

THE EVOLUTION AND SYSTEM-
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UMA AND ITS RELATION TO
THE EVOLUTION OF OTHER
NORTH AMERICAN DES-
ERT REPTILES

KENNETH STAFFORD NORRIS

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INTRODUCTION

THE LIZARD GENUS *Uma*, of the family Iguanidae, is composed of three species, one of which is divided into three distinct subspecies. All are referred to by the common name of fringe-toed lizards. The forms are *Uma scoparia* of the Mojave Desert of California, *Uma notata inornata* of the Coachella Valley of California, *Uma notata notata* of the California and Baja California portions of the Sonoran Desert, *Uma notata rufopunctata* of the Arizonan and Sonoran portions of this desert (see figs. 6, 7), and *Uma exsul* of the Chihuahuan Desert of Coahuila, central Mexico.

Fringe-toed lizards are medium-sized lizards (large adult males may reach 115 mm. in snout to vent length) and are seemingly completely restricted to a sand-dwelling existence. A number of remarkable adaptations are connected with the arenicolous habits of the genus. Most notable of these, but by no means unique to the genus, is a series of elongate valvular scales fringing the lateral edges of certain of the toes (see pl. 46). These fringes widen the toes, giving the animal additional support for locomotion on sand, and serve in effect as "sand shoes" (see Stebbins, 1944). The fringes also assist in movements beneath the surface of the sand (Cowles, 1941). Nasal valves restrict the entrance of sand into the nasal passages. The passages themselves are also specialized for desert living; they are convoluted and have absorbing surfaces which reduce moisture loss through the nasal openings (Stebbins, 1948).

Most of the forms of *Uma* are remarkably adept at burrowing in loose sand, even while running at full speed. This unique behavior pattern has been termed "sand swimming" by Mosauer (1932). *Uma* has several interesting adaptations related to this pattern. The head, body, and tail are quite broad relative to their depth. The head is wedge-shaped in profile, with the lower jaw inset in the upper. The post-brachial, prefemoral, post-femoral, and lateral caudal scales are enlarged, diagonally keeled, and acuminate. These scales seem to act, through movements of the limbs, to force the animal deeper into the sand during burrowing.

The color patterns of members of the genus are fairly uniform. The ventral surface is largely white. The dorsal pattern is a black reticulum, with a subsidiary brown reticulum in most cases, sometimes forming ocelli and sometimes partially assuming a lineate pattern, overlying a whitish or rusty background color. In the case of *Uma exsul*, the ocelli are nearly absent, being replaced by diagonal chevrons. *Uma* varies in color from one locality to another in response to the substrate color. This change is achieved by variations in the intra-ocular colored ring and by changes in background color. The concealing coloration of *Uma* is striking, being one of the best examples of this phenomenon among North American vertebrates.

Uma is almost wholly insectivorous, though small amounts of plant material are eaten occasionally.

The closest relatives of the genus *Uma* are *Callisaurus* and *Holbrookia*, in both of which there are members restricted to sand habitats.

The distinctive habitat of *Uma*, and its complete restriction to this habitat, make it possible to plot closely the total geographic range of the genus. For this reason very specific information can be obtained concerning the range of habitat conditions and habitat associates of *Uma*. This information, in conjunction with a consideration of variation within the genus, when correlated with the geologic history of the present habitat, makes possible a zoogeographic study of considerable precision. The present study is an attempt to integrate knowledge of the ecology, variation, and habitat history of *Uma* into a hypothetical evolutionary history of the genus.

Any zoogeographic study is beset with many difficulties at its beginning; all pertinent evidence must be marshaled and interpreted. Such pertinent information comes from many diverse fields such as ecology, taxonomy, paleontology, geology, and climatology. The justification of such laborious documentation of the history of a single animal lies in the hope that the story that is produced may apply to other animals and plants as well and thus contribute to the detection of fundamental patterns. In this

study one of the main tenets is that the history presented for the genus *Uma* applies for a large number of desert reptile genera, with relatively minor modification in each case.

This scheme is a composite of numerous discussions and seminars at the University of California at Los Angeles, and impressions formulated in the field. The field investigations reported here have involved in excess of 14,000 miles of travel in three years, including visits to all but two of the localities (Tepoca Bay and Laguna Mayrán) at which *Uma* is known to occur. Twenty-five new localities for the genus have been discovered, and the ranges of all forms have been redefined and extended.

I am most grateful to Dr. Raymond B. Cowles for his many suggestions during the course of this work. Dr. Carl Epling has contributed much to the biogeographical scheme presented here through discussions and seminars. I wish to thank Dr. Charles H. Lowe, Jr., who has provided assistance and companionship in the field on several occasions, and who has aided materially in the development of many of the ideas embodied in this study. Dr. Richard G. Zweifel has given me much valuable assistance. He has accompanied me during portions of the field work, and he has helped in many ways during the preparation of the manuscript. Others who have helped with the field work include Dr. Boyd Walker, under whose sponsorship the reconnaissance in southern and middle Sonora was carried out, Mr. R. D. Norris,

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THE ECOLOGY OF *UMA*

STEBBINS (1944) has gathered much information concerning the ecology of *Uma*. His discussion has dealt with the genus largely from the standpoints of behavior and morphology of individual animals. Relatively little new information concerning these aspects of the ecology of *Uma* are here presented. The main emphasis in the present paper is to define geographically the habitat conditions within which *Uma* lives.

Because *Uma* is confined to the deserts of North America and because it occurs in all the major physiographic subdivisions of these deserts, a description of these subdivisions is in itself a rough outline of the habitat conditions of the genus. First the deserts are briefly described, and then information pertaining strictly to the ecologic niche of *Uma* is presented.

THE DESERTS OF WESTERN NORTH AMERICA AND MEXICO

North American deserts are areas of extreme aridity; the evaporation rate exceeds the precipitation rate. There are great diurnal fluctuations in temperature, with characteristic high summer temperatures, which in the California deserts are accompanied by extremely low relative humidity and slight and sporadic rainfall. Vegetation is typically xerophilous and scrubby except when locally modified by ground water.

GREAT BASIN DESERT

The arid region of north to south trending mountains and enclosed basins lying between the Sierra Nevada and the Cascade Mountains on the west and the Rocky Mountains and the Colorado Plateau to the east is termed the Great Basin Desert. This area is a cold desert; winter temperatures average 20° to 35° F. (−6.7° to 1.7° C.) and summer temperatures 65° to 70° F. (18.3° to 21.1° C.). Most of this desert is 4000 to 5000 feet (1220 to 1524 meters) above sea level. It receives snowfall in winter and considerable wind in the springtime. Precipitation averages 4 to 8 inches (101.6 to 203.2 mm.) yearly.

The vegetation type characterizing the Great Basin Desert consists of semi-shrubs. Component plants are small and compact, with an indeterminate growing season. The vegetation of this desert has been described in detail by Shreve (1942).

Sand-dune situations in this area generally support very sparse stands of low vegetation. In the southern portions of the Great Basin Desert such plant genera as *Dalea*, *Franseria*,

Larrea, and *Prosopis* are commonly encountered.

All aeolian situations within the cold Great Basin Desert are uninhabited by *Uma*. In fact, the climatological characteristics listed for this desert can be considered as limiting to the genus *Uma*.

Uma scoparia occurs in the southern portions of Death Valley National Monument, California, an area that is sometimes considered a part of the Great Basin Desert. This northernmost salient of the genus lives at an altitude of approximately 1000 feet (304.5 meters) which is much lower than most of the localities on this desert. I feel that the climate of this locality, as well as its topographic features, place it within the province of the Mojave Desert rather than the Great Basin Desert. In adopting this point of view I therefore consider the genus entirely absent from the Great Basin Desert.

MOJAVE DESERT

The Mojave Desert is here defined in the following manner: It lies almost entirely within the State of California. The west border is formed by the southern Sierra Nevada, Tehachapi, and Sierra Liebre Mountains. The southern border is the San Gabriel, San Bernardino, and the Little San Bernardino Mountains and the north boundary of the Chuckwalla Valley. Eastward the Mojave Desert merges into the Great Basin Desert, but it is generally considered to terminate at the Piute and Ivanpah Mountains (see Baker, 1911). The northern boundary is indefinite

and is arbitrarily assigned to the southern Death Valley-Panamint Valley region passing westward to the Sierra Nevada through the Randsburg area.

The largest part of the Mojave Desert has an altitude of 2000 to 4000 feet, though some areas are near sea level, and occasional high peaks occur. There is no uniform orientation of the mountains in this desert. Winter temperatures average 40° to 50° F. (4.4° to 19° C.) and summer 80° to 85° F. (26.8° to 29.4° C.). Mean annual rainfall is about 4 inches (101.6 mm.), with greater precipitation in upland areas, and as little as 2 inches (50.8 mm.) or less annually in lowland areas. There is some snowfall and frost.

The northern border of the Mojave Desert nearly coincides with the northern limit of the creosote bush (*Larrea divaricata*). Munz (1935) and Shreve (1942) have defined this limit of the desert on the basis of the distribution of *Larrea*. *Larrea-Franseria* association covers about 70 per cent of the Mojave Desert. Typical of the higher slopes is the peculiar Joshua tree (*Yucca brevifolia*) which has counterparts in the Baja California Desert (*Yucca valida*) and in the Chihuahuan Desert (*Yucca australis*). The general vegetative life-form of this desert is shrubby, with semi-shrubs as an understory. The semi-shrubs are mostly similar to, or identical with, those of the Great Basin.

The dunes of this desert are commonly clothed with nearly pure stands of creosote bush. In the more moist dune situations such plants as desert willow (*Chilopsis linearis*), mesquite (*Prosopis chilensis*), and salt grass (*Distichlis* sp.) are common.

Uma scoparia is widespread on the Mojave Desert. The species is known to occur at 25 localities scattered over this area.

SONORAN DESERT

All the desert area south of the Mojave and Great Basin Deserts (excluding the northern Mesa Central of Mexico) is here included in the Sonoran Desert. This embraces the Colorado Desert of California, the southern deserts of Arizona, the deserts of Sonora, Mexico, southward to areas of arid subtropical scrub vegetation, and the Baja California deserts. It would seem difficult to characterize so large and diverse an area, yet

there are features common to the entire region. The Sonoran Desert is typified by small xerophyllous trees and a great diversity of succulents. Mature basin and range topography is general. Elevations are usually less than 1500 feet (457.2 meters). Precipitation occurs as winter rains and summer thunder showers outside California and adjacent northern Baja California; effectual summer rainfall is absent in these latter areas. Average annual rainfall ranges from 2 to 12 inches. Temperatures are less extreme than in the northern deserts, averaging 50° to 60° F. (10° to 15.6° C.) in winter and 80° to 90° F. (26.7° to 32.2° C.) in summer.

Transition from Mojave Desert vegetation to Sonoran Desert vegetation occurs in the vicinity of the Chuckwalla Valley in southern California. The change is striking; small trees become common, and the diversity of type is greatly increased. Stem and leaf succulents become common components of the vegetation. These include many types of cacti. Ironwood (*Olneya tesota*) and paloverde (*Cercidium* sp.) are common small-tree components that occupy the washes. Mesquites (*Prosopis* sp.) assume the stature of trees in contrast to their recumbent life-form on the Mojave Desert and northward. Southward into Sonora the density, height, and diversity of the flora become greater, and the desert finally merges with the arid subtropical scrub of the southern Sonoran and Sinaloan lowlands.

The diversity of types seen in the total flora of the Sonoran Desert is less evident in dune vegetation. Northern Sonoran Desert dunes are clothed largely by such perennials as creosote bush, white bur sage (*Franseria*), indigo bush (*Dalea* sp.), joint fir (*Ephedra* sp.), and incense bush (*Encelia farinosa*), plus numerous species of annuals. To the south the small trees are sometimes common in marginal dune situations. Paloverde (*Cercidium floridum*), iron wood (*Olneya tesota*), and mesquite (*Prosopis chilensis*) are often abundant.

The three subspecies of *Uma notata* (*U. n. notata*, *U. n. inornata*, and *U. n. rufopunctata*) occur on parts of this desert. Only the southern Baja Californian and southern Sonoran portions of the Sonoran Desert do not support populations of *Uma* so far as is known.

CHIHUAHUAN DESERT

This isolated desert is situated on the northern portion of the great tilted plateau known as the Mesa Central of Mexico. Elevations range from 3000 to 6000 feet (914.4 to 1828.8 meters). Summer temperatures average 80° to 85° F. (26.7° to 29.4° C.); winter temperatures, about 45° to 50° F. (7.2° to 10° C.), but sometimes they drop below 0° F. (−17.8° C.). The Mesa Central is the coldest province in Mexico during the winter months, as it is exposed on the north to winter winds from the Great Plains of the United States. In some higher parts of the area, frosts have been known to occur in eight of the 12 months. Relative humidity is low. Rainfall is seasonal, being concentrated largely in the summer months, when it occurs as violent thunder-showers. Ward, Brooks, and Conner (1936) give the average rainfall at the city of Chihuahua as 385 mm., or about 15 inches. There is some precipitation in every month of the year. In winter some of this falls as snow.

The climate and vegetative life-forms are quite similar to those of the Mojave Desert. The major difference lies in the period of precipitation; rainfall occurs predominantly in the summer in the Chihuahuan Desert and in the winter in the Mojave Desert.

The Chihuahuan Desert is florally distinct from the Sonoran Desert to the west. Shreve (1942) lists only three plants common to these two deserts in a list of the 12 most common forms of each desert. These are *Larrea*, *Fouquieria*, and *Prosopis*. This striking floral difference is indicative of the long period during which these two desert regions have remained isolated. The evolution of the genus

Uma also reflects this extended isolation, as is considered in detail below.

The only area from which *Uma* has been taken on the great Mesa Central of Mexico is in the vicinity of the dry lake shown on recent maps as Laguna de Mayrán, on an older map as the Laguna del Muerto (Schmidt and Bogert, 1947). Of this locality they say: "The dunes along the northern edge of the dry lake, Laguna de Mayrán, where the type and paratypes were taken, are relatively low, and composed of fine gray sand. They are not lacking in vegetation. Small mesquite shrubs (*Prosopis chilensis*) on the summits of the dunes provide cover for the lizards and presumably prevent extensive shifting of the dunes."

In summary, *Uma* occupies dune-sand localities on the Mojave, Sonoran, and Chihuahuan Deserts of North America but is absent from the Great Basin Desert. *Uma* can survive moderately severe low temperatures in its habitat, and the highest that exist in North America. This is not survival through physiological tolerance alone but also by means of behavior patterns which allow the lizard to locate and escape to temperatures in which it can exist.

