

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 145

**Systematics and Evolution of the Genus**  
*Uta*  
**(Sauria: Iguanidae)**

BY

**ROYCE E. BALLINGER**

*Department of Biology, Angelo State University, San Angelo, Texas 76901*

AND

**DONALD W. TINKLE**

*Museum of Zoology, University of Michigan  
Ann Arbor, Michigan*

ANN ARBOR

MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN  
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## CONTENTS

	PAGE
ABSTRACT .....	5
INTRODUCTION .....	5
MATERIALS AND METHODS .....	7
SAMPLING .....	7
SCALE CHARACTERISTICS—HEAD .....	10
SCALE CHARACTERISTICS—BODY .....	12
MEASUREMENTS AND RATIOS .....	13
COLOR .....	14
OTHER CHARACTERS EXAMINED .....	16
DATA PROCESSING .....	16
RESULTS .....	17
GENERIC STATUS—HISTORICAL RESUMÉ .....	17
KEY TO THE GENERA <i>Uta</i> , <i>Urosaurus</i> AND <i>Petrosaurus</i> .....	18
KEY TO THE FORMS OF <i>Uta</i> .....	22
<i>Uta antiqua</i> Ballinger and Tinkle .....	24
<i>Uta nolascensis</i> VanDenburgh and Slevin .....	25
<i>Uta palmeri</i> Stejneger .....	27
<i>Uta squamata</i> Dickerson .....	28
<i>Uta stansburiana elegans</i> (Yarrow) .....	29
<i>Uta stansburiana stansburiana</i> Baird and Girard .....	34
<i>Uta stansburiana stejnegeri</i> Schmidt .....	37
<i>Uta stansburiana taylori</i> Smith .....	40
<i>Uta stellata</i> Van Denburgh .....	43
OSTEOLOGICAL COMPARISONS .....	44
KARYOTYPES .....	46
DISCUSSION .....	46
MORPHOLOGICAL RELATIONSHIPS .....	46
PHYLETIC RELATIONSHIPS .....	59
DEFENSE OF THE TAXONOMIC ARRANGEMENT .....	61
EVOLUTIONARY AND ZOOGEOGRAPHIC HISTORY .....	62
HYPOTHESIS OF ORIGIN AND DIVERSIFICATION OF <i>Uta</i> .....	64
SUPPORTING EVIDENCE AND DISCUSSION .....	65
APPENDIX .....	75
LITERATURE CITED .....	79

## ILLUSTRATIONS

FIGURE	PAGE
1. Location map of continental samples .....	8
2. Location map of insular samples .....	9
3. Head scale characteristics .....	10
4. Color pattern types of <i>Uta</i> .....	15
5. Present distribution of the forms of <i>Uta</i> .....	23
6. Scale variation in <i>Uta stansburiana elegans</i> .....	32
7. Scale variation in <i>Uta stansburiana stansburiana</i> .....	36
8. Scale variation in <i>Uta stansburiana stejneger</i> .....	39
9. Scale variation in <i>Uta stansburiana taylori</i> .....	42
10. Morphological relations of <i>Uta stansburiana taylori</i> and <i>U. s. elegans</i> .....	53
11. Scale character distribution in several <i>Uta</i> populations .....	54
12. Chronocline relationships in <i>Uta</i> .....	60
13. Hypothetical phylogeny in <i>Uta</i> .....	62
14. Geography of evolutionary history of <i>Uta</i> .....	65
15. Character state reversals in <i>Uta</i> .....	70



## ABSTRACT

An analysis of the population variation and morphological relationships of 69 populations of the genus *Uta* was made to establish the identity of the species of the genus and the extent of their geographical distribution and variability, and to construct a hypothetical evolutionary history of the group. Nine forms are recognized as distinct taxa including one polytypic continental species and five additional insular monotypic species. The evolutionary history of these taxa is considered to be a result of recent events, principally since the beginning of the Pleistocene. Geographical isolation of the continental populations during glacial maxima appears to have played a major role in the speciation process. Repeated colonization of the Gulf of California islands has resulted in recognizable relictual distributions with more primitive forms on peripherally isolated islands while at least two colonizing stocks are recognizable on certain less isolated islands.

## INTRODUCTION

The side-blotched lizards are a small group of principally ground-dwelling, diurnal species belonging to the sceloporine phylogenetic line of the family Iguanidae. Species of the genus *Uta* have their center of radiation in the deserts of the southwestern United States and northern Mexico and are found from northern Zacatecas and the subtropical tip of Baja California to southeastern Washington, and from the Pacific coast to western Texas. Ecologically, *Uta* may be found in diverse habitats from desert sand dunes to the rocky intertidal zone and from elevations below sea level to above 8,000 feet.

The occurrence of *Uta* on over forty-eight islands along the Pacific coast and in the Gulf of California is of particular interest to evolutionary biologists because it offers opportunity for the study of selection in many different populations in response to environments of varying physiography, climate, and biotic composition. The plasticity that has enabled the colonization of such varied environments is evidently attributable to the great variability in *Uta* which, in turn, has made the diagnosis of the species and their systematic arrangement extraordinarily difficult. Unlike most other groups of North American lizards which have received at least one systematic revision, no attempt has been made to treat the systematics of the entire genus *Uta*. This deficiency has hampered many authors (Van Denburgh, 1922; Linsdale, 1932; and Smith and Taylor, 1950) in their attempts to treat North American reptilian groups in detail.

Species of *Uta* have been used recently as experimental animals in biological studies in ecology (Tinkle et al., 1962; Jorgensen and Tanner, 1963; Tinkle, 1965, 1967; Tinkle and Woodward, 1967; Turner et al., 1965, 1967; Turner and Gist, 1965), ethology (Carpenter, 1962; Irwin, 1965; Ferguson, 1966a, b), physiology (Cowles and Bogert, 1944; Dawson and Bartholomew, 1956; Mullen, 1962; Quay and Wilhoft, 1964; Roberts, 1966;

Alexander and Whitford, 1968; Hadley and Burns, 1968) and reproductive physiology (Tinkle, 1961; Tinkle and Irwin, 1965; Asplund and Lowe, 1964; Christiansen, 1964; Hahn, 1964; Dana and Tinkle, 1965; Hahn and Tinkle, 1965; Hoddenbach, 1965; Cuellar, 1966a, b; Hoddenbach and Turner, 1968). Further comparative studies are now hampered because the systematic relationships within the genus are largely unknown. A systematic revision of the genus should provide much needed information essential to organize and aid, as well as to suggest, future experimental research within this group. As examples we might cite the current studies of Ferguson (pers. comm.) on differences in the mating behavior of two utas that represent what we consider the primitive and advanced stocks in the genus. We might predict that these differences, if phylogenetically consistent, would apply to other utas of the two stocks. Similarly, Tinkle (1969) has correlated the degree of sexual dimorphism in two populations of *Uta stansburiana* with differences in their demographic properties. He noted, however, that such differences in dimorphism also existed between other species in the genus and might have phylogenetic rather than ecological meaning. For the studies cited above, a good understanding of the probable phylogeny of the genus is critical.

The initial procedure was to establish the morphological identity of the species of the genus, to present an analysis of the populational variation in them, and to describe the extent of their geographical distributions. The analysis of morphological relationships between populations was used to construct a hypothetical evolutionary history of the group as well as to point out those areas of specific interest which must be considered in more detail in the future.

For their hospitality and assistance in many ways and for loan of specimens in their care or for assistance in locating such material, we wish to express our gratitude to the following individuals and their institutions: James P. Bacon and Robert F. Inger (Field Museum of Natural History), W. Frank Blair (University of Texas), William B. Davis (Texas A and M University), William G. Degenhardt (University of New Mexico), James R. Dixon (formerly of Los Angeles County Museum), William E. Duellman (University of Kansas), Warren Freihofer and George S. Myers (Stanford University) Alan E. Leviton (California Academy of Sciences), T. Paul Maslin (University of Colorado), W. L. Minckley (Arizona State University), James A. Peters (United States National Museum), Jay M. Savage (University of Southern California), Allan J. Sloan (San Diego Natural History Museum), Hobart M. Smith (formerly of University of Illinois), Robert C. Stebbins (University of California), Wilmer W. Tanner (Brigham Young University), Richard G. Zweifel (American Museum of Natural History), and Charles F. Walker (University of Michigan Museum of Zoology).

Many people have been of valuable assistance in the collection of specimens and in field work connected with this study. Special thanks are due to Orlando Cuellar, Gary Ferguson, and Charles McKinney for their con-



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Computation of the data was made possible through the facilities of the Washington University Computer Center (NSF grant G-22296) and the University of Michigan Computing Center. We extend thanks to James S. Farris, now of the State University of New York at Stony Brook, for statistical advice.

## MATERIALS AND METHODS

External morphological features, principally scale counts and body measurements, were used to indicate similarity. It was assumed that relationship and genetic composition of organisms are reflected in their presumably homologous morphological features. Emphasis has been placed on population variation of these features rather than on the description of individuals.

### SAMPLING

Preserved specimens (3036) representing 32 insular and 37 continental populations plus 79 types and paratypes were examined. Location maps of the samples are presented in Figures 1 and 2. A list of these localities and the sample which they represent is presented in Appendix A. Additional museum material was examined for records of geographical distribution. Specimens from the following institutions were examined: American Museum of Natural History (AMNH); Angelo State College (ASC); Arizona State University (ASU); Brigham Young University (BYU); California Academy of Sciences (CAS); Los Angeles County Museum (LACM); San Diego Natural History Museum (SDNHM); Stanford University, Leland Stanford Museum (SU); Texas A & M University, Texas Cooperative Wildlife Collection (TCWC); University of Texas, Texas Natural History Collection (TNHC); Texas Technological College, Vertebrate Research Collection (TTC); University of Colorado Museum (UCM); University of California, Museum of Vertebrate Zoology (UCMVZ); University of Illinois, Natural History Museum (UI); University of Kansas, Museum of Natural History (UKMNH); University of Michigan, Museum of Zoology (UMMZ); University of New Mexico, Museum of Southwestern Biology (UNMMSB); United States National Museum (USNM).

Quantitative data were collected on 34 meristic characters and 7 measurements, with 10 ratio transformations. The analysis of morphological

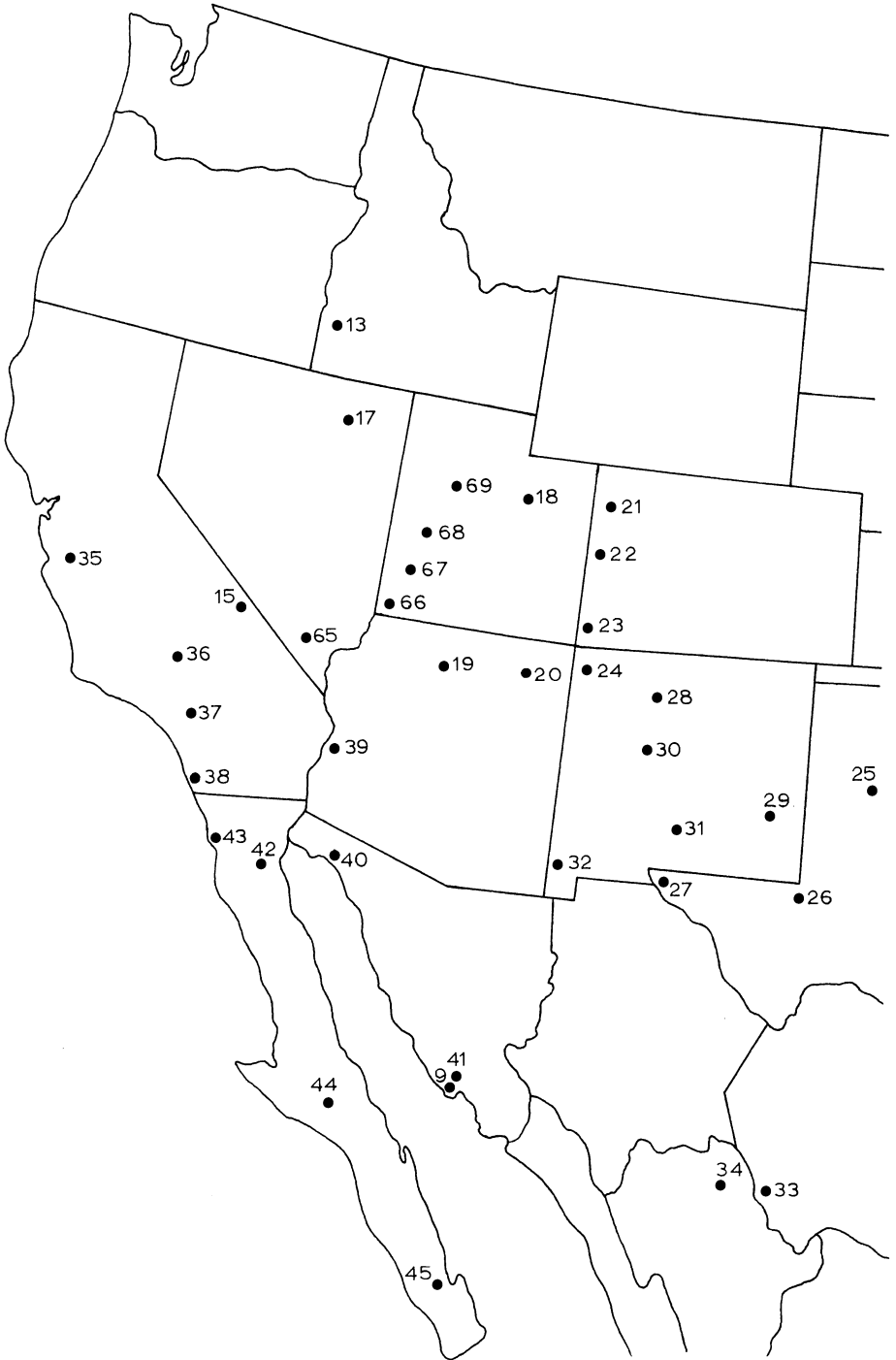


FIG. 1. Location map of samples taken from continental populations. Numbers correspond to the population numbers given in Appendix A.

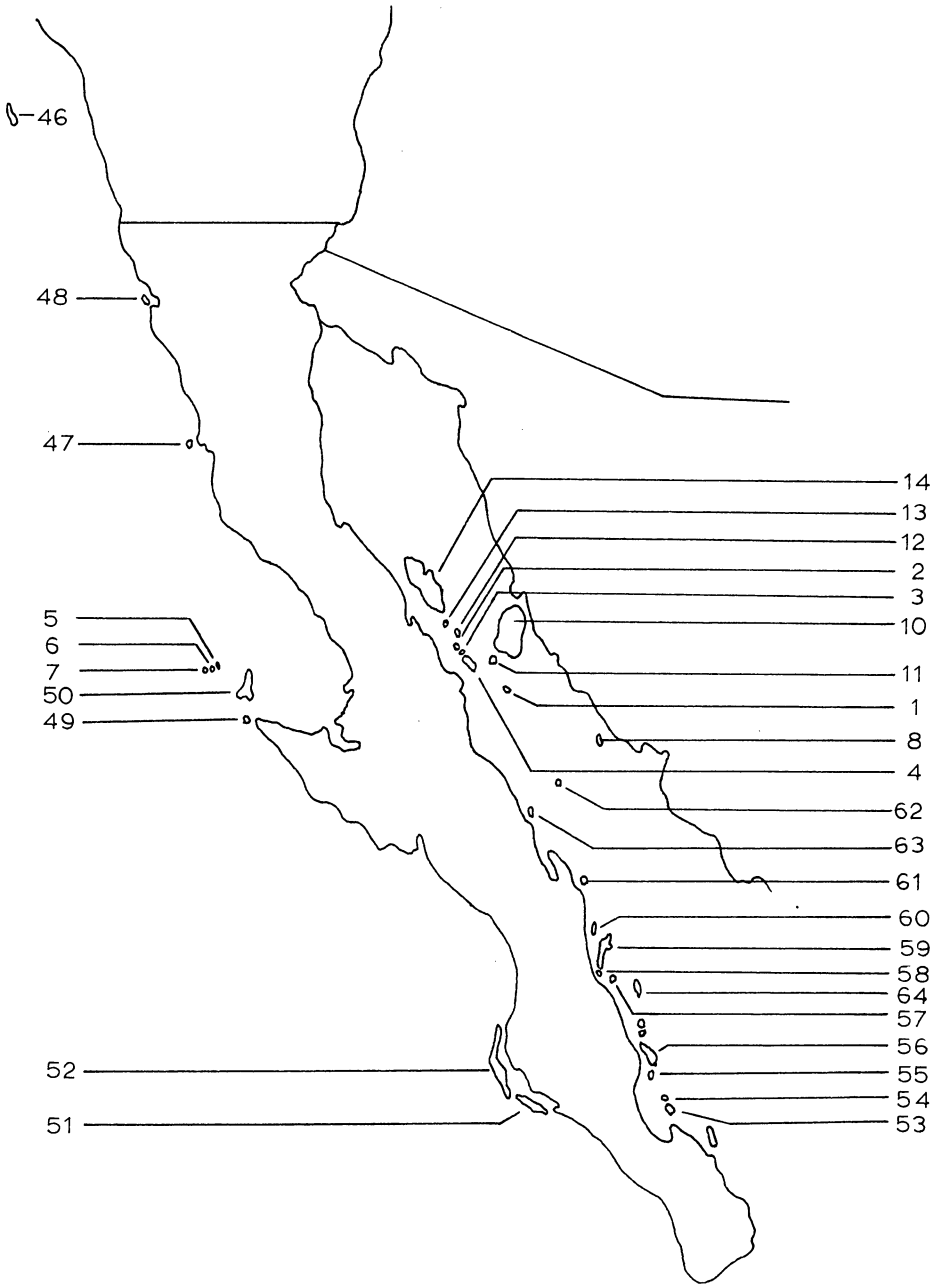


FIG. 2. Location map of samples taken from insular populations. Numbers correspond to the population numbers given in Appendix A.

relationships and geographical variation was based on statistically treated characters (Appendix B), although certain characters proved of descriptive interest only. An attempt was made to include all characters previously considered by other authors, to facilitate comparisons and evaluations of earlier studies of the genus. Additional observations from field experience are presented where pertinent. Qualitative data on color pattern differences were used in certain instances as supporting evidence.

SCALE CHARACTERISTICS—HEAD (FIG. 3)

FRONTAL.—The frontal scale in *Uta* may be a single large plate (entire) or divided (1–3 times) transversely into a number of plates. The number of frontal plates was counted (i.e., entire=1, divided=2, twice divided=3, etc.). In addition, when the frontal is divided into at least three parts the middle

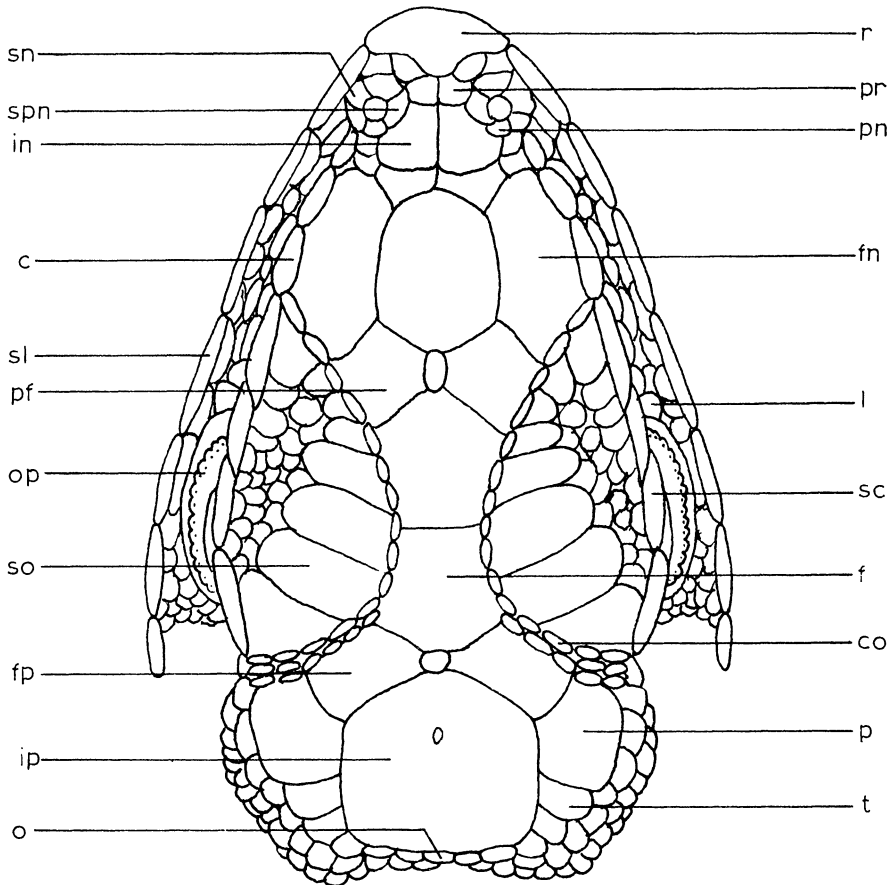


FIG. 3. Head scale characteristics. c=canthal, co=circumorbital, f=frontal, fn=frontonasal, fp=frontoparietal, in=internasal, ip=interparietal, l=loreal, o=occipital, op=orbital papillae, p=parietal, pf=prefrontal, pn=postnasal, pr=postrostral, r=rostral, sc=superciliary, sl=supralabial, sn=subnasal, so=supraocular, spn=supranasal, t=temporal.

part is always entire, whereas the anterior and posterior plates may be divided longitudinally, giving the appearance of a second pair of prefrontals or frontoparietals. This longitudinal division was highly variable and was not considered quantitatively.

**PREFRONTALS.**—The prefrontals are two enlarged scales anterior to the frontals. These scales may be in contact at the middorsal line or separated by the anterior apex of the frontal. The proportion of individuals with contacting prefrontals was noted.

**FRONTOPARIETALS.**—These scales are posterior to the frontal and may be in contact at the middorsal line or separated by the posterior frontal apex. The proportion of individuals with contacting frontoparietals was considered, as well as the number of frontoparietals in the contacting series.

**CIRCUMORBITALS.**—The circumorbital scales on the right side of the head from the posterior superciliary border to and including the posterior canthal were counted. The row adjacent to the enlarged supraoculars was chosen because there may be more than one circumorbital row. The circumorbitals are always in one row in the anterior one-third of the series but often consist of 2–4 scale rows in the posterior two thirds of the series. To quantify this difference, the smallest number of circumorbital scale rows was counted at the position of the parietal, frontoparietal, and frontal. Thus, if at the position of the frontal, the circumorbitals increased from 2 to 3, the number of circumorbital rows was considered 2. Occasionally a 0 was recorded when the circumorbital scale row was incomplete and the frontal and supraocular were in contact.

**SUPRAOCULAR.**—The transversely enlarged supraoculars were counted. The supraocular was considered enlarged if it was twice as large as a representative of the smaller supraoculars at the anterior portion of the series. As this criterion proved somewhat arbitrary, it might be best in future studies to count the total number of scales within the boundary of the circumorbitals and superciliaries as was done by McKinney (1966).

**SUPERCILIARIES.**—The number of superciliaries above the right eye is generally 5 but varies from 4 to 6. The small scales between the enlarged supraoculars and the fourth superciliary were counted. Because the fourth superciliary was always under (i.e., overlapped dorsally by) the third and the fifth, the junction of the third and fifth superciliaries is a convenient reference point for this count.

**FRONTONASAL.**—The single row of frontonasals usually consists of 3 scales although the lateral ones may be subdivided diagonally, producing 5 scales in the series.

**INTERNASALS.**—The number of paired internasals was counted.

**SUBNASAL.**—There is always a single scale between the nasal and the supralabial row.

**SUPRANASAL.**—The scale row bordering the upper margin of the nasal separating the nasal from the internasals is diagnostic of the genus and was used to differentiate *Uta* and *Urosaurus*.

**POSTROSTRAL SCALE ROWS.**—The scale rows posterior to the rostral and anterior to the internasals were counted. Because this number is always 1 or 2, the proportion of individuals with 2 postrostral scale rows was considered in the statistical analysis.

**LOREALS.**—The number of loreal scales in a line from (and including) the posterior canthal to (but excluding) the supralabial was counted on the right side.

**LABIALS.**—The labial (infralabial) count consists of the scales from the corner of the mouth opening to but not including the mental on the lower right jaw.

**ORBITAL PAPILLAE.**—The orbital papillae on the lower lid of the right eye were counted.

**AURICULAR LOBULES.**—The small triangular scales bordering the anterior margin of the ear opening are of two types: the large auricular lobules, which were at least one-half as long as the longest in the series, and the small lobules, less than one-half the length of the longest. The entire series was considered the total auricular lobules.

**OCCIPITALS.**—The number of scale rows between the interparietal and the smaller dorsals varies from 0 to 5. As the number usually decreases lateromedially, this count was taken at the middorsal line.

**CIRCUMINTERPARIETALS.**—The scales immediately adjacent to the interparietal around its entire circumference were counted. This series, which includes the occipitals, temporals, parietals, frontoparietals, and occasionally the frontal, was useful in estimating the number and size of the scales over the posterior portion of the cranium.

#### SCALE CHARACTERISTICS—BODY

**DORSAL SCALES.**—The dorsal scales were counted on a middorsal straight line from the first scale posterior to the interparietal to a point above the posterior insertion of the hind legs.

**NON-KEELED DORSALS.**—The non-keeled dorsal scale count started with the first scale behind the interparietal and terminated either three or four scales posteriorly or occasionally as far posteriorly as the point of termination of the dorsal scale count. This count is a useful estimate of the relative rugosity of the dorsal scales.

**GULAR SCALES.**—The number of scales in a straight line medially from the postmental to and including one enlarged gular fold scale constituted the gular scale count.

**GULAR FOLD SCALES.**—The enlarged scales in a row along the gular fold were counted. The gular fold scales were generally easily distinguished from the nape scales at their lateral origination, but for quantitative purposes the gular fold scales were considered to begin when the scale size increased to one and one-third times an immediately adjacent scale at the ventrolateral nape.

**VENTRAL SCALES.**—The ventrals were counted on a midventral straight line from the first scale behind the enlarged gular fold scale to the last scale bordering the cloacal opening.

**INTERFEMORALS.**—The interfemorals included the number of scale rows between the proximal femoral pore on the right leg and the proximal femoral pore on the left leg.

**DIGITAL LAMELLAE.**—The number of scales on the ventral side of the fourth (longest) toe on the right hind leg was counted. The number of keels or ridges (lamellar spurs) on the lamellae were counted and the maximum and minimum number for each digital lamellar series of the fourth hind toe were recorded.

