephalic scales (100%)

TABLE 4.—Variation in eight mensural and two qualitative characters among the taxa belonging to the *Phrynosoma coronatum* group. Values are mean ±1 SD, observed limits, and samples size (n). Groups C.V. and P.R. of *blainvillii* are from the Central Valley and Peninsular Ranges, respectively. A different superscript letter indicates that samples means are significantly different ($P < 0.05$).

Character	*blainvillii* (C.V.)	*blainvillii* (P.R.)	*cerroense*	*coronatum*	Gulf Coast
Tail length (TL) females	39.79 ± 3.05^{c} 31.90–46.32 $n = 48$	44.16 ± 3.52^{b} 33.30–52.90 $n = 117$	46.89 ± 4.45^{a} 34.50–58.80 $n = 53$	45.95 ± 4.23^{ab} 36.36–57.00 $n = 67$	46.45 ± 6.59^{a} 34.90–52.80 $n = 8$
Tail length (TL) males	47.78 ± 4.04^{c} 40.57–58.76 $n = 61$	53.61 ± 6.04^{b} 33.33–65.26 $n = 108$	54.23 ± 5.91^{ab} 42.60–66.30 $n = 50$	55.75 ± 5.41^{a} 37.93–66.70 $n = 72$	50.85 ± 8.02^{bc} 42.50–61.30 $n = 6$
Parietal shelf (PAR)	21.73 ± 1.87^{d} 17.94–28.24 $n = 114$	23.40 ± 2.17^{c} 15.20–29.80 $n = 242$	23.85 ± 2.07^{c} 19.80–29.53 $n = 108$	29.81 ± 1.86^{b} 24.77–35.10 $n = 139$	31.39 ± 1.48^{a} 28.40–33.10 $n = 14$
Head length (ERD) females	16.72 ± 1.41^{ab} 14.68–21.16 $n = 51$	16.15 ± 1.24^{bc} 13.62–22.40 $n = 122$	15.42 ± 1.22^{c} 13.09–19.50 $n = 55$	16.26 ± 0.92^{bc} 14.50–20.60 $n = 68$	17.66 ± 1.89^{a} 14.80–21.00 $n = 8$
Head length (ERD) males	16.74 ± 0.60^{b} 15.63–18.58 $n = 63$	16.85 ± 1.39^{b} 14.66–23.46 $n = 118$	15.90 ± 1.12^{b} 14.09–18.80 $n = 53$	16.71 ± 0.88^{b} 14.84–19.77 $n = 71$	18.53 ± 1.86^{a} 16.20–21.40 $n = 6$
Postrictal spine (PST)	23.55 ± 3.21^{a} 12.92–33.44 $n = 113$	22.44 ± 3.59^{a} 14.18–35.00 $n = 241$	19.66 ± 3.71^{b} 8.00–27.80 $n = 108$	4.99 ± 3.96^{d} 0–14.28 $n = 139$	12.09 ± 2.42^{c} 8.60–16.40 $n = 14$
Parietotemporal scale (PTM)	14.02 ± 2.48^{bc} 4.88–20.78 $n = 114$	16.42 ± 3.39 7.09–25.82 $n = 242$	13.28 ± 3.08^{c} 8.10–20.50 $n = 108$	21.54 ± 4.47^{a} 10.30–35.10 $n = 139$	21.42 ± 6.83^{a} 10.00–31.00 $n = 14$
Interoccipital spine (IOC) females	15.65 ± 2.50^{c} 9.80–23.62 $n = 50$	18.91 ± 3.13^{bc} 12.80–28.98 $n = 116$	19.78 ± 4.17^{b} 10.10–29.78 $n = 52$	32.42 ± 4.62^{a} 23.00–42.17 $n = 65$	31.14 ± 5.13^{a} 24.60–37.30 $n = 7$
Interoccipital spine (IOC) males	14.99 ± 2.70^{c} 9.09–20.00 $n = 61$	19.59 ± 3.55^{b} 5.19–31.02 $n = 118$	21.82 ± 4.38^{b} 11.76–34.30 $n = 53$	33.62 ± 6.23^{a} 8.82–45.94 $n = 70$	30.27 ± 4.29^{a} 24.00–35.30 $n = 6$
Chinshield gap (GAP) females	7.74 ± 2.28^{a} 3.68–12.86 $n = 51$	4.79 ± 3.21^{b} 0–12.80 $n = 124$	8.53 ± 3.23^{a} 0–16.66 $n = 55$	4.85 ± 2.63^{b} 0–10.96 $n = 69$	2.73 ± 3.36^{b} 0–9.90 $n = 8$
Chinshield gap (GAP) males	6.86 ± 2.58^{a} 0.90–13.47 $n = 63$	4.38 ± 3.57^{ab} 0–17.0 $n = 119$	6.70 ± 3.06^{a} 0–13.21 $n = 53$	4.68 ± 2.32^{ab} 0–10.58 $n = 71$	3.72 ± 2.71^{b} 0–7.30 $n = 6$
Temporal horn length (TMP)	0.97 ± 0.1695^{a} 0.705–1.860 $n = 82$	1.03 ± 0.1209^{a} 0.723–1.520 $n = 198$	0.53 ± 0.1115^{b} 0.291–0.893 $n = 90$	0.57 ± 0.1171^{b} 0.259–0.884 $n = 104$	0.59 ± 0.1012^{b} 0.387–0.708 $n = 11$
Temporal horn orientation (OTH)	Posterolateral^{b} 93 (81.6%) Lateral 21 (18.4%)	Posterolateral^{b} 229 (94.2%) Lateral 14 (5.8%)	Posterolateral^{a} 2 (1.8%) Lateral 106 (98.2%)	Posterolateral^{a} 5 (3.6%) Lateral 135 (96.4%)	Posterolateral^{a} 0 (0%) Lateral 13 (100%)
Subrictal scale position (SUB)	Above^{d} 84 (73.7%) Slightly above 30 (26.3%) In line 0 (0%)	Above^{d} 201 (82.7%) Slightly above 42 (17.3%) In line 0 (0%)	Above^{c} 29 (26.9%) Slightly above 71 (65.7%) In line 8 (7.4%)	Above^{b} 8 (5.7%) Slightly above 71 (50.3%) In line 62 (44%)	Above^{a} 0 (0%) Slightly above 0 (0%) In line 14 (100%)

desert is classified as the Central Coast Division of the Sonoran Desert and is the driest division, receiving scant moisture mainly from summer convectional storms (Crosswhite and Crosswhite, 1982). Hence, the Gulf Coast horned lizard and *cerroense* appear to be adapted to different environmental regimes and likely represent different co-adapted gene