It would appear that the genus has not invaded the numerous Great Basin Desert dune localities because of adverse climatic conditions. Winter rainfall allows cold to penetrate deep into sand dunes in this area. Summer maxima are possibly not sufficient to maintain *Uma*. There is no clue to the actual limiting factor as yet. The absence of *Uma* in this climatic regime is important in the consideration of the history of the genus during the ice advances of the Pleistocene.

SAND DUNES: CLASSES, DISTRIBUTION, AGES, MOVEMENTS, AND COMPOSITION

The genus *Uma* is represented on a large number of completely discontinuous dune localities (see table 1), often isolated by miles of rocky desert. No specimen of *Uma* has ever been captured more than a very short distance from these deposits of aeolian sand. Dr. R. B. Cowles (personal communication) reports capturing a juvenile *Uma* about 50 yards from the nearest dune sand. I captured an adult *Uma n. notata* about 50 yards from

Tule Wash Barchan, Imperial County, California, on January 19, 1957. These records represent the farthest a *Uma* has been taken from its habitat as far as I know. *Uma* is virtually ubiquitous on the dunes. Within a single deposit of sand *Uma* may be found on the hummocks peripheral to the main dune, on densely vegetated sand, and on sterile sand above limits of vegetation. *Uma* is, without doubt, totally restricted to a habitat

of wind-blown sand (in the western deserts at least; I have not observed *Uma exsul* of the Chihuahuan Desert), even juvenile migrations providing dispersal of only the most limited sort.

Questions immediately arise when these facts are considered: (1) How does *Uma* achieve dispersal between suitable habitats at the present time, if at all? (2) How did the genus originally invade the localities within its present range? (3) How long has the genus been composed of the isolated populations we see today? (4) What textures of sand and classes of sand deposits is *Uma* able to occupy?

The answers to these questions are to be found, for the most part, in determinations of the ages, movements, compositions, and histories of formation of the various dune localities. Extensive studies have been made of nearly every dune area occupied by *Uma* and a good many not occupied by the genus, in an attempt to answer the questions formulated above. These studies are summarized here. A more detailed report on the subject of desert dune sand is in preparation.

FORMATION AND CLASSES OF NORTH AMERICAN DESERT AEOLIAN DEPOSITS

Nearly all aeolian materials are derived directly from some type of erosional products. (A notable exception is the gypsum sand deposit of the Tularosa Basin, New Mexico, which is being produced by crystallization.) Before these products are incorporated in wind-blown deposits they are subjected to one to three intermediate sorting processes: (1) the source rock, by virtue of its composition, is eroded directly into "pre-sorted" dune material; (2) the erosional material is sorted by streams or flood waters and later deposited in stream or lake beds; (2) the alluvium is washed into seas or lakes and sorted by wave or tidal action. In western North America all three agencies have been active in sorting material that has subsequently come to rest in dunes. The first process seems to be least important. The only example known to the writer where this process has been of major importance is the dunes near the Vermilion Cliffs of southwestern Utah. There the dunes are derived directly from sandstone of aeolian origin, and thus the erosional material is well

sorted. These dunes are not inhabited by *Uma*.

The second, stream-sorting process has been responsible for nearly all the aeolian concentrations of the Mojave and probably the Chihuahuan Deserts and has been of major importance in the production of the Sonoran Desert dunes. In the Sonoran Desert, important portions of many of the dune deposits appear to have been derived from beach sands.

It is important to note that the lowest basin in each physiographic unit of the Mojave Desert, whether or not now connected by drainage to the other portions of the unit, generally contains the largest deposit of sand. In most cases this distribution seems to be related to paths of Pluvial drainage.¹ For example, the large sand deposits at Kelso, San Bernardino County, California (which are occupied by a large population of *Uma scoparia*), are immediately adjacent to the sump of the Mojave River; Cadiz Dry Lake, San Bernardino County, California, is the terminus of drainage in the Bristol-Lanfair Basin (also occupied by *Uma scoparia*); and the Rice Dunes, Riverside County, California (also occupied by *Uma scoparia*), seem to occupy what was the outlet point of the Mojave and Death Valley drainage during earlier pluvial times (Blackwelder, 1933; R. R. Miller, 1946). The observed regularity seems to be due to two factors: (1) alluvium carried in these drainages accumulates in the lowest place, resulting in greater sand accumulation there, and (2) sand-transporting winds usually blow in the direction of drainage and likewise tend to concentrate sand near the lowest place.

The types of sand accumulations on which *Uma* occurs that the writer has observed on the North American deserts are as follows: sandy plains, sand hummocks or accretion dunes, spring-formed dunes, barchan dunes

¹ The term "Pluvial" is used here in the sense of Hubbs and Miller (1948) who state, "We apply this name (capitalized) to the two or more stages, commonly assumed to be of late Pleistocene (Wisconsin) age, when the western basins were largely filled with lakes which have left definite records of their existence in the form of shore features. . . . We apply the term 'earlier pluvial' to former periods of humidity, so remote that the lakes then formed have left no clear-cut shore features."

(also called barchanes, barkhans, or *medanos*), longitudinal dunes (seif dunes), cliff-margin dunes, sand shadows and drifts, and blow-ups. All these types have been found to harbor *Uma*. Each of the types is considered briefly.

SANDY PLAINS

One of the largest deposits in the Sonoran Desert is of this type. The northern Gran Desierto of Sonora, Mexico, is in part a featureless, nearly level plain covered with a variable thickness of mixed silt and sand. Presumably this deposit resulted from the winnowing of fine sand from the old Colorado River delta (Youngs, 1929). Other sandy plains occur in various localities adjacent to large sand accumulations. Examples are found south of the Sperry Canyon Dunes in San Bernardino County, California, and the East Mesa adjacent to the Algodones Dunes in Imperial County, California.

SAND HUMMOCKS OR ACCRETION DUNES

This type of accumulation is universally peripheral to large deposits of sand. In localities of more limited sand supply, these deposits often form the chief expression of aeolian activity. The typical form of these accumulations is a sand pile within and around bushes. Where the direction of wind is constant, these deposits are oriented with regard to the wind source. The windward slope is composed of coarse sand and is usually truncated close to the base of the bush, while the leeward side, favored for basking by *Uma*, possesses a long stringer of fine sand. The greatest height of such an accumulation is usually within the bush. When sand accumulates around large bushes such as mesquites and desert willows, accretion dunes may reach heights of 30 feet (9.1 meters) or more (see pl. 44, fig. 1).

SPRING-FORMED DUNES

In a few localities, springs or seeps or near-surface water tables have increased plant growth to a marked extent. If these springs lie in the path of wind-blown sand, the vegetation serves to trap the sand in greater quantities than the surrounding, less verdant land. These deposits are actually modified accretion dunes, but they are always distinct be-

cause of their dense vegetation. The Newberry Dunes of San Bernardino County, California, the Indian Wells Dunes, Riverside County, California, and the Kane Spring Dunes of Imperial County, California, are of this type. All of these are occupied by *Uma*. The percolating effect of water from the springs probably has little or no direct effect on sand accumulation. Bagnold (1941) points out that the belief that sand has some miraculous power of drawing up water from the underground water table to an unspecified height by capillary attraction totally lacks support. He states that regardless of the amount of water below a sand layer, the surface tension of the grains is unable to lift the water more than about 15.7 inches (40 cm.). He attributes the moisture often found in barren dunes to preservation of rainfall owing to the extreme insulating properties of sand which prevent rapid evaporation. Moreover, it should be pointed out that the surface layer of sand in these moist dunes is invariably dry except in those dunes containing running springs. Thus, spring-formed dunes, which possess an internal supply of moisture, must accumulate sand by virtue of their vegetation except where the water reaches the surface.

BARCHAN DUNES

Barchans are crescentic dunes produced by unidirectional, sand-moving wind. The two horns of the crescent point in the direction towards which the sand is moving. The windward slope usually stands at a fairly low angle of repose. The highest point of the dune is at the center of the crescent. The leeward face is a concave crescent and stands at the maximum angle of repose of sand, in an active barchan. Barchans move as the wind rolls and blows sand grains over the windward contours of the dune, releasing them down the steep leeward slope, or *drop* slope, and by funneling them around the base of the dune and off the cusps.

Barchans are of particular interest; they have been used in dating the age of Saharan dune deposits by Bagnold (1941, p. 219). Their rate of advance is easily detectable, and thus movements of dune masses can be studied. They are of particular interest in relation to the history of *Uma*, as they are, in effect, a habitat that moves, and may have

been important in the dispersal of their resident biota. Barchans are incorrectly believed to be formed only on hard surfaces, but Bag-nold (*op. cit.*) gives an example of small barchans in sand valleys within a dune mass. Dunes of the barchan type have been observed at Sandy Beach, Imperial County, California, and near Sands, San Bernardino County, California. *Uma* has been captured on these dunes (see pl. 44, fig. 2; pl. 45, fig. 2).

LONGITUDINAL DUNES (SEIF DUNES)

This type of accumulation is formed by a bidirectional wind source. The dunes consist of longitudinal ridges often with irregular drop slopes, demonstrating their relation to barchans (H. T. U. Smith, 1949) (see pl. 45, fig. 1).

CLIFF-MARGIN DUNES

These dunes are found at the edge of sea cliffs. Greatest development is at the edge of the cliff. In general, these dunes do not extend far back from the cliff. Their occurrence at Puerto Libertad, Sonora, and Punta San Felipe, Baja California, and elsewhere can be explained by sand-bearing winds that blow towards the coast from upland valleys, the velocities of which are checked at the cliff edge by rising air at the cliff face. The prevalence of these updrafts along the sea cliffs is known to all who have watched sea birds soaring and circling in such places.

Lower seashore deposits, as those found at Punta Peñasco (inhabited by *Uma*) and Kino Bay, Sonora, Mexico, are formed largely by wave and tidal action, as evidenced by a high content of shell fragments (Holtenberger, 1913).

SAND SHADOWS AND DRIFTS

When sand-bearing winds are forced to rise, they are slowed and drop their sand. For this reason, large accumulations are often found on the lee side of hills and ridges. These accumulations are termed sand shadows.

When winds sweep down narrow passes or into gaps and then emerge into more open situations, the wind velocity is first increased, and sand transport is likewise increased temporarily, only to be reduced again, as velocity decreases when the air spreads out over the hill slopes. This process is termed funneling,

and the resultant deposits are called drifts. In some areas where sand accumulations are poorly developed, knowledge of these drifts can be put to good use in assisting collecting. On the western slopes of the Alvord Mountains, San Bernardino County, California, sand forms a thin veneer on the alluvial slope. By looking for gaps formed by two hills close to each other, one can travel to the areas of greatest sand accumulation without being able to see them. *Uma* was found to be far more common in these localized areas than anywhere else on the slope.

BLOW-UPS

When sand-bearing winds blow against a mountain face, they are slowed and sand is deposited. These deposits are actually a special kind of drift but are so widespread and so often inhabited by *Uma* as to deserve special attention. Often the sand extends up ravines and spills over the top to form a sand shadow on the other side of the ridge. Blow-ups are often intermixed with detritus from the mountain and thus are not so well sorted in some cases as the larger valley dunes.

MOVEMENT AND AGE OF DUNES

Several dune localities on the western deserts allow interpretation of the age or the movement of their sand deposits and hence may throw light on the distributional history of *Uma*. Some of these examples are cited below.

PISGAH CRATER, SAN BERNARDINO COUNTY, CALIFORNIA

The fresh lavas of this crater are believed to be of recent age. Thus the sands that now occur on the flows must have been deposited in the last few thousand years. The source of this wind-blown sand has not been determined. Sand has accumulated on the lava not by the encroachment of a large dune mass but by winds which carried relatively little sand at any one time.

KELSO DUNES, SAN BERNARDINO COUNTY, CALIFORNIA

The barchans of the Kelso Valley near Sands Siding, the cusps of which point eastward, are good evidence of eastward sand

movement. No estimates of speed of movement have been made.

In addition to the presence of "moving dunes" such as barchans, further evidence of movement within the main dunes at Kelso is offered by the complete obliteration of an old automobile road which connected Kelso and Amboy. This road, which passed between the main dune mass and a smaller, more easterly mass, was abandoned a number of years ago. It is now impossible to follow for more than a short distance, as it leads to an area of deep sand completely impassable to automobile traffic. *Uma scoparia* is common over the entire dune area.

NEWBERRY DUNES

A rather extensive deposit of dunes and sand hummocks occupies the floor of the Lower Mojave Valley, San Bernardino County, California, in the vicinity of the town of Newberry. Thompson (1929) has related this deposit to the water table which is close to the surface (10–15 feet) in the area covered by sand. The water table abruptly becomes much deeper at the eastern border of the dunes. Fairly dense plant growth, growing in response to the readily available water, has accounted for the sand accumulation. *Uma* is common on these dunes.

The presence of *Uma* on these dunes is of particular interest, as good evidence is available for the existence of a permanent Pluvial lake covering the entire area now occupied by dunes (Free, 1916; Ellsworth, 1933; Campbell and Campbell, 1937; Buwalda, 1914; Bode, 1937; Blackwelder and Ellsworth, 1936). Thus it is obvious that *Uma* must have invaded the dunes in post-Pleistocene time during or after the time the dunes were formed. As the dunes are now isolated from the nearest inhabited deposit by several miles of inhospitable terrain, it is interesting to speculate on the lizard's method of invasion.

DALE DRY LAKE, SAN BERNARDINO COUNTY, CALIFORNIA

An automobile road east of Dale Dry Lake has been rendered practically impassable by blown sand. This road passed between the Virginia Dale Mining District and the Rice (Blythe Junction) road. The direction of sand movement has not been accurately de-

termined but, if one can judge from the coarse texture of the sands west of Dale Lake, the movement is probably towards the south-east, a movement that would finally bring the sand to the large Rice Dunes. In this case, as in others mentioned, *Uma* has moved with the migration of sand.

PALEN DRY LAKE, RIVERSIDE COUNTY, CALIFORNIA

The surface of this playa was formed in Pluvial times. Dune sand has covered a large portion of the playa and seems to be moving in a southeasterly direction. Amid the large dunes at the southwest corner of the playa, stretches of the old playa surface can be seen underlying the dunes. *Uma* is common at this locality.