**FEMORAL PORES.**—The total number was counted.

**INTERPOSTANALS.**—This count was of the number of small scales in a line between the enlarged postanals in males.

In addition to the above scale characters the following descriptive characters were considered: size and shape of the enlarged postanals; size and shape of the interparietal; frontal size; postnasal size; prenasal size; rostral length and apex description; mental size and shape; postmental size; gular scale shape; auricular lobule size; supratemporal size and shape; parietal size and shape; size, shape, and keel description of posterior and anterior femorals, dorsals, basal caudals, ventrals and subcaudals; and presence or absence of interdorsals.

#### MEASUREMENTS AND RATIOS

The following body measurements, taken to the nearest millimeter, were converted to ratios to standardize the measurement in relation to body size.

*Snout-vent length* was measured along the midventral line from the anterior border of the mental to the anterior lip of the cloacal opening.

*Snout-gular length* was measured from the anterior border of the mental to the posterior edge of the enlarged gular fold scales.

*Femoral length* was measured as an external representation of the femur length. With the rule resting on the dorsal surface of the thigh, and pressed against the body at the proximal end, we measured to the joint with the tibia.

*Tibia length* was taken from the joint of the femur and tibia to the heel base.

*Foot length* was taken from the base of the fifth toe to the distal tip of the longest (fourth) toe excluding the claw.

*Fourth-toe length* was measured from the base to the distal end excluding the claw.

The following ratios were computed to represent size, shape, and body proportions. In the text, these are referred to by their abbreviations.

- RSGSV = snout-gular length/snout-vent length
- RFMSV = femur length/snout-vent length
- RTBSV = tibia length/snout-vent length
- RFTSV = foot length/snout-vent length
- RTOFT = fourth toe length/foot length
- RDSV = number dorsal scales/snout-vent length
- RNKD = number non-keeled dorsals/number of dorsals
- RVSV = ventral scales/snout-vent length
- RGSG = number gular scales/snout-gular length
- RLMTO = number lamellae/fourth toe length

#### COLOR

Available specimens did not allow a quantitative analysis of the color pattern variation. The occurrence of polymorphic patterns described by Ballinger and McKinney (1967) is common in certain members of the genus while other members are essentially monomorphic. In this study no pattern analysis beyond the recognition of monomorphism and polymorphism was made; in certain descriptive sections side-blotch coloration, general ventral coloration, and general dorsal coloration were noted.

There is generally sexual dimorphism in the coloration of each species, the males being more brightly colored with superficial orange and yellow spotting and blue flecks. The blue flecks are a good sexual indicator and are never obvious in females. The blue to blackish spot in the axillary region is present in both males and females and is responsible for the common name applied to the genus (side-blotched lizards). The absence of the axillary spot in populations on Carmen, Danzante and Coronados Islands has been used in the past as a diagnostic characteristic; however, this blotch is reduced or absent in other populations so its diagnostic validity is questionable. Zweifel (1958) discussed a possible explanation for the absence of the axillary spot and suggested that it was highly ecotypic.

In an analysis of polymorphism in West Texas populations of *Uta stansburiana stejnegeri*, Ballinger and McKinney (1967) designated four different pattern types as "striped," "barbed," "chevron," and "patternless" (Fig. 4). Some of these patterns were discernible in other members of the genus. However, the basic difference between taxa appears to be between striped and non-striped pattern types. Additional variation in pattern types



may be found in *Uta* but the most obvious differences are shown in Figure 4 and discussed below.

The patternless type is rare but present in Texas and New Mexico populations of *Uta stansburiana stejnegeri*. A single such individual was found in the material examined from Cedros Island, indicating a similar rare occurrence of the patternless type in *Uta stansburiana elegans*. The entire population of *Uta nolascensis* is patternless.

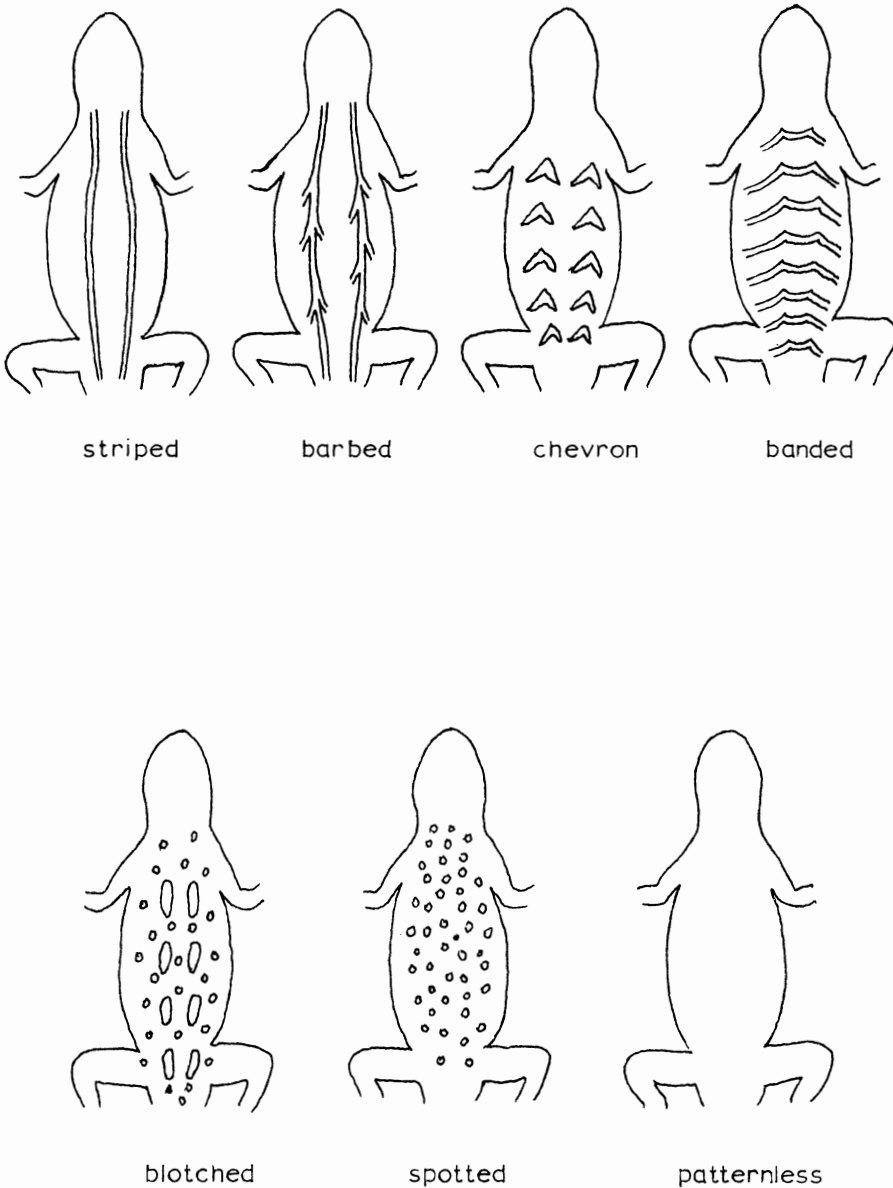


FIG. 4. Diagrammatic representation of color pattern types in the lizard genus *Uta*.

The spotted pattern type is characteristic of *Uta palmeri*, *stellata*, *antiqua*, *stansburiana taylori*, and *stansburiana stansburiana*.

The blotched pattern type occurs in certain populations of *Uta stansburiana taylori* and *stansburiana elegans*.

The striped, barbed, chevron, and banded types were found in *Uta stansburiana stejnegeri* and *stansburiana elegans*.

#### OTHER CHARACTERS EXAMINED

X-rays were made of several representatives of each form of *Uta*. From these, counts were made of presacral vertebrae, preautotomous caudal vertebrae, caudal vertebrae with transverse processes that were conspicuously enlarged compared with those on more posterior vertebrae, and phalangeal bones in each finger and toe. Prepared skeletons of some forms provided additional comparisons.

Karyotypes of most forms were prepared from bone marrow of the hind limbs using the method of Pennock et al. (1968). Chromosome counts were made, as were measurements of chromosome arms.

#### DATA PROCESSING

Standard statistical estimates were obtained for all of the quantitative characters (Appendix B). The mean, standard deviation, standard error, variance, and coefficient of variability were computed for each character for each sample.

Three tests of differentiation were considered. Graphic representation proved too laborious since the number of graphs required was prohibitively large. A limited number of graphs have been employed in the discussions of geographical variation. The multiple Student's "t" test computed for all characters and sample combinations was used where statistical significance of small differences was in question.

The coefficient of difference (C.D.) test (Mayr et al., 1953) proved satisfactory for comparisons of differences between populations. This statistic estimates the percentage nonoverlap of partially overlapping curves of character state frequencies. Because the C.D. test evaluates character differences between two populations one at a time, the following method was used to treat all characters and populations simultaneously.

A coefficient of difference matrix was prepared by calculating a mean coefficient of difference between all possible population samples. This was done by calculating each coefficient of difference for each character for each population and then averaging these coefficients of difference for each population comparison. In turn, a mean coefficient of difference for each taxon was calculated by averaging the mean coefficients of difference for each population in that taxon. Because of the enormous size of these matrices, only the taxon against taxon CD matrix is shown (Table 3). Taxonomic difference sufficient for subspecific recognition between populations

was generally considered to be a coefficient of difference of 1.28 (see Mayr, Linsley and Usinger, 1953, p. 146) at which level about 90% of the individuals of one population are separable from 90% of the individuals of the other. However, we have not hesitated to use other criteria for recognition of subspecies when we thought that the recognition provided a clearer picture of evolutionary relationships in the genus.

In the following presentation we first describe the taxa which appear worthy of recognition and then discuss the morphological relationships and bases for recognition of the taxa and their probable evolutionary history.

## RESULTS

### GENERIC STATUS—HISTORICAL RESUMÉ

The generic status of *Uta* has been controversial since it was first described by Baird and Girard in 1852. Various species assigned to the genus after that time were divided among three additional genera by Mittleman (1942). Mittleman recognized *Uta* as a distinct genus including only the side-blotched, small-scaled, utiform iguanids with homogeneous dorsal scutellation. He recognized *Urosaurus* (Hallowell, 1854) which had been synonymized with *Uta* by Baird (1859), and *Petrosaurus* (Boulenger, 1885) which was ignored and considered synonymous with *Uta* by Cope in 1887, as distinct genera. An additional genus, *Streptosaurus*, was erected by Mittleman (op. cit.) to include *Uta mearnsi* (Stejneger, 1894) and *Uta slevini* (Van Denburgh, 1894). Most authors before Mittleman's work (notably Baird, 1859; Cope, 1898; Ditmars, 1907; Stejneger and Barbour, 1923; Dickerson, 1919; Schmidt, 1921 and 1922; Woodbury, 1931; and Smith, 1935) had synonymized *Urosaurus* and *Petrosaurus* with *Uta*, and only Van Denburgh (1922) had recognized them (as subgeneric taxa). Like most authors since 1942 (notably Stejneger and Barbour, 1943; Smith, 1946; Smith and Taylor, 1950; Shaw, 1950; Brown, 1950; Lowe, 1964; Leviton and Banta, 1964), we have followed Mittleman's generic designations. However, Mittleman failed to present sufficient diagnostic data in support of his separation of the genera and many authors (Oliver, 1943; Schmidt, 1953; Stebbins, 1954; and Cagle, 1957) continued to recognize only the single genus *Uta*.

Savage (1958) found no evidence to support recognition of *Petrosaurus* and suggested that only subgeneric distinction be made. However, Etheridge (1964) pointed out that *Petrosaurus* is osteologically the most distinct sceloporine genus, and sufficiently different to warrant generic status distinct from *Uta*. Etheridge indicated that there was no osteological basis on which to recognize *Streptosaurus* as a genus distinct from *Petrosaurus* and suggested synonymy of the two.

Savage (1958) found differences in the sternal and pectoral girdle elements as well as in scutellation between *Urosaurus* and *Uta* that warranted their separation as two genera. Etheridge (1964) found no consistent differences in osteology which could be used to separate *Uta* and *Urosaurus*. Carpenter (1962) pointed to behavioral differences between *Urosaurus* and

*Uta* which he felt were of sufficient magnitude to characterize two genera.

On the bases suggested by Mittleman (1942), Savage (1958), and Carpenter (1962), *Urosaurus* and *Uta* can be justifiably treated as distinct genera. We further contend in our evolutionary hypothesis presented later that *Uta* is a derivative of *Petrosaurus*. Until a study is made of relationships among sceloporine genera, *Uta* and *Urosaurus* should definitely be treated as separate genera to avoid a probably artificial assemblage of polyphyletic origins.

KEY TO THE GENERA *Uta*, *Urosaurus* AND *Petrosaurus*<sup>1</sup>

- 1a Enlarged supraoculars in 2 or 3 rows, superciliaries 8 or 9, dorsals 160–250, not keeled; ventrals more than 100. . . . . *Petrosaurus*
- 1b Enlarged supraoculars in a single row, superciliaries 3–6, dorsals 70–150, keeled, ventrals fewer than 90 (usually fewer than 70). . . . . 2
- 2a Supranasals absent, subcaudals keeled to within 5 mm of cloacal aperture and mucronate<sup>2</sup>, keels of caudal scales run entire scale length at same height producing a series of continuous parallel longitudinal ridges surrounding the tail, vertebral and paravertebral scale rows greatly enlarged and bordered by smaller scales<sup>3</sup>, blue to black ventrolateral band in males. . . . . *Urosaurus*
- 2b Supranasals present, subcaudals never keeled except on posterior one-third of tail, keels on caudal scales approximately one-half length of scale and higher at posterior end, not producing continuous ridges the length of the tail, vertebral and paravertebral scale rows not greatly enlarged, axillary spot (blue to black) present in both sexes<sup>4</sup> . . . . . *Uta*

The internasal-rostral contact as used by Savage (1958) to separate *Uta* and *Urosaurus* is not absolute. In *Uta* the internasals never contact the rostral while in *Urosaurus* this character is variable; the contact is absent in *ornatus*, *auriculatus*, *clarionensis*, and *graciosus* but present in *gadovi*, *nigricaudus*, *bicarinatus*, and *microscutatus*. While the above key reflects a closer relationship between *Uta* and *Urosaurus* than between *Uta* and *Petrosaurus* this is probably not the case (Table 1). In support of the separation of *Uta*, *Urosaurus* and *Petrosaurus*, taxonomic diagnoses of the three genera are presented below with the major differences summarized in Table 1.

<sup>1</sup> Key based on the following material examined: *Urosaurus* (265) including *gadovi* (62), *auriculatus* (15), *nigricaudus* (4), *clarionensis* (20), *graciosus* (8), *bicarinatus* (25), *microscutatus* (17), *ornatus* (113) including *symmetricus*, *wrightii*, *linearis*, *schmidti*; *Petrosaurus* (20) including *repens*, *thalassinus*, *mearnsi*; *Uta* (3055) presented in the following review.

<sup>2</sup> Subcaudals in *Urosaurus auriculatus* not keeled at extreme base but spinose, keels begin approximately 2–4 cm from base of tail.

<sup>3</sup> Absent in *microscutatus* and *nigricaudus*.

<sup>4</sup> Occasionally lost or modified in *Uta stansburiana elegans*.

TABLE 1.  
COMPARISON OF DIAGNOSTIC CHARACTERISTICS  
OF *Uta*, *Urosaurus*, AND *Petrosaurus*

<i>Character</i>	<i>Uta</i>	<i>Urosaurus</i>	<i>Petrosaurus</i>
Enlarged supraoculars	single row	single row	double row
Supranasals	present	absent	present
Caudals	short keeled non-aligned	long keeled aligned	short keeled non-aligned
Dorsals	homogeneous granular to keeled	heterogeneous usually with enlarged para- vertebral dorsals	homogeneous granular

#### Genus *Petrosaurus* Boulenger

*Petrosaurus* Boulenger, 1885, Cat. Liz. Brit. Mus., vol. 2, page 205.

TYPE-SPECIES.—*Uta thalassina* Cope, 1863, Proc. Acad. Nat. Sci. Phila., p. 104.

DIAGNOSIS.—Enlarged supraoculars in 2 or 3 rows; superciliaries 8 or 9; dorsals homogeneous, small, granular, not keeled, more than 160; ventrals more than 100; supranasal always present; subcaudals never keeled; body size large (maximum 175 mm); internasals not in contact with rostral; total femoral pores 32 to 50; interfemorals 12 to 31; gulars more than 60; 1–2 subnasals; frontonasals not enlarged, occurring in 2 rows 6 scales across or in single row with medium one enlarged and lateral ones bifurcated diagonally; four sternal ribs.

DISTRIBUTION.—Extreme southern California, Baja California, and on the islands of Mejia, Angel de la Guarda, El Muerto, Danzante, Espiritu Santo, and Partida Sur, Gulf of California.

REMARKS.—As recognized here, *Petrosaurus mearnsi mearnsi*, *P. mearnsi slevini*, and *P. thalassinus* are referable to this genus.

#### Genus *Urosaurus* Hallowell

*Uro-saurus* Hallowell, 1854, Proc. Acad. Sci. Phila., vol. 7, p. 92.

TYPE-SPECIES.—*Urosaurus graciosus* Hallowell, 1854, *ibid.*

DIAGNOSIS.—Enlarged supraoculars in a single row; superciliaries 3–6; greatly enlarged vertebral and paravertebral scale rows bordered by smaller

scales; supranasal always absent; subcaudals keeled, usually to within 0.5 cm of cloacal aperture; keels of caudal scales run entire length of scale at approximately equal height producing a series of continuous parallel longitudinal ridges surrounding the tail; total femoral pores 16–28; inter-femorals 8–18; one subnasal; gulars fewer than 40; 3 enlarged frontonasals in single row; three sternal ribs; ventrolateral blue to black belly patch in males.

DISTRIBUTION.—Central Texas and northern Mexico west to eastern California and south through Baja California; Utah south along the Pacific coast of Mexico to Chiapas; islands bordering Baja California in the Pacific and Gulf of California; the Revillagigedo Archipelago.

REMARKS.—As recognized here, *Urosaurus* includes those forms reviewed by Mittleman (1942). The genus is in need of careful revision in view of the failure of Mittleman to provide quantitative diagnoses for the taxa he recognized.

#### Genus *Uta* Baird and Girard

*Uta* Baird and Girard, 1852, in Stansbury, Exploration and survey of the valley of the Great Salt Lake of Utah. . . . . pp. 344–345.

TYPE-SPECIES.—*Uta stansburiana* Baird and Girard, 1852, *ibid.*

DIAGNOSIS.—Enlarged supraoculars in a single row; superciliaries 4–6; dorsals fewer than 150 and never including enlarged vertebrales or paravertebrales; ventrals fewer than 90; supranasals always present; subcaudals keeled only on posterior one-third of tail; keels on caudal scales approximately one-half the length of the scale and higher at the posterior aspect, not producing continuous ridges the length of the tail; total femoral pores 21–37; interfemorals 4–20; three sternal ribs.

DESCRIPTION.—Frontal entire or divided transversely 1–3 times; when twice divided posterior- and anterior-most plates occasionally divided longitudinally, longer than length of interparietal, greatest width never exceeding internarial distance, anterior apex truncate to triangular, posterior apex truncate or rarely triangular; prefrontals in series of 2 in contact medially or separated by anterior apex of frontal, or in series of 3–4 in contact with 1–2 smaller interprefrontals between larger lateral prefrontals; frontoparietals in series of 2 in contact medially or separated by posterior apex of frontal, or in series of 3–6 with 1–4 small interfrontoparietals between larger lateral ones; circumorbitals 10–26 from posterior-most superciliary to and including the posterior-most canthal, 1–3 minimum circumorbital scale rows between enlarged supraoculars and parietal, 0–2 between supraocular and frontoparietal or frontal; 3–6 enlarged supraoculars; 1–4 scales between enlarged supraocular and fourth superciliary; 4–6 superciliaries, fourth superciliary always under third and fifth, first through third imbricate; 3 frontonasals, median one hexagonal, slightly larger,

lateral ones in contact with posterior canthals, occasionally bifurcated diagonally yielding 4 or 6 frontonasals; 2 rows of paired internasals or occasionally 3, third row often discontinuous, separated medially by anterior portion of medial frontonasal and usually consisting of 4-6 scales; 1 subnasal; 2-4 postnasals; rostral a single scale separating right and left supralabials, length greater than internarial distance but never extending beyond nasal, posterior rostral apex well developed, mucronate to truncate often separating scales in first row of postrostrals, or not developed and rounded, but never absent; 1-2 rows of postrostals consisting of 2-4 scales, anterior row occasionally separated medially by rostral apex; canthal ridge of 3-4 scales, 2-5 scales separating posterior canthal and supralabials; 0-7 loreals in one or 2 rows; infralabials 6-13 on one side from angle of jaw to mental; mental a single pentagonal scale separating right and left infralabials, width one-third of rostral width, posterior apex sharp and triangular; 10-18 orbital papillae on lower eyelid; 1-5 large auricular lobules bordering anterior margin of ear opening, width at base varying from one-half to one and one-half times the length, size variable but largest generally extending one-half to three-fourths distance across ear opening, shape triangular; total auricular lobules 2-7 including large auricular lobules and 1-4 smaller lobules less than one-half length of large ones located dorsal or ventral to the large ones; 2-5 enlarged nuchals in 1-2 rows anterior to auricular lobules but separated from them by 1-2 rows of smaller scales; 2-4 supratemporals one-half to one-third size of parietal; parietal a single scale on either side of head, subtriangular, 2 times size of frontoparietal; 1-4 rows of occipitals at middorsal line increasing to 2-6 rows laterally; single enlarged interparietal, width equal to or slightly greater than height of ear opening, shape triangular to semicircular or pentagonal, parietal foramen visible and centrally to anterocentrally located; 10-25 circuminterparietals; dorsals 70-132, juxtaposed to imbricate, smooth to carinate, increasing in size from anterior to posterior, mucronate to spinose when keeled; basal caudals larger than dorsals, imbricate, carinate, spinose; non-keeled dorsals comprising the first 2-132 scales in the dorsal series; lateral scales granular, not carinate, 15-18 rows at midbody between ventrals and dorsals increasing to 25-30 at femoral and axillary regions, laterals about one-tenth size of ventrals; 54-86 ventrals, smooth, imbricate, decreasing in size posteriorly, triangular to diamond shaped; subcaudals smooth, slightly larger than ventrals, imbricate; 22-45 gulars, smooth, juxtaposed to imbricate posteriorly, rounded to triangular, increasing in size posteriorly; 12-25 gular fold scales larger and anterior to granular gular fold scales, equal to or one and one-half times the size of anterior ventrals; 4-20 interfemorals; 21-37 total femoral pores; 21-33 digital lamellae on fourth hind toe; digital lamellae with 3-7 spurs projecting distally; postanals in males not enlarged to greatly enlarged; postanals in females small; interpostanals in males 1-4 small scales separating two greatly enlarged postanals; postfemorals small granular scales posterior from femoral pores to midway to dorsal thigh, size equal

to or smaller than laterals; anterior femorals enlarged, size similar to dorsals, carinate, imbricate. Number of presacral vertebrae usually 23 (21-24); usually 6 or fewer preautotomous caudal vertebrae; total number of caudal vertebrae 36-44; phalangeal formula 2-3-4-5-3 for front toes, 2-3-4-5-4 on rear toes. Chromosome number  $2n=34$  with 6 pairs of macrochromosomes, 11 pairs of microchromosomes; the males heterogametic.

DISTRIBUTION.—Northern Zacatecas, Mexico north to southeastern Washington and south to southern Sonora and Baja California; western Texas to the Pacific coast; islands in the Gulf of California and Pacific coastal islands (Fig. 5).

REMARKS.—Forms referable to *Uta* are reviewed in the following report.

#### KEY TO THE FORMS OF *Uta*

- 1a Ventrals 75 or more, gulars generally more than 38.....2
- 1b Ventrals 74 or fewer, gulars generally fewer than 37.....3
- 2a Dorsals 103 or more.....*palmeri*
- 2b Dorsals fewer than 95.....*antiqua*
- 3a Auricular lobules poorly developed (width at base equal to or greater than length), usually 2-3; dorsals not imbricate, widely spaced with intervening granules conspicuous.....*stellata*
- 3b Auricular lobules well developed (width at base less than length), usually more than 3, dorsals varied but not as above.....4
- 4a Venter completely dark; dorsal pattern unicolor; superciliaries 6 (60%) or 5 (40%), dorsals always more than 95.....*nolascensis*
- 4b Venter light; dorsal pattern not unicolor; superciliaries 4-5, rarely 6 (1%); dorsals variable in number, but commonly fewer than 95..5
- 5a Two scales between posterior canthal and supralabial; scales between enlarged supraocular and third superciliary 1-2; ventrals more than 65 .....*antiqua*
- 5b Scales between posterior canthal and supralabial usually more than 2; scales between enlarged supraocular and third superciliary usually more than 2; ventrals varied but usually fewer than 65.....6
- 6a Prefrontals not in contact, separated by an anterior projection of the frontal; dorsals usually 80 or fewer and never more than 84; non-keeled dorsals 10 or fewer, scales at tail base predominantly green .....*squamata*
- 6b Prefrontals in contact or separated by a small scale, rarely separated by an anterior projection of the frontal; dorsals more than 83, rarely fewer than 80 (except Angel de la Guarda where non-keeled dorsals usually more than 10); non-keeled dorsals averaging more than 10 .....7
- 7a Dorsal color pattern generally composed of dorsolateral light stripes at least just behind head; body size of adult males greater (maximum 58 mm); males rarely spotted.....8



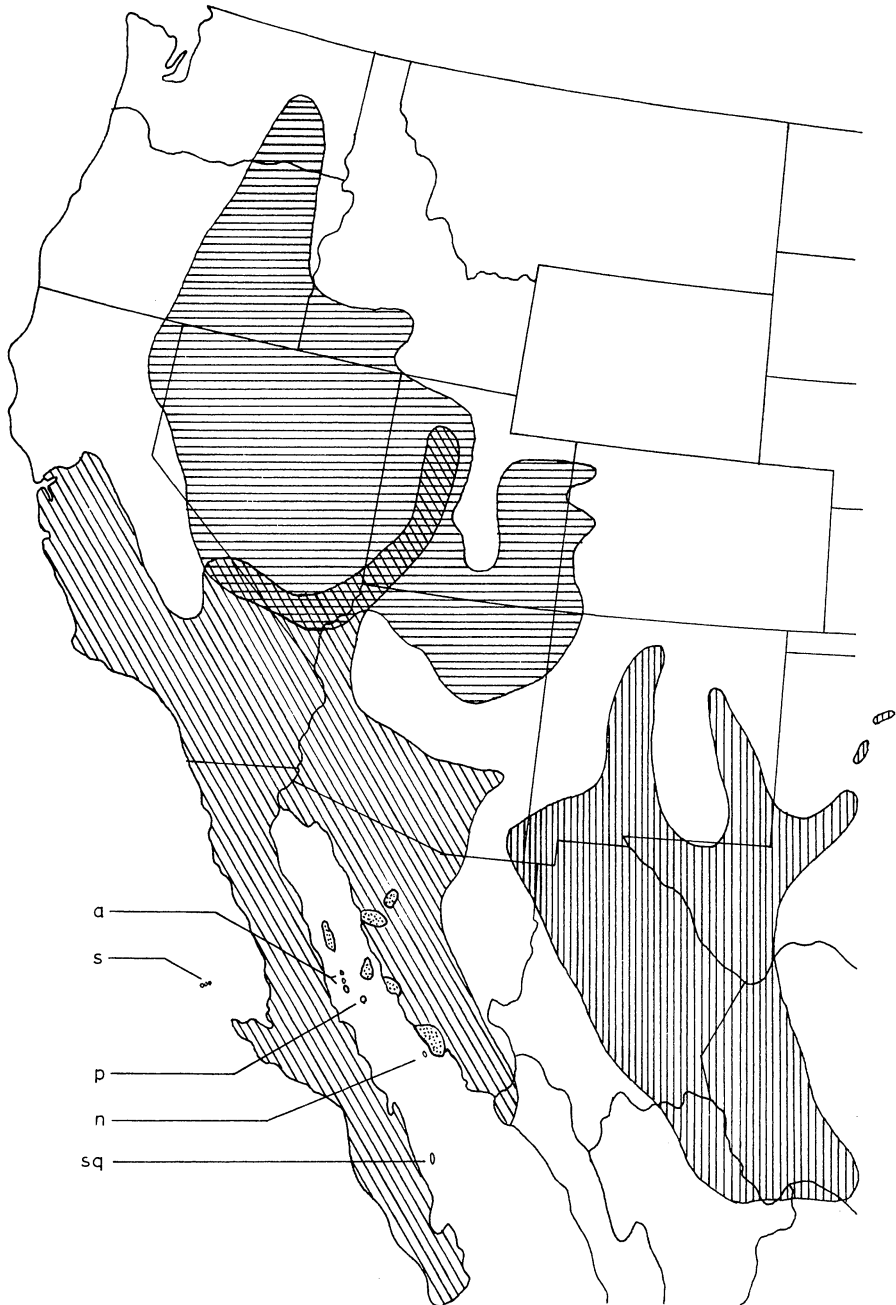


FIG. 5. Present distribution of the forms of *Uta*. Horizontal lines=*stansburiana stansburiana*, diagonal lines =*stansburiana elegans*, cross-hatch=intergrade zone between *stansburiana stansburiana* x *stansburiana elegans*, vertical lines=*stansburiana stejnegeri*, stipple=*stansburiana taylori*, a=*antiqua*, s=*stellata*, p=*palmeri*, n=*nolascensis*, sq=*squamata*.