TABLE 5.—Variation in seven meristic characters among the taxa belonging to the *Phrynosoma coronatum* group. Values are mean ±1 SD, observed limits, and sample size (n). Groups C.V. and P.R. of *blainvillii* are from the Central Valley and Peninsular Ranges, respectively. A different superscript letter indicates that sample means are significantly different ($P < 0.05$).

Character	*blainvillii* (C.V.)	*blainvillii* (P.R.)	*cerroense*	*coronatum*	Gulf Coast
CHN	4.94 ± 0.31^{b} 4–6 $n = 114$	5.37 ± 0.58^{a} 4–7 $n = 243$	4.59 ± 0.60^{c} 3–6 $n = 108$	4.99 ± 0.24^{b} 4–6 $n = 141$	5.14 ± 0.36^{ab} 5–6 $n = 14$
BAS	5.76 ± 1.19^{b} 3–9 $n = 114$	5.71 ± 1.36^{b} 2–9 $n = 243$	6.92 ± 1.06^{a} 3–10 $n = 108$	5.72 ± 1.04^{b} 4–8 $n = 141$	4.21 ± 1.25^{c} 3–7 $n = 14$
GUL	8.98 ± 0.88^{c} 7–11 $n = 114$	9.65 ± 1.03^{b} 8–12 $n = 243$	8.41 ± 0.80^{c} 7–11 $n = 108$	10.78 ± 1.07^{a} 8–14 $n = 141$	11.00 ± 1.24^{a} 10–14 $n = 14$
PRE	4.22 ± 0.46^{b} 4–6 $n = 114$	4.20 ± 0.42^{b} 4–6 $n = 243$	4.07 ± 0.45^{b} 2–5 $n = 108$	5.11 ± 0.33^{a} 4–6 $n = 141$	4.86 ± 0.36^{a} 4–5 $n = 14$
FRG	17.67 ± 3.56^{b} 9–26 $n = 114$	19.95 ± 3.88^{b} 7–34 $n = 241$	19.96 ± 4.52^{b} 3–30 $n = 108$	23.16 ± 3.47^{a} 3–30 $n = 141$	23.79 ± 4.64^{a} 15–30 $n = 14$
IRS	11.75 ± 1.23^{b} 8–15 $n = 114$	11.22 ± 1.62^{b} 7–16 $n = 243$	12.00 ± 1.59^{b} 8–15 $n = 108$	9.42 ± 1.27^{c} 6–13 $n = 141$	13.36 ± 1.01^{a} 12–16 $n = 14$
INC	0.32 ± 0.47^{bc} 0–1 $n = 114$	0.56 ± 0.52^{ab} 0–2 $n = 243$	0.09 ± 0.29^{c} 0–1 $n = 108$	0.38 ± 0.49^{bc} 0–1 $n = 141$	0.86 ± 0.36^{a} 0–1 $n = 14$

complexes that are maintaining independent evolutionary trajectories, despite any gene exchange. The Gulf Coast horned lizard and *cerroense*, after differentiating in allopatry, may have established secondary contact by early Pleistocene (see discussion below). If this time frame is correct, these two groups of horned lizards would by now have merged into a single population if gene flow were unrestricted and hybrid fitness were equal to that of the parental genotypes.

The Gulf Coast horned lizard is morphologically similar to the southernmost form, *coronatum*, but the two differ in the mean number of cephalic scales, with only modest overlap in variation (IRS; Table 5). Nine of the 14 specimens from the Gulf coast desert have 12–13 scales; the remaining five have a higher number of scales. By comparison, only 14 of 141 (9.9%) specimens of *P. coronatum* have 12–13 scales; the remaining 127 specimens have a lower number. The two groups also show a statistically significant difference in the character PST (Table 4), with only modest overlap; in terms of color characters, they differ discretely in CFS, CSB, CTH, and ISC (Table 3).

The Gulf Coast horned lizard and *coronatum* appear to be allopatric and may be isolated from each other by both geographic (Sierra del La Giganta) and vegetational (Arid Tropical Scrub) barriers. What little is known about the habitat preferences of the Gulf Coast horned lizard suggests that the habitat characteristics dominating the Sierra de la Giganta are unsuitable and likely to impede or restrict gene exchange between these horned lizard populations. However, field studies are needed in the southern peninsula to clarify their distributional and ecological relationships. The preponderance of currently available evidence supports the hypothesis that the Gulf Coast horned lizard population is an independent lineage and merits taxonomic recognition as a phylogenetic species.

The forms *coronatum* and *cerroense* are tentatively regarded as distinct species; they differ in terms of the color of the interparietal scale (ISC; Table 3). Also, the cephalic scales in *coronatum* are relatively large and have distinct white borders compared with those of *cerroense*. In several local populations of *cerroense*, white borders are present between some of the scales, but these borders are relatively pale and narrow compared to their expression in *coronatum*. In *coronatum*, the postrictal scale is rudimentary or relatively short, but generally much longer in *cerroense* (PST; Table 4). Only 7 of 108 cerroense (6.5%) have a PST within the range of variation observed in *coronatum*. However, a higher proportion of *coronatum* (35 of 141 specimens; about 25%) has a longer PST that falls within the lower limit observed in *cerroense*. There is relatively greater overlap in the range of variation of the parietal shelf in these two forms (PAR; Table 4). Forty of 108 *cerroense* (37%) and 66 of 140 *coronatum* (47%) fall within the limits of overlap.