SQUEAKY SPRING-SANDY BEACH-KANE SPRING, IMPERIAL COUNTY, CALIFORNIA

A series of disjunct sand dunes of spring-formed and barchan type is located along the western edge of the Salton Sea, from McCain Spring southward to Kane Spring. In addition to these dunes that occupy the old Lake LeConte beach,² considerable sand has accumulated in three areas in canyons and depressions along the low ridge of hills separating the Cahuilla Basin from the Borego Valley. These latter deposits are located between Zacatón Spring and Harper's Well.

The barchan dunes near Sandy Beach are nearly perfect examples of this type of dune. The horns of the dunes indicate a northwest wind source. As J. S. Brown (1923) suggests, much of the sand material forming these dunes has been derived from old (Pluvial and recent) beach deposits. However, these do not seem to be the sole, or even the only, important source. Numerous wide washes dissect the hills west of the old lake bed, and large quantities of alluvium are deposited in their lower portions and on the old beaches. These must form important sources of aeolian material, as well as representing the probable pathway for *Uma*, between Clark Dry Lake and the Cahuilla Basin.

² Lake LeConte is the name given to all the various lakes that have occupied the Cahuilla Basin (Salton Trough) during the geologic history of the trough.

It is interesting that nearly all these western accumulations are below sea level.

A large body of evidence summarized by Hubbs and Miller (1948) indicates that the Cahuilla Basin has been filled intermittently by fresh water from the Colorado and by salt water from tidal action in the Gulf. The marked beach lines of the basin are the result of a Pluvial fresh-water lake. In recent time (estimated as between 1000 and 400 years ago) the Cahuilla Basin was occupied by a transient fresh-water lake that rose to the overflow level (Mendenhall, 1909b; Rodgers, 1939). Evidence also indicates a fairly recent but restricted salt-water lake (Hubbs and Miller, 1949).

If the Cahuilla Basin has been filled as recently as evidence suggests, then these dunes may have moved rapidly. Some of the dunes at Sandy Beach occur $4\frac{1}{2}$ miles below the old beach line. If the conservative estimate of 1000 years since the last high-level filling of the basin be used, these dunes have moved 23 feet per year. This figure is based on the assumption that the dunes were formed above the ancient beach line, though of course they all probably were not. Some of them are very close to the old beach edge. This beach line is close to the base of the hills in this area. Therefore we may assume that the average rate of advance of the barchans in this area is probably less than 23 feet per year. Mendenhall (1909a) indicates that two large dunes near McCain Spring are practically stationary. During the early stages of a barchan dune, movement is more rapid than in larger accumulations, which adds a further complication (Bagnold, 1941). At any rate, barchans have been shown to be moving dunes (Bagnold, 1941; van Dieren, 1934; Cornish, 1897), and their movements across the Cahuilla Basin during dry periods may have been an important source of sand for the great Algodones Dunes to the southeast. They may also have supplied an important mode of movement for populations of *Uma*.

ALGODONES SAND HILLS, IMPERIAL COUNTY,
CALIFORNIA (ALSO CALLED SANDY HILLS
OR YUMA DUNES)

The largest dune-sand deposit of California, and one of the largest in the United States, stretches along the southeastern bor-

der of the Cahuilla Basin for about 40 miles. This dune mass is the home of the largest existing population of *Uma n. notata*. The dunes are a long narrow series of ridges, with a maximum width of about 6 miles.

The sand hills, at their northern end, lie just above the old Pluvial Lake LeConte shore line. The large size and apparently stable nature of the Algodones Dunes and their position above the old lake lines all point towards a considerable antiquity. The deposit is certainly not post-Pluvial in origin and may have had its genesis in mid-Pleistocene after the recession of the Pliocene sea. Conditions favoring the formation of the Algodones Dunes were probably initiated with the development of the Cahuilla Basin. Most of its sands rest upon the deltaic dam of the Colorado River which isolated the Cahuilla Basin from the sea at the beginning of the Pleistocene.

The deposit represents the end accumulation of most of the wind-blown sand in the Great Salton Trough, a depression about 120 miles in length, flanked by great fault block mountains that reach altitudes of over 10,000 feet (3048 meters) at its northern end.

Before the present paved highway crossing the dunes was built, automobiles traveled across the sand on a plank road. This road was constructed of heavy timbers nailed to one another by means of large spikes, with a thick iron strip along each end of the plank. Since this road was abandoned in favor of the pavement, it has been twisted and ripped to pieces by the sand excavation and replacement.

The destruction of the Yuma Plank Road and the topography suggest a continual flux within the dune mass, but not necessarily migration of the deposit as a whole.

The Algodones Dunes appear to be of sufficient antiquity to have harbored *Uma* during a considerable portion of the Pleistocene. It seems probable that this population of *Uma* and the one on the Gran Desierto of Sonora, Mexico, may have acted as a reservoir of the genus during fluctuations and extinctions of the more transient habitat sites and their populations.

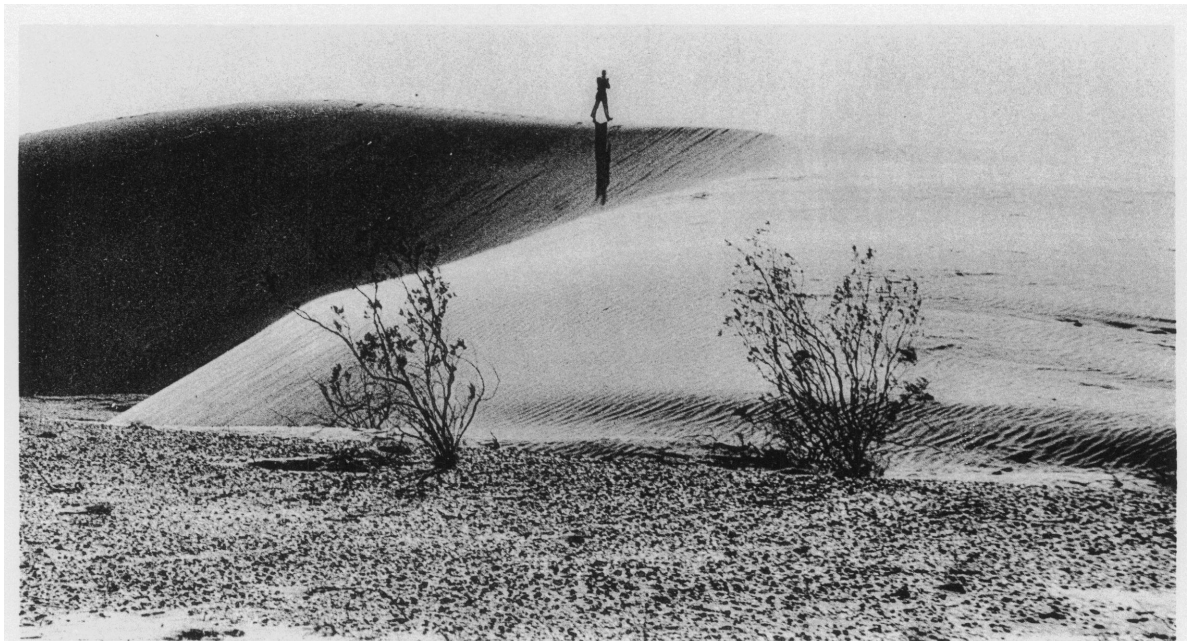
In summary, the ages of the various western desert dune masses occupied by *Uma* are often subject to reasonable approxima-



Uma notata notata, adult male, 107 mm. in snout to vent length. Captured at Lone Barchan, Tule Arroyo, Imperial County, California, January 19, 1957



1



2

1. Accretion dunes near 1000 Palms Junction, Riverside County, California
2. Barchan dune at Sandy Beach, west edge of Salton Sea, Imperial County, California

tion. In general, the small dune deposits adjacent to the playas of the desert seem to be of recent origin. Their sources can be traced either directly to the playa surface or to the reworking of materials from the old Pluvial beach dunes. Most of such dunes are small and in relatively instable situations which either do not allow the deposition of large quantities of sand or only foster deposits under rather specific wind conditions. A primary type of dune structure is uniformly exhibited by these dunes. H. T. U. Smith (1949) has pointed out that barchans, transverse dunes, and wind shadows are usually primary dune forms. These recent deposits include El Mirage, Harper Lake, Newberry, Alvord Mountains, Cronise Dry Lake, Devil's Playground, Silver Lake, Sperry Canyon, Saratoga Springs, Lavic Dry Lake, Pisgah Crater, Palen Dry Lake, Ford Dry Lake, Blythe Escarpment, Clark Dry Lake, Borego, North Pattie Basin, and South Pattie Basin.

The larger dune masses such as those at Kelso, Rice, Cadiz Dry Lake, and the Algodones Dunes probably antedate the last Pluvial period. The Cadiz Dunes occupy a portion of the playa of Cadiz Lake and must have been reworked since Pluvial times. No secondary dune morphology is apparent on any of these large dunes. Their size and position at the sumps of their respective Pleistocene drainage basins indicate a considerable antiquity.

When the present complete restriction of *Uma* to aeolian sand and the recent origin of many of the dunes on which it now occurs are considered, it must be concluded that at least intermittent connections between these deposits existed at one time or another in the immediate geologic past. These connections may have consisted of actual physical connection between two deposits or of migration by a segment of one deposit into another. The optimum period of dune-sand accumulation on our deserts would seem to be largely past. The optimum may have occurred during the waning of Pluvial times when desert streams were intermittent but carried more water than they do today, and hence more alluvium. The intermittency would have allowed winds to winnow the sands of these exposed stream courses. The largest transport of alluvium doubtless came during pluvial maxima, and

hence these may have been the times of maximum dune building. What is more probable is that in certain situations, as along long desert stream courses, such as that of the Mojave River, dune development was maximum during waning pluvial times, while in large lake-filled basins, such as the Cahuilla Basin, dune building was at a maximum during the height of pluvial times when transport of alluvium was greatest and longshore sand transport and sorting most active within the lakes themselves. Dune deposits may have been more or less continuous along river banks during these times. Since then deposits have been concentrated and stabilized and thus isolated from one another, the animals being isolated with them. Some minor genetic differentiation seems to have resulted in *Uma*, as is discussed in detail below.

Observed dune movements are adequate to explain the passage of *Uma* over low divides into unoccupied drainage systems. The genus occupies dunes on such divides today between the Amargosa River and the Mojave River drainages at Silurian Lake, San Bernardino County, California, and between the Laguna Salada and Cahuilla Basin drainages at Cerro Pinto, Baja California, Mexico.

SAND TEXTURES

In order to obtain information regarding the texture of the habitats upon which *Uma* occurs, sand samples from most of the localities discussed in this report have been analyzed for the extent of sorting (see table 1).

The samples tested were selected according to certain criteria. First, samples were taken from drop slopes wherever possible in order that the finest sand of the deposit might be obtained. At several localities (Coachella Valley, Dale Lake, Pattie Basin, and others) it was noted that *Uma* tended to select the areas of finest sand for burrowing. Thus the finest diameter present on the dunes is critical with respect to habitation by *Uma* (Stebbins, 1944, p. 314). For example, on the windward slopes of some of the dunes in the Coachella Valley, average grain size is greater than 1 mm., while on the lee slopes it may average only about 0.3 mm. *Uma* nearly always selects the lee slopes, and thus the sand-grain diameter of 0.3 mm. is taken as the critical measurement. The largest figure for minimum

grain size of the various deposits occupied by *Uma* is taken to indicate approximately the coarsest sand habitable to *Uma*. The degree of compaction sometimes affects the movements of *Uma*, but this factor is so sporadic that I ignore it in this classification.

Second, samples were taken from areas as far from the edges of the deposit as possible in order that contaminating effects of local alluviation might be avoided.

An Emery settling tube was used to obtain the sorting data. Poole and Butcher (1950) have shown that the data so obtained from sand samples are fully as accurate as data obtained by sieving. Sorting coefficients were calculated for each sample by use of the formula

$$S_0 = Q_3/Q_1$$

in which

$$\begin{aligned} S_0 &= \text{sorting coefficient,} \\ Q_1 &= 25\% \text{ coarser, } 75\% \text{ finer} \end{aligned}$$

and

$$Q_3 = 75\% \text{ coarser, } 25\% \text{ finer}$$

(Krumbein and Pettijohn, 1938). A sample of absolutely uniform grain size would give a coefficient of 1.0. All sands tested gave sorting coefficients indicating considerable uniformity of grain size compared to most alluvial materials. However, a significant range is shown by the sorting coefficients.

Several sand samples gave grain-size distribution curves which were bimodal (see table 1). In most of these cases either two periods of accumulation appear to have been present, or the deposit seems to have been built from two sources. For example, the sand at Bond's Corners, Imperial County, California, gives a bimodal sorting curve.

This deposit is located along the bank of the Alamo River and was inundated during the filling of the Cahuilla Basin in 1905-1907 when the present Salton Sea was formed. Consequently, wind-sorted sand is mixed with fine, water-borne silt. A similar sorting curve is shown by sand from the Gran Desierto of northwestern Sonora. The plain upon which a large part of this huge deposit rests was once a part of the Colorado River delta. The deposits have apparently resulted from wind sorting of sands from river-deposited material and consequently contain much silt. The bimodal curves of other deposits could have resulted from seasonal wind changes in velocity or source.

The coarsest sand on which *Uma* is known to occur was found at the west side of Dale Dry Lake, San Bernardino County, California. At this location the median grain diameter for the finest sand was 0.375 mm. The average median diameter for all localities tested was 0.205 mm. The finest sands were those at El Papalóte, Sonora, Mexico, with a median diameter of 0.11 mm.

Thus *Uma* occupies sands of which the grain sizes vary within relatively narrow limits. As grain sizes become larger, mechanical resistance to burrowing increases, burrowing being noticeably retarded in sand of 2-mm. average grain size (Stebbins, 1944). The tendency of sands to pack is increased as the average grain size becomes smaller. The cushioning effect of air between wind-borne sand particles prevents rounding of grains at about 0.08 mm. (Bagnold, 1941). Consequently sands composed of grains below this diameter are angular grained and are more subject to consolidation than are larger, rounded grains.