- 7b Dorsal color pattern never composed of dorsolateral light stripes; body size of adult males less (maximum 54 mm (9a), 56 mm (9b)); males spotted . . . . . 9
- 8a Interfemorals usually fewer than 8 (average 6.8) . . . *stansburiana stejnegeri*
- 8b Interfemorals usually more than 8 (average 12.4) . . . *stansburiana elegans*
- 9a Dorsal scales weakly keeled not conspicuously imbricate nor spinose; non-keeled dorsals usually more than 30 and as many as 70; spotted pattern in males (spots small); female pattern of small dark spots over lighter background . . . . . *stansburiana stansburiana*
- 9b Dorsal scales keeled to strongly keeled, imbricate, mucronate to spiny; non-keeled dorsals usually fewer than 30, never more than 38, mean number varying from 12 to 26; spots on males conspicuously larger; female pattern variable but not as above . . . . . *stansburiana taylori*

*Uta antiqua* Ballinger and Tinkle

*Uta antiquus* Ballinger and Tinkle, 1968, Occ. Paps., Mus. Zool., Univ. Mich., no. 656, pp. 1-6.

*Uta stansburiana elegans* Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 240-247 (part); Smith and Taylor, 1950, Bull. U.S. Nat. Mus., vol. 199, pp. 148-149 (part).

TYPE.—UMMZ 127386, D. W. Tinkle and O. Cuellar, collectors.

TYPE LOCALITY.—Isla Salsipuedes, Gulf of California.

DIAGNOSIS.—Two scales between posterior canthal and labial; one or two scales between enlarged supraoculars and fourth superciliary; ventrals more than 65; dorsals fewer than 93; maximum size of adult males, 69 mm (Isla San Lorenzo Norte).

DESCRIPTION.—**Head:** Frontal once or twice divided transversely, rarely divided three times, never entire; prefrontals in contact or separated by single small scale, never separated by anterior projection of frontal; frontoparietals separated by single scale or posterior apex of frontal or rarely by 2-3 scales; circumorbitals 15-20 (aver. 17.2); 1 circumorbital scale row between frontoparietal and enlarged supraoculars; 2 (83%), occasionally 1 (17%), circumorbital scale rows between parietal and enlarged supraoculars; 1 circumorbital row between frontal and enlarged supraoculars; 5, rarely 4 (4%) enlarged supraoculars; 2, rarely 1 (10%) scales between enlarged supraoculars and fourth superciliary; 5 superciliaries; 3 frontonasals; 2 rows of internasals; 1 subnasal; 1 or 2 (51%) postrostral scale rows; 1 or occasionally 2 (20%), rarely 3 (7%) loreals; 2, occasionally 3 (20%) scales between postcanthal and labial; right labials 8-10 (aver. 9.9); 13-16 orbital papillae (aver. 14.1); large auricular lobules 1-3 (aver. 2.5); total auricular lobules 3-5 (aver. 4.2), largest longer than basal width; 2, occasionally 3 (16%), occipital scale rows at midline behind interparietal; 14-18 circum-

interparietals (aver. 16.6). **Body:** Dorsals 79–94 (aver. 86.5); non-keeled dorsals 16–38 (aver. 25.9); dorsals at midbody carinate, mucronate to spiny; dorsals at tail base carinate and spinose; gulars 31–37 (aver. 33.7), gular fold scales 13–20 (aver. 16.6); ventrals 66–76 (aver. 70.0); interfemorals 13–19 (aver. 15.7); total femoral pores 27–33 (aver. 30.0); 24–30 lamellae on fourth toe (aver. 26.8); maximum lamellar spurs average 6.1; interpostanals in males average 2.3 (2–3). **Ratios:** RDSV average 1.79; RNKD average .30; RSV average 1.45; RGSG average 2.06; RLMTO average 3.04. **Size and Proportions:** Maximum snout-vent length 58 mm in males, 57 mm in females; RSGSV average .34; RFMSV average .22; RTBSV average .25; RFTSV average .32; RTOFT average .58. **Color in alcohol:** Dorsum gray to brown with scattered light spots, blue flecks in males; venter light; gular region dark blue to black; axillary spot prominent, dark blue to black.

**VARIATION.—Sexual:** There is little or no sexual dimorphism in coloration. Females are generally smaller and have slightly shorter appendages in relation to body length; they have smaller scales and higher ratios of scales per unit area than males although actual numbers of scales do not differ significantly between the sexes. There is more sexual dimorphism in the Salsipuedes population based on scale counts, external measurements, and ratios than in either of the San Lorenzo populations. The numbers of characters which differ between the sexes at the 0.01 level (t test) are 13 (Salsipuedes), 8 (San Lorenzo Sur) and 5 (San Lorenzo Norte). **Geographical:** There are no significant taxonomic differences in any characters between the Salsipuedes population and the populations on north and south San Lorenzo. Interfemorals are slightly fewer (10–16) in the San Lorenzo populations compared with those on Salsipuedes.

**DISTRIBUTION.—**Isla Salsipuedes, Isla San Lorenzo Norte and Isla San Lorenzo Sur, Gulf of California (Fig. 5).

**HABITAT.—***Uta antiqua* may be found in a variety of habitats. On San Lorenzo Sur *antiqua* is common in the sandy flats and rocky arroyos as well as along the rocky beach and on cliffs above the beach. On Salsipuedes and San Lorenzo Norte it is found commonly along the rocky beach and on hillsides and has been observed to feed on isopods of the intertidal zone.

**MATERIAL EXAMINED.—**UMMZ 127386 (type); UMMZ 127387 (82) (Salsipuedes Island, paratypes); UMMZ 127449 (47) (San Lorenzo Sur Island); CAS 51247–56, 95103–19, SDNHM 45054–56, 44149–50, 51210–49 (San Lorenzo Norte Island).

*Uta nolascensis* Van Denburg and Slevin

*Uta nolascensis* Van Denburgh and Slevin, 1921, Proc. Calif. Acad. Sci., ser. 4, vol. 11, pp. 395–396. Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 223–225.

**TYPE.—**CAS 50508; Joseph R. Slevin, collector.

**TYPE LOCALITY.**—Isla San Pedro Nolasco, Sonora, Gulf of California.

**DIAGNOSIS.**—Pattern unicolor, green above, no dark or light markings, blue flecks in males; venter dark blue, superciliaries 6 or 5 (37%); circum-orbital scale rows between supraoculars and frontoparietal 2 or 1 (20%).

**DESCRIPTION.**—**Head:** Frontal once or twice transversely divided, rarely entire; prefrontals in contact or separated by a single scale, never separated by anterior projection of frontal; frontoparietals separated by 1–3 small scales, never separated by posterior projection of frontal; circumorbitals 16–21 (aver. 18.2); 2 occasionally 1 (20%) circumorbital scale rows between supraoculars and frontoparietal; 2 occasionally 3 (10%) circumorbital scale rows between supraoculars and parietal; 1 occasionally 2 (10%) circumorbital row between supraoculars and frontal; 4 enlarged supraoculars, occasionally 5 (20%) rarely 6 (7%); 2 occasionally 1 (14%) small scale rows between enlarged supraoculars and fourth superciliary; superciliaries 5 (37%) or 6 (63%); 3 frontonasals in single row never subdivided; 2 inter-nasal scale rows, rarely 3 (3%); 1 subnasal; 1 postrostral scale row, occasionally 2 (30%); 2 loreals, occasionally 3 (20%); 3–4 scales in a straight line between posterior canthal and supralabials; 10 right labials or 9 (26%); orbital papillae 12–14 (aver. 13.0) on lower eyelid; auricular lobules of one small scale on either side of 2 (2–4) large scales, length of largest scale equal 1.5–2 times width, 1–3 times length of smaller lobules, total complement generally 4, rarely 5 or 6; 2–4, usually 3, occipital rows; 14–20 circuminter-parietals (aver. 17.7). **Body:** Dorsals 95–108 (aver. 101.5); non-keeled dorsals 17–41 (aver. 31.8); dorsals at midbody carinate, slightly to not imbricate, mucronate not spiny; dorsals at tail base carinate, imbricate, weakly spinose; gulars 30–38 (aver. 33.5), smooth; gular fold scales 15–20 (aver. 16.7), not greatly enlarged; ventrals 64–72 (aver. 66.8), smooth; interfemorals 12–15 (aver. 13.4); total femoral pores 28–36 (aver. 30.6); digital lamellae on fourth hind toe 25–30 (aver. 27.3); maximum lamellar spurs average 5.9; postanals enlarged in males; interpostanals 2–3 (aver. 2.5). **Ratios:** RDSV average 2.11; RNKD average .31; RSV average 1.39; RGS average 2.12; RLMTO average 3.01. **Size and Proportions:** Maximum snout-vent length 55 mm in males, 50 mm in females; RGS average .33; RFMSV average .22; RTBSV average .26; RFTSV average .33; RTOFT average .57. **Color:** Dorsal color pattern uniform green, blue flecks in males; venter dark blue; gular dark blue; axillary spot prominent, darker blue than venter.

**VARIATION.**—**Sexual:** Characters significantly different between the sexes at the 0.01 level (t test) included total femoral pores, number of digital lamellae on fourth toe, RTBSV, RDSV, RSV, and RGS. No sexual dimorphism in color except blue flecks noted above; females slightly smaller than males.

**DISTRIBUTION.**—San Pedro Nolasco Island, Gulf of California, Sonora (Fig. 5).

**HABITAT.**— *Uta nolascensis* is abundant on the rocky slopes of Isla San Pedro Nolasco where it basks on rocks along the ridges or in the arroyos and is extremely wary, seeking shelter under huge rocks when alarmed. It is not found on the rocky beach or cliffs overlooking the beach.

**MATERIAL EXAMINED.**—CAS 50508 (type): UMMZ 128905 (40); ASC 2097–2098.

*Uta palmeri* Stejneger

*Uta palmeri* Stejneger, 1890, North American Fauna, vol. 3, p. 106.  
Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 221–223.

**TYPE.**—USNM 16002; Edward Palmer, collector.

**TYPE LOCALITY.**—Isla San Pedro Martir, Sonora, Gulf of California.

**DIAGNOSIS.**—Ventrals 75–86 (aver. 79.9); gulars 36–45 (aver. 40.8) femoral pores 30–37 (aver. 33.6); interfemorals 15–20 (aver. 17.3); body size large, maximum 80 mm in males.

**DESCRIPTION.**—**Head:** Frontal once divided, rarely entire (7%); prefrontals in contact or rarely separated by 1 or 2 small scales, never separated by anterior apex of frontal; frontoparietals in contact or rarely separated by one scale, never separated by posterior apex of frontal; circumorbitals 16–22 (aver. 19.5); 1 circumorbital row between supraocular and frontoparietal, rarely 3 (3%); 1 circumorbital row between supraoculars and frontal; 2 circumorbital rows, rarely 3 (3%) between supraocular and parietal; 4 enlarged supraoculars, occasionally 5 (13%); 3 scale rows between supraoculars and fourth superciliary, occasionally 2 (14%); 5 superciliaries, rarely 6 (6%); 3 frontonasals in single row, lateral ones occasionally subdivided diagonally; 2 internasal scale rows, occasionally 3 (16%); 1 subnasal; 1 postrostral scale row; 1–3 loreals (aver. 1.8); 2–4 scales (aver. 3.2) in a line between posterior canthal and supralabial; 9–12 right labials (aver. 10.6); 15–18 orbital papillae (aver. 16.1) on lower eyelid; 1 small auricular lobule on either side of 2–3 large auricular lobules or 1 small one ventral to 3–4 large lobules, largest lobe 2–4 times smallest, 2–3 times longer than wide; 2–3 (aver. 2.5) occipital scale rows; 12–18 (aver. 15.4) circuminterparietals. **Body:** Dorsals 103–121 (aver. 108.5), not imbricate, intervening granules prominent, weakly to not carinate, rarely mucronate and not spinose; non-keeled dorsals 38–60 (aver. 47.0); dorsals at tail base carinate, weakly mucronate to weakly imbricate; gulars 36–45 (aver. 40.8); gular fold scales 17–25 (aver. 20.0); ventrals 75–86 (aver. 79.9); interfemorals 15–20 (aver. 17.3); total femoral pores 30–37 (aver. 33.6); digital lamellae on fourth toe 25–30 (aver. 26.8); maximum lamellar spurs 6–8; interpostanals in males 2–3 (aver. 2.6). **Ratios:** RDSV average 1.82; RNKD average .43; RVSV average 1.34; RGSG average 2.06; RLMT0 average 2.63. **Size and Proportions:** Maximum snout-vent length 80 mm in males, 67 mm in females; RSGSV average .33; RFMSV average .22; RTBSV average .25; RFTSV

average .32; RTOFT average .53. **Color in alcohol:** Dorsum light gray with uniformly spaced small light spots, males with blue flecks; no sexual dimorphism in color pattern; venter light, dark or black coloration increasing from pectoral region to gular, gular region black; axillary spot black.

**VARIATION.—Sexual:** Characters differing between sexes at the .01 level of significance include number of interfemorals, number of gulars, number of large auricular lobules, number digital lamellae on fourth toe, number right labials, RFMSV, RTOFT, RDSV, RVSV, RGSG, and RLMT0.

**DISTRIBUTION.—***Uta palmeri* occurs at high densities along the boulder beaches of Isla San Pedro Martir and may feed extensively on marine isopods and other arthropods of the intertidal zone. It is found commonly on the cliffs behind the beach and also occurs on the plateau above.

**MATERIAL EXAMINED.—**USNM 16002 (type); USNM 16003–14 (paratypes); UMMZ 127198 (14), 127200 (67); TTC 3542 (2), 3543 (2).

#### *Uta squamata* Dickerson

*Uta squamata* Dickerson, 1919, Bull. Amer. Mus. Nat. Hist., vol. 41, p. 471; Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 249–251; Schmidt, 1922, Bull. Amer. Mus. Nat. Hist., vol. 46, p. 656; Smith and Taylor, 1950, Bull. U.S. Nat. Mus., vol. 199, p. 149.

**TYPE.—**USNM 64259, C. H. Townsend, collector.

**TYPE LOCALITY.—**Santa Catalina Island, Gulf of California.

**DIAGNOSIS.—**Prefrontals rarely in contact, separated by an anterior projection of the frontal; dorsals fewer than 85; non-keeled dorsals 10 or fewer; dorsals strongly keeled, imbricate and mucronate to spinose.

**DESCRIPTION.—Head:** Frontal divided once transversely, rarely twice divided or entire; prefrontals rarely in contact, separated by anterior frontal apex; frontoparietals usually separated by posterior frontal apex, occasionally separated by single scale or rarely in contact; circumorbitals 15–22 (aver. 18.7); circumorbital scale rows between frontoparietal and supraocular usually 1 (94%), rarely 0 (3%) or 2 (3%); circumorbital scale rows between parietal and supraocular usually 2 (83%), rarely 1; circumorbital scale rows between frontal and supraocular usually 1 (90%), rarely 0; 4 or 5 (13%) enlarged supraoculars; number of scales between enlarged supraoculars and fourth superciliary, 2 (77%) or 3; superciliaries 5, rarely 6 (6%); frontonasals 3; internasals in 2 rows; 1 subnasal; postrostral scale rows one, rarely 2 (3%); loreals 1 or 2, rarely 3 or 4 (aver. 1.3); scales between posterior canthal and labial usually 3 (aver. 2.9), rarely 2 or 4; 8–10 right labials (aver. 8.8); orbital papillae 14–16 (aver. 15.1); large auricular lobules 1–3 (aver. 2.7); total auricular lobules 2–5 (aver. 3.4); 2 occipital scale rows, occasionally 1 (17%) or 3 (7%); 13–19 circuminterparietals (aver. 16.0). **Body:** Dorsal scales 70–84 (aver. 77.9), large, rugose, strongly carinate and

mucronate; non-keeled dorsals 2–10 (aver. 5.2), basal caudals carinate and spinose; gulars 26–32 (aver. 28.6); gular fold scales 13–16 (aver. 14.0); ventrals 58–67 (aver. 61.9); interfemorals 10–16 (aver. 13.4); total femoral pores 25–33 (aver. 28.5); digital lamellae on fourth toe 25–30 (aver. 27.3); maximum lamellar spurs 5–6 (aver. 5.2); interpostanals in males 1–2 (aver. 1.8). **Ratios:** RDSV average 1.61; RNKD average .07; RSV average 1.28; RGSG average 1.77; RLMT0 average 2.92. **Size and Proportions:** Maximum snout-vent length 57 mm in males, 52 mm in females; RSGSV average .34; RFMSV average .22; RTBSV average .25; RFTSV average .33; RTOFT average .59. **Color:** Dorsum brown, profusely light spotted blue to green at middorsum to yellow and orange on sides; dorsolateral light stripe present just behind eye to above insertion of foreleg or slightly beyond; males with bright green tails and blue flecks; venter white in females, light blue in males; gular faint blue in females, light blue in males, with lighter spots along labial margins; axillary blotch variable, dark in males to very light in females.

**VARIATION.—Sexual:** Characters which differ significantly between the sexes at the 0.01 confidence level (t test) include RFMSV, RTBSV, RFTSV, RTOFT, ROSV, RSV, RGSG, RLMT0.

**DISTRIBUTION.—**Santa Catalina Island, Gulf of California (Fig. 5).

**HABITAT.—**Most abundant on hillsides in association with cacti or shrubs and in arroyos between hills where it is seldom found far from dense cactus thickets or other vegetation; not notably saxicolous nor associated with beaches.

**MATERIAL EXAMINED.—**USNM 64259 (type); UMMZ 128892 (20), 128906 (49) (Santa Catalina Island, Gulf of California).

*Uta stansburiana elegans* (Yarrow)

*Uta elegans* Yarrow, 1882, Proc. U.S. Nat. Mus., vol. 5, p. 442; Schmidt, 1922, Bull. Amer. Mus. Nat. Hist., vol. 46, pp. 656–657..

*Uta stansburiana elegans* Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 240–247 (part); Smith and Taylor, 1950, Bull. U.S. Nat. Mus., vol. 199, pp. 148–149; Zweifel, 1958, Amer. Mus. Nov., no. 1895, pp. 7–9.

*Uta concinna* Dickerson, 1919, Bull. Amer. Mus. Nat. Hist., vol. 41, p. 470; type locality, Cedros Island, Baja California, USNM 64257, C. H. Townsend, collector.

*Uta mannophorus* Dickerson, 1919, Bull. Amer. Mus. Nat. Hist., vol. 41, pp. 470–474; type locality, Carmen Island, Gulf of California; USNM 64260, C. H. Townsend, collector; Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 252–254.

*Uta stansburiana hesperis* Richardson, 1915, Proc. U.S. Nat. Mus., vol. 48, pp. 415–418; type locality, Arroyo Seco Cañon, near Pasadena, Los Angeles County, California, UCMVZ 892, J. Grinnell, collector.

*Uta parva* Dickerson, 1919, Bull. Amer. Mus. Nat. Hist., vol. 41, p.

471, type locality, San Bartolome Bay, Baja California, USNM 64258, C. H. Townsend, collector.

*Uta martinensis* Van Denburgh, 1905, Proc. Calif. Acad. Sci., vol. 4, pp. 18–19; type locality, San Martin Island, Baja California, CAS 4698, R. H. Beck, collector.

*Uta stansburiana martinensis* Zweifel, 1958, Amer. Mus. Nov., no. 1895, pp. 9–10.

TYPE.—USNM 12666, L. Belding, collector.

TYPE LOCALITY.—La Paz, Baja California.

DIAGNOSIS.—Dorsolateral light stripes conspicuous at least just behind head; interfemorals not reduced in number, usually more than 8; maximum snout-vent length in adult males 58 mm.

DESCRIPTION.<sup>5</sup>—**Head:** Frontal usually divided transversely once or twice, rarely entire or divided three times; prefrontals in contact or separated by a single scale or rarely by anterior frontal apex (9%); frontoparietals in contact or separated by 1–2 scales or occasionally separated by posterior frontal apex (20%); circumorbitals 15–25 (aver. 20.0); circumorbital scale rows 1 or 2 (20%) between supraoculars and frontoparietal, 2 rarely 1 (1%) or 3 (1%) between supraocular and parietal, 1 or 0 (3%) between supraocular and frontal; 4 or 5 (58%) enlarged supraoculars; 2–4 (aver. 2.7) scale rows between supraoculars and fourth superciliary; 5 superciliaries; frontonasals usually 3, median scale rarely divided producing 4, lateral ones rarely divided producing 5; 2 or 3 (5%) internasal scale rows; 1 subnasal; postrostral scale rows 1 or 2 (17%); loreals 1–6 (aver. 2.8); 3–5 scales between the postcanthal and labial (aver. 3.7); right labials 9–11 (aver. 9.4); 12–16 orbital papillae (aver. 14.1); 2–4 large auricular lobules (aver. 2.8); total auricular lobules 3–6 (aver. 4.4); 1 or 2 (88%) occipital scale rows; 13–20 circuminterparietals (aver. 16.4). **Body:** Dorsals 82–102 (aver. 91.3); non-keeled dorsals 2–19 (aver. 13.0); dorsals keeled, imbricate, mucronate to spinose at tail base; gulars 28–37 (aver. 30.4); gular fold scales 13–20 (aver. 16.8); ventrals 56–67 (aver. 61.8); interfemorals 6–15 (aver. 10.3); total femoral pores 24–32 (aver. 28.1); digital lamellae on fourth toe 23–30 (aver. 25.8); maximum lamellar spurs average 4.9; 1–3 interpostanals (aver. 1.9). **Ratios:** RDSV average 2.04; RNKD average 1.41; RVSV average 1.38; RGSG average 1.95; RLMT0 average 3.02. **Size and Proportions:** Maximum snout-vent length 58 mm in males, 53 mm in females in continental populations; RSGSV average .35; RFMSV average .22; RTBSV average .26; RFTSV average .30; RTOFT average .64. **Color:** Dorsal pattern variable but continental populations generally similar to *U. stansburiana stejnegeri*; dorsolateral light lines present at least in neck region but may be incorporated into pattern types similar to *U. s. stejnegeri* on the back i.e., striped, barbed, chevron (Fig. 4). An additional pattern type (banded) peculiar to

<sup>5</sup> Description based on topotypes, La Paz, Baja California.



the Tortuga Island population is considered a modification of the chevron type. In zones of intergradation with *stansburiana stansburiana* or *stansburiana taylori*, paired dorsal dark blotches form a row on each side of the midline. These dark blotches are not prominent and do not alter the pattern types which we have recognized. Similar dark blotches are prominent in certain *U. s. taylori* populations and not uncommon in *U. s. stejnegeri* populations. Insular populations of *U. s. elegans* are extremely variable in dorsal color pattern but the dorsolateral light stripe is retained at least in the neck region. Venter light; gular region light to dark blue; axillary blotch prominent or lost on the islands of Carmen, Danzante, Coronados, lost or greatly reduced on Isla Magdalena and in certain southern Baja California populations; dark blotch prominent on each shoulder, two additional blotches between shoulder blotches on either side of middorsal line forming a series of four dark blotches across the neck. This ring of neck blotches is of common occurrence in populations of California and Baja California (particularly along the Pacific coast) and is very prominent in certain insular populations (e.g., Carmen Island). The occurrence of a uniform pattern type in a single individual from Cedros Island (CAS 79907) is possibly homologous to the supposed "mutant" form found in *U. stansburiana stejnegeri* (Ballinger and McKinney, 1967).

**VARIATION.—Sexual:** Dorsolateral light stripes are more prominent in females. Males have conspicuous light blotches and blue flecks that obscure the dorsal pattern type. Males are larger than females. The numbers of characters which differ between the sexes at the 0.01 level (t test) are 0 (San Benito), 5 (Kern), 9 (San Diego), 6 (Pt. Penasco), 1 (Guaymas), 4 (San Felipe), 3 (Ensenada), 4 (San Ignacio), 5 (La Paz), 1 (Riverside), 6 (Yuma), 5 (San Clemente), 7 (San Martin), 7 (Todos Santos), 6 (Natividad), 3 (Cedros), 5 (Santa Margarita), 6 (Magdalena), 8 (Espiritu Santo), 5 (Partida Sur), 8 (San Francisco), 5 (San Jose), 5 (Monserate), 5 (Danzante), 7 (Carmen), 5 (Coronados), 4 (San Ildefonso), 8 (Tortuga), and 3 (San Marcos). **Geographical:** Significant differences between continental populations of *Uta stansburiana elegans* occur in the number of dorsal scales (Fig. 6) which decrease in number from north to south and from west to east. There is little difference in the color pattern types, but considerable geographical variation in general coloration (e.g., blotching and melanism) with lighter colors predominating in desert regions and darker colors in coastal areas. It is to populations displaying this type of color variation that many taxonomic names have been applied. We do not consider such variations as local adaptations significant enough to warrant taxonomic recognition.