Finally, the morphological patterns of divergence among the coast horned lizard groups strongly parallel the genetic units in *Urosaurus*, which was analyzed by Aguirre-Leon et al. (1999). Populations 1–3 of *Urosaurus* correspond to *coronatum* from the Cape Region; populations 5–7 (4 is insular) correspond to the unnamed population from the Gulf Coast; and a northern group of *Urosaurus* (populations 8–12) corresponds to *blainvillii*. The morphological discontinuities in *Phrynosoma* are largely concordant with the major genetic breaks in *Urosaurus* and many other species (Murphy and Aguirre-Leon, 2002). The congruent patterns suggest that the morphological groups in *Phrynosoma* have a genetic basis.

The different forms of coast horned lizards readily interbreed in captivity and produce viable, fertile hybrids (Baur, 1984). Although these observations fall short of clarifying the interactions of horned lizard populations in nature, they do indicate the absence of genetically based premating and postzygotic isolating mechanisms and the potential for gene exchange. Obviously, there is need for fine-grained molecular studies in areas where the different forms potentially meet to determine the nature and extent of any gene exchange.

The four coast horned lizard groups could be treated as subspecies of a single polytypic species (sensu Mayr, 1942). Despite the controversies concerning the use of the subspecies concept (Frost and Hillis, 1990), it has merit, in my opinion, when used judiciously in comprehensive studies, and especially when the taxa denote historical groups. Speciation is a temporally extended process (de Queiroz, 1998) involving intermediate stages of divergence where this taxonomic category might be usefully, and appropriately, applied (Smith et al., 1997). To regard these groups merely as informal pattern classes (Grismer, 2002*a*) would underestimate biodiversity and seriously neglect the historical reality of these entities. The preponderance of the evidence obtained from my study supports the view that these four groups of coast horned lizards represent independent historical lineages that are little affected by gene exchange and qualify for recognition as distinct phylogenetic (sensu Cracraft, 1983) or evolutionary (sensu Wiley, 1978) species. This proposed classification seems to best reflect the historical events (see below) that have led to the diversification of these populations.

Biogeography

Prior to the development of plate tectonic models of Earth history, Savage (1960) explained the origin of the peninsular herpetofauna in terms of dispersal from continental deserts, coincident with late Pleistocene through Holocene climatic oscillations. However, a new scenario for the origin of the peninsular herpetofauna based on late Neogene vicariance is now becoming widely accepted. Murphy (1983) formulated a paleogeographic scenario for the peninsula of Baja California that is drawn from geologic evidence and distributional patterns of the peninsular herpetofauna. He hypothesized that the peninsula was fragmented into islands that were reconnected several times during its geologic history. Upton and Murphy (1997), for the first time, presented molecular genetic evidence (sequence data from mtDNA cytochrome b and ATPase 6 genes) for a mid-peninsular seaway in their phylogenetic analysis of side-blotched lizards (Uta). Subsequently, Aguirre-Leon et al. (1999) demonstrated that cladogenetic patterns in *Urosaurus* derived from isozyme analysis were congruent with two ancient trans-peninsular seaways—one at mid-peninsula, the Vizcaíno Seaway, and the other at the Isthmus of La Paz. Patterns of molecular divergence in other vertebrate taxa were found to be geographically concordant with these hypothesized ancient seaways. For example, Radtkey et al. (1997), using mtDNA cytochrome b sequence data, identified several clades in *Cnemidophorus tigris* associated with the mid-peninsular and Isthmus of La Paz ancient seaways. Using mtDNA ND4 gene and three t-RNA genes, Rodriguez-Robles and De Jesus-Escobar (2000) detected north and south clades of *Pituophis catenifer* associated with the mid-peninsular seaway. Hollingsworth (1998) described two "pattern classes" of *Sauromalus* in the mid-peninsular region, and sequence data from the mtDNA cytochrome b gene (Petren and Case, 1997, 2002) suggested that different northern and southern haplotypes are associated with this presumptive barrier. Additional evidence of historical vicariance in the mid-peninsular region comes from five rodent taxa that display haplotype divergence in the mtDNA cytochrome oxidase subunit 3 gene (Riddle et al., 2000*a*), and from Le-Conte's Thrasher (*Toxostoma lecontei*) that diverge at the mtDNA cytochrome b gene (Zink et al., 1997). Other studies of rodents (Riddle et al., 2000*b*,*c*) provided further evidence for the vicariance history of the Cape Region. Hence, phylogroup distributions from a wide array of vertebrate taxa now offer strong support for historical vicariance events in central Baja California (Vizcaíno Seaway) as well as the Cape Region (Isthmus of La Paz).

Although the biological evidence for the Vizcaíno Seaway is compelling, geological evidence is wanting, and arguments against the hypothesis of a mid-peninsular seaway have been made (Grismer, 2002*b*). Furthermore, Irwin (2002) demonstrated with theoretical models that deep phylogeographic breaks (in mtDNA or cpDNA) could form within a continuously distributed species even when there are no barriers to gene flow. The likelihood of observing phylogeographic discontinuities increases as the average individual dispersal distance and population size decrease. However, Irwin (2002) offered two criteria by which such breaks can be attributed to geographic barriers (as opposed to stochastic processes). First, if multiple sources of evidence (e.g., morphology, several independent genetic markers) all show discontinuities in the same region and, second, if several different species exhibit discontinuities in the same region, then it is likely that such patterns have resulted from a geographic barrier to gene flow. The available evidence (e.g., multiple taxa, morphology, allozymes, and mtDNA data) for the mid-peninsular seaway satisfies both criteria advanced by Irwin.