HABITAT SELECTION

Animals living in the most extreme portions of the desert are never active in more than a small fraction of the available temporal or thermal environment. Retreat of one sort or another (hibernation, estivation, or daily inactivity) is the unbroken rule for desert reptiles. In general, this retreat is caused by temperature extremes in both winter and summer. The highest critical maximum tem-

peratures for desert lizards are near 47.5° C. (117.5° F.) (*Dipsosaurus d. dorsalis*; Cowles and Bogert, 1944). They state that the lethal temperature for *Uma* is close to 45° C. (113° F.). The work of Fry (1947) has shown that determination of the biokinetic range of any species involves techniques that were not used in the pioneer work of Cowles and Bogert; thus these figures, which are the only

TABLE 1

SUMMARY OF LOCALITIES INHABITED BY THE GENUS *Uma* IN WESTERN UNITED STATES
AND NORTHWESTERN MEXICO

Locality	Drainage System	Estimated Size of Deposit ^a	Age Estimate	Predominant Vegetation	Median Sand Grain Diameter	Sorting Coefficient	Sorting Curve Class	Dune Types	Species in Occupancy
MOJAVE DESERT									
Peck's Butte and adjacent area	Mojave River (Pluvial)	200 acres ±	Recent	Creosote bush, Joshua tree, burro weed	0.178	1.44	Bimodal	Blow-ups, accretion dunes	<i>scoparia</i> ^b
El Mirage Dry Lake	Mojave River (Pluvial)	100 acres ±	Recent	Creosote bush, Joshua tree, burro weed	—	—	—	Blow-ups, accretion dunes	<i>scoparia</i> ?
Harper's Dry Lake	Mojave River (Pluvial)	2 or 3 square miles	Recent	Creosote bush, burro weed	0.180	1.60	Bimodal	Blow-ups, accretion dunes	<i>scoparia</i>
Hodge	Mojave River	½ square mile	Recent	Creosote bush, desert willow	0.210	1.57	Unimodal	Stream-edge, accretion dunes	<i>scoparia</i>
Daggett-Newberry	Mojave River	3 to 5 square miles	Recent	Mesquite, screwbean, desert willow, creosote bush	0.150	1.31	Unimodal	Accretion dunes	<i>scoparia</i>
Coyote Dry Lake	Mojave River (Pluvial)	2 to 3 square miles	Recent	Creosote bush, indigo bush	0.180	1.78	Bimodal	Accretion dunes, drifts	<i>scoparia</i>
Sperry Canyon	Amargosa River	5 square miles	Pleistocene?	Creosote bush, burro weed, indigo bush	0.218	1.55	Unimodal	Longitudinal dunes, interconnected barchans	<i>scoparia</i>
Troy Dry Lake	Mojave River (Pluvial)	Several small areas	Recent	Creosote bush, indigo bush	0.300	1.56	Unimodal	Sand shadows	<i>scoparia</i> ?
Cronise Dry Lake	Mojave River	1000 acres ±	Recent	Creosote bush, salt bush, desert willow	0.170	1.44	Bimodal	Accretion dunes, blow-ups	<i>scoparia</i>
Crucero flood plain	Mojave River	Large area from Afton Canyon to Bristol Dry Lake	Recent	Creosote bush, palo-verde, desert willow	—	—	—	Accretion dunes	<i>scoparia</i>
Silver Lake	Mojave River	10 acres	Recent	Creosote bush	0.285	1.42	Unimodal	Blow-ups	<i>scoparia</i>
Kelso Dunes	Mojave River	96 square miles	Pleistocene	Creosote bush, desert willow	0.230	1.22	Unimodal	Longitudinal dunes, accretion dunes, interconnected barchans	<i>scoparia</i>
Dale Dry Lake	Lucerne Trough	—	Recent?	Creosote bush, indigo bush	0.375	1.86	Unimodal	Accretion dunes	<i>scoparia</i>
Cadiz Dry Lake	Bristol-Lanfair Basin	40 square miles	Pleistocene	Creosote bush	—	—	—	Barchans, longitudinal dunes, accretion dunes	<i>scoparia</i>
Rice Dunes	Colorado River (Pluvial)	20 square miles ±	Pleistocene	Paloverde, salt grass, creosote bush, mesquite	—	—	—	Accretion dunes	<i>scoparia</i>

^a The sizes of sand deposits listed here come from three sources: from topographic maps when deposits are indicated, from literature references, or from estimates made by eye. They probably are useful only as an indication of order of magnitude.

^b Exterminated?

TABLE 1—(Continued)

Locality	Drainage System	Estimated Size of Deposit	Age Estimate	Predominant Vegetation	Median Sand Grain Diameter	Sorting Coefficient	Sorting Curve Class	Dune Types	Species in Occupancy
SONORAN DESERT									
Palen Dry Lake	Colorado River (Pluvial)	4 square miles ±	Recent	Tamarix, creosote bush, salt bush, salt grass	0.120	1.36	Unimodal	Interconnected barchans, accretion dunes	<i>scoparia</i>
Ford Dry Lake	Colorado River (Pluvial)	1000 acres ±	Recent	Salt bush, tamarix, creosote bush	0.20	1.78	Bimodal	Accretion dunes	<i>scoparia</i>
Blythe Escarpment	Colorado River	1000 acres ±	Recent	Mesquite	0.142	1.22	Unimodal	Sand shadows	<i>scoparia</i>
Thousand Palms	Cahuilla Basin	85 square miles	Pleistocene	Creosote bush, indigo bush, burro weed	0.285	1.94	Bimodal	Accretion dunes	<i>notata inornata</i>
Chuck-a-walla Ranch, north of Indio	Cahuilla Basin	Same deposit as Thousand Palms	Pleistocene	Mesquite, creosote bush	0.120	1.37	Unimodal	Accretion dunes	<i>notata inornata</i>
Sandy beach	Cahuilla Basin	—	Recent	No vegetation	0.123	1.25	Unimodal	Barchans	<i>notata notata</i>
Lone barchan	Cahuilla Basin	5 acres ±	Recent	No vegetation	—	—	—	Barchan	<i>notata notata</i>
Borego Dunes	Cahuilla Basin (Pluvial)	100 acres ±	Recent	Creosote bush, salt bush, burro weed	0.178	1.69	Bimodal	Accretion dunes	<i>notata notata</i>
Jaspar District	Cahuilla Basin	250 acres ±	Recent	Creosote bush, tamarix	0.159	1.26	Bimodal	Accretion dunes	<i>notata notata</i>
Algodones Dunes (north)	Cahuilla Basin	160 square miles	Pleistocene	Creosote bush, incense bush, buckwheat	0.225	1.13	Unimodal	Longitudinal dunes, interconnected barchans	<i>notata notata</i>
Pattie Basin (north dunes)	Colorado River (Pluvial)	100 acres ±	Recent	Creosote bush, joint fir, paloverde	0.138	1.15	Unimodal	Accretion dunes, sand shadows	<i>notata notata</i>
Pattie Basin (mouth of Tajo Canyon)	Colorado River (Pluvial)	35 square miles ±	Pleistocene?	Mesquite, joint fir, paloverde, tamarix, creosote bush	0.181	1.25	Unimodal	Accretion dunes	<i>notata notata</i>
Pattie Basin (south entrance)	Colorado River	Part of Pattie Basin (mouth of Tajo Canyon) deposit	Pleistocene?	Creosote bush, joint fir	0.192	1.24	Unimodal	Blow-ups, accretion dunes	<i>notata notata</i>
Yuma Mesa, at airstrip	Colorado River	—	Pleistocene?	Creosote bush, joint fir, burro weed	0.161	1.41	Bimodal	Accretion dunes	<i>notata rufopunctata</i>
15 miles south of San Luis, Sonora, Mexico	Colorado River	Very large, part of extensive Gran Desierto; perhaps 900 square miles	Pleistocene	Creosote bush, joint fir	0.187	1.63	Bimodal	Sandy plains, accretion dunes	<i>notata rufopunctata</i>
Punta Peñasco (beach)	Gulf of California	350 acres	Recent	Creosote bush, burro weed	0.196	1.37	Bimodal	Beach dunes	<i>notata rufopunctata</i>
El Papalóte	Gulf of California	Part of Gran Desierto; perhaps 900 square miles	Pleistocene	Mesquite, creosote bush	0.11	1.23	Unimodal	Accretion dunes	<i>notata rufopunctata</i>

available information for North American lizards, must be considered as close approximations. As the temperatures within the microclimate in which *Uma* lives often exceed 45° C., the genus is able to survive only because it possesses various morphological and behavioral adaptations which make possible control of its internal temperature. Prominent among these adaptations are ones related to burrowing.

The extreme summer temperature recorded for a locality inhabited by *Uma* is 54.4° C. (130° F.) at Amos, a railroad siding at the north end of the Algodones Dunes in Imperial County, California (Sprague, 1941). Actually this summer temperature does not present an accurate picture of the extremes of the habitat of *Uma*. The above record was taken in a standard weather shelter 5 feet above the ground. Temperatures are much greater near the surface where *Uma* lives. Cowles and Bogert (1944) report a surface temperature of 87° C. (189° F.) taken with a black-bulb thermometer during the last week in May when shade temperatures did not exceed 45° C. (113° F.). In July, in the same general area, I have repeatedly recorded shade temperatures (1 cm. above the sand) of 50° C. (122° F.) or higher in the middle of the day.

Also, the relatively mild winter temperatures of the deserts cause retreat of the reptile fauna. With the exception of certain small forms able to reach activity temperature ranges in a short period of time (i.e., *Uta stansburiana*, *Xantusia vigilis*), hibernation during the winter months is the rule (Cowles, 1941).

The winter-temperature extremes endured by the genus are approximately -17.8° C. (0° F.) (Sperry Canyon, Laguna Mayrán?). A winter-temperature extreme of -15° C. (5° F.) has been recorded as far south as Blythe, Riverside County, California (Sprague, 1941).

Although adaptations related to temperature control allow a sizable reptile fauna to exist in desert areas, the period during which reptiles may be active is often very restricted. The vacant thermal environments are open to invasion by animal types able to cope with the thermal problems these environments present. It is interesting that the reptiles that endure the highest environmental temperatures are vegetarians (i.e., *Dipsosaurus dorsalis* and *Sauromalus obesus*). Presumably a carnivorous type would be unable to invade the vacant environment until its prey had become adapted to this environment.

HABITAT ASSOCIATES

Few reptilian associates occur with *Uma* over its entire range. *Uta stansburiana* occasionally occurs on sand dunes in southern California and Sonora and probably in the Chihuahuan Basin. The genus *Cnemidophorus* is present to the limit of the vegetation on western sand dunes and is represented in the Chihuahuan Basin. The genus *Urosaurus* is now known to be closely associated with *Uma* almost everywhere. I have recently taken *Urosaurus graciosus* from the Sperry Canyon Dunes, 4 miles south of the northern record for *Uma*, and on the slopes of the Alvord Mountains a few miles east of Barstow, San Bernardino County, California. Of the western populations of *Uma*, only those at Wilsona, El Mirage, Harper's Lake, and Peck's Butte are outside the known range of *Urosaurus*. A recent record of *Urosaurus ornatus schmidtii* for the region of Parras, Coahuila

(Chrapliwy and Fugler, 1955, p. 124), extends the range of the genus south on the central plateau to include the area inhabited by *Uma exsul*.

The closest relatives of *Uma* are *Callisaurus* and *Holbrookia*. One or the other occurs with *Uma* everywhere. *Callisaurus* is present in the densest populations of *Uma* in very small numbers and is usually peripheral to these populations. *Callisaurus* has been noted on open sand dunes close to the limit of vegetation along the All American Canal in the Algodones Dunes. The association of members of the genus *Holbrookia* with *Uma exsul* may be similar. Schmidt and Bogert (1947) report finding *Holbrookia dickersoni* on the flats north of the type locality of *exsul* but state that it was not seen at the type locality.

The genera *Phrynosoma*, *Crotaphytus* (*wislizeni*), and *Coleonyx* are closely associated

with *Uma* throughout its range. Snake associates occurring over the entire range in the same habitat are *Crotalus* and *Masticophis*. The range of the genus *Arizona* is incompletely known, and it may well be a close associate over the entire range. At present it is not known from middle coastal Sonora, though it almost certainly occurs there, nor has it been reported from the southern portions of the Chihuahuan Desert.

The genera *Rhinocheilus*, *Leptotyphlops*, *Sonora*, *Pituophis*, *Lampropeltis*, and *Salvadora* occur over all or nearly all the specified range, but none is specifically limited to habitats of wind-blown sand.

It is obvious that the paucity of widespread associates is not due to a unique evo-

lutionary history but to highly specialized habitat requirements, with relatively few associates at any locality. The uniqueness of *Uma* lies in adaptation to a specific edaphic habitat within the desert climatic regime.

Though habitat associates are few, climatic associates occurring over the whole range include many genera of desert reptiles. In general, many of these genera must have arisen in genetic response to the same vegetative, climatic, and geologic changes that, through natural selection, have molded the genus *Uma*. It is to be expected that the histories of many of these desert reptiles will ultimately prove to be similar, in a general sense, to the history of *Uma*. This idea is expanded and documented in the section on biogeography.

CONCEALING COLORATION

Two main classes of coloration are found within the genus *Uma*: (1) sexual coloration, and (2) concealing coloration. Sexual coloration varies among the different forms of the genus, and because it is discussed at length in the descriptions of species and subspecies, it is not considered here.

Concealing coloration within the genus is highly complex and variable. It is best analyzed on the local population level. It has reached a remarkable degree of development in *Uma*, perhaps as effective as that of any North American lizard. There are apparent reasons for this development. The habitat of *Uma* consists of sand, generally remarkably uniform in color within the confines of each deposit. Thus color-matching adaptation can occur by use of genetic materials contributed by animals within the entire area of each locality. The areas of different sand deposits are highly variable, but the number of animals occupying each of them is usually large. Vegetation and other forms of cover are limited on most dune areas. A large part of the daily activity period of each animal is spent on open sand, without the protection of cover of any sort. Therefore the selective stress produced by predators towards development of concealing coloration is unusually intense.

Sand color varies considerably in different deposits. Sand source, nearness to source, age of deposit, and the size of the accumulation

all have an effect on color. In general, the presence of quantities of mica or heavy minerals produces grayish sands. Sands near their source tend to be poorly sorted, variable in constituent mineral types, and relatively unweathered (see fig. 1, upper). These factors make such deposits internally variable in color and more often whitish than deposits of which the sands have been transported long distances. Deposits distant from their source are usually uniform in color, as they are composed of grains of relatively uniform size and composition (see fig. 1, lower). The grains of such deposits are commonly covered with a rusty, iron oxide film. Old age deposits tend to be rusty in color for the same reason. Small deposits are easily contaminated by local alluviation and are often variable in color.