**DISTRIBUTION.—**All of Baja California and adjacent major islands of Magdalena, Santa Margarita, Natividad, Cedros, Todos Santos, San Martin, Espiritu Santo, Partida Sur, San Francisco, San Jose, Monserate, Carmen, Coronados, San Ildefonso, San Marcos, and additional minor islets; north in California to Contra Costa County and adjacent islands of San Clemente, Santa Catalina, Ana Capa, Santa Cruz; east to Santa Cruz County, Arizona

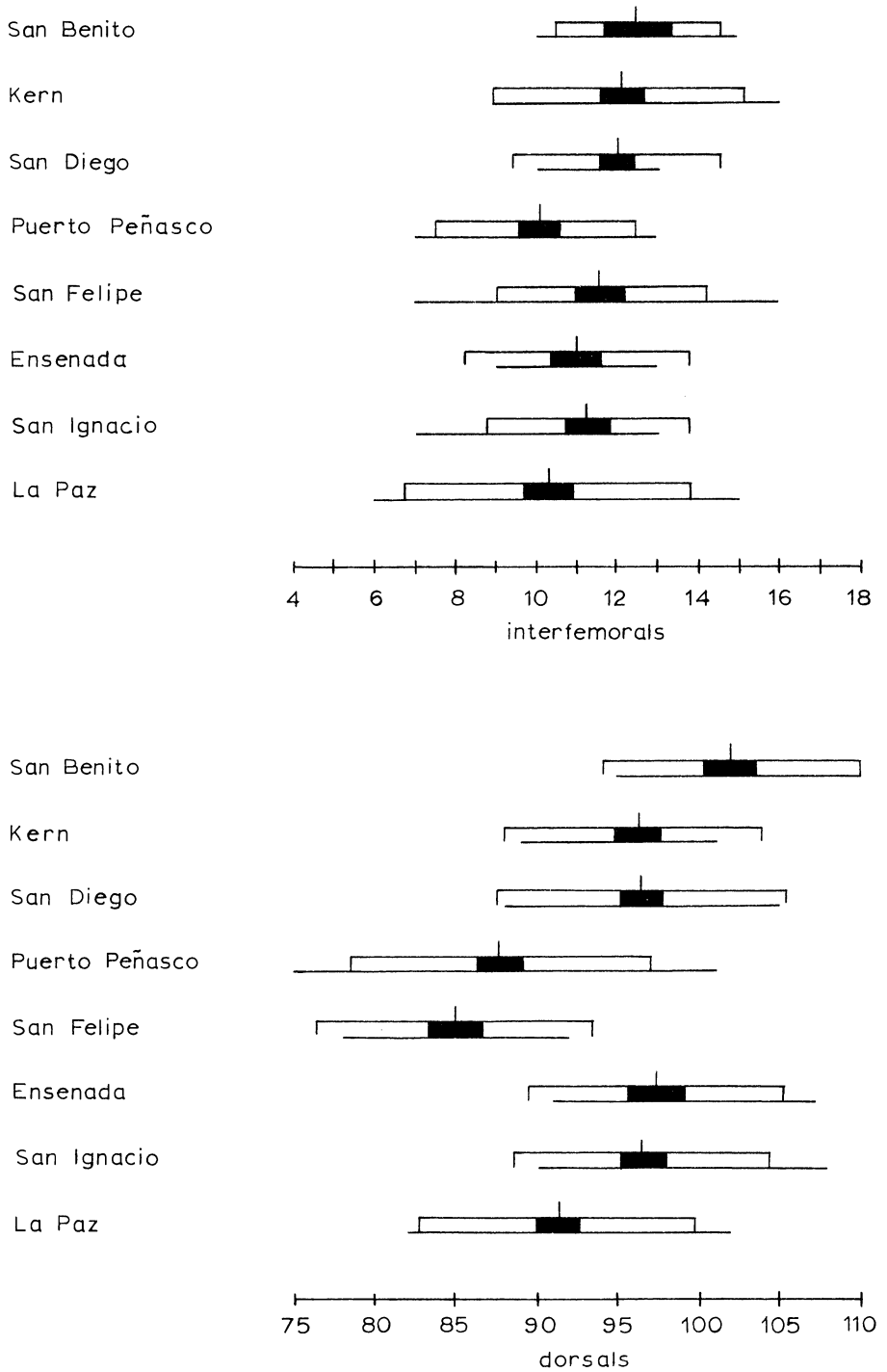


FIG. 6. Geographical variation in dorsal scales and interfenorals in *Uta stansburiana elegans*. Baseline=range, open bar=2 x standard deviation, solid bar=2 x standard error, vertical line=mean.

and south at least to Guaymas, Sonora. Intergrades with *s. stansburiana* in northwestern Arizona, southern Nevada, and southwestern Utah and in lowland river valleys in eastern Nevada and central to western Utah north as far as Tooele County (Fig. 5).

**HABITAT.**—*Uta stansburiana elegans* occurs in a variety of habitats from desert sands to rocky hillsides. Other authors have discussed various aspects of the ecology of *U. s. elegans* (Wood, 1933; Von Bloeker, 1942; Smith, 1946; and Shaw, 1950).

**MATERIAL EXAMINED.**—USNM 12666 (10), 12668 (4 cotypes); USNM 64257 (type *concinna*), AMNH 5399–5406 (paratypes *concinna*); USNM 64260 (type *mannophorus*), AMNH 5440–46 (paratypes *mannophorus*); UCMVZ 892 (type *hesperis*), SU 1255–56, 1260, 1310–14, 1316–19, 1321–36 (paratypes *hesperis*); USNM 69258 (type *parva*), AMNH 5427, 5429–32 (paratypes *parva*); CAS 4698 (type *martinensis*); UMMZ 128893 (26), 128910 (76) (Carmen Island); UCMVZ 9685–90, 13849–53, 45294–304, 51075, CAS 79771–910 (Cedros Island); SDNHM 6740–46, 30065–76, 51523–56 (Coronados Island); CAS 52151–61, 95166–68, SDNHM 6737–39, 44568–69, 44571–74, 51495–522 (Danzante Island); SDNHM 3960–61, 7237–41, 31041–50, 44563, 51397–428, SU 14158–68, 17169–70 (Espiritu Santo Island); CAS 55998–56030, SDNHM 6696–97, 30097–106, 31095–96, 10250, 10269, (Magdalena Island); CAS 52199–238 (Monserrate Island); CAS 56387–426, SDNHM 7557, 17436 (Natividad Island); SDNHM 7242–43, 6715, 51730, UMMZ 128912 (43) (Partida Sur Island); LACM 5097, 5100, 5102, 5104, 5106, 5108, 5111, 5115–16, 5119, 5121, 5126–28, 5133, 5138–39, 5141, 5144, 5150, 5152–56, 5158–76, 5178, 5180–81, 5183, 5248, 5724, 5727 (San Clemente Island); UMMZ 128891 (57) (San Francisco Island); SDNHM 6675–92, 3951–55, 51557–93, SU 14227–39, 17188 (San Ildefonso Island); UMMZ 128887 (13), 128911 (30) (San Jose Island); SU 14240–43, UMMZ 128915 (35) (San Marcos Island); SDNHM 11613–19, 17437–45, 31061, 52964, UCMVZ 9671–84, 51043–45, 59688–99, 59701–02 (San Martin Island); SDNHM 6669–73, 28568, 30091–96, CAS 56076, 56106–27, UCMVZ 13500–01 (Santa Margarita Island); CAS 56796–835, UCMVZ 51180–84 (South Todos Santos Island); ASC 2099, UMMZ 128895 (56) (Tortuga Island); UCMVZ 1768–98 (Arizona, Yuma Co.); CAS 8591, 8555–57, 8559–60, 8603–16, 8642–44, 57572 (Baja California, Ensenada); CAS 46685–99, 90600, 90962, 91009, UCM 29418–23, 29426–31, UCMVZ 11560–62, 11689, 73449–66 (Baja California, La Paz); SDNHM 19025–33, 37797–98, 37801–03, 37805, 38125–26, 38141–52, UCMVZ 9533–40, 9542–43, 50133–40, 68529 (Baja California, San Felipe); SDNHM 3975–87, UCMVZ 13300–50 (Baja California, San Ignacio); UCMVZ 74795–811, 76045–73 (California, Kern Co.); UMMZ 128894 (45) (California, Riverside Co.); UCMVZ 21145–68, 21311–13, 51303–04, 51306–07, UI 4430–31 (California, San Benito Co.); SDNHM 34–35, 123, 919, 11627, 11629, 11706, 11862, 13224–26, 13233, 13303, 13305–07, 13318, 13504, 13507, 13512, 14060, 14062–65, 14067, 14071, 14074, 14076,

14078-81, 14083, 14096, 14099, 14114, 14122, 14126, 15567, 16333-35, 16338, 18649, 18682, 18691, 22484, 25309-10, 32544, 39239, 39999, 40000, 41147 (California, San Diego Co.); SDNHM 4036, UMMZ 128878 (25), 128923 (26) (Guaymas, Sonora); UMMZ 128888 (52) (Puerto Penãasco, Sonora).

*Uta stansburiana stansburiana* Baird and Girard

*Uta stansburiana* Baird and Girard, 1852, in Stansbury, Exploration and survey of the Valley of the Great Salt Lake of Utah . . . , 1852, pp. 344-345.

*Uta stansburiana stansburiana* Van Denburgh, 1922, Proc. Calif. Acad. Sci., vol. 1, pp. 227-233; Smith, 1946, pp. 277-281.

*Uta stansburiana nevadensis* Ruthven, 1913, Proc. Biol. Soc. Wash., vol. 26, pp. 27-30; type locality, Cortez Range, west of Carlin, Nevada, UMMZ 43848, F. Gaige, collector.

TYPE.—USNM 2753 (4 cotypes), Captain H. Stansbury, collector.

TYPE LOCALITY.—Utah, Valley of the Great Salt Lake.

DIAGNOSIS.—Dorsal color pattern never composed of dorsolateral light stripes, females with dark spots, males with light spots and blue flecks; dorsal scales weakly keeled, small, not conspicuously imbricate; non-keeled dorsals usually more than 30, as many as 70.

DESCRIPTION.<sup>6</sup>—**Head:** Frontal once or twice divided transversely, rarely divided three times; prefrontals in contact or separated by a single scale or separated by anterior frontal apex (10%); frontoparietals in contact or separated by 1-3 scales or separated by posterior projection of frontal (7%); circumorbitals 17-21 (aver. 18.8); circumorbital scale rows 1 between supraocular and frontoparietals, 2 between supraocular and parietal, 1 between supraocular and frontal; 4 enlarged supraoculars; 3, rarely 4 (6%) scale rows between enlarged supraoculars and fourth superciliary; 5, rarely 4 (4%) superciliaries; 3, rarely 4 (3%) frontonasals in single row; 2, rarely 3 (3%) rows of internasals; 1 subnasal; postrostral scale rows 2 (56%) or 1 (44%); loreals 1-3 (aver. 1.6); 3 scales between posterior canthal and labial, occasionally 4 (26%); right labials 9-11 (aver. 9.8); 13-16 orbital papillae (aver. 14.3); large auricular lobules 3-5 (aver. 3.7); total auricular lobules 5-7 (aver. 5.1); 2, occasionally 1 (20%), occipital scale rows; 15-22 circuminterparietals (aver. 17.6). **Body:** Dorsals 102-117 (aver. 107.8); non-keeled dorsals 23-73 (aver. 42.3); dorsals weakly keeled, not conspicuously imbricate or mucronate to weakly imbricate and mucronate at tail base; gulars 30-38 (aver. 32.1); gular fold scales 16-22 (aver. 18.6); ventrals 64-74 (aver. 68.2); interfemorals 11-16 (aver. 13.4); total femoral pores 25-34 (aver. 30.1); digital lamellae on fourth toe 24-28 (aver. 26.5); maximum lamellar spurs average 4.9; 2, rarely 3 (5%) interpostanals in males. **Ratios:** RDSV average 2.39; RNKD average .39; RVSV average 1.51; RGSG average 2.16; RLMTO

<sup>6</sup> Description based on series from Montezuma County, Colorado.

average 3.38. **Size and Proportions:** Maximum snout-vent length 54 mm in males, 53 mm in females; RSGSV average .33; RFMSV average .21; RTBSV average .25; RFSV average .28; RTOFT average .63. **Color:** Dorsal color pattern in males composed of a profuse scattering of light spots over darker brown background, with blue flecks; females with dark spots over lighter background with some scattered light spots; venter white to pale blue or grey; gular region light blue, darker in males with large light (white to yellow) spots along labial margin.

**VARIATION.—Sexual:** The number of characters which differ significantly between the sexes at the 0.01 confidence level (t test) include 9 (Ada Co., Idaho), 5 (Elko Co., Nevada), 3 (Rio Blanco Co., Colorado), 5 (Mesa Co., Colorado), 7 (Montezuma Co., Colorado), and 6 (San Juan Co., New Mexico). **Geographical:** *Uta s. stansburiana* is extremely uniform in meristic characters. Of the six major populations considered, only two significant differences were found. Elko County specimens differed from those from San Juan County in the number of postrostral scale rows at the 94% level (coefficient of difference). Mesa County utas differed from Montezuma County utas in the number of orbital papillae at the 90% level. For comparative purposes the variation in the number of interfemorals and dorsals in *Uta s. stansburiana* is presented in Figure 7.

**DISTRIBUTION.—***Uta s. stansburiana* occurs from southwestern Washington south through east and central Oregon, western Idaho, western Colorado, northwestern New Mexico, northeastern Arizona, Nevada and adjacent eastern California. Intergrades with *U. s. elegans* in northwestern Arizona, southern Nevada, southwestern Utah, and lowland river valleys in eastern Nevada and central to western Utah (Fig. 5).

**HABITAT.—**The ecology of *U. s. stansburiana* in Colorado has been considered by Tinkle (1967). *Uta s. stansburiana* is found in rocky habitats more than other *stansburiana* sub-species, and at higher elevations.

**TAXONOMIC COMMENT.—**The four syntypes upon which the name *Uta stansburiana* is based come from an area of intergradation between *U. s. elegans* and *U. s. stansburiana* and three of them are distinctly striped like *elegans*. The name *U. s. stansburiana* has been associated with predominantly unicolored populations that occur in eastern Utah, western Colorado and northern New Mexico. We have not designated a lectotype from among the syntypes because Charles O. McKinney and Wilmer W. Tanner are completing a more detailed study of the western *elegans* populations and will deal with the nomenclatural problem raised here.†

† In papers appearing after this went to press, Pack and Tanner, 1970 (Great Basin Nat. 30:71–90) applied the new name of *U. stansburiana uniformis* to the forms in eastern Utah and western Colorado, and McKinney, 1971 (Copeia 1971:596–613) suggested that *U. stansburiana nevadensis* be resurrected to apply to the populations in Nevada, Oregon, Washington, and Idaho.

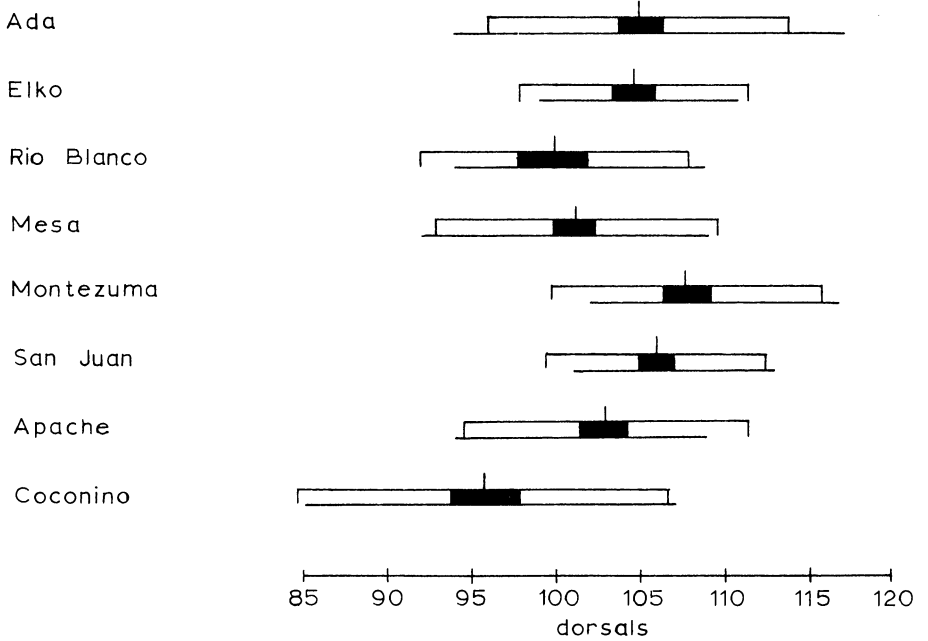
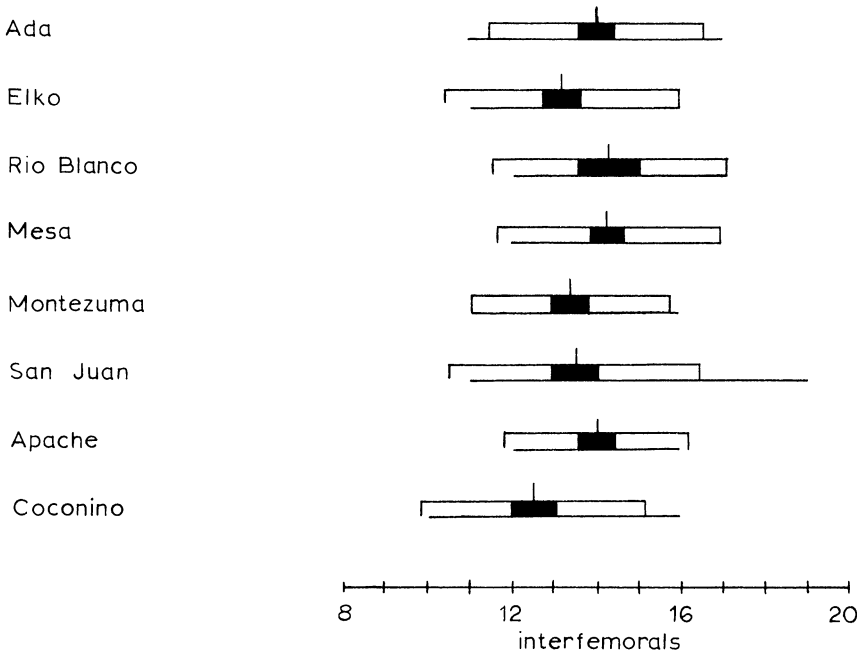


FIG. 7. Geographical variation in interfenorals and dorsal scales in *Uta stansburiana stansburiana*. Explanation as in Figure 6.

MATERIAL EXAMINED.—USNM 2753 (4 syntypes); UCMVZ 76436-64 (Arizona, Apache Co.); SDNHM 12936-76, 12978-90 (Arizona, Coconino Co.); CAS 65250-96, 65672-75 (California, Inyo Co.); TTC 3432 (53) (Colorado, Mesa Co.); UCM 11544-77 (Colorado, Montezuma Co.); UCM 4083-98 (Colorado, Rio Blanco Co.); BYU 625-26, 1707-08, 1710, 1712-48, 1750-52, 1758-62 (Idaho, Ada Co.); UMMZ 43799-812, 43814, 43816-20, 43823-29, 43831-39, 43841-46 (paratypes *nevadensis*; Nevada, Elko Co.); UNMMSB 2951, 2954-57, 2959-61, 2963, 3003, 3005-06, 3027, 3169, 3171-74, 3177-80, 3213-16, 3227, 3357-60, 3362-63, 3365, 3369-72, 6673-74 (New Mexico, San Juan Co.); AMNH 47007-08, BYU 3957, 3961-66, 13029-33 (Utah, Duchesne Co.). Intergrade populations (*s. stansburiana* x *s. elegans*): UMMZ 128590 (115) (Nevada, Nye Co.); AMNH 22882-92, CAS 38047-75 (Utah, Beaver Co.); UI 2041-55 (Utah, Millard Co.); AMNH 14438, 14440-54, 14456-72, 14474, 14476, 14480-81, 14489 (Utah, Tooele Co.); AMNH 22893-904, TNHC 28061-65, UCM 13867-77, UI 27766-79 (Utah, Washington Co.).

*Uta stansburiana stejnegeri* Schmidt

*Uta stansburiana stejnegeri* Schmidt, 1921, Amer. Mus. Nov., no. 15, pp. 1-2; Schmidt, 1922, Bull. Amer. Mus. Nat. Hist., vol. 46, pp. 654-655; Smith, 1946, Handbook of Lizards, pp. 283-286; Smith and Taylor, 1950, Bull. U.S. Nat. Mus., vol. 199, p. 150.

*Uta stansburiana elegans* Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 240-247 (part).

TYPE.—AMNH 348, A. G. Ruthven, collector.

TYPE LOCALITY.—Mouth of Dry Cañon, Alamogordo, Otero County, New Mexico.

DIAGNOSIS.—Dorsolateral light stripes conspicuous at least just behind head; interfemoral scales greatly reduced in number (usually 4-8). Maximum snout-vent length in adult males 58 mm.

DESCRIPTION.<sup>7</sup>—**Head:** Frontal once or twice divided; prefrontals in contact or separated by a single scale or separated by anterior frontal apex (7%); frontoparietals in contact or separated by 1 or 2 scales or separated by posterior projection of frontal (4%); circumorbitals 16-22 (aver. 18.2); circumorbital scale rows between supraocular and frontoparietals 1 or 2 (16%), between supraocular and parietal 2 or 3 (16%), between supraocular and frontal 1; 4-6 (aver. 4.5) enlarged supraoculars; 2 or 3 (58%) scale rows between supraocular and fourth superciliary; superciliaries 4-6 (aver. 4.9); 3 frontonasals; 2 rows of internasals; 1 subnasal; postrostral scale rows 1 or 2 (10%); 1-5 loreals (aver. 3.2); 2-4 scales between postcanthal and labial (aver. 3.4); 3-10 right labials (aver. 8.7); 12-15 orbital papillae (aver. 13.3); 2-3 large auricular lobules (aver. 2.6); 4-5 total auricular lobules (aver. 4.1);

<sup>7</sup> Description based on topotypes from Alamogordo, Otero Co., New Mexico.

2-3 occipital rows (aver. 2.2); 13-20 circuminterparietals (aver. 15.9). **Body:** Dorsals 77-93 (aver. 85.1); 3-19 non-keeled dorsals (aver. 10.6); dorsals keeled to strongly keeled, imbricate, mucronate to spinose at tail base; gulars 23-30 (aver. 27.2); gular fold scales 14-19 (aver. 16.4); ventrals 57-67 (aver. 62.4); interfemorals 5-8 (aver. 6.6); total femoral pores 28-34 (aver. 30.1); digital lamellae on fourth toe 23-27 (aver. 25.4); maximum lamellar spurs average 5.4; 1-3 interpostanals in males (aver. 1.9). **Ratios:** RDSV average 1.86; RNKD average .12; RSV average 1.37; RGSG average 1.79; RLMT0 average 3.13. **Size and Proportions:** Maximum snout-vent length 58 mm in males, 52 mm in females; RSGSV average .33; RFMSV average .21; RTBSV average .24; RFTSV average .28; RTOFT average .64. **Color:** Dorsal pattern composed of dorsolateral light lines beginning posterior to the eye and continuing past the shoulder, these lines may vary from chevrons to barbed lines to continuous straight lines (Ballinger and McKinney, 1967). The dorsolateral light markings have dark brown borders, females with some sparse light spots on middorsum, males profusely light (white, yellow, and orange) spotted and blue flecked. The blue flecks increase posteriorly so that the tail may be predominantly blue. Non-patterned morph of rare occurrence (Ballinger and McKinney, 1967); venter white, occasionally light blue in pectoral region; gular light to dark blue with white to orange spots along labial borders; dark shoulder blotch rare.

**VARIATION.—Sexual:** Number of characters which differ significantly between the sexes at the 0.01 confidence level (t test) include 6 (Armstrong Co., Texas), 7 (Bernalillo Co., New Mexico), 6 (Chaves Co., New Mexico), 9 (Otero Co., New Mexico), 9 (Winkler Co., Texas), 3 (Hidalgo Co., New Mexico), 4 (San Pedro, Coahuila, Mexico), and 6 (Mapimi, Durango, Mexico). **Geographical:** Geographical variation in the interfemorals and dorsals is presented in Figure 8. The Armstrong Co., Texas, population has a higher percentage of individuals with 2 postrostral scale rows (86%) and differs from Bernalillo Co., New Mexico (6%) at the 91% level (C. D. test) and at the 90% level from Hidalgo Co., New Mexico (7%). This trend to a lower number of postrostral scales from east to west is not universal as 13% of specimens from Winkler Co., Texas, have 2 while 17% of those from El Paso Co., Texas, and 24% from Socorro Co., New Mexico, have 2. The unusually high percentage in the Armstrong population may in part be due to lack of gene flow as a result of its relatively isolated position (Knopf, 1963). Coahuila utas have an increased foot size in relation to snout-vent length and differ significantly from Armstrong at the 90% level, from Bernalillo at the 92% level, and from Hidalgo at the 95% level (C. D. test) in this character.

**DISTRIBUTION.—***Uta s. stejnegeri* occurs from north central New Mexico and northwestern Texas (Carpenter et al., 1961, have reported *Uta s. stejnegeri* in extreme southwestern Oklahoma although it is not common) south to northern Zacatecas and Durango, Mexico. It occurs from western Texas (Howard Co.) west to Cochise Co., Arizona (Fig. 5).