The mid-peninsular Vizcaíno Seaway is considered a "cryptic" vicariance event, not previously revealed by morphological and geological analyses (Riddle et al., 2000*a*). However, in my multivariate analysis, the detected patterns of morphological divergence within the *P. coronatum* group give further support for vicariance events in both regions of the peninsula. The species *blainvillii* and *cerroense* are juxtaposed, and *cerroense* and the unnamed Gulf Coast horned lizard population apparently meet and hybridize in the general area of the Vizcaíno Seaway. During the period of maximum inundation of the mid-peninsular region, the progenitor of *blainvillii* may have existed on the northern segment of the peninsula; the ancestor of *cerroense* may have been isolated on several persisting islands (Isla de Cedros, Sierra Vizcaíno, and Sierra Santa Clara), whereas *coronatum* may have evolved in the Cape Region when it was an island separated from the rest of the peninsula by the Isthmus of La Paz (Fig. 6). The occurrence of *coronatum* on the Plain of Magdalena, north of the Isthmus of La Paz, can be explained by northward dispersal after the seaway receded or by over-water rafting prior to receding. Both trans-peninsular seaways may have existed at various times during the geologic past, most recently about 3 MYA, but were fully receded by the early Pleistocene (Murphy and Aguirre-Leon, 2002), providing opportunity for secondary contact between previously isolated populations of coast horned lizards. Therefore, coast horned lizard diversification appears to have occurred primarily via allopatric speciation, facilitated by these repeated vicariance events. Whether this scenario based on morphological data will gain further support in the genetic structure and phylogeography of these populations of coast horned lizards remains to be determined.

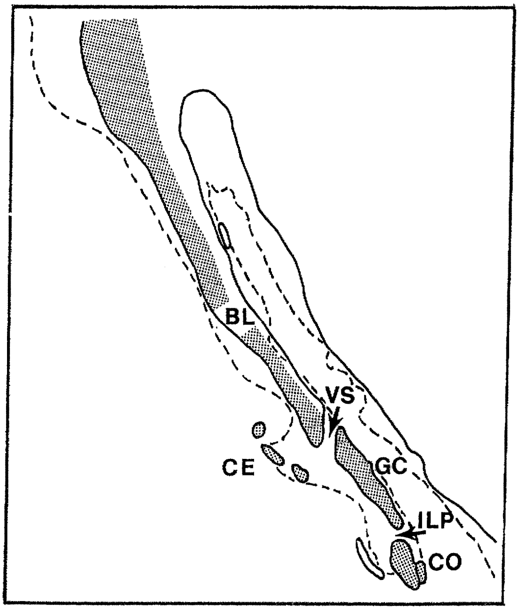

FIG. 6.—Paleogeographic reconstruction (3 MYA) of the subaerial regions of the peninsula of Baja California, showing possible areas of evolutionary origin for *Phrynosoma blainvillii* (BL), *P. cerroense* (CE), *P. coronatum* (CO), and the unnamed Gulf Coast taxon (GC). Ancient seaways are Vizcaíno Seaway (VS) and Isthmus of La Paz (ILP). Modified from Murphy and Aguirre-Leon(2002).

Description of a New Species

Populations of coast horned lizards from the Gulf of California side of the peninsula are shown by univariate and multivariate analyses to differ from all other recognized populations by several discrete and nearly discrete characters. Therefore, I propose to call this new horned lizard:

Phrynosoma ***wigginsi*** sp. nov.

Phrynosoma coronatum jamesi: Jennings, 1988*a*:428.2 (part); Klauber, 1936:103 (part); Linsdale, 1932:349 (part); Reeve, 1952:884 (part); Smith and Taylor, 1950*a*: 321(part), 1950*b*:102 (part); Stejneger and Barbour, 1939:73 (part); Stejneger and Barbour, 1943:93 (part); Tevis, 1944: 13 (part).

Suggested common name.—Gulf Coast horned lizard.

Holotype.—CAS-SU 11377, adult male (Figs. 7, 8B), collected from Cuesta Coyote, Bahía Concepción, Baja California Sur, Mexico, by T. H. Work and I. L. Wiggins (original field no. 362), on 14 November 1946.

Paratypes.—Thirteen specimens: LACM 138363–64; MVZ 204255; SDSNH 30234–41, 53059–60.

Etymology.—This species of coast horned lizard is named for Ira L. Wiggins, in recognition of his important contributions to the knowledge of the flora of the Sonoran Desert.

Diagnosis.—*Phrynosoma wigginsi* differs from *P. blainvillii* in having the fourth temporal horn (counting from rear) greatly reduced, producing a "gap" in the temporal series. Its temporal horns, especially the third, are directed laterally or anterolaterally, rather than posteriorly as in *P. blainvillii*. It also has a much more extensive PAR, a longer IOC, and a PST that is on average nearly half as long as that of *P. blainvillii*.

Phrynosoma wigginsi can be distinguished from *P. cerroense* by having a more extensive PAR. Also, all *wigginsi* examined have the subrictal scale in line with the chinshields, whereas 92.6% of the *cerroense* have the subrictal above the chinshield row. The frontal and supraocular scales in *P. wigginsi* are gray-brown with darker pigmentation limited only to the crests of the scale rugosities; the interparietal scale and the temporal horns also have a gray-brown color. By contrast, *P. cerroense* has extensive charcoal to black pigmentation on the frontal-supraocular area; the interparietal scale is whitish; and the temporal horns have a pale cream or pinkish color, contrasting with the dark pigmentation on the dorsal surface of the head.

Phrynosoma wigginsi differs from *P. coronatum* in having a higher number of IRS, with about 10% of 141 specimens of *P. coronatum* falling within the lower limit of variation for *P. wigginsi*. On average, the PST is nearly twice as long in *wigginsi* as it is in *coronatum*, but there is overlap in the range of variation, with about 15.6% of *P. coronatum* falling within the lower limit of variation in *P. wigginsi*. The frontal and supraocular areas (including the interparietal scale) and the temporal horns of *P. wigginsi* are grayish-tan, but, in *P. coronatum*, the cephalic areas are a rich chocolate or black with distinct, whitish scale borders, and the temporal horns are cream to pinkish red.