Thus the concealing coloration within the genus is that of populations that have adapted to local edaphic conditions.

Standard color analysis, using color dictionaries such as Ridgway (1912) or Maerz and Paul (1930), are not useful for the definition of variations of dorsal coloration in *Uma*, because this color results from the summation of a series of color patterns superimposed one upon another. The component colors are of minor importance compared to the resultant blended color.

The use of a General Electric recording spectrophotometer to record a summation of

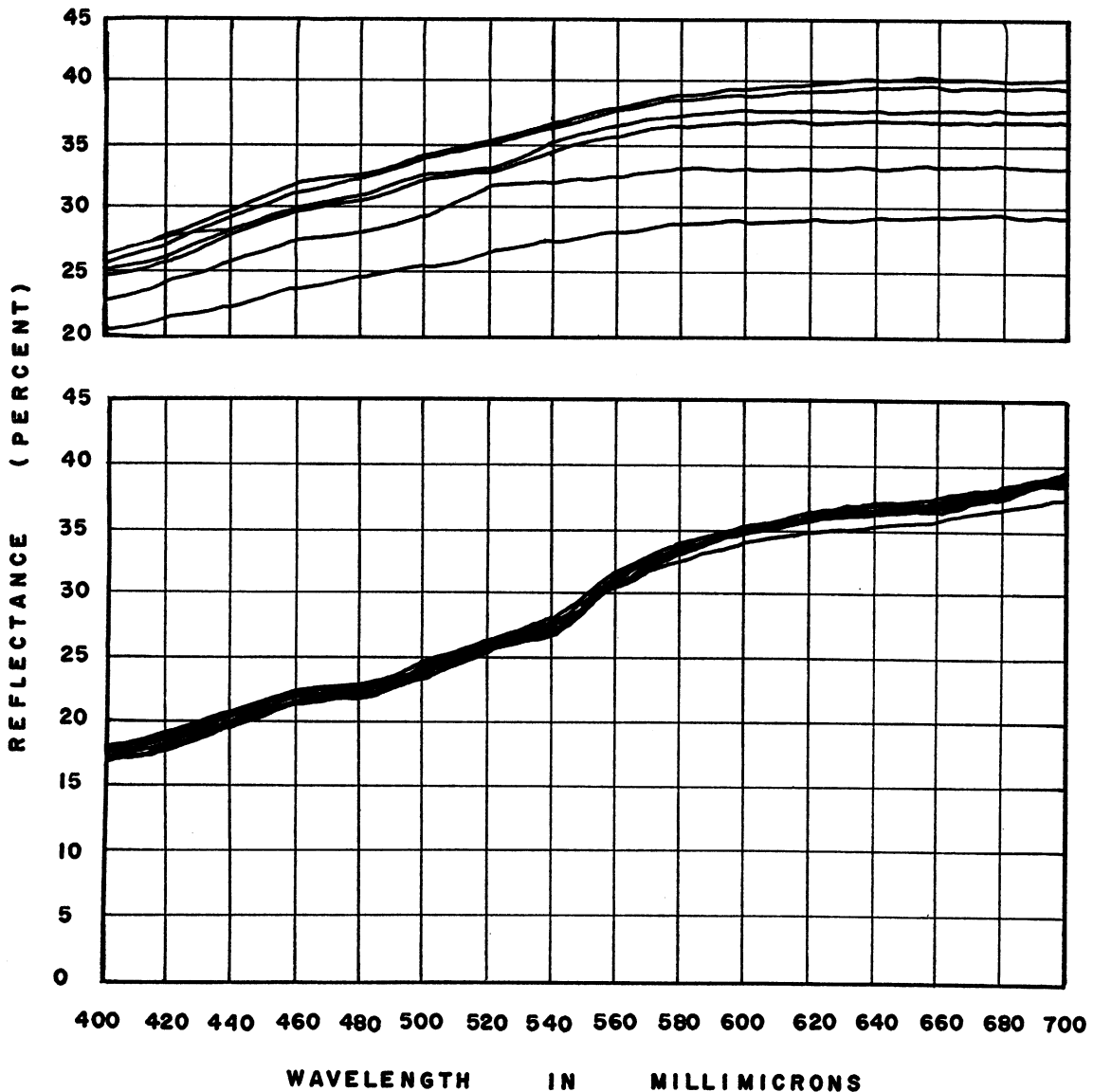


FIG. 1. *Upper:* Sand color, Thousand Palms Junction, Riverside County, California. Six samples taken at half-mile intervals. Note the wide color variation. This deposit is close to its various sources and is relatively unweathered and unsorted. *Lower:* Sand color, Algodones Dunes, Imperial County, California. Seven samples taken at half-mile intervals. Note the homogeneous color of this well-weathered and well-sorted deposit. Curves for a series of animals from these two localities closely approximate the conditions shown by the sand in each case.

the entire dorsal coloration of various lizards has proved simple and useful in the solution of this problem. This machine records either transmitted or reflected light. It consists of a source of white light which is directed through a prism which alternately shines the monochromatic beam on a white magnesium car-

bonate blank and through a transmittal chamber to a reflecting opening. If, as is the case with living animals, reflected light is to be measured, the test object is placed over the reflecting opening. The amount of reflected light is compared with the magnesium carbonate blank by a photoelectric cell which

controls a small electric motor driving a worm gear to which a pen is attached. Graph sheets are placed on a revolving drum geared to the selecting knife-edge, and the pen records the amount, in per cent, of each wavelength reflected as to that reflected by the white blank. The reflecting beam, which impinges upon the test animal, is approximately $1\frac{1}{4}$ inches in diameter, a size sufficient to allow summation of the colors of various components of the dorsal pattern of *Uma*. Substrate colors have been recorded by making a glass "sandwich" containing sand taken from the point of capture of the animal. To equalize the effect of reflectivity of the glass, similar sheets of glass were placed between the animal and the reflecting beam. The photometric accuracy of this machine is 0.5 per cent. It records the percentages of reflected or transmitted light from 400 to 700 millimicrons in either 2.5 or 5.0 minutes per reading. The former speed was used in this analysis because higher speed of recording might aid in summation.

In this brief analysis, the following methods were employed. When the colors of animals were recorded, a square of glass was taped over the reflecting beam orifice. Animals of which the dorsal area was sufficient to cover the reflecting beam were selected and placed between a spring-held clamp and the glass sheet covering the orifice. The entire photoelectric cell sphere and the animal were covered with a heavy black cloth to eliminate outside light. The animal was held in place while the reading was taken. When glass "sandwiches" containing sand samples were used, the taped glass was removed. All glass surfaces were cleaned prior to recording reflectivity. In cases in which it was desired to compare the animal and its substrate, the graph sheet was left on the machine, and both curves were recorded on the same sheet.

All animals were heated to activity temperature before their color was recorded. Cloacal temperature was recorded before and after each reading. It proved very difficult to control the body temperature of the animals while they were being tested. The change of color with changes of temperature in *Uma* is very slight, and the records presented here are thought to be virtually free from melanophore expansion effects (Atsatt, 1939) (see fig. 2,

lower). The control of body temperature of other animals, such as *Phrynosoma*, presents more difficulties.

To determine the exact percentage of reflected light of a given wave length, two corrections must be applied to the data presented here. The first correction involves the imperfect reflectivity of the comparison magnesium carbonate blank. Correction curves for the reflectivity of this material may be obtained in an article by Benford *et alii* (1948). At all wave lengths recorded by the machine, magnesium carbonate has a reflectivity of over 97 per cent. In the two-thirds of the spectrum nearest the red end its reflectivity is somewhat over 99 per cent.

The second correction is necessary to account for the absorbency of the glass plate that was placed over the reflecting opening during the recording of these data. This correction is presented in figure 2, as compared to a gray disc. These corrections need not be applied here, as the animal-substrate relationships are unaffected by them.

The population of *Uma* at Ford Lake (an area of very uniform sand color) is remarkably uniform in dorsal coloration (see fig. 3, lower). The dorsal color of the animals at Ford Lake closely approximates the color of the sand (see fig. 3, upper). The curve slope for the Ford Lake animals indicates a reddish coloration. The continued upsweep of the curve at the red end of the spectrum is typical of pinkish or reddish *Uma*.

Pisgah Crater near Ludlow, San Bernardino County, California, presents a unique situation with regard to color adaptation. The recent lava flow of Pisgah Crater has spread out over the desert in a series of jagged ridges 2 to 6 feet high near the edge of the flow. This lava is virtually unweathered and black in color. In the interstices between these lava ridges, light-colored, wind-blown sand has been trapped. *Uma* is common on this limited sand. The deposit is actually a network of little ridges and piles of sand heaped against the lava, and nowhere does it cover any considerable area. *Uta stansburiana* is common on the lava. The *Uta* is black and the *Uma* is one of the lightest forms occurring on the Mojave Desert. This example of adaptation to substrate color is even more remarkable, in one respect, than that pointed out by Benson

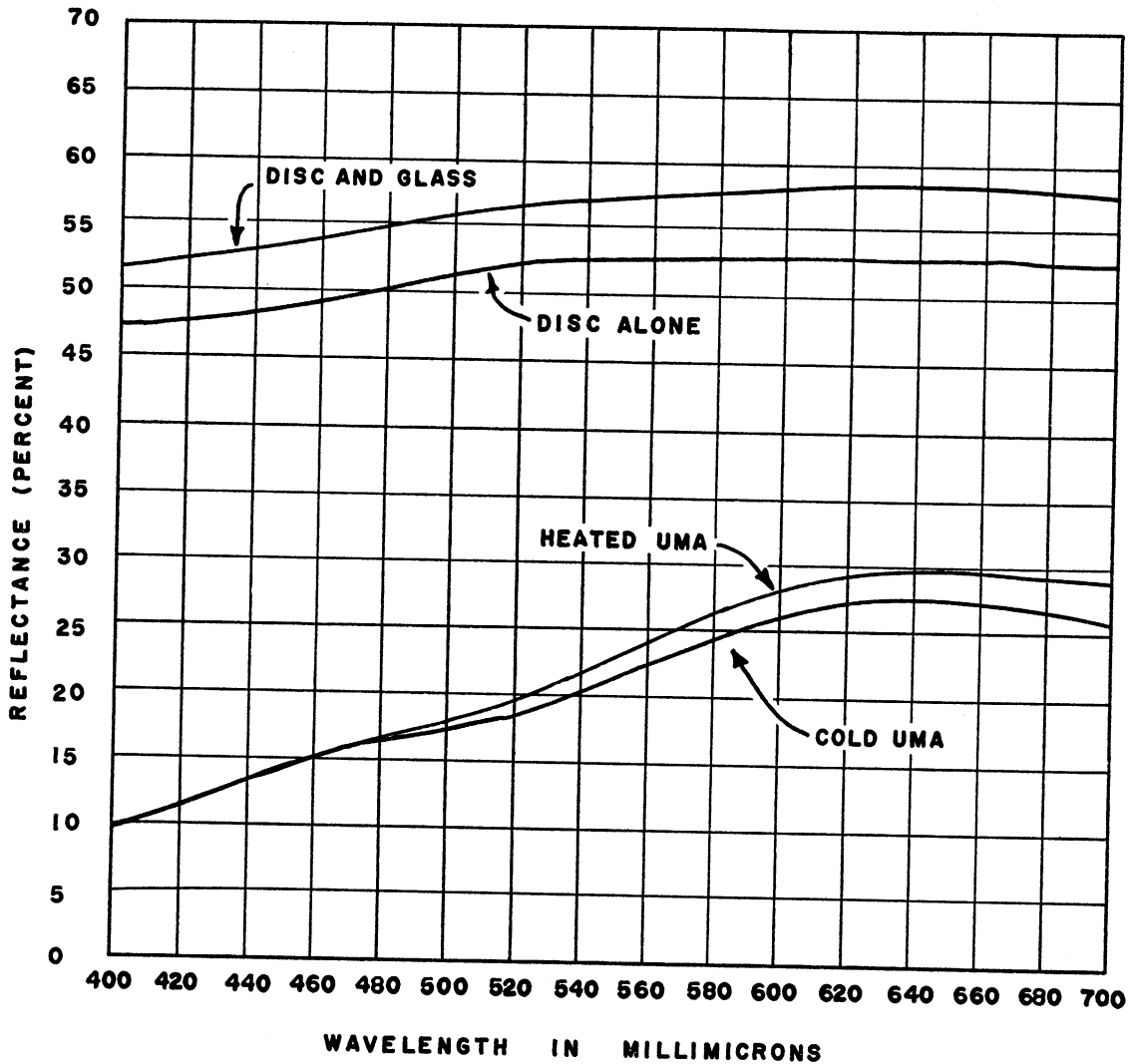


FIG. 2. *Upper*: Correction for glass sheet. The degree of increase in reflectivity caused by the glass plate is the difference between the two upper curves, or about 5 per cent for all wave lengths. *Lower*: Change in reflectivity of *Uma*. Note the slight shift at the red end of the spectrum (600–700 millimicrons). Cold *Uma* (start to finish): 24.2° C.–23.9° C. Warm *Uma* (start to finish): 38.2° C.–30.3° C. See text.

(1933) for the mammals of the White Sands and Carrizozo Lava Beds of the Tularosa Basin in New Mexico. In that case, black lava and white sand occupy two geographically distinct areas nearly in contact with each other. In this case, the habitats are interdigitated with each other completely and occupy the same area. Unfortunately, up to this time I have been unable to obtain adult *Uma* large enough to be used for spectrophotometric analysis. A similarly colored adult *Uma* was captured from near-by Newberry

Dunes and compared to the sand in figure 4 (upper). Even though the curves of sand and *Uma* are not closely matched they are similar in slope and highly different from the curves presented by *Uta* from the flows and the lava sample.