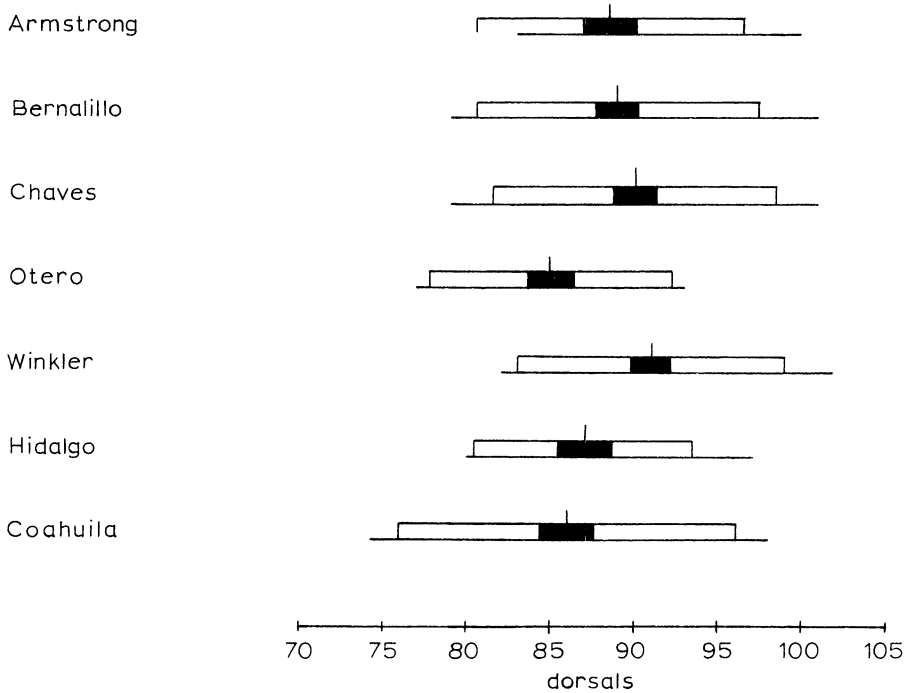
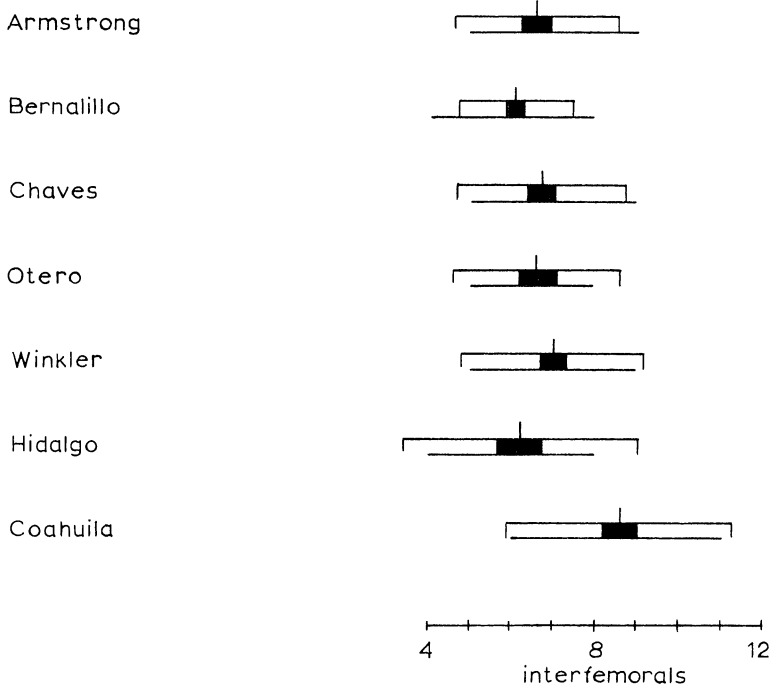


FIG. 8. Geographical variation in interfenemorals and dorsal scales in *Uta stansburiana stejneri*. Explanation as in Figure 6.

HABITAT.—*Uta stansburiana stejnegeri* is found in typical lowland habitat of the Chihuahuan Desert and in sandy ecotonal areas and river valleys which extend northward in the short-grass prairies. Tinkle (1967) has treated the ecology of *Uta s. stejnegeri* in western Texas.

MATERIAL EXAMINED.—AMNH 348 (type); USNM 105892–942 (Coahuila, San Pedro); TTC 3470 (30) (Durango, Mapimi); UNMMSB 1472, 4328–32, 4760, 5073–79, 5163, 5166, 5411–12, 5414, 7398–400, 10254–55, 11031, 11057, 11079, 11272, 11290–94, 11474, 12122–24, 12341–43, 12542, 12558, 12902, 12969–71, 13082, 13084, 12174, 13176 (New Mexico, Bernalillo Co.); UNMMSB 1400, 7209–12, 11085, 12231–32, 12547–51, 12671, 12738–47, 12790–96, 12903–04, 12906, 12972–73, 13001–03, 13320–21, 13323–28, 13330–32 (New Mexico, Chaves Co.); UK 72039–51, 74652–76 (New Mexico, Hidalgo Co.); ASC 1886–87, 1894, UMMZ 128600 (26) (New Mexico, Otero Co.); UNMMSB 1407–08, 1468–69, 1479, 4380, 4858, 5081–82, 7007–11, 7015, 12291–92, 12436, 12543–46, 12619, 12851–52 (New Mexico, Socorro Co.); UMMZ 128897 (29) (Texas, Armstrong Co.); UCM 6448–62, UI 1529, 12779–81, 40394, 6740–42 (Texas, El Paso Co.); UMMZ 128599 (60) (Texas, Winkler Co.).

*Uta stansburiana taylori* Smith

*Uta taylori* Smith, 1935, Univ. Kansas Sci. Bull., vol. 22, pp. 158–166; Smith and Taylor, 1950, Bull. U.S. Nat. Mus., vol. 199, p. 150.

*Uta stansburiana taylori* Lowe and Norris, 1955, Herpetologica, vol. 11, p. 92.

*Uta stansburiana klauberi* Lowe and Norris, 1955, Herpetologica, vol. 11, pp. 91–92, type locality Isla San Esteban, Gulf of California, SDNHM 6642, J. R. Pemberton, collector.

TYPE.—CNHM 100097, E. H. Taylor, collector.

TYPE LOCALITY.—10 miles northwest of Guaymas, Sonora, Mexico.

DIAGNOSIS.—Dorsal pattern never of dorsolateral light stripes; dorsal scales extremely variable in number but always keeled to strongly keeled, imbricate and mucronate; non-keeled dorsals usually fewer than 30; dorsal pattern of light spots in males, light spots or double row of dark middorsal blotches with dorsolateral chevrons in females.

DESCRIPTION.<sup>8</sup>—**Head:** Frontal once divided transversely, rarely entire or twice divided; prefrontals in contact, occasionally separated by a single scale, rarely separated by anterior frontal apex; frontoparietals in contact, occasionally separated by 1–3 small scales or occasionally separated by posterior projection of frontal; circumorbitals 16–25 (aver. 19.1); 1, rarely 2 circumorbital scale rows between frontoparietal and supraocular, 2, rarely 1 or 3 between parietal and supraocular, 1, rarely 2 between frontal and

<sup>8</sup> Description based on topotypes from San Carlos Bay, Sonora, Mexico.

supraocular; 3–5, usually 4, enlarged supraoculars; 2, occasionally 3 scale rows between enlarged supraocular and fourth superciliary; superciliaries 5, rarely 6 (9%); 3 frontonasals; 2 rows of internasals; 1 subnasal; 1 row of postrostrals occasionally 2 (20%); loreals 0–4 (aver. 2.5); 2–5 (aver. 3.4) scales between posterior canthal and labial; 9–12 right labials (aver. 9.6); 12–16 orbital papillae (aver. 13.9); 2–4 large auricular lobules (aver. 2.9); 3–5 total auricular lobules (aver. 4.5); 2 occipital scale rows, rarely 1 or 3; 15–21 (aver. 17.0) circuminterparietals. **Body:** Dorsals 87–115, keeled, imbricate, and mucronate to spinose posteriorly and at tail base; non-keeled dorsals 10–38 (aver. 20.7); gulars 25–34 (aver. 29.4); gular fold scales 17–22 (aver. 18.2); ventrals 55–67 (aver. 61.0); interfemorals 9–16 (aver. 11.8); total femoral pores 25–33 (aver. 29.5); digital lamellae on fourth toe 22–28 (aver. 24.7); maximum lamellar spurs average 4.5; 2–3 interpostanals in males. **Ratios:** RDSV average 2.27; RNKD average .20; RVSV average 1.37; RGSG average 1.91; RLMT0 average 2.96. **Size and Proportions:** Maximum snout-vent length 56 mm in males, 54 mm in females; RSGSV average .35; RFMSV average .22; RTBSV average .26; RFTSV average .30; RTOFT average .64. **Color:** Dorsum light spotted in males, females with paired dark brown blotches on either side of middorsal line with scattered to profuse light spots varying in intensity; venter white; gular region light blue bordered with light yellow to white spots; axillary blotch prominent, dark blue.

**VARIATION.—Sexual:** The number of characters which differ significantly between the sexes at the 0.01 confidence level (t test) include 7 (San Carlos, Sonora, Mexico), 7 (Isla Tiburon), 6 (Isla San Esteban), 8 (Isla Raza), 4 (Isla Angel de la Guarda). **Geographical:** Graphic representation of those characters most divergent between populations of *Uta stansburiana taylori* is presented in Figure 9. In addition the number of large auricular lobules is higher on Partida Norte. The number of ventrals in utas from Raza is higher and differs from Angel de la Guarda utas at the 91% level (C. D. test). The number of digital lamellae of Raza lizards is higher and differs from the mean of San Carlos lizards at the 90% level (C. D. test). Geographical variation in pattern types indicates that Angel de la Guarda, Partida Norte, and San Carlos are most alike with the blotched pattern type predominant in females. San Esteban and Raza lizards are predominantly spotted with larger spots on San Esteban lizards and more spots per unit area on Raza lizards. Tiburon lizards have a pattern type somewhat intermediate between those of San Carlos and those of San Esteban. Increased variability in utas on Tiburon suggests intergradation with *Uta stansburiana elegans* of the Sonora mainland.

**DISTRIBUTION.—***Uta s. taylori* is reported from the vicinity of La Playa, Bahia San Pedro, Bahia Tepoca, El Banuri, and Bahia San Carlos, all in Sonora. Populations on the islands of Tiburon, San Esteban, Raza, Partida Norte, and Angel de la Guarda are referable to *U. s. taylori* (Fig. 5).

**HABITAT.—**In Sonora *U. s. taylori* is found typically in rocky habitats, particularly on low altitude hillsides and along cliffs overlooking the Gulf.

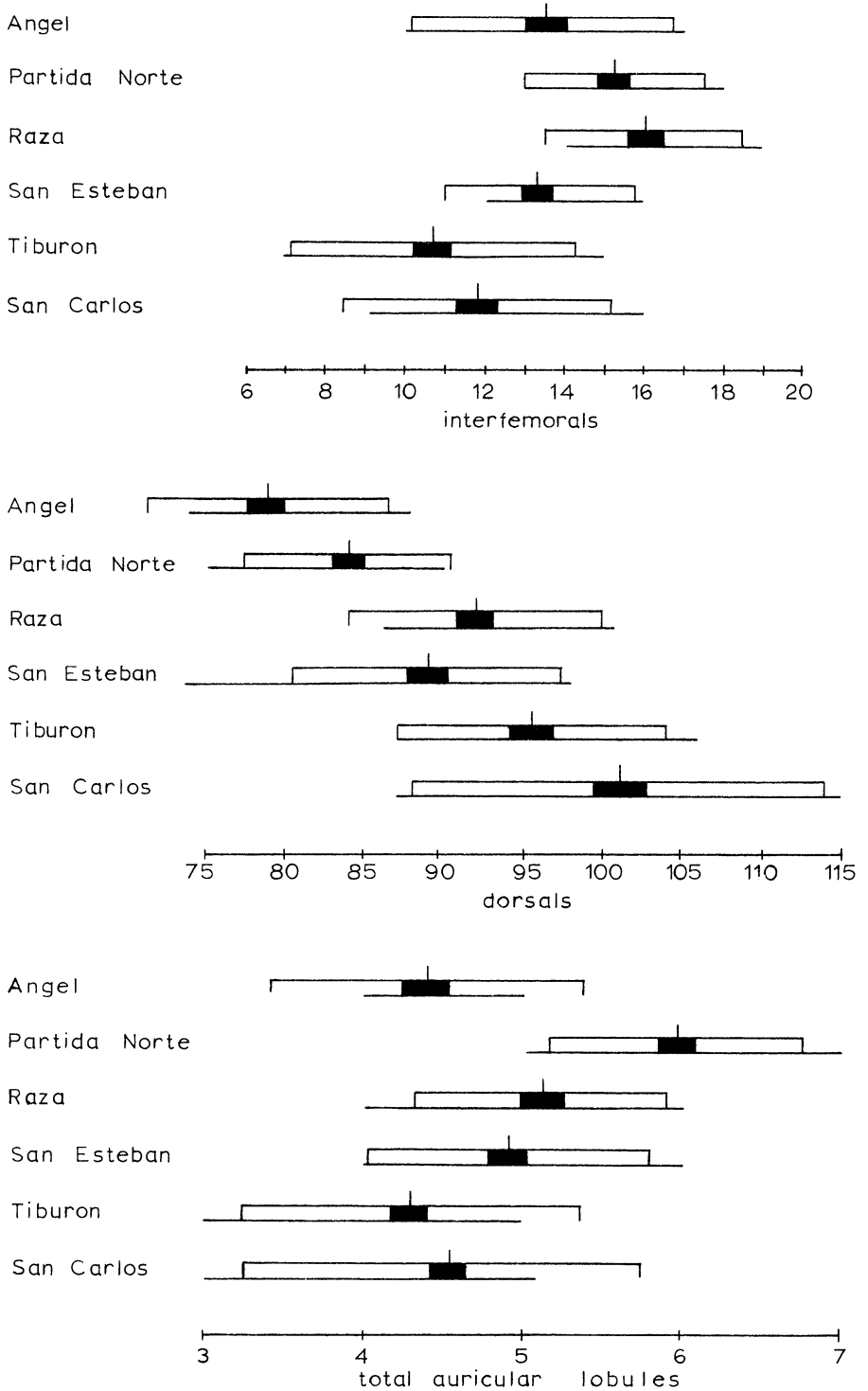


FIG. 9. Geographical variation in interfenorals, dorsals, and auricular lobules in *Uta stansburiana taylori*. Explanation as in Figure 6.

MATERIAL EXAMINED.—CNHM 100097 (type); UI 27446–50 (paratypes); SDNHM 6701–03, 17588–89, 38536, 51646–52, 51721–29, UMMZ 128889 (28) (Angel de la Guarda Island); UMMZ 128913 (51) (Partida Norte Island); SDNHM 51255–73, UMMZ 128914 (33) (Raza Island); UMMZ 128904 (44) (San Esteban Island); UMMZ 128886 (21), SDNHM 6709, 51770–91 (Tiburón Island); ASC 2516–2542, UNMMSB 4682–87, UMMZ 128923 (26), 128924 (8) (Sonora, San Carlos).

*Uta stellata* Van Denburgh

*Uta stellata* Van Denburg, 1905, Proc. Calif. Acad. Sci., vol. 5, pp. 21–22; Van Denburgh, 1922, Occ. Pap. Calif. Acad. Sci., vol. 10, pp. 225–227; Smith and Taylor, 1950, Bull. U.S. Nat. Mus., vol. 199, p. 150.

*Uta stansburiana stellata* Zweifel, 1958, Amer. Mus. Nov., no. 1895, p. 10.

TYPE.—CAS 4704, R. H. Beck, collector.

TYPE LOCALITY.—San Benito Islands, Baja California.

DIAGNOSIS.—Auricular lobules greatly reduced in size and number, width of largest lobule 2–4 times its height, largest lobules 2–3, with a single smaller lobule on either side below or above the larger ones, or no smaller lobules at all; dorsals small with intervening granules, weakly keeled to not keeled, not imbricate; non-keeled dorsals comprising anterior 40%–50% of dorsal count, occasionally 90%–100%; body size moderately large, maximum snout-vent length 64 mm in males.

DESCRIPTION.—**Head:** Frontal once divided, rarely entire or twice divided; prefrontals in contact or separated by a single scale (37%) or rarely separated by anterior frontal apex (1%); frontoparietals in contact or separated by 1–2 scales or occasionally separated by posterior frontal apex (21%); circumorbitals 17–24 (aver. 20.1); circumorbital scale rows between supraocular and frontoparietal 1–2, between supraocular and parietal 2, rarely 1 (9%), between supraocular and frontal 1; 4, rarely 5 (6%) enlarged supraoculars, 2–3 scales between enlarged supraocular and fourth superciliary; 5 superciliaries; 3 frontonasals, lateral ones rarely divided; 2 rows of internasals; 1 subnasal; postrostral scale rows 1 or 2 (27%); loreals 1–4 (aver. 2.5); 2–5 scales between posterior canthal and labial (aver. 3.8); right labials 9–12 (aver. 10.2); orbital papillae 11–16 (aver. 13.5); auricular lobules small, largest lobule wider at base than long, one small lobule on either or both sides of 2–3 large lobules, or no small lobules; occipital rows 1–3 (aver. 2.0); 14–23 circuminterparietals (aver. 18.2). **Body:** Dorsals 101–132 (aver. 112.2), weakly to not keeled, small with intervening granules conspicuous, not mucronate, not imbricate; non-keeled dorsals 20–132 (aver. 46.5); dorsals at tail base weakly keeled, not mucronate to keeled and weakly mucronate; gulars 28–37 (aver. 32.6); gular fold scales 15–21 (aver. 17.0); ventrals 63–78

(aver. 68.8); interfemorals 11–19 (aver. 14.2); total femoral pores 26–33 (aver. 29.7); digital lamellae on fourth toe 25–31 (aver. 27.9); maximum lamellar spurs average 5.6; interpostanals in males 2–3 (aver. 2.1). **Ratios:** RDSV average 2.10; RNKD average .42; RSV average .13; RGSG average 1.79; RLMT0 average 2.87. **Size and Proportions:** Maximum snout-vent length 64 mm in males, 61 mm in females; RSGSV average .34; RFMSV average .21; RTBSV average .25; RFTSV average .28; RTOFT average .65. **Color:** Dorsum grey to brown, blue flecks in males, light spots yellowish tan to rust, females with paired series of middorsal dark spots, occasional light lateral band on anterior dorsum, venter light; gular region deep blue, bordered with bright orange spots (Zweifel, 1958). Axillary spot dark blue.

**VARIATION.—Sexual:** The number of characters which differ significantly between the sexes at the 0.01 confidence level (t test) include 7 (East San Benito Island), 6 (Middle San Benito Island), and 4 (West San Benito Island). **Geographical:** *Uta stellata* consists of three separate insular populations; however, the interpopulation isolation is probably incomplete as no significant differences in morphological characters were found among the island populations. The gene flow between each island or uniformity of selection pressures is apparently sufficient to prevent divergence.

**DISTRIBUTION.—**East, West, and Middle San Benito Islands, Baja California, Mexico.

**HABITAT.—**Zweifel (1958) found *Uta stellata* under rocks. Murray (1955) noted that petrel burrows served as retreats for *stellata*.

**MATERIAL EXAMINED.—**CAS 4704 (type); CAS 56644–76, 56678–84, UCMVZ 5163–73, 77082 (East San Benito Island); CAS 8834–37, 56641–43, SDNHM 8904–10, 27662, 42685, 52961–62, UCMVZ 51051–58, 51074 (Middle San Benito Island); CAS 56601–40; UCMVZ 77081, 77083, 51059–62 (West San Benito Island).

#### OSTEOLOGICAL COMPARISONS

X-ray analysis is particularly well suited for comparison of skeletal features of lizards, but not so valuable for detailed comparisons. Therefore, only a few characteristics have been compared from the X-ray studies. Additional observations on some forms are available from prepared skeletons. Because of the non-uniformity of data on each form, such characters were not used in the analysis of morphological relationships.

A comparison of the nine recognized forms of utas on the basis of five osteological characters is shown in Table 2. In all forms, as in most iguanids, there is a modal number of 23 presacral vertebrae. There are consistently 5 (modal) preautotomous caudal vertebrae. The number of caudal vertebrae, however, differs between species, but the limited samples of individuals with complete tails preclude detailed considerations. The anterior caudal vertebrae bear lateral processes that are distinctly enlarged and generally

TABLE 2  
OSTEOLOGICAL COMPARISONS OF NINE FORMS OF THE GENUS *Uta*

<i>Character</i>	<i>Uta palmeri</i>	<i>Uta antiqua</i>	<i>Uta nolascensis</i>	<i>Uta stellata</i>	<i>Uta squamata</i>
				21-1	
Number presacral vertebrae	22-1 23-13 24-4	22-2 23-25 24-2	23-13 24-1	23-2	22-2 23-12 24-1
Number preauto-tomous caudals	5-12 6-6 38-1	4-1 5-20 6-7	5-9	4-1 5-2	5-10 6-4
Total caudals	40-1 41-1	41-1 42-2 43-1	39-1	41-1	40-2 41-1
Number of caudals with distinctly elongated processes	5-18	4-4 5-22 6-1	4-4 5-12	4-1 5-5	4-3 5-12
Phalangeal formula	2-3-4-5-3 front 2-3-4-5-4 rear	2-3-4-5-3 front 2-3-4-5-4 rear	2-3-4-5-3 front 2-3-4-5-4 rear	2-3-4-5-3 front 2-3-4-5-4 rear	2-3-4-5-3 front 2-3-4-5-4 rear

TABLE 2 (cont.)

<i>Character</i>	<i>Uta stansburiana stansburiana</i>	<i>Uta stansburiana taylora</i>	<i>Uta stansburiana elegans</i>	<i>Uta stansburiana stejneri</i>
Number presacral vertebrae	22-1 23-24 24-1	22-11 23-46 24-2	22-4 23-72 24-6	22-2 23-33 24-1
Number preauto-tomous caudals	4-2 5-15 6-5 7-1 36-2 37-1 38-3	4-5 5-54 6-10 7-3	4-2 5-55 6-20 7-1	5-28 6-4
Total caudals	39-3	40-1 41-1 42-3 43-2 44-1	39-2 40-1 41-4 42-1 43-2 44-1	39-1 41-3 42-1 43-1 44-1
Number of caudals with distinctly elongated processes	5-24 6-1 7-1	5-55 6-2	5-55	4-7 5-31
Phalangeal formula	2-3-4-5-3 front 2-3-4-5-4 rear	2-3-4-5-3 front 2-3-4-5-4 rear	2-3-4-5-3 front 2-3-4-5-4 rear	2-3-4-5-3 front 2-3-4-5-4 rear

obviously differentiated in size from those of the posterior caudals. However, in all forms the first five caudal vertebrae generally bear the elongated processes.

The phalangeal formula of 2-3-4-5-3 and 2-3-4-5-4 for front and rear feet, respectively, is characteristic of all forms of utas. Maxillary tooth counts are unavailable for all the forms, but have proved taxonomically valuable in at least one instance in distinguishing *Uta antiqua* from *U. palmeri* (Ballinger and Tinkle, 1968).

#### KARYOTYPES

Pennock, Tinkle, and Shaw (1968) have presented detailed comparisons of karyotypes in all of the forms of utas and readers are referred to this paper for quantitative information. All of the forms have  $2n=34$  chromosomes with 6 pairs of macrochromosomes and 11 pairs of microchromosomes. Apparently in all forms the male is heterogametic (Pennock and Tinkle, 1969). Significant differences in arm ratios between the different forms could not be demonstrated. We were unable to confirm a previous count of  $2n=30$  for *U. s. stejnegeri* and consider this count to be in error (Hahn, 1964).

Both skeletal comparison and karyotype studies, while producing essentially no evidence of relationship or degree of divergence, support the hypothesis of recent evolution and differentiation of the species in the genus *Uta*.

#### DISCUSSION

##### MORPHOLOGICAL RELATIONSHIPS

The foregoing descriptions and analyses of variation of the nine recognized forms of *Uta* provide a basis for the taxonomic recognition of these taxa. Although a description of the variation of the natural populations represented by these taxa necessarily preceded the grouping of the populations, we have omitted a detailed treatment of each of the 69 populations for practical reasons of presentation and economy. Such descriptions not only become boring and redundant but are largely unnecessary in understanding the relations as a whole; however, some attention must be given to individual populations in a consideration of their evolutionary histories.

The following discussions of morphological relationships are based on the mean coefficients of difference (Table 3) derived from characters 1-28 (Appendix B) for all populations. Additional qualitative differences in color and in characters 29-44 are considered where taxonomically important. Significant differences mentioned in the following section refer to differences between character means which are as great or greater than 1.28 as determined by the coefficient of difference test (Mayr, Linsley, and Usinger, 1953).

*Uta palmeri* is most closely related phenetically to *U. stellata*. Of the other species, *palmeri* is most unlike *squamata* and *stansburiana* and most similar to *nolascensis* and *antiqua* (Table 3). Color pattern indicates a com-



TABLE 3  
 MEAN COEFFICIENTS OF DIFFERENCE AND RANGE OF VARIATION IN CD'S  
 IN INTRATAXA AND INTERTAXA COMPARISONS. NUMBERS IN PARENTHESES  
 ARE NUMBERS OF POSSIBLE COMPARISONS.

	<i>Uta palmeri</i>	<i>Uta nolascensis</i>	<i>Uta stellata</i>	<i>Uta antiqua</i>	<i>Uta stansburiana stejnegeri</i>
<i>Uta palmeri</i>		.82(1)	.71(3)	.88(3)	1.30(10)
			.70-.74	.75-.96	1.03-1.50
<i>Uta nolascensis</i>	.82(1)		.50(3)	.49(3)	.79(10)
			.43-.57	.38-.60	.60-.92
<i>Uta stellata</i>	.71(3)	.50(3)	.21(3)	.53(9)	.70(30)
	.70-.74	.43-.57	.18-.24	.43-.57	.58-.84
			intrataxon		
<i>Uta antiqua</i>	.88(3)	.49(3)	.53(9)	.38(3)	.57(30)
	.75-.96	.38-.60	.43-.57	.32-.45	.35-.81
				intrataxon	
<i>Uta stansburiana stejnegeri</i>	1.30(10)	.79(10)	.70(30)	.57(30)	.26(45)
	1.03-1.50	.60-.92	.58-.84	.35-.81	.14-.43
					intrataxon
<i>Uta squamata</i>	1.44(1)	1.06(1)	.84(3)	.70(3)	.74(10)
			.82-.86	.61-.86	.51-.90
<i>Uta stansburiana taylori</i>	1.05(6)	.64(6)	.58(18)	.47(18)	.50(60)
	.89-1.24	.53-.87	.45-.75	.29-.63	.28-.70
<i>Uta s. elegans</i>	1.13(30)	.66(30)	.58(90)	.54(90)	.48(300)
	.81-1.53	.43-.93	.34-.82	.30-.82	.19-.82
<i>Uta s. stansburiana x elegans</i>	1.03(5)	.53(5)	.52(15)	.48(15)	.48(50)
	.95-1.14	.49-.63	.40-.59	.36-.67	.38-.59
<i>U. s. elegans (insular)</i>	1.15(17)	.66(17)	.61(51)	.56(51)	.52(170)
<i>U. s. elegans (mainland)</i>	1.09(13)	.65(13)	.54(39)	.50(39)	.42(130)
<i>U. s. stansburiana</i>	.91(10)	.54(10)	.50(30)	.61(30)	.73(100)
	.81-1.10	.48-.64	.38-.61	.34-.72	.38-.91

TABLE 3 (cont.)