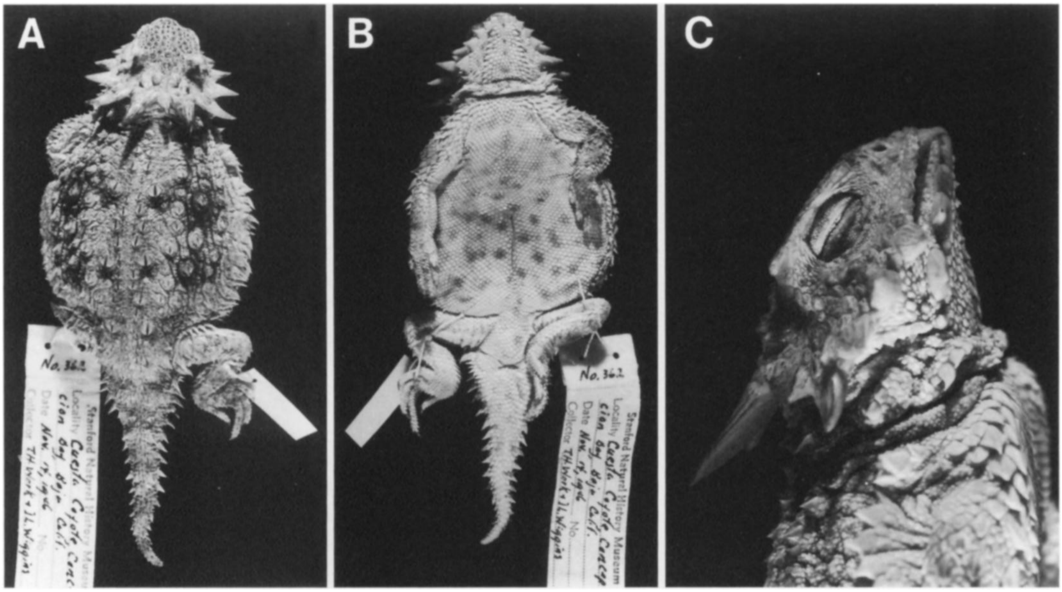

FIG. 7.—Holotype of *Phrynosoma wigginsi* (CAS-SU 11377). (A) dorsal aspect, (B) ventral aspect, (C) right lateral aspect of head.

Tables 3–5 present a summary of comparisons among the four taxa.

Description of holotype.—Adult male, SVL 79 mm, tail length 47 mm. Interparietal to rostral distance 14 mm. Parietal shelf flared and expansive, not greatly depressed; parietal length 6.6 mm. Four conical preoccipitals (a median fifth may have been lost). Length of right parietotemporal scale 3.6 mm. Length of interoccipital spine 4.9 mm. Base of interoccipital spine narrowly separated from flanking occipital horns. One reduced, pointed scale in "gap" of temporal horn series on both left and right sides. "Pre-gap" and "post-gap" temporal horns directed laterally. "Pre-gap" temporal horns directed at downward angle. Length of postrictal spine about 2 mm on both left and right sides. Subrictal scale in line with row of chinshields. Ten gular scale rows. Five chinshields on left and right sides. Chinshield–subrictal gap narrow; one scale between last chinshield and subrictal scale on left and right sides. No incipient chinshields. Seven basirictals on left and right sides. Lower abdominal fringe row with about 28 enlarged scales on left and right sides.

Color pattern of holotype in alcohol.—Dorsal surfaces of head, body, limbs, and tail yellowish brown. Frontal-supraocular scales with black pigmentation confined to crests of rugosities. Interoccipital spine and occipital horns yellowish with medium brown tips and medium brown striations; temporal horns yellowish with few, narrow, pale brown striations. Nuchal blotches charcoal; two rows of charcoal body blotches, each with median pair of small spots and lateral pair of large blotches; median spots bordered posteriorly by pale whitish dots; left anterior median spot with two whitish dots; a third dorsal row, just anterior to the rump, pale gray-brown, scarcely discernible except for pair of whitish dots; large lateral blotches of anterior row nearly coalescing with those in second row; median spots in first row continuous with lateral blotches; median spots in second row separated from lateral blotches. Tail with six gray-brown transverse dorsal bands; first two bands with faint whitish posterior border. Gular area and abdomen yellowish white with gray spots; underside of tail with faint indications of gray spots.

Variation.—Occipital horns may be divergent or directed straight back. In one specimen (SDSNH 53059), the horns are directed upward, but, in most specimens, they have