It would be desirable to compare animals from El Papalóte and Punta Peñasco, Sonora, for reflectivity differences. These two areas, within 3 miles of each other, support populations that have completely different dorsal coloration. The animals of the beach dunes of

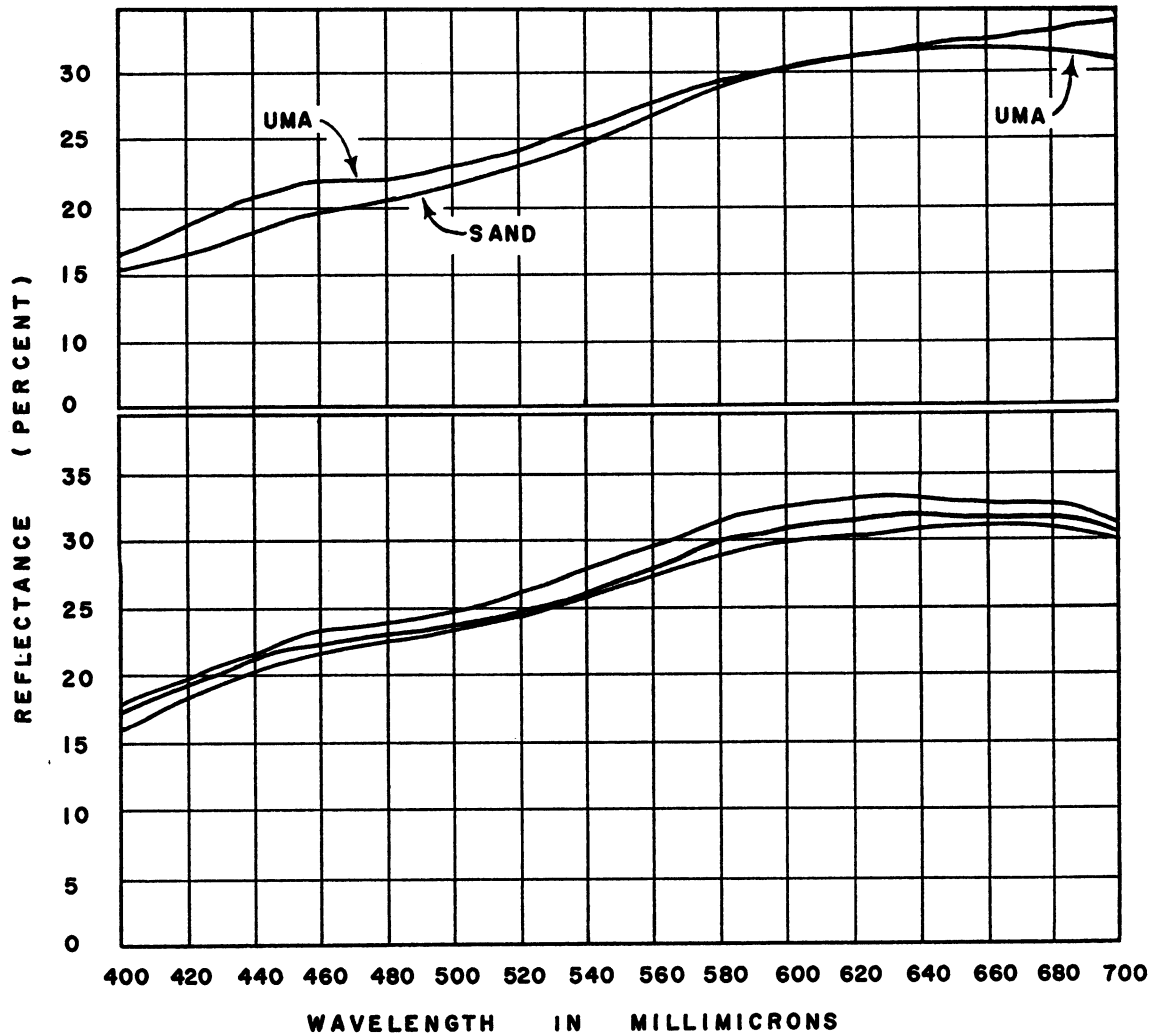


FIG. 3. *Upper: Uma and sand color. Uma scoparia*, Ford Dry Lake, Riverside County, California. Cloacal temperature (start to finish), 34.1° C.–32.3° C. *Lower: Dorsal color uniformity, Uma scoparia*, Ford Dry Lake, Riverside County, California. Cloacal temperatures (start to finish), (1) 33.8° C.–31.8° C.; (2) 33.0° C.–32.0° C.; (3) 37.0° C.–31.5° C.

Punta Peñasco are grayish white, while the inland El Papalóte animals are rusty in color. Again, living animals of sufficient size have not yet become available. This difference is of about the same magnitude as the difference shown in figure 4 (lower) in which a rusty-colored animal from the Ford Lake Dunes is compared to a white animal from Thousand Palms Junction.

The difference between the reflectivity of the venter and the dorsum of most species of ground-dwelling desert lizards is striking. The relationships are shown in figure 5. The adap-

tive significance of this abrupt shift in coloration is not entirely clear. Cott (1940) suggests that white ventral coloration might serve to reflect light into the shadows created by the animal and eliminate them to some extent, aiding concealment by making the outline of the animal more cryptic. Raymond B. Cowles (personal communication) points out that white surfaces faithfully reflect colors, whereas colored surfaces reflect only certain colors; thus a white-ventered animal will appear to be nearly the same color (ventrally) as any substratum upon which it rests. This conten-

tion has been borne out by subsequent field observation. Grinnell (1924) has suggested that the white coloration of the under parts of certain birds that feed in rock crevices and dark places aids the animal in finding food by

reflection of light into the darkness. It is difficult to conceive how such an explanation could apply to diurnal lizards which search for food on a uniform substratum such as a sand dune. Another explanation seems to of-

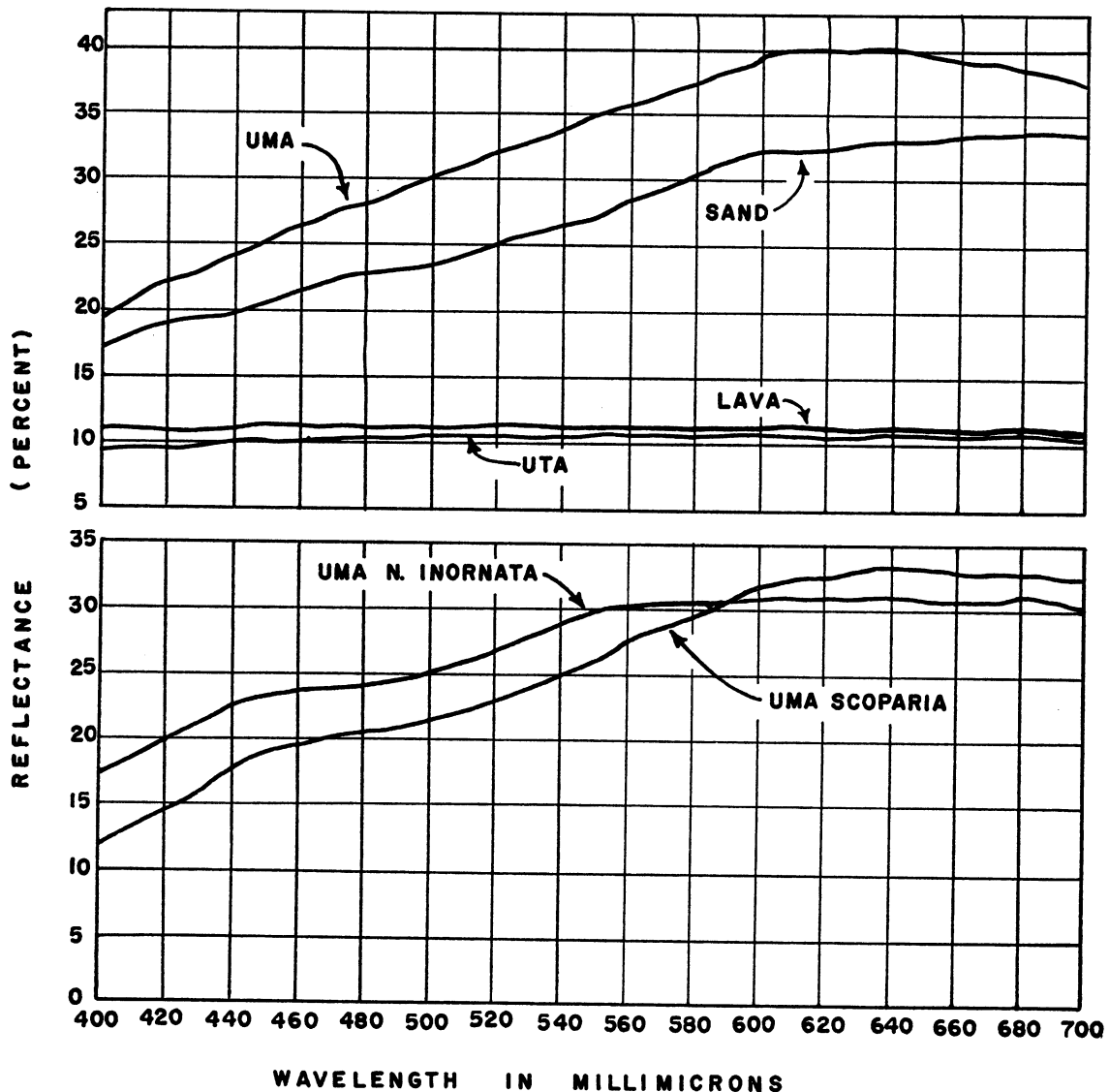


FIG. 4. *Upper:* Substrate color matching, Pisgah Crater, San Bernardino County, California. The lower curves are of black *Uta stansburiana* and the black lava upon which it lives. The upper curves are of the pale peach-colored sand interspersed among the lava flows and for *Uma scoparia* from the nearby Newberry Dunes. A specimen large enough to be tested was not taken from the Pisgah sand. The correlation between sand and animal would most likely be higher if a Pisgah animal had been used. *Lower:* Comparison of white and pink *Uma*. *Uma n. inornata* (white) from Thousand Palms Junction, Riverside County, California (start to finish cloacal temperatures: 33.1° C.–31.7° C.). *Uma scoparia* (pink) from Ford Dry Lake, Riverside County, California (start to finish cloacal temperatures: 34.5° C.–32.3° C.).

fer at least a partial solution. Some lizards, living in the coastal regions of California, show light ventral surfaces which contrast rather strongly with the dorsal color (i.e., *Phrynosoma coronatum*, *Sceloporus occidentalis*, *Uta stansburiana*, *Eumeces skiltonianus*). In each case, the contrast is much less striking than that demonstrated by desert forms. For example, consider *Callisaurus*, *Uma*, *Phrynosoma platyrhinos*, *Phrynosoma m'calli*,

and *Dipsosaurus dorsalis*. Could the pigmented white venter of ground-dwelling desert lizards be partly an adaptation for temperature regulation? The high reflectivity theoretically would allow the lizard to remain active on soils far too hot to be tolerated by a dark-ventered animal. The desert lizards mentioned above lift their bodies off the substratum during the heat of the day. They can be seen running along on their heels, with the

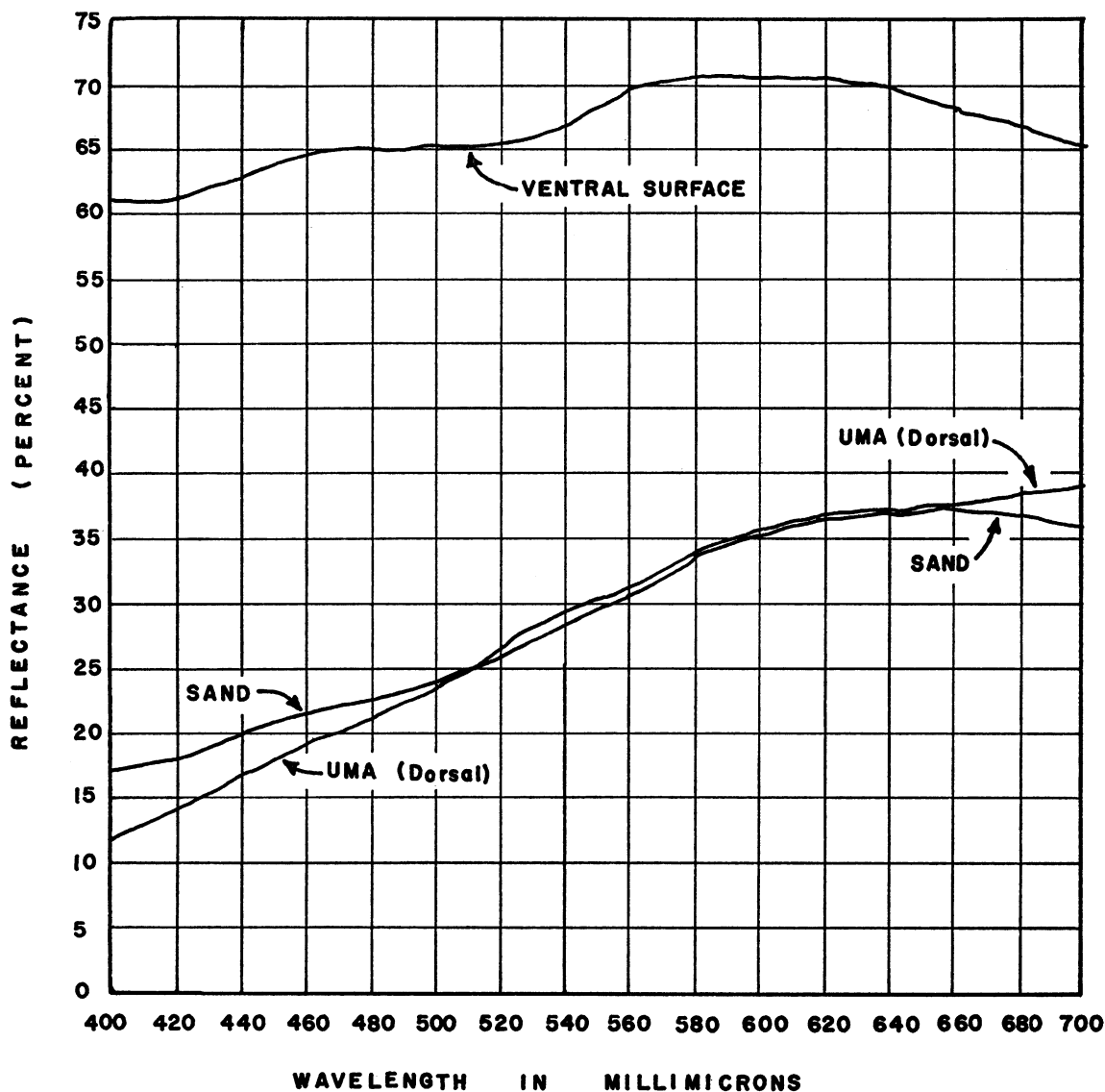


FIG. 5. Comparison of ventral and dorsal color matching. *Uma n. notata* from Algodones Dunes, Imperial County, California. Cloacal temperature (start to finish) 39.6° C.-33.4° C. Note the high reflectivity of the venter.

toes reflexed and the body well raised above the soil. Thus the soil-skin contact is eliminated, and heat conduction from the soil is prevented. Conducted heat is not affected by the color of surfaces in contact, but radiant heat is materially affected by surface color. Figure 5 shows that approximately 65 per cent of all incident light is reflected by the ventral white surface. Probably the explanation of white ventral coloration in diurnal desert lizards is that it is an adaptation to shadow elimination, color matching, and heat reflection.