	<i>Uta squamata</i>	<i>Uta stansburiana taylora</i>	<i>Uta stansburiana elegans</i>	<i>Uta stansburiana stansburiana x. s. elegans</i>
<i>Uta palmeri</i>	1.44(1)	1.05(6) .89-1.24	1.13(30) .81-1.53	1.03(5) .95-1.14
<i>Uta nolascensis</i>	1.06(1)	.64(6) .53-.87	.66(30) .43-.93	.53(5) .49-.63
<i>Uta stellata</i>	.84(3) .82-.86	.58(18) .45-.75	.58(90) .34-.82	.52(15) .40-.59
<i>Uta antiqua</i>	.70(3) .61-.86	.47(18) .29-.63	.54(90) .30-.82	.48(15) .36-.67
<i>Uta stansburiana stejnegeri</i>	.74(10) .51-.90	.50(60) .28-.70	.48(300) .19-.82	.48(50) .38-.59
<i>Uta squamata</i>		.66(6) .50-.79	.68(30) .46-1.03	.71(5) .65-.75
<i>Uta stansburiana taylora</i>	.66(6) .50-.79	.40(15) .22-.60 intrataxon	.44(180) .20-.89	.38(30) .26-.56
<i>Uta s. elegans</i>	.68(30) .46-1.03	.44(180) .20-.89	.39(465) .17-.99 intrataxon	.38(150) .18-.66
<i>Uta s. stansburiana x s. elegans</i>	.71(5) .65-.75	.38(30) .26-.56	.38(150) .18-.66	.20(10) .13-.27 intrataxon
<i>U. s. elegans (insular)</i>	.68(17)	.48(102)		.44(85)
<i>U. s. elegans (mainland)</i>	.68(13)	.39(78)		.31(65)
<i>U. s. stansburiana</i>	.93(10) .61-1.13	.55(60) .23-.77	.56(300) .20-.89	.47(50) .19-.62

TABLE 3 (cont.)

	<i>Uta stansburiana elegans</i> (insular only)	<i>Uta stansburiana elegans</i> (mainland only)	<i>Uta stansburiana stansburiana</i>	<i>Uta stansburiana</i> average
<i>Uta palmeri</i>	1.15(17)	1.09(13)	.91(10) .81-1.10	1.06
<i>Uta nolascensis</i>	.66(17)	.65(13)	.54(10) .48-.64	.66
<i>Uta stellata</i>	.61(51)	.54(39)	.50(30) .38-.61	.59
<i>Uta antiqua</i>	.56(51)	.50(39)	.61(30) .34-.75	.55
<i>Uta stansburiana stejnegeri</i>	.52(170)	.42(130)	.73(100) .38-.91	
<i>Uta squamata</i>	.68(17)	.68(13)	.93(10) .61-1.13	.75
<i>Uta stansburiana taylori</i>	.48(102)	.39(78)	.55(60) .23-.77	
<i>Uta s. elegans</i>			.56(300) .20-.89	
<i>Uta s. stansburiana x elegans</i>	.44(85)	.31(65)	.47(50) .19-.62	
<i>U. s. elegans</i> (insular)	.50(126) intrataxon	.44(221)	.63(170)	
<i>U. s. elegans</i> (mainland)	.44(221)	.32(78) intrataxon	.52(130)	
<i>U. s. stansburiana</i>	.63(170)	.52(130)	.39(45) intrataxon	

parable relationship. *Uta palmeri*, *stellata*, *antiqua*, and *nolascensis* have relatively simple uniform to spotted patterns while the pattern of *stansburiana* is occasionally more complex and basically some derivative of the stripe pattern. The forms of *U. stansburiana* (i.e., *s. taylori* and *s. stansburiana*) which have a spotted dorsal pattern not unlike *U. palmeri* are also less divergent from *palmeri* in morphological characters (Table 3). *Uta palmeri* is characterized by high numbers in meristic characters, notably in femoral pores, interfemorals, ventrals, gulars, and orbital papillae. In addition *palmeri* is characterized by a long fourth toe in relation to the hind foot length. Also *palmeri* has more lamellar spurs than most mainland and some insular populations and has significantly more right labials than *s. stejnegeri* and most *s. elegans* populations.

*Uta stellata* is morphologically most similar to *U. nolascensis* and differs significantly from the latter only in characters 3 and 22 (Appendix B). The two forms may be easily separated on the basis of coloration (see description) and by the development of the auricular lobules which are short in *stellata*, the basal lobule width equal to or as great as twice the length, but long in *nolascensis* (length of the largest lobule always exceeding its width). The two forms are also easily recognized on the basis of total body size; *nolascensis* is small (maximum snout-vent length 55 mm), while *stellata* is larger (maximum snout-vent length 64 mm). *Uta stellata* is equally similar to but differs significantly from *U. antiqua* in the number of dorsal scales. Of the *stansburiana* races, *stellata* is most similar to *s. taylori*, *s. stansburiana*, *s. elegans* and to intergrades of the latter two forms; it is most divergent from *s. stejnegeri*. Zweifel (1958) suggested that *Uta stellata* should be regarded as a subspecies of *stansburiana*; however, we have retained it as a species because of its close similarity to *Uta palmeri*, *antiqua* and *nolascensis*. *Uta stellata* is characterized by high numbers of dorsals, non-keeled dorsals, ventrals, right labials, and interfemorals. The dorsal color pattern indicates affinities as previously discussed for *Uta palmeri*.

*Uta antiqua* is also very similar in morphology to *U. s. taylori*. Color pattern indicates similar affinity. *Uta antiqua* is characterized by a general decrease in numbers of scales as compared to *palmeri*, *stellata*, and *nolascensis*, with a significant decrease in the number of dorsal scales. *Uta antiqua* is characterized by an increase in numbers of scales, particularly ventrals, interfemorals and gulars, when compared to subspecies of *U. stansburiana*.

*Uta nolascensis* is most similar to *Uta stellata* and *Uta antiqua*. Of the *stansburiana* races, *nolascensis* is most similar to *s. stansburiana*, not strongly dissimilar from *s. taylori* and *s. elegans*, and quite dissimilar from *s. stejnegeri*. Morphologically *nolascensis* is most different from *squamata* and *palmeri*. The green coloration of *squamata* and *nolascensis* is certainly a case of convergence. *Uta nolascensis* differs from *palmeri* in a lower number of ventrals, gulars, and interfemorals while having a significantly higher number of gulars and interfemorals than *squamata* and *s. stejnegeri*, and a higher number of maximum lamellar spurs than most *stansburiana* popu-

lations except *s. stejnegeri*. The shorter hind foot in relation to snout-vent length significantly differs from most populations of *s. stejnegeri* and *s. stansburiana*. The high number of superciliaries is significantly different from all populations and the high number of non-keeled dorsals differs significantly from *s. stansburiana*. The uniform color pattern of *nolascensis* is unique (excepting the mutant form found in *s. stejnegeri*, Ballinger and McKinney, 1967), although by inference from morphological similarities, we have considered it most closely related to the spotted pattern of *palmeri*, *antiqua*, *stellata*, *s. taylori*, and *s. stansburiana*. Soulé and Sloan (1966) considered *nolascensis* a race of *stansburiana* although no specific nomenclatural reference was made nor data presented. Due to the strong similarity to *antiqua* and *stellata*, we feel that the retention of *nolascensis* as a distinct species is more indicative of its true relationship than to consider it as a subspecies of *stansburiana*.

*Uta squamata* is found only on Isla Santa Catalina. *Uta squamata* is most similar to *stansburiana taylori* and *stansburiana elegans*, although more similar to *antiqua* than to the species *stansburiana* as a whole (Table 3). *Uta squamata* is characterized by significantly fewer dorsals and non-keeled dorsals than nearly all *Uta* populations, fewer scales in most other characters when compared with *palmeri*, *stellata*, and *nolascensis*, fewer gulars than *antiqua*, more interfemorals than *stansburiana stejnegeri* and by prefrontals which are rarely in contact as opposed to the contacting prefrontals in most other populations.

*Uta stansburiana taylori* occurs on five islands and has a restricted distribution on the Sonoran mainland. The relatively high interpopulational divergence (Table 3) is not surprising since a higher divergence level would be expected between its disjunct insular populations than between contiguous continental populations. *Uta s. taylori* is most divergent from *palmeri*, *squamata*, *nolascensis* and *stellata*, in that order, and is most similar to *antiqua* and *s. stansburiana*. Of the *stansburiana* populations, *s. taylori* is most similar to *s. stansburiana* x *s. elegans* intergrades and mainland *s. elegans*, and this similarity is probably due to the low divergence level of *s. elegans* which is a result of the heterogeneous origin of *stansburiana elegans* (see discussion p. 69). Characters diagnostic of *Uta stansburiana taylori* are few due to its intermediacy between other forms in most characters. It is, however, greatly different from *U. s. stejnegeri* in its higher number of interfemorals. It has significantly fewer interfemorals, ventrals, gulars, orbital papillae and maximum lamellar spurs than *Uta palmeri*. The San Carlos population has fewer digital lamellae than most insular populations of *s. elegans* and *stellata*. The population of Isla Partida Norte has a significantly higher number of auricular lobules than most populations. The same is not true for other populations of *s. taylori* although a slight increase in the number of auricular lobules occurs in the Raza population, significantly separating it from *stellata* as well as from certain insular *stansburiana elegans* populations.

*Uta stansburiana taylori* was first described as a distinct species by Smith (1935) who indicated later that it was completely sympatric with *s. elegans* (Smith and Taylor, 1950) although Taylor (1936) had previously noted its restriction to rocky hillsides while *s. elegans* inhabits the flats of the Sonoran deserts. Lowe and Norris (1955) regarded *taylori* as a subspecies of *stansburiana* due to this ecological separation and suggested that intergradation occurred along the boundary of the two habitats, but they failed to produce data to support this contention. We have collected *U. s. taylori* at the type locality and surrounding area and find that the ecological separation of the two forms is great. We have failed to find a zone of intergradation. The comparison of morphological characters of a population of typical *U. s. elegans* near Guaymas with typical *U. s. taylori* of nearby San Carlos suggests that the two forms are distinct with some indication of introgression (Fig. 10). Under laboratory condition the two forms have produced hybrids, indicating at least some genetic compatibility. Likewise, *U. s. taylori* does not discriminate behaviorally from *U. s. elegans* in laboratory studies of mate preference (Ferguson, pers. comm.). Therefore, the mechanism of separation of the two forms in nature is not understood. Although intergradation apparently may not occur, the close phenetic relationship of *s. taylori* to *s. elegans* suggests its subspecific rather than specific distinctness.

The sample from Tiburon Island which we consider *U. s. taylori* shows a character state distribution indicative of an intergrade population (Fig. 11), which again supports the subspecific status of *s. taylori*. However, when this sample was collected, we were unaware of the possibility of two forms occurring on such a shallow water island, and were therefore not selective in collecting in specific habitats. We obtained animals from hillsides as well as arroyos and desert flats, so that the sample may be of mixed populations. However, if the ecological separation of the two forms does occur on Tiburon, the separation is not nearly so evident as that which occurs at San Carlos. McKinney (1966; 1969) found only a slight decrease in number of animals produced in hybridization experiments between utas from Guaymas and Tiburon compared with controls; however, his sample from Tiburon was taken at the same time as ours and could likewise have been mixed.

*Uta stansburiana klauberi* (Lowe and Norris, 1955; San Esteban Island) is considered synonymous with *U. s. taylori* since there are no significant morphological differences between the two forms. Minor color differences considered diagnostic by Lowe and Norris are not sufficient to warrant its recognition; at least 20 additional insular populations could likewise be recognized on that basis. The extremely adaptive nature of such minor color variations has been demonstrated in other groups (Sheppard, 1960). Such minor changes are not sufficient to warrant diagnostic weight for these characters. The color pattern type of the San Esteban population is not different from some other insular forms of *Uta s. taylori*.

*Uta stansburiana stansburiana* is distributed in the Great Basin Desert

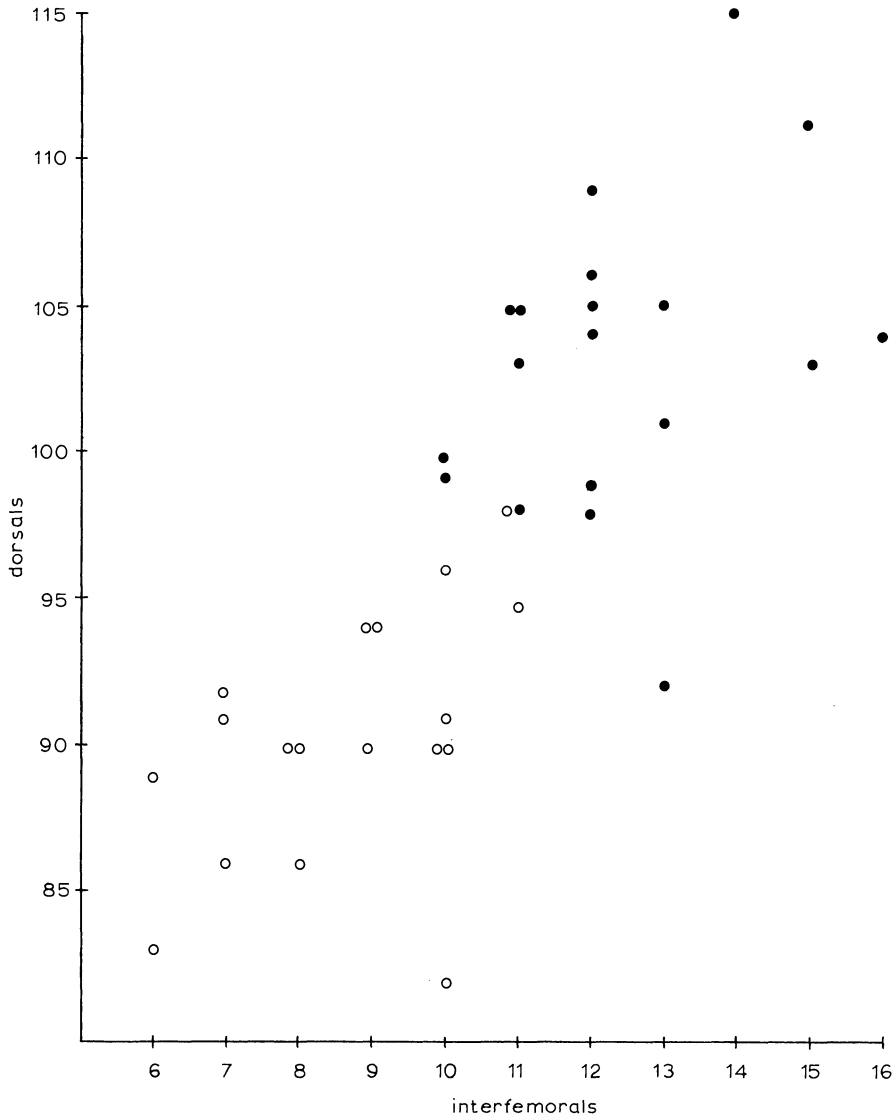


FIG. 10. Morphological relationship between populations of *Uta stansburiana taylori* and *Uta stansburiana elegans* on the basis of two scale characteristics. Dots represent males from San Carlos; circles represent males from Guaymas.

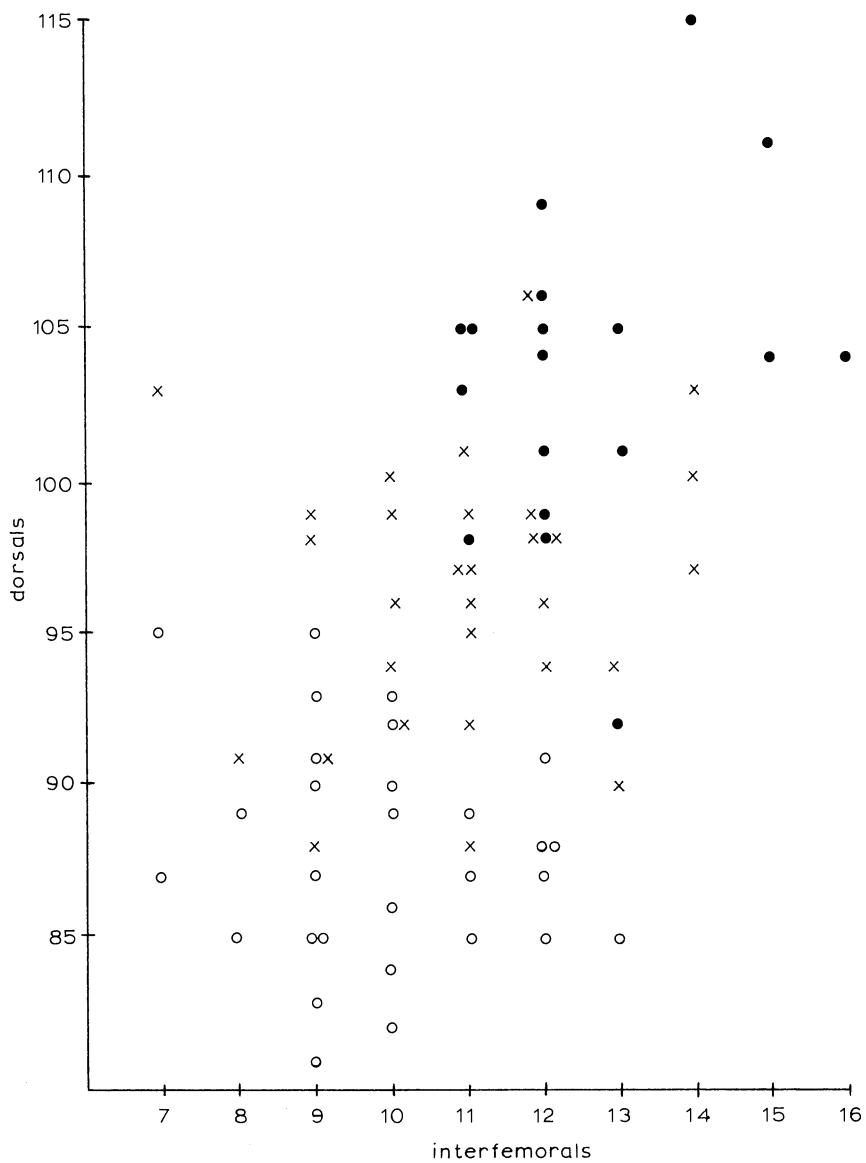


FIG. 11. Distribution of two scale characters in the Tiburon population compared to Pt. Peñasco and San Carlos populations. Dots represent males from San Carlos, circles males from Puerto Peñasco, x's males from Tiburon.



and surrounding plateaus and represented in our analysis by ten populations. *Uta s. stansburiana* is most divergent from *palmeri* and *squamata*, most similar to *stellata* and intermediately similar to *nolascensis* and *antiqua*. Intraspecific comparisons indicate that *s. stansburiana* is most similar to *s. stansburiana* x *s. elegans* intergrade populations, as would be expected, and to *s. taylori* and mainland populations of *s. elegans*. The similarity to *s. elegans* is likely due to gene flow between the two forms since a large area of intergradation occurs in southern Nevada and southwestern to central Utah. *Uta s. stansburiana* is most dissimilar (intraspecifically) from *s. stejnegeri* and certain insular populations of *s. elegans*. *Uta s. stansburiana* is significantly different from *palmeri* in the smaller number of ventrals, gulars, labials and maximum lamellar spurs and from *s. stejnegeri* in the larger number of interfemorals and in the large size of the gulars in relation to snout-gular distance, an increase particularly evident in the Colorado populations. Duchesne, Apache, and Ada populations have a significantly shorter foot in relation to snout-vent length when compared to insular *s. elegans*. A lower percentage of individuals in the Duchesne population have frontoparietals in contact when compared to *s. stejnegeri*. Apache specimens show an increase in the per cent of individuals with two postrostral rows as compared to most other populations. Color pattern indicates a similar close relationship to *s. taylori* and an affinity to *stellata* and *antiqua* rather than to *s. elegans* or *s. stejnegeri*.

*Uta stansburiana nevadensis* described by Ruthven (1913) is considered synonymous with typical *s. stansburiana*. The color pattern type of *s. nevadensis* is the same as typical *s. stansburiana*. We considered the paratype series of *s. nevadensis* in our analysis (Elko Co., Nevada) and found no basis on which the distinction of this form could be recognized. However, Charles McKinney (now at the University of Texas) and Wilmer Tanner of Brigham Young University are making a more detailed study of "nevadensis" and other western *stansburiana* populations and we defer additional comment pending the outcome of their studies (see footnote on p. 35).

*Uta stansburiana stejnegeri*, represented in our analysis by ten populations, occurs principally in the Chihuahuan desert and river valleys in scrubland east of the Sierra Madre Occidental Mountains of Mexico and the Chiricahuas of southeastern Arizona. *Uta s. stejnegeri* is relatively more divergent (Table 3) than other *Uta* taxa except *palmeri* and *squamata*. However, *U. s. stejnegeri* is only superficially distinguishable from *s. elegans*, differing significantly in only a single character (interfemorals) from most *s. elegans* populations. A zone of intergradation between *s. stejnegeri* and *s. elegans* has yet to be discovered; the two forms appear to be completely allopatric at present. Such a zone would be difficult to recognize since the color patterns of the two forms are essentially identical. *Uta s. stejnegeri* occurs in the desert flats of southwestern New Mexico and southeastern Arizona east of the Chiricahua Mountains, while *s. elegans* occurs in the Sonoran Desert west of this area. There is a gap in the locality records between the two forms.

*Uta s. stejnegeri* is characterized by reduction in the numbers of scales particularly when compared to *palmeri* and a significant reduction in number of interfemorals and number of gulars when compared to *antiqua* and *stellata*. All populations of *s. stejnegeri* are significantly different from all other *uta* populations in the low number of interfemorals except when compared to La Paz, Magdalena, Santa Margarita and San Martin populations.

*Uta stansburiana elegans* occurs from southern Sonora, Mexico to central California and south through all of Baja California and adjacent islands along the Pacific coast and in the Gulf of California. The interpopulational divergence level of the mainland populations is considerably lower than that among insular populations of *s. elegans* (Table 3). These data demonstrate that continuously distributed mainland populations are less divergent between themselves than their disjunct insular counterparts. Therefore, we elected to treat the mainland populations of *U. s. elegans* as a group when comparing levels of divergence with other taxa and to treat each island population as a distinct unit, comparing each to all of the other mainland forms.

As indicated in the above discussion *Uta s. stejnegeri* is most closely related to *s. elegans* although data in Table 3 indicate that *s. elegans* is slightly more similar to *s. taylori*. This similarity is likely due to gene flow between *s. elegans* and *s. taylori* and to intergradation between *s. elegans* and *s. stansburiana* which is phenetically similar to *s. taylori*. *Uta s. stejnegeri* is isolated from and not influenced by these interactions.

Due to the extreme variability of *U. s. elegans*, its distinctness from other taxa is difficult to demonstrate. Like other races of *Uta stansburiana*, *U. s. elegans* is characterized by a decrease in most scale counts when compared to *Uta palmeri*. The more complex dorsal color pattern of *U. s. elegans* differs from all taxa except *s. stejnegeri*. The number of interfemorals is significantly greater than found in *s. stejnegeri* except for certain southern Baja California populations of *s. elegans* as discussed above.

We have not recognized *Uta stansburiana hesperis* which was described by Richardson (1915) from California and northern Baja California for a number of reasons. The low level of interpopulational divergence between mainland *U. s. elegans* populations indicated that further separation of this group is unwarranted. The high number of dorsal scales on which Richardson's original description of *hesperis* was based is clinal, with dorsals increasing in number from south to north and from the hotter desert region of the east to the cooler coastal climate of the west. We have failed to find a definite area of intergradation with *U. s. elegans*. The differences in coloration of the California populations are minor and vary in a geographic pattern identical to the dorsal scale variation.

The morphological divergence of insular populations of *U. s. elegans* is presented in Table 4. With two exceptions, all insular populations of *s. elegans* are more similar to the nearest continental population and/or their

TABLE 4  
 COMPARISON OF INSULAR POPULATIONS OF *Uta s. elegans* WITH  
 OTHER SUBSPECIES OR SPECIES POPULATIONS OF *Uta stansburiana*

Insular <i>elegans</i> populations	<i>stansburiana</i>	<i>stejnegeri</i>	<i>elegans</i>	mainland <i>elegans</i>	island <i>elegans</i>	<i>taylori</i>	nearest island population	nearest continental population
	A <sup>1</sup>	B	C	D	E	F		
San Clemente	.53	.74	.65	.56	.72	.65	.48	.35
San Martin	.68	.41	.45	.42	.50	.46	.38	.38
Todos Santos	.51	.45	.41	.33	.47	.44	.38	.27
Natividad	.43	.58	.52	.47	.56	.53	.48	.45
Cedros	.47	.40	.34	.29	.38	.31	.48	.26
Santa Margarita	.54	.35	.34	.31	.36	.35	.27	.18
Magdalena	.75	.35	.46	.42	.50	.45	.88	.33
Espiritu Santo	.61	.45	.39	.36	.41	.39	.24	.21
Partida Sur	.62	.44	.41	.37	.44	.41	.24	.26
San Jose	.67	.51	.46	.43	.46	.46	.42	.37
Monserrate	.70	.50	.47	.45	.59	.45	.34	.44
Danzante	.68	.52	.45	.44	.47	.47	.47	.44
Carmen	.63	.58	.46	.43	.49	.51	.47	.36
Coronados	.66	.59	.49	.44	.51	.46	.42	.49
San Ildefonso	.72	.65	.55	.54	.56	.57	.64	.58
Tortuga	.78	.49	.55	.50	.60	.59	.63	.54
San Marcos	.52	.50	.41	.37	.44	.41	.63	.24
San Francisco	.76	.70	.60	.58	.61	.63	.42	.48

<sup>1</sup> Each number under A-F represents the mean Coefficient of Difference for that comparison.

nearest insular neighbor or to mainland populations of *Uta s. elegans* as a whole (Table 4). The Natividad population is more similar to *U. s. stansburiana* although not differing significantly in any character from the nearest mainland population considered in our analysis. The Tortuga population differs from the closest mainland sample (San Ignacio) in having significantly fewer non-keeled dorsals and is slightly more similar to populations of *s. stejnegeri* than to those of *s. elegans*. The Tortuga population shows significant differences from *s. stejnegeri* in three characters (femoral pores, interfemorals, and non-keeled dorsals), and is different from *s. elegans* populations in only the number of non-keeled dorsals. We have, therefore, considered it as *s. elegans*. The morphological similarities of the Tortuga utas to *s. stejnegeri* are probably due to the recent colonization of this island discussed in a later section. Four of the insular *s. elegans* populations show marked divergence from their nearest mainland counterparts. The population on Isla Coronados differs from La Paz utas in having a greater number of digital lamellae (C.D.=1.28). Isla San Ildefonso utas differ from those from San Ignacio in having fewer circumorbitals (C.D.=1.55) and fewer

labials (C.D.=1.34). The utas of Isla San Francisco differ from La Paz specimens in having more orbital papillae (C.D.=1.28) and more digital lamellae (C.D.=1.28). San Martin utas differ from Ensenada ones in having fewer dorsals (C.D.=1.40). These slight differences do not seem sufficient to warrant a separation of these insular populations into distinct taxa.