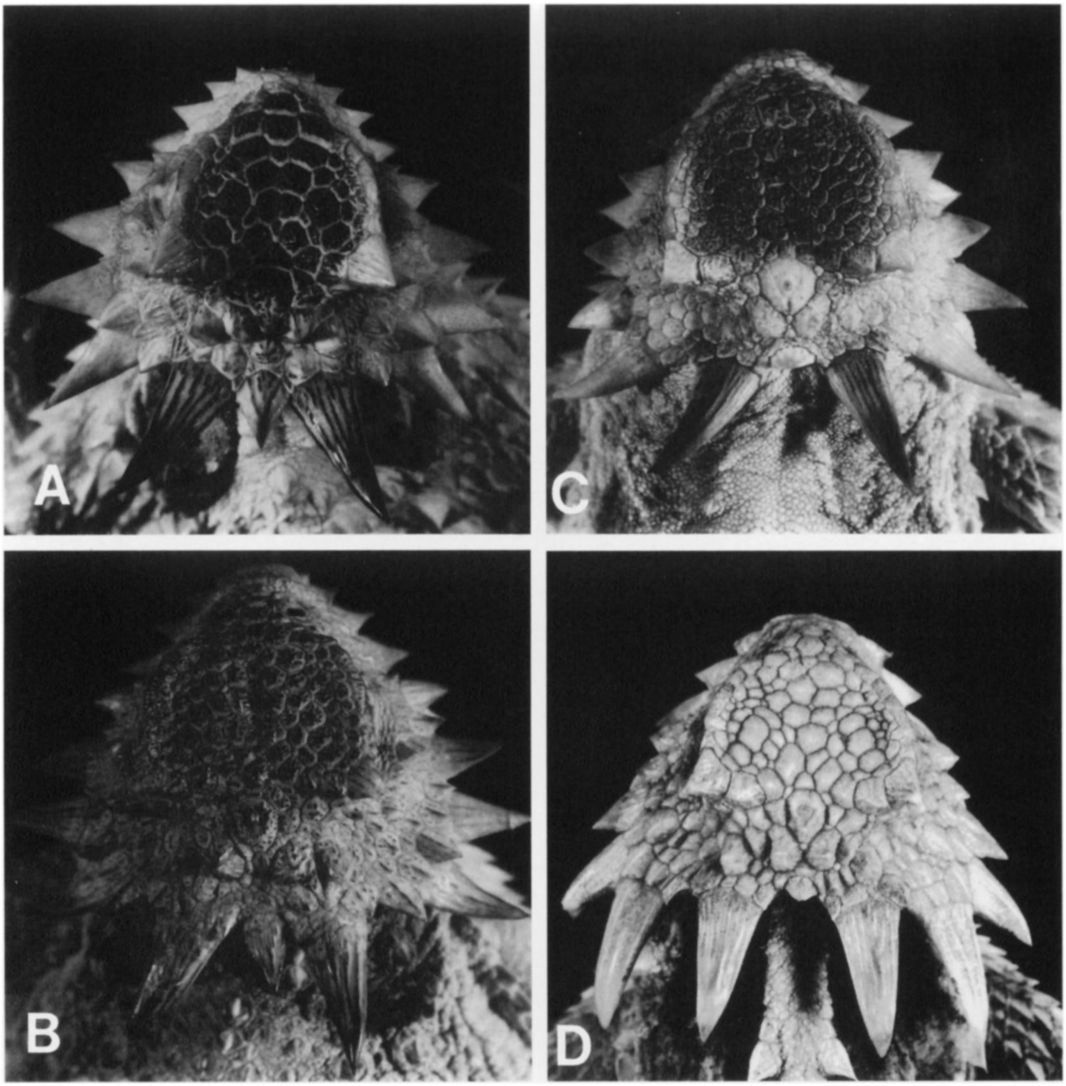

FIG. 8.—Comparison of the head regions of (A) *Phrynosoma coronatum* (RRM 2479), (B) *P. wigginsi* (holotype, CAS-SU 11377), (C) *P. cerroense* (CAS 147787), and (D) *P. blainvillii* (RRM 2395). The temporal horns project laterally in the former three taxa, compared with the posterolateral orientation in *P. blainvillii*. In *P. coronatum* and *P. wigginsi*, the distance from the parietal "eye" to the base of the interoccipital spine is greater than that in *P. cerroense* and *P. blainvillii*.

a nearly horizontal orientation. In two specimens (LACM 138364, CAS-SU 11377 [the holotype]), only four conical preoccipital scales are present; a median fifth preoccipital appears to be absent in both due to previous injury (granular scales noted in the area). In at least two specimens (SDSNH 30241, 53060), the temporal "gap" is reduced and the small spinous scale positioned there is actually positioned above the line of the temporal horns.

The dorsal ground color varies from yellowish brown to tan or gray. The dorsal blotches may vary from dark brown to charcoal, but in some specimens (e.g., SDSNH 53060) the dorsal marks may be faint. The dark dorsal blotches may be bordered posteriorly by whitish dots, or these may be lacking entirely.

The dark spots or blotches forming rows may be more or less connected to produce irregular transverse bands. The laterally positioned dorsal blotches may coalesce with those of adjacent rows to produce a longitudinal dark zone above the upper row of lateral fringe scales. The dark pigmentation on the head scale rugosities varies from dark brown to black; the head pattern is reminiscent of the early stages of color pattern ontogeny noted in juvenile and subadult *P. cerroense* and *P. coronatum*. The gular area may have a dark suffusion or scattered spots; in some specimens, the spots form a pattern of chevrons. The underside of the tail in most specimens has gray spots arranged in transverse rows, but, in a few, it is immaculate.

Distribution.—*Phrynosoma wigginsi* occurs in the peninsula of central Baja California, on the Gulf of California side of the Sierra de Guadalupe (= Sierra de Santa Lucia; Sierra San Pedro), and Sierra de La Giganta, from about latitude 27° 19′ N to about 26° N. It is known from the following localities: Bahía Concepción at Cuesta Coyote; 30.4 km S Canipole; Loreto; Mulegé; between Loreto and Mulegé; 53.9 km S Rancho Rosarito; Santa Rosalía; and 9.6 km S Santa Rosalía. At the northern limit of its range near Santa Rosalía, *P. wigginsi* may extend westward along foothills just south of Volcan de Las Tres Virgenes, contacting populations of *P. cerroense*. There may be other narrow valleys (e.g., SW of Bahía Concepción; W of Loreto) through which contact may occur with Pacific slope populations. The southern limit of the range of *P. wigginsi* and whether it meets *P. coronatum* are not known (Fig. 9).

Misidentified specimens.—The results of the principal components analysis, followed by taxonomic assignments, revealed several misidentifications in the literature. Reeve (1952) lists MVZ 9777 twice, under *blainvillii* and *coronatum*; it belongs to the former taxon and is from Valladares, which is misspelled in both listings. Specimen MVZ 9779 is also *blainvillii*, not *coronatum*, and is from San José (near 31° N latitude), not San José del Cabo. Reeve classified several specimens (SDSNH 18091, 18517, 18520) as *jamesi*, but these are *blainvillii*. Reeve also shows a locality near Punta San Juanico (also plotted by Jennings, 1988*a*) that I have not been able to match with his list of museum specimens. However, Reeve listed *jamesi* from Punta San Jacinto (approximately 30° 52′ N), a collection site much farther north for this taxon than shown by his range map. I believe he confused the two localities and incorrectly plotted SDSNH 18520 near Punta San Juanico. Also, MVZ 37333 is from 4 mi. (6.4 km), not 14 mi. (22.4 km) SE El Arco. Specimen MVZ 13626 is from 30 mi. (48 km) N of San Ignacio, not 20 mi. (32 km) as listed by Reeve.