As is noted above, the change in reflectivity of *Uma* with changes in temperature is very slight (see fig. 2, lower). Atsatt (1939) recorded little color change in *Uma* at high and low temperatures. It seems logical that reflectivity (albedo) changes in lizards are geared closely to their temperature regulating mechanism (Atsatt, *ibid.*).

When most species of lizards emerge from their retreats in the morning, they are both cold and dark colored. Theoretically, a dark animal is better able to absorb heat and thus warm up more rapidly than a light-colored animal. Of course, this idea is not new (Klauber, 1939; Atsatt, 1939), but if it is the

proper explanation, why is color change in *Uma* from a cold to a warm animal so slight? The answer lies, I believe, in the emergence habits of the animal. In the evening, *Uma* usually buries itself in unvegetated sand on a drop slope, if the sand concentration is large enough to produce such a formation. It remains in this situation during the night. The following morning, the sun warms the sand covering the animal and surrounds it with a warm medium which heats the lizard by conduction, regardless of its color. The lizard reaches its activity temperature range before emergence. In fact, *Uma* usually comes closer to the surface and thrusts its head partially out of the sand before emerging. A reluctance to emerge before a cloacal temperature of 26° C. (78.8° F.) was reached has been noted by Cowles and Bogert (1944) for individuals of *Uma n. notata* and *Uma n. inornata*. Among the temperature records I have accumulated, not one is below the range within which *Uma* is perfectly active. The seemingly anomalous lack of significant albedo change with temperature differences in *Uma* supports the theory that change in reflectivity is an adaptation for temperature control rather than argues against it.

SUMMARY

Uma is totally restricted to a habitat of aeolian sand, the finest sands of which are composed of material of median grain diameter no coarser than 0.375 mm. (Dale Dry Lake). The average median diameter for all localities tested is 0.205 mm. Very little material over 1 mm. or under 0.04 mm. was present in most of the samples. Locally, as on the windward side of sand hummocks, the median may exceed 1 mm.

Several sand deposits on the western deserts give evidence of movement. These movements are of sufficient magnitude to explain much of the spread of *Uma* in Pluvial and post-Pluvial times.

The dunes inhabited by *Uma* are all Pleistocene or recent in age so far as is known. Most of the small deposits are definitely referable to recent time, whereas a few of the large deposits appear to be older.

The dominant plant associates of *Uma* are

fairly uniform over the entire known range of the genus. Creosote bush (*Larrea divaricata*) and mesquite (*Prosopis chilensis*) occur with it over its entire range. *Ephedra* sp. and burro weed (*Franseria dumosa*) are common associates over most of the range of *Uma*.

Uma is the only diurnal lizard in North America known to occupy regularly areas totally barren of vegetation. Even *Uma* does not penetrate these sterile areas very far.

Reptilian habitat associates at any one locality are few and include various arenicolous species.

Predators include badgers, various snakes, such as *Arizona elegans*, *Crotalus cerastes*, and *Masticophis flagellum*, hawks, shrikes, road-runners, and coyotes (Stebbins, 1944).

The extreme habitat temperatures within the range of the genus are approximately -17.8° C. (0° F.) and 87.2° C. (189+° F.).

Uma is able to select and exist in a small

portion of the thermal range of its various habitats. This is accomplished by various morphological and behavioral temperature-control mechanisms. A close approximation of the "selected" environment of *Uma n. inornata* and *Uma n. notata* is given by Cowles and Bogert (1944) as follows: Minimum emergence temperature, 26° C. (78.8° F.); activity range, 35° to 40.5° C. (95° to 104.9° F.), with an average of 38.8° C. (101.3° F.). The putative lethal temperature is said to be "close to 45° C." (113° F.). These figures correspond closely with similar data gathered by the present author.

The localities occupied by *Uma* range in altitude from 244 feet below sea level (−74.3 meters) at the edge of the Salton Sea, Imperial County, California, to approximately 3700 feet (1127.8 meters) at Laguna Mayrán,

Coahuila, Mexico. The latter is the only known locality above 3000 feet (914.4 meters).

Rainfall in the various localities varies from no rain at all to 7 to 9 inches (213.4 to 274.3 mm.) during any one year. Precipitation occurs as winter rains in the western portions of the range and chiefly as torrential summer thundershowers in the Chihuahuan Desert.

The various populations of *Uma* show remarkable color adaptation to the dune sand upon which they live. This fact is seemingly correlated with strong selection towards color matching engendered by predator pressures in the open habitat of the genus. The white ventral coloration of diurnal desert lizards, including *Uma*, is suggested to be an adaptation to shadow elimination, color matching, and heat reflection.

VARIATION IN THE GENUS *UMA*

KEY TO THE SPECIES AND SUBSPECIES OF THE GENUS *UMA*

1. Dorsal pattern of reticulated black and gray lines, emphasized at intervals to form distinct diagonal black chevrons. A prominent black shoulder blotch. No subdigital scales between the fringes and the lamellae of the toes *Uma exsul*
Dorsal pattern of reticulated black and brown lines forming ocelli and sometimes emphasized to form interrupted lines over the shoulders. Shoulder blotch small or absent. Subdigital scales intercalated between the toe fringes and the lamellae of the toes . . . 2
2. Dorsal pattern of ocelli not emphasized over the shoulder to form interrupted black lines. Internasal scales usually five. Three enlarged black blotches in prefemoral pocket and on anterior surface of femur. Gular pattern of dark, posteriorly directed chevrons, widest medially *Uma scoparia*
Dorsal pattern of ocelli emphasized over the shoulder to form interrupted black lines. Internasal scales usually three. No enlarged black blotches in the prefemoral pocket or on the anterior surface of the femur. Gular pattern of thin, posteriorly directed chevrons, absent or faint medially 3
3. Ventrolateral black blotch wholly absent or evident as a minute cluster of black dots *Uma n. inornata*
Ventrolateral black blotch present, prominent 4
4. A bright, permanent, abdominal, ventrolateral, red patch (in adults), usually not evident in preserved animals. *Uma n. notata*
Abdomen immaculate in adults and young except during breeding season when it is tinged with pink along the lateral margins *Uma n. rufopunctata*

GENUS *UMA* BAIRD

Uma BAIRD, 1858, Proc. Acad. Nat. Sci. Philadelphia, vol. 10, p. 253.

Callisaurus COPE, 1896, Amer. Nat., vol. 30, p. 1049 (part).

RELATIONSHIPS: *Uma* is a small genus of iguanid lizards, most closely related to *Callisaurus* and *Holbrookia*. It differs from *Callisaurus* by possession of enlarged denticulate auricular scales, two to six in number, and a much larger and heavier body, two times more broad than deep at its widest point. In

Callisaurus, the body is much less broad in relation to its depth. *Uma* has a naked tympanic membrane and valvular digital fringes which separate it from the genus *Holbrookia*.

MORPHOLOGY: Body depressed. An abdominal cross section broadly rounded dorsally, ventrally flat or somewhat concave. Viewed laterally, the head is wedge-shaped. Dorsally, the snout is rounded and the head roughly V-shaped, widest at the angle of the mouth and narrowing very slightly at the neck. Abdomen reaching its widest point slightly over two-thirds of the distance from the axilla to the anterior insertion of the femur. Tail much depressed, slightly constricted at base (more evident in males than females because of hemipenes), broadening rapidly to maximum width and then tapering slowly to tip. Ratio of tail length to total length: 0.49 to 0.64. Lower jaw countersunk in upper. Maximum recorded total length: 244 mm. (*Uma n. notata*). A skin fold extends along the lateral edge of the body between the limbs. Front legs moderately long, reaching from two-thirds of the distance to anterior insertion of femur to slightly beyond the anterior insertion of femur, when adpressed to sides. Adpressed hind limb reaching between gular fold and snout. Lower and upper portion of hind limb approximately equal in length. The cloacal opening covered by a crescentic flap, occasionally triangular and overhanging the cloacal opening.

SCUTELLATION: Lower jaw bordered with a row of smooth, imbricate, diagonally placed, infralabial scales, 11 to 17 on each side. Anteriorly these rows are in contact with a medial series of larger, subrectangular, pavimentous, sublabial plates which become confluent laterally, along the lower surfaces of the jaw, with a series of four to six rows of similar scales. The anterior medial scale of this series, the post-mental, is triangular and either occluded posteriorly or passes between the two lateral scales as an elongate process or as a series of small fragmented scales. Medial to the sublabial series are the small flat plates of the gular area, granular at the contact and enlarging slightly at the center of the fold. A definite mental groove extends

posteriorly from the post-mental scale, one-third to one-half of the distance to the gular fold. This groove is further differentiated by extremely fine granular scales which line it. Gular area wrinkled into one or two indefinite transverse folds. Posterior margin of gular area limited by a transverse row of slightly enlarged scales forming a gular fold. Posteriorly several rows of fine granular scales about the fold. The scales of this series enlarge posteriorly and merge with the pectoral plates.

On the lateral surface of the head a canthal ridge of elongate carinate scales extends from the posterior corner of the eye to the lateral edge of the large, obliquely placed nostrils. Below the eye is a series of three to eight elongate, keeled, subocular scales extending from the posterior margin of the eye and making contact with the canthal ridge just anterior to the eye. The median scale of this series is often enlarged by fusion with adjacent scales of the series. The eyelids are covered with very small granular scales and fringed at the edge of the eye with a series of 10 to 15 elongate lappets or festoons. The upper jaw is bordered by a series of seven to 10 keeled supralabial scales. The enlarged half-circular or triangular rostral scale forms the anteriormost member of this series. The series ends at the angle of the mouth, where a patch of fine granular scales is located. The ear is fringed on its anterior margin by two to six enlarged, flat, acuminate scales or lappets. Post-rostral rows are small, generally two in number. Internasals are three to five. Other anterior cephalic plates are flat and fairly uniform in size. Supraocular scales are imbricate and smaller than scales of supra-orbital semicircles, 10 to 12 across the orbit. Supraorbital scales encircling supraoculars are largest anteriorly, becoming part of the anterior cephalic series, nearly always two rows at mid-orbit, separated from the enlarged inter-parietal scale by two to five scale rows. Inter-parietal scale rounded or flask-shaped, with a translucent central area bearing a parietal eye.

Prebrachial scales of shoulder are enlarged, imbricate, and slightly mucronate. Two or three rows of similar prebrachial scales extend the length of the upper arm and the upper part of the lower arm. Infrabrachials and infra-antibrachials small, slightly imbricate. Enlarged valvular digital fringes border both

edges of the second, third, and fourth toes, with approximately equal development on either edge of the toe, the largest scales being on the fourth toe. Patches of enlarged, rectangular, diagonally carinate scales are located on the anterior surface of the thigh, the posterior surface of the thigh, and the posterior surface of the lower hind leg. Fringes border both edges of the second, third, and fourth toes of the hind feet, much larger on the posterior edge of the toes. Fourth toe longest, approximately equal in length to lower hind limb.

Ventral abdominal plates imbricate, flat, triangular in shape, and truncated at the apex. Femoral pores larger in males than females, 18 to 47 in number. Medially, pores piercing an enlarged scale, with two smaller scales appended to its posterior margin. Often some enlarged scales in femoral pore row are not pierced by pores. Occasionally a double row of pores composed of smaller pores inset above, below, and between the larger pores. A post-cloacal row or rows of enlarged scales, usually composed of two large, semicircular scales in males and four or five less distinctly enlarged ones in females. Often completely absent in females.

The tail is ringed with slightly enlarged caudal whorls separated by four slightly smaller rows. Ventrally, the tail is covered with transverse rows of truncated, triangular, subcaudal plates which become narrower and more pointed posteriorly. Laterally, the tail is covered with rectangular plates, keeled diagonally, and acuminate at the dorsoposterior corner.

COLOR AND PATTERN: The gular area is striped with diagonal black lines converging medioposteriorly, either absent medially or thickest there. Posterior to the gular fold, a transverse line of indistinct gray blotches or none. Abdomen immaculate white except where marked by the lower portions of the ventrolateral black blotch. Small percentages of the specimens have two small black punctations medial to the anterior insertion of the femur, two small black spots anterior to the cloacal opening, or two small black spots at the lateral edges of the cloacal opening. The posterior one-half of the tail is marked with black blotches anteriorly which widen into transverse bands posteriorly.

The dorsal pattern is variable, being com-



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1. Longitudinal dunes extending from eastern slopes of Superstition Mountain, Imperial County, California

2. Miniature barchan dunes, Superstition Mountain, Imperial County, California. These small dunes were 6 inches across the cusps, on the average. They were composed of dry sand and were noted to move several feet per hour across a harder moist sand substratum. A miniature of typical interconnected barchan topography can be seen on left-hand side of picture. This topography results when the quantity of sand becomes great and individual barchans coalesce and is the most typical type found in large dune areas such as the Kelso and Algodones Dunes of California (see R. M. Norris, 1956)



Digital fringes of right hind foot of *Uma n. notata*

posed of a black reticulum of longitudinal interrupted lines, ocellations, or diagonal chevrons, with a subsidiary reticulum of brown or gray. Black shoulder blotches range from prominent to faint or absent. Three pre-femoral blotches are often present. Color matching with the substratum is remarkably well developed and usually a function of

changes in the secondary brown or gray reticulum and the background color. Dorsal color ranges from gray to reddish brown. Juvenile color closely resembles that of adults, though the pattern is more cryptic. Preserved specimens of juveniles often assume a bluish cast.

PROPOSED SYSTEMATICS

The specimens of *Uma* deposited in various museums have been collected from a remarkably small number of localities. Little has been recorded concerning the nature of the sand deposits upon which *Uma* occurs. Thus, at the beginning of this study, it appeared possible that overlapping, intergradient, or intermediate populations might be found. The gaps between the range limits of the western forms were not great, and their morphologic separation is such that the discovery of intergradation or overlap would not have been surprising.

Extensive field work in the critical areas has shown the disjunction between all forms to be more certain than ever. It now seems highly doubtful that populations showing intermediacy, intergradation, or overlap will be found. The problem of the relative systematic rank of these isolated groups remains.