Likewise, the previously recognized *Uta stansburiana martinensis* (San Martin Island), *Uta concinna* (Cedros and Natividad Islands), and *Uta mannophorus* (Carmen, Danzante and Coronados Islands) are considered synonymous with *s. elegans* since differences attributed to these forms are not of a significant magnitude to warrant recognition. In the case of the San Martin *Uta*, the distinctive appearance (i.e., large body size and minor color characteristics) is likely due to an ecological response to an insular environment that is not uncommon in *Uta* (Soulé, 1966). Of the other diagnostic characters discussed by Zweifel (1958) the axillary blotch size is unreliable as a diagnostic character. The dorsal scale number of the San Martin *Uta* which differs slightly from those of the nearest mainland populations (Ensenada) does not differ consistently at a statistically significant level from other populations of *s. elegans* to make it a useful diagnostic character. Zweifel (1958) quite properly put less emphasis on the number of postrostral scale rows than previous authors. When large series of *Uta* are considered, the number of postrostral scale rows simply is not diagnostic of any population. The synonymy of *Uta concinna* (Cedros and Natividad Islands) was discussed by Zweifel (1958), with whom we agree and can only add that among all meristic characters examined by us the population on Cedros has no significant differences when compared to continental populations while Natividad populations have slightly more dorsal scales than certain southern and eastern continental populations of *s. elegans*. Populations previously considered as *U. mannophorus* are considered synonymous with *U. s. elegans* because of the lack of diagnostic characteristics. Smith and Taylor (1950) used axillary blotch as diagnostic for these populations, but this character is not sufficient to separate them from other populations in which similar color variations occur.

Although the insular populations are more similar to and statistically inseparable from *s. elegans*, the relative degree of similarity of island *U. s. elegans* populations to *s. stansburiana* or to *s. stejnegeri* is of interest. Based on the mean C.D. of 28 characters all insular populations of *s. elegans* are more similar to *s. stejnegeri* than to *s. stansburiana* with the exceptions of the *Uta* of San Clemente and Natividad Islands which are more similar to *s. stansburiana* (Table 4). However, if a consideration is made of only those characters which are significantly different (C.D.  $\geq$  1.28), island populations of *s. elegans* are more similar (i.e., differ significantly in fewer characters) to *s. stansburiana* with the exception of San Martin and Magdalena populations, which are more similar to *s. stejnegeri*. This similarity to *s. stansburiana* and a possible explanation for it are discussed in a later section.

## PHYLETIC RELATIONSHIPS

The analysis of morphological divergence between *Uta* populations reveals the basis on which we have recognized nine forms and indicates that additional forms previously described are not morphologically distinct. In addition, the analysis of the morphological relationships provides the data from which the probable phyletic relationships can be determined by using the principles outlined by Maslin (1952). Briefly, Maslin pointed out that related organisms exhibit varying degrees of similarity which can be represented by a "morphocline" or a series of groups (taxa, populations, individuals, etc.) illustrating a gradual change in a particular character or character complex from one type to another, the intermediate groups being more similar than groups at opposite ends of the cline. Furthermore, morphoclines are derived from chronoclines, being partially identical to the actual phylogenetic series. The polarity or probable evolutionary direction of a morphocline can be determined by applying Maslin's principles of divergence, precurrence, relicts, etc. The polarity of one morphocline is generally determined by comparing similar clines in closely related taxa of the same rank in which the phylogenetic sequence of character change is known. Brown (1965) pointed out that appropriate chronoclines are not always available for such comparisons and suggested that the rule of evolutionary reduction (i.e., "a phylogenetic change in number much more frequently results in a decrease than in an increase") be used as an aid in determining polarity of a morphocline.

It becomes apparent that the number of different possible clines is directly proportional to the number of characteristics used to construct the morphoclines. The usefulness of a morphocline then depends on the usefulness of the particular character on which the morphocline is based. Although all morphoclines generally differ in some respects, after many such clines have been constructed, a sequential pattern common to all clines is usually evident and can be expressed in a single cline derived from the mean value of all characters used. Based on ten scutellation characters, the species of *Uta* form a morphocline as follows: *palmeri* ( $\bar{x}=40.23$ ), *stellata* ( $\bar{x}=37.80$ ), *nolascensis* ( $\bar{x}=34.61$ ), *antiqua* ( $\bar{x}=31.92$ ), *stansburiana* ( $\bar{x}=31.58$ ), and *squamata* ( $\bar{x}=28.59$ ). The polarity or evolutionary direction of this morphocline becomes apparent on the basis of a number of criteria. Using the rule of evolutionary reduction (Brown, 1965), *palmeri* would be considered primitive because of its greater number of scales. *Uta palmeri* would also be considered primitive since it most closely resembles the condition found in the closely related and relict genus *Petrosaurus*, which presumably represents the ancestral stock. Based on ten characters, the subspecies of *Uta stansburiana* form a morphocline as follows: *s. stansburiana* ( $\bar{x}=34.93$ ), *s. stansburiana* x *s. elegans* intergrades ( $\bar{x}=31.82$ ), *s. elegans* insular populations ( $\bar{x}=31.19$ ), *s. elegans* continental populations ( $\bar{x}=31.02$ ), *s. taylori* ( $\bar{x}=30.95$ ), and *s. stejnegeri* ( $\bar{x}=29.57$ ). The polarity of this morphocline becomes apparent using similar criteria. The combination of the two mor-

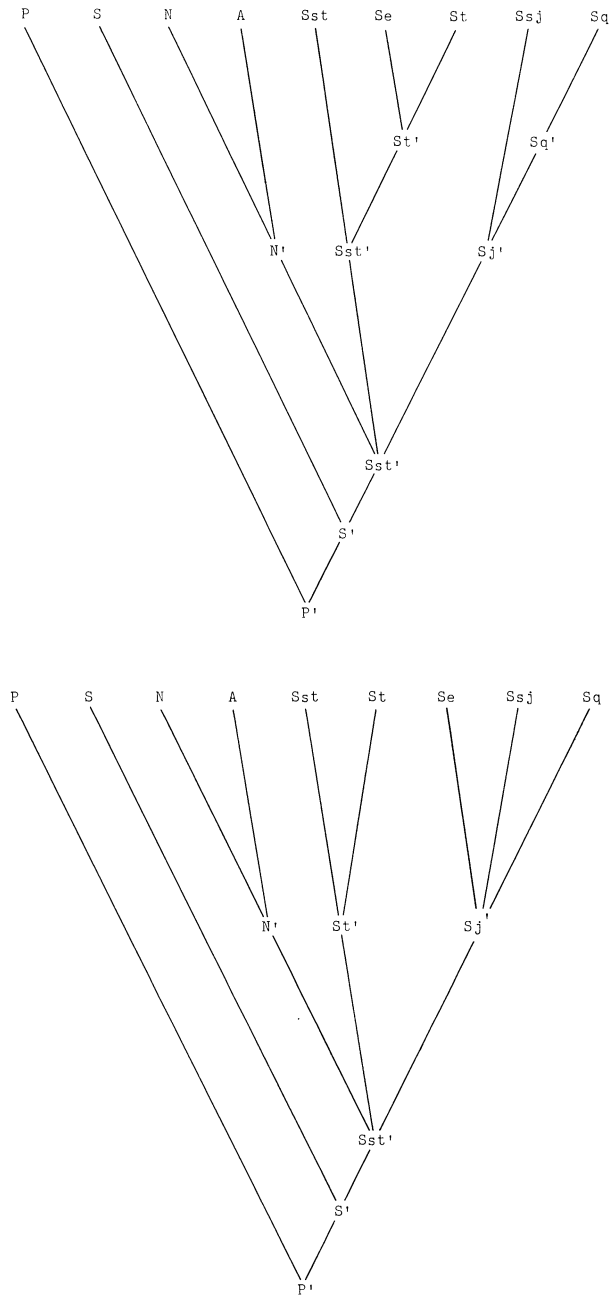


FIG. 12. Chronocline relationships in the genus *Uta*. P=*palmeri*, S=*stellata*, N=*nolascensis*, A=*antiqua*, Sst=*stansburiana stansburiana*, Se=*stansburiana elegans*, St=*stansburiana taylora*, Ssj=*stansburiana stejneri*, Sq=*squamata*. Prime abbreviations represent hypothetical ancestors. A. Dorsal scales included in estimation of phenetic relationship. B. Dorsal scales not included in estimation of phenetic relationship.

phoclines and the representation of the chronoclines from which they were derived, is seen in Figure 12A. According to the chronocline (Fig. 12A), the complex pattern of *U. s. elegans* and *U. s. stejnegeri* has arisen independently in two lines of descent, an improbable explanation. Re-examination of the morphoclines reveals that if a single character, the dorsal scales, is deleted, all relationships remain the same with the exception of *s. taylori* and *s. elegans* which are reversed in their position. A chronocline can then be constructed which is more compatible with the probable phyletic origin of the striped dorsal pattern as well as other characters (Fig. 12B). However, the relationship between this representation and the true phylogenetic sequence is conjectural. The chronocline in Figure 12B has been converted to a conventional phylogenetic representation in Figure 13 to illustrate the probable phyletic relationships of the forms of the genus *Uta*.

#### DEFENSE OF THE TAXONOMIC ARRANGEMENT

Before proceeding with a general theory of the causal events in the diversification of utas, we wish to defend our proposed taxonomic arrangement of the genus. This will involve mention of our zoogeographic theory that will be treated in detail in a later section, but we will not attempt to defend statements that will be clarified later.

The genus *Uta* is geologically young as indicated by close similarity of the taxa and has undergone most of its divergence on islands. Within the genus there are several taxa with simple uniform color patterns and generally with high counts of meristic characters. This pattern is present on the mainland in varying degrees in *Uta s. stansburiana* and *U. s. taylori*. We think that these general similarities bespeak evolutionary relationships rather than convergences.

The most divergent of the species is *Uta palmeri*, but its characters are clustered to suggest relationship with *Uta stellata*, *nolascensis* and *antiqua*. The latter three show almost identical average coefficients of difference (approximately 0.5) when compared *inter se*. In fact, the differences are not great enough to designate them as subspecies. However, their behavior, color and size are quite different and we have little doubt that they are biologically quite distinct; certainly they are completely isolated from gene flow with each other. All of these four species, we think, are relicts of a once widespread radiation of a small-scaled, simple-patterned mainland *Uta*, of which *s. stansburiana* and *s. taylori* are the remainder.

The more complexly patterned utas are *squamata*, *s. elegans* and *s. stejnegeri*. Thus, within the species *stansburiana* we have types representing what we believe to be two phyletic lines. The lines can be separated in the insular forms because isolation and the altered environments of the islands have allowed greater divergence. On the mainland the lines are still in contact, and it is this fact that has forced us to base our taxonomy on an evolutionary picture rather than the reverse.

For example, what we call *Uta s. elegans* has a rather low average co-

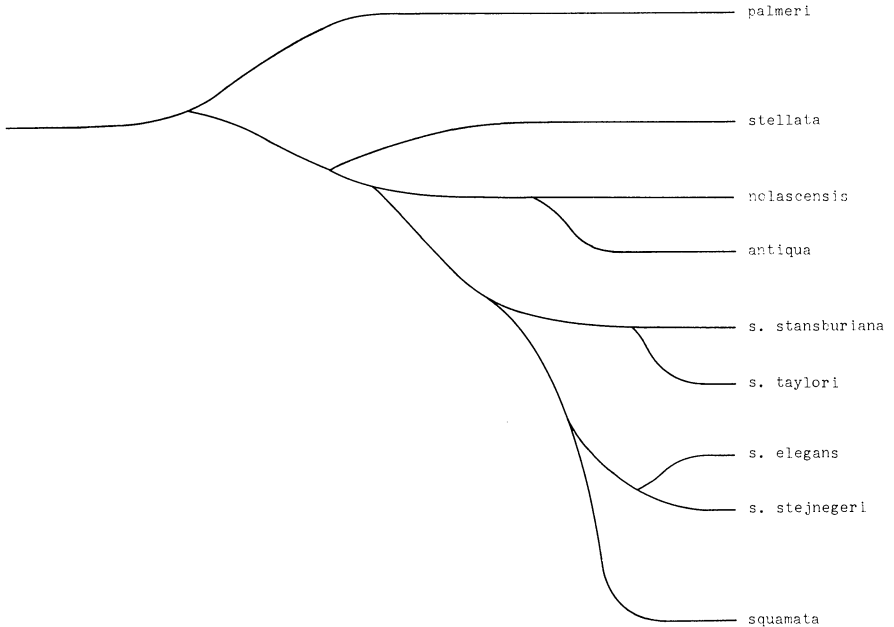


FIG. 13. Hypothetical phylogeny of the recognized taxa in the genus *Uta*.

efficient of difference from other mainland races of *stansburiana*. However, to leave it unnamed ignores the fact that it is a large evolutionary unit of western utas that beautifully closes the gap between the races *s. stansburiana* and *s. stejnegeri*. *Uta s. stejnegeri* has a very high coefficient of difference from *Uta s. stansburiana* and from most of the island utas; yet it differs only slightly from *Uta s. elegans* which, in turn, intergrades broadly with *s. stansburiana*.

In summary, the taxonomic arrangement is one which attempts to recognize what appear to be the evolutionary units within the genus.

#### EVOLUTIONARY AND ZOOGEOGRAPHIC HISTORY

An appreciation of the general outline of geologic and climatic history of western North America is necessary to understand the causal events involved in the speciation of *Uta*. The present distribution of *Uta* in a lowland desert environment suggests that the origin and subsequent adaptive radiation could hardly have occurred prior to the origin of the North American deserts approximately in the middle Pliocene (Axelrod, 1948). The deserts are a result of the rain shadow produced by the mountain building in western North America which began with the mid-Cretaceous orogeny (King, 1958) and continued into the Tertiary. Final phases of this extensive uplift which created the Rocky Mountains-Sierra Madre Occidental and the Sierra Nevada-Baja Peninsular Ranges continued through late



Pliocene at which time, combined with the effects of decreasing temperature and increased aridity, desert fauna and flora began to appear in the rain-shadow area at the head of the Gulf of California.

Prior to the appearance of the deserts in western North America, humid tropical forest reached as far north as southern Canada in early Tertiary times. By Eocene, warm temperate Arcto-Tertiary forests had pushed as far south as Wyoming (Chaney, 1940; MacGinitie, 1958, 1962) with subtropic forest extending southward and grading into the humid tropical flora in northern Mexico. During the Oligocene there was a general decrease in temperature and rainfall although no major vegetational changes occurred until the Miocene when the more xeric Madro-Tertiary flora began to develop along the mountain chains, and by late Miocene thorn-scrub elements of the Madrean flora dominated the region which subsequently was to become the deserts in the middle Pliocene. By the end of the Pliocene, the desert vegetation rapidly developed in areas of low rainfall, establishing the modern floral elements found in the deserts today.

The establishment of the deserts in the Pliocene, however, was not the end to ecological changes in this area. Temperature and rainfall fluctuated in the Pleistocene correlated with the advance and retreat of the continental ice sheets (Martin, 1958). Desert elements may have been forced south during glacial maxima and returned to essentially their present location during glacial minima. While the deserts were not destroyed but simply displaced geographically, it is important to note that the impinging Madrean flora forced the segmentation of the deserts into three refugia as noted by Savage (1960). In fact, Orr (1960) and Savage (1960) have questioned whether there was much desert at all in the Baja California peninsula during maximum glacial advance. The Gulf of California and the Sierra Madre Occidental served as barriers separating desert elements in Southern Baja California, Sinaloa, and the Mexican Plateau. Since each succeeding postglacial period became drier than the previous one and produced a corresponding expansion of the deserts, the most complete separation of desert elements likely occurred in the early Pleistocene. This single phenomenon of desert contraction provided the necessary geographical isolation for potential speciation and likely had a profound influence on the evolution of *Uta*.

Additional refugia for desert species probably occurred on the deep-water islands in the Gulf of California as the surrounding water could have served as a partial buffer against the advancing elements of the Madrean flora. The present configuration of the Gulf had been established by early Pliocene (Anderson, 1950; Moore and Buffington, 1968) and the deep-water islands exclusive of Tortuga (of Pleistocene volcanic origin) all originated before the close of the Miocene or in early Pliocene. The shallow-water islands which became connected to the Baja California peninsula during glacial maxima are likely not to have been so important in the evolution of *Uta* as previously suggested (Soulé, 1964; Soulé and Sloan, 1966) because these islands would have been subjected to the advancing Madrean flora as

well as to the retreating desert fauna, although certain of these islands along the extreme tip of Baja California may have been contiguous with the Baja desert refugium. In other words the important Pleistocene event providing geographical segregation of *Uta* was the separation of the deserts rather than the eustatic sea level changes.

#### HYPOTHESIS OF ORIGIN AND DIVERSIFICATION OF *Uta*

Elements of the "Young Northern Herpetofauna" associated with the rise of the Madro-Tertiary Geoflora began to predominate by mid-Miocene after being spawned from neotropical groups in the Oligocene (Savage, 1960). According to Savage the immediate ancestor to *Petrosaurus* appeared by early Pliocene. The subsequent evolution of *Uta* may have involved four major periods. A summary of these periods is as follows (see also Fig. 14): 1) *Period of initial development*. Proto-*Uta* separated from *Petrosaurus* with the initial division of the deserts in early Pleistocene and remained isolated in the Sinaloa desert refugium long enough for sufficient development of genetic and ecological integrity. 2) *Period of expansion*. As the deserts expanded during the subsequent interglacial period, the primitive stock of *Uta* rapidly spread from the Sinaloan refugium into the new habitat available, extending its range into Baja California and colonizing most of the islands. The continental populations gradually changed, becoming the precursor to *Uta stansburiana stansburiana*. Certain insular populations became distinct and remained relatively unchanged due to differential rates of evolution and extinction while other insular populations changed with or parallel to the mainland form. The unequal rate of evolution and isolation likely allowed *palmeri* to become distinct at this time. Before the end of this period *Uta* entered the deserts east of the Rocky Mountains. 3) *Period of contraction and differentiation*. Climatic and subsequent biotic changes brought about by advancing glaciation again separated the deserts into three refugia and isolated *Uta* in all three. Insular isolates became more different genetically, with *stellata*, *antiqua*, and *nolascensis* becoming distinct. Sufficient divergence occurred in the separated continental deserts to allow subspecific differentiation of *Uta stansburiana stansburiana* developing in Baja California, *Uta stansburiana taylori* in the Sinaloan desert, and *Uta stansburiana stejnegeri* in central Mexico. 4) *Period of final development and interaction*. As the deserts expanded during a subsequent interglacial, so did the three continental isolates of *Uta stansburiana*. *Uta s. stansburiana* spread northward well into the Great Basin and eastward around the head of the Gulf of California. This spread brought it into contact with the Sinaloan stock (now recognized as *U. s. taylori*) somewhere in Sonora. The *U. s. taylori* was almost completely absorbed or competitively displaced during this spread.

The Chihuahuan isolate which we now recognize as *U. s. stejnegeri* also spread northward out of Mexico and westward into most of the southwestern United States and the Baja California peninsula. During this time

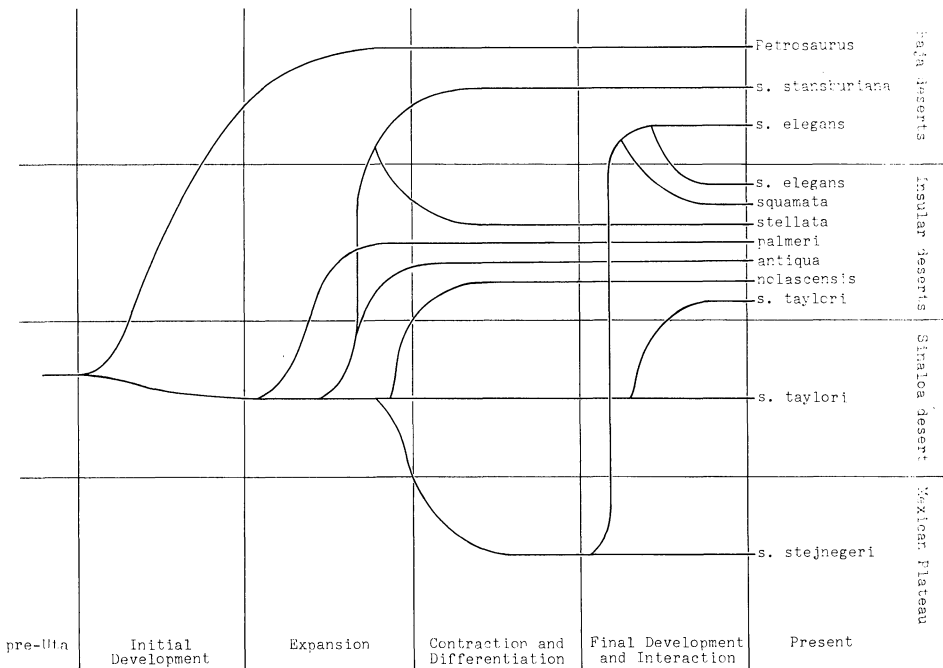


FIG. 14. Diagrammatic summary of the geography of the evolutionary history of *Uta* showing events during the phases discussed in the text.

it was interacting with the *U. s. stansburiana* stock to produce a widespread form of hybrid origin that we now recognize as *U. s. elegans*. Later changes, perhaps very recent ones, served to isolate what we now call *U. s. elegans* from *U. s. stejnegeri* somewhere in southeastern Arizona.

During the period of expansion of the *stejnegeri*-like stock, the *U. s. stansburiana* stock was displaced or absorbed in most of Baja California. However, the former presence of this stock in Baja California is suggested by the similarities of some of the populations of the southern Gulf islands to it.

#### SUPPORTING EVIDENCE AND DISCUSSION

*Period of Initial Development.* The exact time of separation of the ancestral stock into the progenitors of modern *Petrosaurus* and *Uta* is difficult to ascertain in the absence of a fossil record. Two hypotheses for this separation are plausible. 1) This separation occurred with the initial development of the deserts in mid-Pliocene. 2) This separation occurred with the initial division of the deserts in early Pleistocene. The second hypothesis is favored.

In addition to the *Petrosaurus-Uta* lineage other closely related sceloporine genera were evolving after initiation of the Young Northern Group in early Miocene (Savage, 1960). The morphological relationship

between *Petrosaurus* and *Uta* is much closer than between these and other genera (*Sator*, *Sceloporus*, *Urosaurus*), so the division of *Petrosaurus* from the latter groups likely occurred before the separation of *Petrosaurus* from *Uta*. The more xerically distributed *Petrosaurus* of today likely evolved with the initiation of the desert while the more mesically distributed *Sceloporus*, etc., became associated with the oak-woodland chaparral and thorn-scrub of the early Madrean flora. Savage (1960) suggested that *Sator* represents a remnant associated with thorn-scrub community and entered Baja California as early as mid-Miocene. The separation of *Uta* and *Petrosaurus* stocks likely occurred with the initial separation of the deserts during the Nebraskan glaciation, and judging from the present distribution, the stock forced into southern Baja California was the *Petrosaurus* stock while the precursor of *Uta* followed the desert south into the Sinaloa refugium. As the deserts expanded in the Aftonian interglacial the genetic and ecological separation of the two stocks was sufficient to prevent interbreeding or to reinforce the divergence even if some interbreeding occurred. The recognition of this simple division of *Uta* and *Petrosaurus* from a common ancestor seemingly contradicts the contention that the two should be considered generically distinct. However, a breakthrough into a new adaptive zone seems to have occurred because there was an increase in the rate of evolutionary change in *Uta* (far more change has occurred in *Uta* since its origin in early Pleistocene than has occurred in *Petrosaurus* during the same interval if indeed the two did have a common ancestor as we contend) as well as a period of increased speciation (see discussion of the period of expansion below). Simpson (1944, 1953) has pointed out how rapidly a new type may reach a new phylogenetic "grade" and remain essentially stable afterward. It is for these reasons that we have elected to separate the two forms generically. The relatively significant difference in skeletal characteristics between *Uta* and *Petrosaurus* (Etheridge, 1964) supports this view. We consider *Streptosaurus* and *Petrosaurus* congeneric; although *Streptosaurus* can be distinguished morphologically from *Petrosaurus*, no new adaptive zone is apparent.

*Period of expansion.* The primitive stock of *Uta*, most similar to the present day *Uta palmeri*, spread with the desert expansion during the first interglacial and colonized most of the gulf islands. Because the most primitive species (i.e., *palmeri*) is found on one of the most remote islands (San Pedro Martir Island), *Uta* undoubtedly could have reached less isolated islands at least as easily. The occurrence of more advanced forms on other deep-water islands (e.g., Angel de la Guarda, Raza, etc.) suggests that additional differentiation in the mainland stock occurred before the colonization of these islands although alternative suggestions are possible. Evolutionary rates in the insular populations may have been different from those on the mainland due to their isolation. The more isolated the population, the less likely were its chances of remaining similar to the continental stock or to less isolated insular populations. The more primitive populations on

distant islands (i.e., *palmeri* and *antiqua*) likely represent temporal escapees. Other island populations (i.e., *Uta s. taylori*) maintained a comparable evolutionary rate to continental populations due to the greater gene flow and/or similar environmental changes. Because many islands in the Gulf of California contain similar species, while others contain quite divergent ones, we must recognize that a single genetic stock from a mainland invasion has diverged in response to selection on different islands or that there was divergence of the mainland stocks between invasions so that the different insular stocks such as *U. palmeri* versus *U. squamata* represent different invasive mainland stocks and possible competitive replacement of earlier taxa by subsequent invaders. We think that the different stocks of island utas do represent different mainland invasives. The close similarity, for example, of *Uta nolascensis* to mainland populations of *Uta stansburiana* that no longer border the Gulf of California suggests either convergence or genetic relationship of the two. Because examples of such similarities are common and would require numerous convergences, we feel that convergence is unlikely as the explanation.

On the other hand, evolutionary divergence of isolated insular populations may have been independent of the mainland stock in response to specific island environments and insular populations may be more divergent not because they are older or more primitive, but because of their independent evolution. This view is supported by Soulé (1966) who suggested that the adaptive radiation of *Uta* on the islands is a result of specific environmental selective trends. A more detailed discussion of these two viewpoints is given on page 73.

Gradual change in the spreading continental stock during interglacial expansion of the desert resulted in the appearance of the progenitor of *Uta stansburiana stansburiana* as previously discussed. This stock undoubtedly became widespread, as *Uta stellata* of the San Benito Islands is an apparent derivative of it. It is impossible to tell how extensively *Uta* populated the deserts east of the Rocky Mountains. Certainly some of this stock reached there, because *stansburiana stejnegeri* likely developed in the Mexican Plateau during a later desert contraction from stock which must have entered that area during this or a later period of expansion.