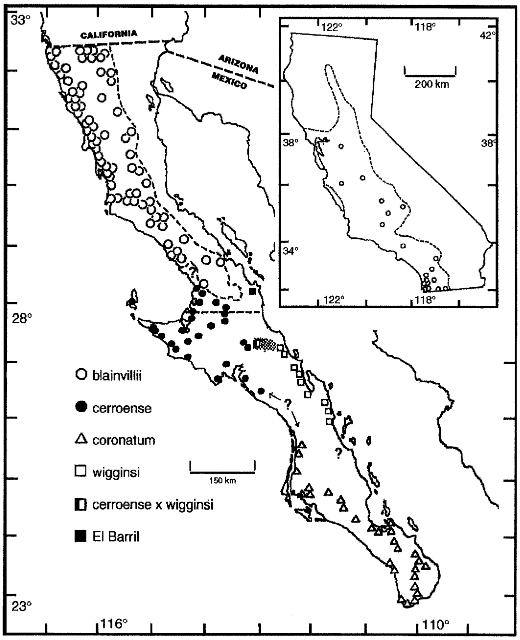

FIG. 9.—Distribution of species of the *Phrynosoma coronatum* group in the peninsula of Baja California. Dashed lines indicate hypothesized range limits of *P. blainvillii*. Stippled area indicates putative zone of hybridization. Question marks and arrows denote uncertain distributional limits. Inset: distribution of *P. blainvillii* in California (dashed line) and localities sampled.

Questionable records.—The type locality for *P. c. schmidti* (= *blainvillii*) was originally designated as Cerros Island (= Isla de Cedros; Barbour, 1921). However, Banta (1968) questioned the occurrence of this taxon on the island, and Jennings (1985) presented evidence in support of Banta's contention. *Phrynosoma cerroense* occurs in low sandy habitat in the Vizcaíno Desert and presumably in similar habitat on Isla de Cedros. However, the island has considerable area above 915 m, with one peak reaching 1204 m elevation. This elevation gradient provides a range of habitats from xerophilic flora to coastal chaparral and relict, disjunct stands of pinyon-juniper woodland, the more mesic habitats supporting populations of *Sceloporus occidentalis* (Grismer and Mellink, 1994), which is found abundantly and in sympatry with *P. blainvillii* in the northern portion of the peninsula. It is possible, but perhaps improbable, that both *cerroense* and *blainvillii* occur on the island in parapatric association along an elevation gradient. Until high elevation areas of the island are more thoroughly searched for horned lizards, I do not consider this question completely resolved.

RESUMEN

Un análisis de componentes principales basado en 24 cáracteres morfológicos y de color para 634 especimenes revela cuatro groupos distintos dentro de *Phrynosoma coronatum*. Estos groupos parecen tener distribuciones alopátricas, pero la evidencia morfológica sugiere que donde existe una zona de contacto entre dos groupos, se occure la hibridisación. Los cuatro groupos difieren por cáracteres distintos de color y cáracteres morfológicos casi distintos. La correlación entre los patrones de la divergencia en *Phrynosoma* y la divergencia genetica en *Urosaurus* sustenta el argumento que los groupos de *Phrynosoma* tienen una base genetica. Por eso, yo reconozco los cuatro groupos como especies distintas. Los nombres latinos (*blainvillii, cerroense, coronatum*) son aprovechables por tres de los cuatro groupos. El analisis de componentes principales no puede distinguir las subespecies *frontale* y *schmidti*, y se las ponen en la sinónimia de *P. blainvillii*. Además, se describe una especie nueva, *Phrynosoma wigginsi*, de lado oriental de la Sierra de Guadalupe y Sierra de la Giganta en la región central de la costa del Golfo de California. Diez cáracteres que tienen valores altos en el componente primero no demuestran patrones fuertes de la variación clinal a través de California y la peninsula de Baja California. Los patrones de la divergencia morfológica en *Phrynosoma* presentan más evidencia para dos vias maritimas antiguas.

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APPENDIX I

Specimens Examined

The following specimens of *Phrynosoma coronatum* were examined in this study. Sample sizes used in the PC analysis are given in parentheses following the locality and may be less than the total examined from a given locality. Museum acronyms follow Leviton et al. (1985).

CALIFORNIA: *Locality 1.* San Benito County: Pinnacles National Monument (12): MVZ 19251, 36189–90, 36424, 83581–84, 83586–88, 83611. *Locality 2.* San Joaquin County: Lathrop (17): MVZ 3551–55, 3568–72, 4796–4803. *Locality 3.* Fresno County: E of Mendota (15): MVZ 39297–98, 80223–29, 80230–35. *Locality 4.* Tulare County: Earlimart (32): MVZ 2512–40, 6790–92. *Locality 5.* Kern County: San Emigdio Plain (16): MVZ 3784–97, 4900–01. *Locality 6.* Near Bakersfield (15): MVZ 2548–51, 2552–57, 43497–43500, 43504. *Locality 7.* 10 km N of Weldon (7): MVZ 2899–2905. *Locality 8.* Los Angeles County: Pasadena (16): MVZ 851, 853–54, 2412–13, 2480, 3557–58, 4787–89, 43480–84. *Locality 9.* Riverside County: San Jacinto Mountains (26): MVZ 76–77, 102, 146, 184–86, 212, 233, 273–76, 322–23, 336, 344–48, 573–77. *Locality 10.* San Diego County: Near San Diego (19): MVZ 43490, 43496, 43503; USNM 157, 10779, 13893, 13948, 14587, 14777, 53692–93, 53700–02, 54365, 55105, 293191–92, 293239, 293241–45. *Locality 11.* National City and Tijuana River (12): MVZ 43491–95, 43502; SDSNH 11864, 23953; USNM 21968–70, 21980. *Locality 12.* La Mesa (5): SDSNH 46244; USNM 53688–91. *Locality 13.* Near Campo (9): SDSNH 47840, 49066, 56988, 56997–99; USNM 21973, 21971, 21993. *Locality 14.* Near Jacumba Hot Springs (13): SDSNH 26841, 56485; USNM 21981, 21982–85, 21986–91. *Locality 15.* Near Jamul Creek (4): SDSNH 49063; USNM 21965–67. *Locality 16.* Near Lakeside (4): SDSNH 15570, 56996; USNM 53698–99. *Locality 17.* Near Escondido (10): SDSNH 56986, 56993; USNM 16997, 44947, 53694–97, 64285–86. *Locality 18.* Mt. Palomar (10): SDSNH 59227–34, 59237–38. *Locality 19.* La Jolla (5): MVZ 43485–89.