*Period of contraction and differentiation.* As the next glaciation again forced the desert southward, *Uta* became divided into three segments. *Uta stansburiana stansburiana* developed in the Baja California peninsular refugium, *Uta stansburiana taylori* in the Sinaloa desert, and *Uta stansburiana stejnegeri* in the Mexican plateau. The close morphological relationship of the insular *stansburiana elegans* populations along peninsular Baja California to *Uta stansburiana stansburiana* (Table 4 and page 58) suggests that *stansburiana stansburiana* or at least its progenitor once inhabited the peninsular desert and initially colonized most of the nearby islands. Two other alternative explanations for the close affinity of *stansburiana stansburiana* and some insular *stansburiana elegans* can be con-

sidered. The insular populations are similar to *stansburiana stansburiana* due to convergence because of similar environmental pressures. The surrounding water possibly produced a climate similar to continental climates further north. The probability that at least fifteen such instances occurred independently on different islands while not occurring on seemingly similar islands (Islas Magdalena and San Martin) is very low. Another explanation would be that the insular populations of *stansburiana elegans*, and indeed the continental population as well, are similar to *stansburiana stansburiana* due to gene flow from the zone of intergradation. The distance over which such gene flow must have occurred is sufficient to question this possibility. The fact that the same gene flow has not affected equally nearby islands (e.g., San Martin and Magdalena) suggests that the similarity of *stansburiana stansburiana* and certain insular *stansburiana elegans* populations is due to a previous colonization by the *stansburiana stansburiana*-like stock and not to convergence or gene flow.

*Uta stansburiana taylori* represents a portion of the *stansburiana stansburiana*-*stansburiana taylori* progenitor that was separated from the Baja California populations by the Gulf of California during glacial maxima and developed in the desert refugium in Sinaloa. The present distribution of *stansburiana taylori* in parts of Sonora supports this statement. Likewise the occurrence of *stansburiana taylori* on islands near the Sonoran side of the Gulf suggests that *stansburiana taylori* rather than another form was isolated and developed in the Sinaloan desert during a glacial maximum.

The occurrence of *stansburiana stejnegeri* only east of the Rocky Mountain-Sierra Madre Occidental barrier suggests that the progenitor of *stansburiana stejnegeri* was isolated in the Mexican Plateau desert refugium.

During this period of contraction and differentiation, immigration to insular populations was probably low as the center of continental distribution was displaced southward. This reduced colonization pressure allowed insular isolates to strengthen their genetic divergence with *stellata*, *antiqua*, and *nolascensis* becoming distinct.

*Period of final development and interaction.* As the deserts again expanded, the three continental isolates of *Uta* spread. *Uta stansburiana stansburiana* and *stansburiana taylori* likely interbred in the vicinity of northwestern Sonora. The close phenetic relationship between *stansburiana stansburiana* and *stansburiana taylori* (Table 3) suggests that their similarity is a result of factors in addition to their common ancestry. *Uta stansburiana stejnegeri*'s progenitor supposedly developed from the same stock as *stansburiana taylori* and *stansburiana stansburiana*, yet *stansburiana stejnegeri* is significantly more divergent from *stansburiana taylori* and *stansburiana stansburiana* than *stansburiana taylori* and *stansburiana stansburiana* are from each other. The closer relationship of *stansburiana taylori* and *stansburiana stansburiana* may be a result of gene exchange following their isolation and subsequent expansion or to the incomplete or shorter period of isolation as compared to *stansburiana stejnegeri*, or to both. An unequal

evolutionary rate or differential time of separation could have produced similar results.

*Uta stansburiana stejnegeri* stock succeeded in replacing *stansburiana stansburiana* in Baja California, restricting *stansburiana stansburiana* primarily to the Great Basin. There is little doubt that this replacement was a result of rapid expansion of *stansburiana stejnegeri* rather than casual gene flow from east to west. Populations on San Martin Island, Magdalena Island, and in southern Baja California (e.g., La Paz) are morphologically scarcely distinguishable from *stansburiana stejnegeri* populations east of the Rocky Mountains, suggesting that *stansburiana stejnegeri* stock once inhabited the entire Baja California peninsula. Such a situation is not unique, for Davis (1951) has produced evidence that the southernmost populations of some towhees are more similar to eastern (Arizona and New Mexico) populations than to populations on Baja California or to other western populations. *Uta stansburiana stejnegeri* likewise displaced *stansburiana taylori* in Sonora, greatly restricting the continental distribution of the latter while influencing only one of the insular populations (Tiburón Island). The restricted distribution of *stansburiana taylori* in Sonora may indicate that *stansburiana stejnegeri* did not completely replace *stansburiana taylori* or that *stansburiana taylori* has subsequently reinvaded the mainland from nearby islands.

Partial or complete discontinuity between *stansburiana stejnegeri* populations east of the Rocky Mountains and *Uta* populations further west has restricted the gene flow between the two, allowing divergence of *stansburiana elegans*. This separation may have been more extensive during some past period, although even the present degree of separation is sufficient to have produced the same result. Gene flow from the zone of intergradation of *stansburiana stansburiana* and *stansburiana elegans* as well as from insular relicts of *stansburiana stansburiana* stock has resulted in the heterogeneous origin of *stansburiana elegans*. This gene flow likely has given *stansburiana elegans* its diagnostic separation from *stansburiana stejnegeri* and has resulted in at least partial state reversals in some characters (Figure 15). Although *stansburiana elegans* is a derivative of *stansburiana stejnegeri*, certain of its characters appear more primitive due to gene flow from the more primitive *stansburiana stansburiana*.

The exact time of each hypothesized period of *Uta* evolution is impossible to ascertain. In fact, additional periods may have been involved although only two periods of contraction of the deserts are required to explain the present distribution and relationships with the genus *Uta*. The fact that the most effective separation of the deserts occurred during the first glacial periods suggests that the segmentation of the populations was most effective in early Pleistocene, although this does not mean that later glacial periods were not sufficient to produce the same result. The relatively significant difference in skeletal characteristics of *Uta* and *Petrosaurus* (Etheridge, 1964) suggests a reasonably long period of development; however, if

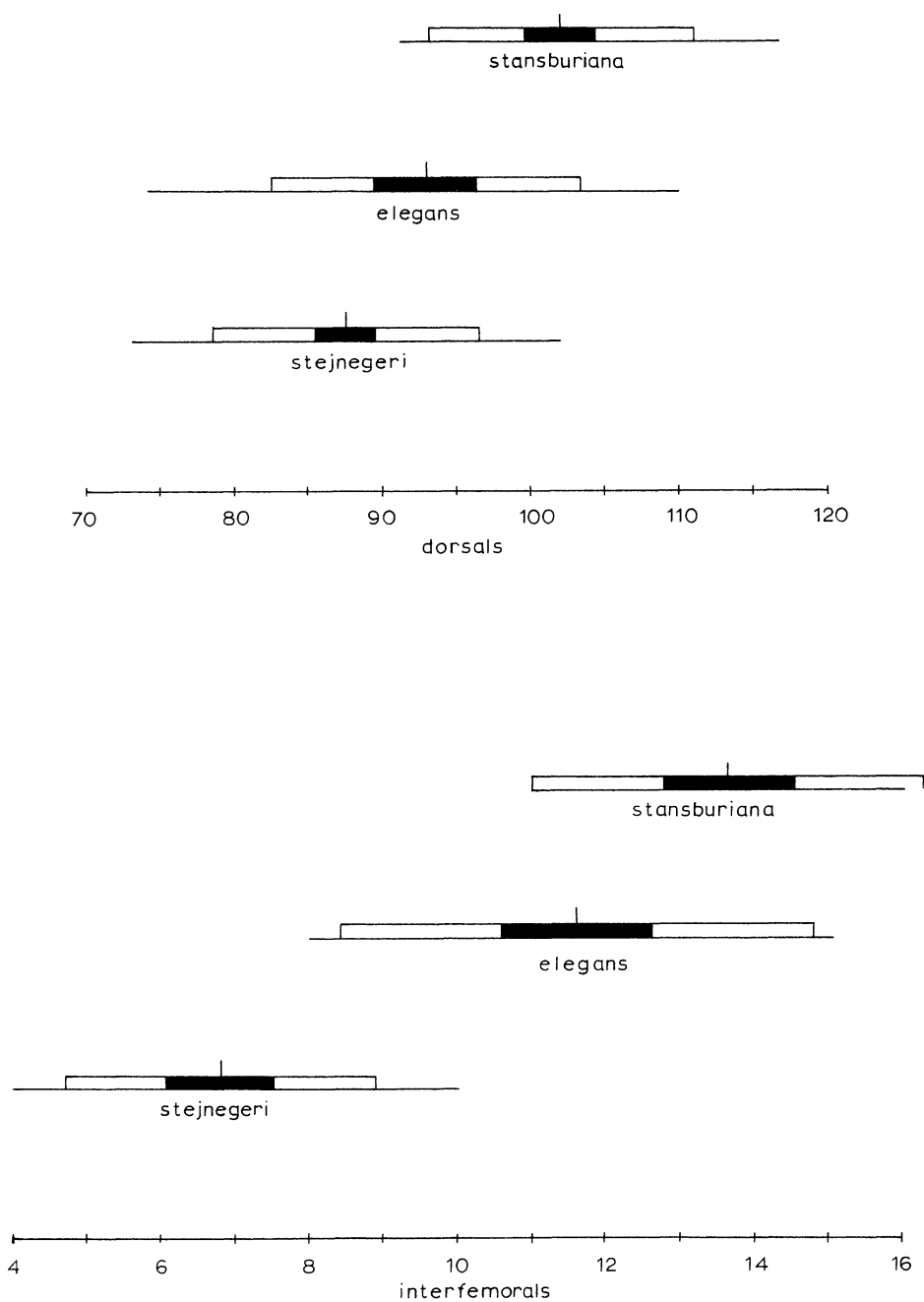


FIG. 15. Character state reversals. Interfemorals and dorsal scales in *Uta stansburiana elegans* as compared to *stansburiana stejnegeri* and *stansburiana stansburiana*. Explanation as in Figure 6.



only one additional glacial period (in addition to that resulting in separation of *Uta* and *Petrosaurus* stocks) resulted in the present configuration of the genus *Uta*, the remaining glacial periods somehow did not produce a similar influence on the distribution of *Uta*.

Because the shallow-water islands along the Baja California peninsula were connected to the mainland during the last glaciation it is unreasonable to assume that the mainland populations were unable to swamp these smaller insular populations so that any evidence of previous colonization was masked beyond recognition. However, as previously discussed, shallow-water island populations do show evidence of previous colonization. Some *stansburiana elegans* populations are more similar (see page 58) to *stansburiana stansburiana* than to their closest relative, *stansburiana stejnegeri*. Therefore, it is likely that the last expansion of *Uta*, involving the *stansburiana stejnegeri* stock, occurred after the last glacial period when the islands again became more isolated from mainland influence, and specifically from that of the spreading *U. s. stejnegeri*.

The difference between the number of glacial periods since the probable origin of the genus and the number of periods which we have hypothesized as necessary to explain the present distribution suggests one or two alternatives. Either there was a sufficient gap between the initial development of the genus and its most rapid radiation, or the evolution of the genus was much more complex with additional periods of development which are undetectable in the present distribution. The fact that there is a significant gap in the morphological relationship between *palmeri* and the remaining forms supports this latter possibility. Also, the significant gap between *stansburiana stejnegeri* and other *stansburiana* forms may be a similar indication of a broader time interval than is hypothesized. Nevertheless, the evolution and adaptive radiation of *Uta* seems explicable on the basis of the theory of relicts and "centrifugal speciation" (as discussed by Brown, 1957). This does not imply a special type of speciation process, but is a result of geographical speciation as championed by Mayr (1963). This model seems contradictory to that which has previously been proposed for the evolution of *Uta* (Soulé, 1966); therefore, an evaluation of the two theories seems necessary.

The two theories are not completely exclusive and have a number of complementary if not identical components, and indeed the "phenetic" relationships proposed are remarkably similar (compare Soulé's [1966] phenogram Fig. 2, p. 30 with the morphological relationships presented here). Both models suggest geographical separation and natural selection as the governing factors of divergence. The major disagreement lies in the interpretation of the origin (i.e., colonization) of the insular populations.

We suggest that different islands have been subjected to immigration by different mainland stocks and have proposed how such differences in these mainland stocks could have arisen. The islands have been continually subjected to gene flow from the mainland and since there has been a con-

tinual change in the mainland populations it is certain that stocks of different genetic constitutions have colonized various islands at different times. Because the shallow-water islands are subjected to a higher level immigration (than the deep-water islands) due to their proximity to the source of the different genetic stocks, they have continually undergone changes in the direction of the mainland stocks due to repeated colonization. In addition, the rate of change in the continental stocks has fluctuated due to their origin and divergence during population contractions. The colonization of the islands has likewise been cyclic with periods of distinctly different colonizing stocks (e.g., first *palmeri*-like, then *stansburiana*, then *stejnegeri*) rather than a gradual change which would be less detectable. The recognition of at least two founding stocks on the southern Gulf shallow-water islands supports our contention of cyclic colonization.

Deep-water islands have been subjected to a proportionately lower level of immigration due to their greater distance from the source (MacArthur and Wilson, 1963, 1967). Not only have these islands received less immigration, but the time interval between possible colonizations has been greater, so that the probability of resisting additional colonists has been enhanced because of the better adaptation of the insular populations to the particular island than would be expected of any recent immigrant form. These two factors alone would increase the probability that earlier stocks (therefore more primitive forms) would persist on deep-water islands versus shallow-water islands. The fact that more advanced forms occur on deep-water islands is an exception but is not incompatible with this theory. *Uta stansburiana elegans* occurs on the deep-water Tortuga Island. This is not surprising since Tortuga is the youngest island in the Gulf (of Pleistocene volcanic origin, Anderson, 1950) and likely was not available for colonization until very recently. Additional deep-water islands that have relatively advanced forms on them include Angel de la Guarda (*Uta stansburiana taylori*) and Santa Catalina (*Uta squamata*). Both islands are relatively large compared to other deep-water islands and might be expected to receive a greater number of immigrants due to larger land area. In addition, Santa Catalina is relatively close (25 kilometers) to the mainland compared to other deep-water islands. Other deep-water islands such as Partida Norte and Raza (both with *Uta stansburiana taylori*) are likely close enough to Angel de la Guarda as to behave as satellite islands while San Esteban (*Uta stansburiana taylori*) is sufficiently close to Tiburon Island to have received repeated immigrations from the latter. Therefore, the effect of differential colonization alone could account for the evolutionary and zoogeographic pattern observed in *Uta* regardless of what evolution took place on the islands after they were colonized. This model is essentially identical to the theory of relicts (Brown, 1957).

Soulé states (1966: 60) that "at least one theory with which the results (his) are completely incompatible, is the 'relict theory'." Since he does not discuss how his theory differs from the relict theory, he must interpret the

“distinctive peripheral isolates” (i.e., *palmeri*, *antiqua*, *stellata*, *nolascensis*) as not representing primitive, relict populations as suggested here but as “explicable in terms of the selective effects of the environmental variables” (op. cit., p. 60) he discusses. This is to say that the more isolated (deep-water island) populations are more divergent not because they are older or founded by a different mainland stock but because of their independent evolution in response to specific environmental conditions. It is reasonable that the insular populations have evolved independently due to different selective forces on islands of varying physiography, climatography, and biotic composition. To assume that the entire divergence of the populations is a result of these forces, one must assume that the islands were initially colonized by stocks of essentially the same composition. Not to assume colonization by similar stocks is to admit that differential colonization has occurred and that repeated colonization was probable, all of which is compatible with the theory of relicts. Soulé admits (1966: 51) that “populations on the deep-water islands probably have been extant for a considerably greater length of time than those on the shallow-water islands” and that “the probable lower rate of waif migration to them, together would account for the uniqueness of their populations.” This is not incompatible with the theory of relicts; therefore, from a zoogeographic standpoint the two theories seem to be in agreement. It is unfortunate that Soulé did not analyze the mainland populations and integrate these into his theory.

Because the two theories are in agreement with the theory of relicts from a zoogeographic standpoint, Soulé presumably must present data in his analysis of phenetic relationships to substantiate his contention that the theory of relicts is incompatible with his own theory of the adaptive radiation of *Uta*. He must show that the distinctive, peripheral, isolate populations do not represent primitive, relict populations. If we assume that the characters of the most primitive populations are indeed primitive, then judging from Soulé's (1966: 50) “phenogram” (cf. Mayr, 1965) of relationships among the populations, he must have considered those characters which are found in the complex of San Ildefonso, Monserrate, and particularly Carmen and Coronados (for reference convenience we designate these as Group A) to be most primitive. Group B (San Lorenzo, San Lorenzo Norte, Salsipuedes, Tonopah, and San Pedro Martir) is less primitive, while group C (Raza, San Esteban, Santa Catalina, Partida Norte, and Angel de la Guarda) and group D (Bahia de los Angeles, Espiritu Santo, Tiburon, San Jose, Tortuga, and San Francisco) are the least primitive and most derived. Considering the same groups, although our separation of them is somewhat different, we propose the evolutionary sequence B, C, A, D from most primitive to derived (Figure 12). Using his example of dorsal scales, we will attempt to trace the evolutionary development of this single character in the manner which his “phenogram” predicts. Using data from this analysis the mean numbers of dorsal scales are roughly 95 for group A, 91 for group B, 84 for group C, and 91 for group D.

The evolutionary sequence in the dorsal scales, therefore, appears to be a reduction in number until group D, where a shift to an increased number occurs. Considering the possible adaptive nature of the dorsal scales (Fox, 1948; Fox et al., 1961; Hellmich, 1951), this reversal of direction is not entirely unexpected. In this instance group B (which includes the primitive relictual populations in question) is indeed not the most primitive group. In an attempt to see if the same results are obtained when using additional characters, we will consider two characters which seem more useful in determining evolutionary relationship. Again using data from this analysis, the mean numbers of ventrals and interfemorals, respectively, for each group are 63 and 13 (A), 71 and 14 (B), 62 and 14 (C), and 63 and 11 (D). These data show an increase in the number of scales from A to B and then a decrease from B to D. Additional characters show a similar pattern. The occurrence of character state reversals is obvious and apparently common according to Soulé's model.

However, it has generally been considered that such reversals are uncommon (Sokal and Sneath, 1963). Character state reversals, exclusive of those observed in *Uta stansburiana elegans* (Fig. 15) that apparently result from intergradation, are extremely rare in *Uta*. The increased number of auricular lobules in the Partida Norte population (*stansburiana taylori*), the increased number of superciliaries in *Uta nolascensis*, and the increase in the number of loreals in southern *elegans* populations are considered character state reversals. All other character states in *Uta* conform to the general rule of evolutionary reduction.

The sequence and direction of character change that contains the fewest reversals are, in our view, the most probable. To accept Soulé's model of evolutionary development that the distinct peripheral isolates are less primitive than certain less distinct shallow-water island populations, we must accept the contradictions that character state reversals are common and that the probability that phenetically similar organisms are related is no more likely than that they are convergent.

## APPENDIX

## A—SUMMARY OF POPULATION SAMPLES

The numbers in the left column refer to population numbers shown in Figures 1 and 2.

Species	Population name in text	N	Locality
<i>Uta palmeri</i>			
1	San Pedro Martir	86	San Pedro Martir Island, Gulf of California, Mexico
<i>Uta antiqua</i>			
2	Salsipuedes	81	Salsipuedes Island, Gulf of California, Mexico
3	San Lorenzo Norte	80	San Lorenzo Norte Island, Gulf of California, Mexico
4	San Lorenzo Sur	48	San Lorenzo Sur Island, Gulf of California, Mexico
<i>Uta stellata</i>			
5	E. San Benito	50	East San Benito Island, Baja California, Mexico
6	M. San Benito	43	Middle San Benito Island, Baja California, Mexico
7	W. San Benito	46	West San Benito Island, Baja California, Mexico
<i>Uta nolascensis</i>			
8	San Pedro Nolasco	39	San Pedro Nolasco Island, Gulf of California, Mexico
<i>Uta squamata</i>			
64	Santa Catalina	63	Santa Catalina Island, Gulf of California, Mexico
<i>Uta stansburiana taylori</i>			
9	San Carlos	57	10 miles northwest Guaymas (Bahia San Carlos), Sonora, Mexico
10	Tiburón	51	Tiburón Island, Gulf of California, Mexico
11	San Esteban	43	San Esteban Island, Gulf of California, Mexico
12	Raza	45	Raza Island, Gulf of California, Mexico
13	Partida Norte	64	Partida Norte Island, Gulf of California, Mexico
14	Angel de la Guarda	44	Angel de la Guarda Island, Gulf of California, Mexico

*Uta stansburiana stansburiana*

- |    |            |    |  |
|----|------------|----|--|
| 15 | Inyo       | 49 | Nemo Canyon, Panamint Mtns.,<br>Inyo County, California        |
| 16 | Ada        | 41 | Snake River below Melba and<br>Swan Falls, Ada County, Idaho   |
| 17 | Elko       | 40 | Near Carlin, Elko County, Nevada                               |
| 18 | Duchesne   | 14 | Ioka and Roosevelt,<br>Duchesne County, Utah                   |
| 19 | Coconino   | 30 | Near Roaring Spring, Grand<br>Canyon, Coconino County, Arizona |
| 20 | Apache     | 25 | 20 miles west of Chinle,<br>Apache County, Arizona             |
| 21 | Rio Blanco | 14 | 2 miles south of Rangely,<br>Rio Blanco County, Colorado       |
| 22 | Mesa       | 53 | Colorado National Monument,<br>Mesa County, Colorado           |
| 23 | Montezuma  | 32 | 30 miles west of Cortez,<br>Montezuma County, Colorado         |
| 24 | San Juan   | 40 | Chaco Canyon National Monument,<br>San Juan County, New Mexico |

*Uta stansburiana stejnegeri*

- |    |            |    |  |
|----|------------|----|--|
| 25 | Armstrong  | 30 | 29 miles southwest of Claude,<br>Armstrong County, Texas |
| 26 | Winkler    | 60 | 6 miles south of Kermit,<br>Winkler County, Texas        |
| 27 | El Paso    | 17 | El Paso, El Paso County, Texas                           |
| 28 | Bernalillo | 47 | Albuquerque, Bernalillo County,<br>New Mexico            |
| 29 | Chaves     | 43 | East of Roswell,<br>Chaves County, New Mexico            |
| 30 | Socorro    | 25 | Socorro, Socorro County,<br>New Mexico                   |
| 31 | Otero      | 30 | Alamogordo, Otero County,<br>New Mexico                  |
| 32 | Hidalgo    | 28 | Rodeo, Hidalgo County,<br>New Mexico                     |
| 33 | Coahuila   | 45 | 13 miles west of San Pedro,<br>Coahuila, Mexico          |
| 34 | Durango    | 30 | 3 miles east of Mapimi,<br>Durango, Mexico               |

*Uta stansburiana elegans*

- |    |            |    |   |
|----|------------|----|---|
| 35 | San Benito | 32 | 2 miles southeast of Panode,<br>San Benito County, California |
| 36 | Kern       | 44 | 7 miles southeast of Weldon,<br>Kern County, California       |

37	Riverside	46	5 miles southeast of Oasis, Riverside County, California
38	San Diego	54	San Diego, San Diego County, California
39	Yuma	31	10 miles south of Cibola, Yuma County, Arizona
40	Puerto Peñasco	53	Puerto Peñasco, Sonora, Mexico
41	Guaymas	41	10 miles north of Guaymas, Sonora, Mexico
42	San Felipe	36	San Felipe, Baja California, Mexico
43	Ensenada	24	Ensenada, Baja California, Mexico
44	San Ignacio	36	San Ignacio, Baja California, Mexico
45	La Paz	46	La Paz, Baja California, Mexico
46	San Clemente	49	San Clemente Island, Los Angeles County, California
47	San Martin	55	San Martin Island, Baja California, Mexico
48	Todos Santos	49	South Todos Santos Island, Baja California, Mexico
49	Natividad	40	Natividad Island, Baja California, Mexico
50	Cedros	48	Cedros Island, Baja California, Mexico
51	Santa Margarita	26	Santa Margarita Island, Baja California, Mexico
52	Magdalena	42	Magdalena Island, Baja California, Mexico
53	Espiritu Santo	65	Espiritu Santo Island, Gulf of California, Mexico
54	Partida Sur	41	Partida Sur Island, Gulf of California, Mexico
55	San Francisco	59	San Francisco Island, Gulf of California, Mexico
56	San Jose	43	San Jose Island, Gulf of California, Mexico
57	Monserate	40	Monserate Island, Gulf of California, Mexico
58	Danzante	36	Danzante Island, Gulf of California, Mexico
59	Carmen	82	Carmen Island, Gulf of California, Mexico

60	Coronados	50	Coronados Island, Gulf of California, Mexico
61	Ildefonso	72	San Ildefonso Island, Gulf of California, Mexico
62	Tortuga	51	Tortuga Island, Gulf of California, Mexico
63	San Marcos	39	San Marcos Island, Gulf of California, Mexico

*Uta stansburiana stansburiana* x *stansburiana elegans* intergrades

65	Nye	50	Mercury, Nye County, Nevada
66	Washington	36	St. George, Washington County, Utah
67	Beaver	39	Newhouse, Beaver County, Utah
68	Millard	10	65 miles west of Delta, Millard County, Utah
69	Tooele	38	Grantsville, Tooele County, Utah

B—LIST OF QUANTITATIVE CHARACTERS

See text for discussion of each character.

No.*	Name
1	total femoral pores
2	interfemorals
3	dorsals
4	non-keeled dorsals
5	ventrals
6	gulars
7	large auricular lobules
8	total auricular lobules
9	circumorbitals
10	orbital papillae
11	percent postrostral scale rows=2
12	digital lamellae
13	maximum lamellar spurs
14	right labials
15	per cent prefrontals in contact
16	number prefrontals in series
17	per cent frontoparietal in contact
18	number frontoparietal in series
19	RSGSV—snout-gular length/snout-vent length ratio
20	RFMSV—femur length/snout-vent length ratio
21	RTBSV—tibia length/snout-vent length ratio
22	RFTSV—foot length/snout-vent length ratio
23	RTOFT—fourth toe length/foot length ratio
24	RDSV—number dorsal scales/snout-vent length ratio
25	RNKD—number of non-keeled dorsal scales/total dorsal scales ratio



- 26 RSV—number ventral scales/snout-vent length ratio
- 27 RGS—number gular scales/snout-gular length ratio
- 28 RLMT—number toe lamellae/fourth toe length ratio
- 29 frontal
- 30 supraoculars
- 31 scale rows between supraocular and superciliary
- 32 circumorbital rows at frontoparietal
- 33 circumorbital rows at parietal
- 34 circumorbital rows at frontal
- 35 internasals
- 36 subnasal
- 37 frontonasal
- 38 scale rows postcanthal to labial
- 39 gular fold scales
- 40 occipital rows
- 41 loreals
- 42 circuminterparietals
- 43 superciliaries
- 44 interpostanals

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\* Referred to in the text

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