BAJA CALIFORNIA: *Locality 20.* Near Ensenada (16): CAS 177; CAS-SU 178; CAS 179–80; CAS-SU 11925; CAS 181370–72; LACM 4303, 52795, 101491–96. *Locality 21.* 37 km E of Ensenada (1): MVZ 75890. *Locality 22.* Rancho Agua Blanca (1): CAS 181382. *Locality 23.* Mision Santa Catarina (1): CAS 181381. *Locality 24.* Las Cabras (1): CAS 57609. *Locality 25.* 5 km W of San Vicente (1): MVZ 9586. *Locality 26.* Mike's Sky Ranch (2): MVZ 140824, 140826. *Locality 27.* Meling Ranch (= Rancho San José) (6): MVZ 9587, 9779, 51095, 140821, 140823, 140825. *Locality 28.* Near San Telmo (4): MVZ 9778, 37319; SDSNH 18517, 18520. *Locality 29.* Near Valladares (9): CAS 57492, 181373–77; MVZ 9777, 51096, 140822. *Locality 30.* Colonia Guerrero (25): CAS 84784–86, 181378; LACM 107934; MVZ 9776, 37320, 161187–204. *Locality 31.* Near Bahía San Quintin (20): CAS-SU 11374, 11926, 11936, 12130–31, 12133; CAS 59703; LACM 19908, 25060, 61493, 62552, 63477, 101487–89; MVZ 37321–24; SDSNH 42613. *Locality 32.* El Rosario (2): MVZ 37326, 80246. *Locality 33.* Near El Arenoso (4): CAS 84789–90; LACM 101490; MVZ 37328. *Locality 34.* Near El Marmol (3): LACM 4309; SDSNH 18091, 39216. *Locality 35.* Near Catavina (4): CAS-SU 11375; CAS 84804; MVZ 161208, 182123. *Locality 36.* 16 km S of Laguna Seca Chapala (4): LACM 4310–11; MVZ 50071–72. *Locality 37.* Arroyo San Javier, NE of Miller's Landing (1): LACM 4333. *Locality 38.* Near Punta Prieta (3): LACM 63478; MVZ 37329–30. *Locality 39.* Near Bahía de Los Ángeles (3): LACM 4308; MVZ 161207, 182262; SDSNH 39003, 47841. *Locality 40.* Rancho El Barríl (4): SDSNH 18082–85. *Locality 41.* Cedros Island (4): SDSNH 17369–70, 24357; USNM 11977. *Locality 42.* Miller's Landing (6): CAS 143430–32; LACM 63479; MVZ 37331–32. *Locality 43.* ENE of Guerrero Negro (21): CAS 147787; LACM 63480–99; MVZ 189975. *Locality 44.* S of Guerrero Negro (3): LACM 126153,137910; MVZ 161210–11. *Locality 45.* 5 km W of Calmallí (1): MVZ 13625.

BAJA CALIFORNIA SUR: *Locality 46.* Near El Arco (9): CAS-SU 11376; LACM 4331; MVZ 37333, 50074–76, 161209, 182152; SDSNH 18087. *Locality 47.* Cerro Elefante (5): LACM 4325–29. *Locality 48.* Near Bahía Tortugas (8): LACM 4315–21; USNM 64450. *Locality 49.* Scammon's Lagoon, S side (1): SDSNH 47839. *Locality*

50. Near El Vizcaíno (22): CAS 143525, 152096–99; MVZ 161212–20, 161222–27, 182256. *Locality 51.* NW of San Ignacio (14): LACM 4330; MVZ 13626–27, 73557, 117461–66, 182154; SDSNH 42010, 42117, 42506. *Locality 52.* San Andres and San Rafael (6): LACM 4312–14, 4322–24. *Locality 53.* Bahía Ballenas and Punta Abreojos (8): CAS 147740, 147755; LACM 4332; SDSNH 38939, 38945, 38972, 40077–78. *Locality 54.* Near San José de Gracia (2): CAS 87371; MVZ 73556. *Locality 55.* San Ignacio (5): MVZ 10660, 13637–40. *Locality 56.* 10 km S of Santa Rosalía (1): SDSNH 53059. *Locality 57.* Between Loreto and Mulegé (1): LACM 138363. *Locality 58.* Bahía Concepción (1): CAS-SU 11377. *Locality 59.* 54 km S of Rancho Rosarito (1): MVZ 204255. *Locality 60.* Loreto (9): LACM 138364; SDSNH 30234–41. *Locality 61.* 30 km S of Canipole (1): SDSNH 53060. *Locality 62.* Médaño Blanco (2): LACM 4304; MVZ 73555. *Locality 63.* 53 km NW of El Centenario (1): LACM 126152. *Locality 64.* Near Santo Domingo (3): CAS 90530; MVZ 37334, 13629. *Locality 65.* 94 km NW of La Paz (2): LACM 101507, 126254. *Locality 66.* La Paz, at El Sombrero Trailer Park (84): CAS 143851–52, 145174–76, 145180, 145185, 145187–202, 147475; MVZ 171587, 171589, 171594–95, 171598–99, 171601, 171605, 171616–24, 171626–27, 171629, 171631, 171637, 171641–43, 171648–59, 171669–70, 171673, 171675, 171683, 171689–91, 171693–97, 171699–171700, 171705, 171707–09, 171711–13, 171715. *Locality 67.* Near Santiago (3): LACM 19904–06. *Locality 68.* Todos Santos (8): CAS 46840–41; MVZ 11734–39. *Locality 69.* Eureka (27): MVZ 11741–67. *Locality 70.* Miraflores (3): MVZ 13634–36. *Locality 71.* San José del Cabo (10): CAS-SU 18824, 2995–3001; CAS 46837–38.