The systematic problem presented by the genus *Uma* is of the most difficult sort. Statistical analysis has revealed major and minor levels of difference. The fact that all forms are completely isolated eliminates the possibility of obtaining direct criteria for name giving. The systematics of such a group must be based on the opinions of the taxonomist.

Once relationships within a group have been elucidated, the problem of defining those relationships in the hierarchy might seem a secondary matter. This is not true. Names are one of the most important products of such a study; they are important for the connotations they carry. It is the duty of a name giver to use the facts as he sees them to devise a name that will reflect those facts to the largest number of biologists. Unfortunately, the connotations carried by taxonomic names vary widely with different taxonomists. It is said of the taxonomic species that

it should reflect the phylogenetic history of the form, the absence of interbreeding, actual or potential, the degree of morphologic differentiation, and that it should imply the presence of dichotomous characteristics. For a matter that is opinion to a large extent, this compounding of demands upon systematics reduces the system to a mass of names derived not only from taxonomic intuition but also from the particular school of thought to which each systematist belongs.

Reptilian taxonomy is one of the more orderly portions of classification. As I see it, the trend in cases in which forms are isolated has been to make the species represent a degree of differentiation comparable to that of species based on overlap criteria. This sort of species difference can be perceived, whereas to base a taxonomic name on "potential interbreeding" is to carry this perception one step further by making an untestable inference from it (Myers, 1950). Taxonomic names said to be based on potential interbreeding criteria are actually based on differences of one sort or another which impress the particular student. The method of arriving at names is the same for those based on "levels of difference" or "potential interbreeding." I can see no reason for including the insupportable assumption of presence or absence of "potential interbreeding" in the connotations of a taxonomic name.

The named forms of *Uma* recognized in the current taxonomy are all 100 per cent distinct from one another on the basis of at least one morphologic characteristic. The degree of distinctness of each of the nominate forms is quite variable (see table 2). *Uma exsul* is the most deviant form. *Uma scoparia* also stands by itself, though it is more closely related to *Uma n. notata*, *Uma n. rufopunctata*, and *Uma inornata* than to *U. exsul*. Of the first three

forms *scoparia* appears to be most closely related to *U. n. rufopunctata*. *Uma n. notata*, *U. n. rufopunctata*, and *U. inornata* appear closely related to one another.

Variability within some of the nominate forms has been detected. Most of these differences are color variations developed as genetic responses to different sand colors.

These color variants are duplicated in widely separated areas and across specific barriers. Certain scutellation and pattern variations have been noted within the species *scoparia*. These either are very limited, small-population effects or are trends of such minor magnitude that naming them would magnify their true importance. Within *Uma n. rufopunctata*

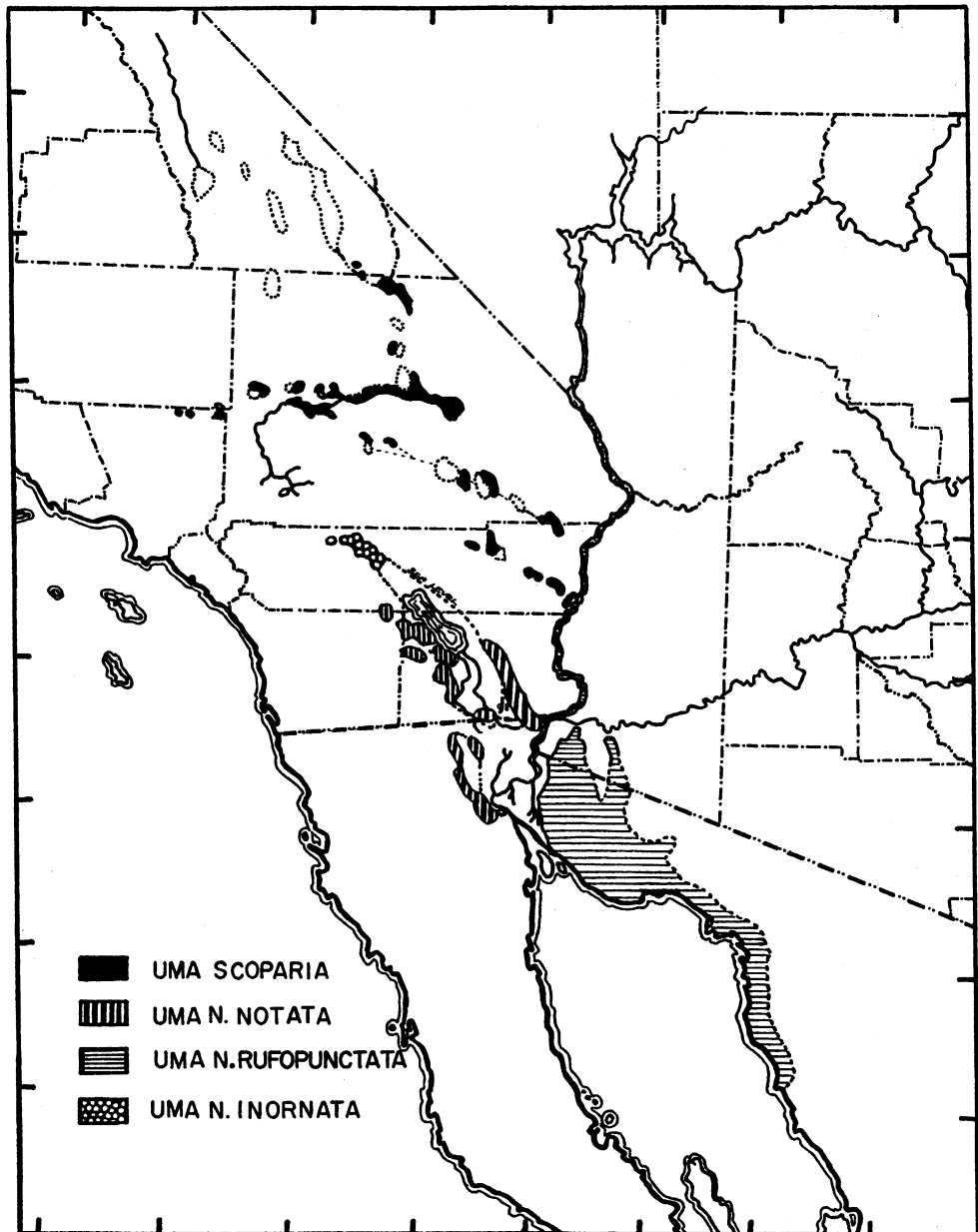


FIG. 6. The occurrence of the genus *Uma* in the western United States and western Mexico. The localities for *Uma exsul* in Coahuila, Mexico, are not shown.

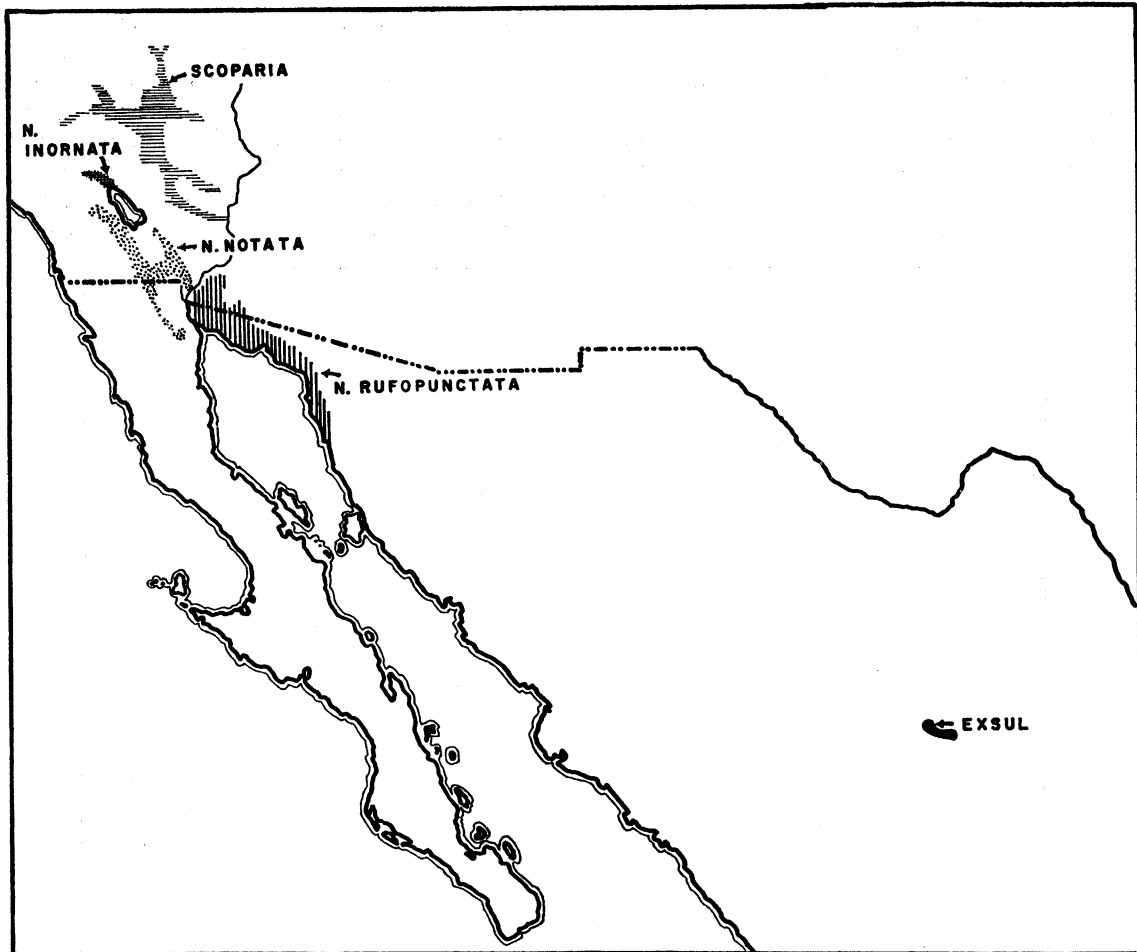


FIG. 7. Range map for genus *Uma*, showing location of the isolated populations of *Uma exsul* in relation to the western forms of the genus.

there is a wide difference in ventrolateral blotch width, the Tepoca Bay animals being rather strikingly different. When more collecting has been done in the area it may become advisable to recognize another form within the presently defined range of *U. n. rufopunctata*. Series are not now on hand that could be used adequately to define a new entity.

Three major levels of difference exist within the genus *Uma*. Considering these levels in relation to the rest of reptilian taxonomy, I propose that *Uma exsul*, *Uma scoparia*, and *Uma notata* be recognized as species. In addition, I propose that *Uma notata* include the subspecies *notata*, *inornata*, and *rufopunctata*.

The only changes from present nomenclature suggested are that the species *scoparia* be revived and that Cope's *rufopunctata* be revived for the form presently called *Uma notata cowlesi* Heifetz. *Uma scoparia* is the most distinctive of the western forms and is felt to warrant specific rank.

The name *rufopunctata* was applied by Cope (1895) to a *Uma* from the "Yuma Desert, Arizona." The redefinition of the range of the Sonora-Arizona form throws Heifetz' name "*cowlesi*" into synonymy. It is possible that it will be revived when more is known of the Sonoran coastal *Uma* from which he described it. These taxonomic changes are followed in the remainder of this paper.

MATERIALS AND METHODS

This variational study is based on the examination of 446 preserved animals. Of this number about one-third were collected by the author, and many more than the total were observed in the field but not captured. All measurements were taken on preserved material. Live specimens of all forms except *Uma exsul* have been maintained in the laboratory. The numbers of each form examined are as follows:

Uma n. notata, 154
Uma n. inornata, 64
Uma n. rufopunctata, 96
Uma scoparia, 125
Uma exsul, 9

The counts and descriptions of *Uma exsul* given by Schmidt and Bogert (1947) were used in this analysis. The small series of *exsul* was used as comparative material. In the statistical analyses, the series were limited to 50 animals, chosen at random except when the data required groupings such as all adults or all females.

Measurements were taken with double-break dividers and a millimeter rule. The limit of accuracy is approximately 0.25 mm. Scale counts were made with the use of a dissecting microscope where necessary. Color variation was studied by use of both a Maerz and Paul color dictionary (1930) and by use of a General Electric recording spectrophotometer.

Sexes were determined by three criteria used for all specimens: first, sexual pattern dimorphism was noted; second, postanal scale configuration was checked; and third, internal examination was made. At times, the determination was difficult on small specimens.

The following determinations were made for each specimen: Snout to vent length, sex, interparietal scale shape, number and configuration of femoral spots, number of groin

blotches, presence or absence of enlarged shoulder blotches, width of base of tail, femur length (from medial femoral pore to knee), tibia length (knee to instep), gular to mental length (gular fold to anterior edge of mental scale), internasal scale count, supraocular scale count (across the center of the orbit), blotch width (width at lateral fold), width of head at posterior corner of the eye, anterior canthal separation (distance between the outside edges of the anterior canthal scales), upper arm length (from mid-body at level of shoulder to inside elbow when limb was held at right angles to body), number of scales in the lower eyelid, femoral pore count (where doubling occurred it was noted, and counts were made without the extra scales being taken into consideration, as doubling is considered to be a separate characteristic from femoral pore count). The scales of the normal and doubled rows may be differentiated. Pore scales not pierced by pores were not counted. The digital fringe was counted (from first elongate fringe scale at base of toenail to last keeled scale of same row on the fourth digit of the hind foot).

Special measurements and counts were made on specimens of *Uma scoparia* in addition to those done for all animals. They are as follows: configuration of post-gular spots, configuration of post-mental scale, width of head at angle of jaw, interparietal to rostral length, configuration of the supralabial scales, number of complete gular crescents, and the number of scales separating the interparietal and post-parietal scales.

Statistical analysis was made with the use of a Friden automatic calculator. All figures were calculated twice to insure accuracy. Some of the measurements listed above do not appear in the following systematic summary. These did not prove of use in the elucidation of variation within the genus.

ACCOUNTS OF SPECIES AND SUBSPECIES

Uma exsul Schmidt and Bogert

COAHUILA FRINGE-TOED LIZARD

Uma exsul SCHMIDT AND BOGERT, 1947, Amer. Mus. Novitates, no. 1339, p. 1, figs. 1, 3, 4; type A.M.N.H. No. 67404, 12 miles north of San Pedro de Las Colonias, Coahuila, Mexico.

DIAGNOSIS: A highly distinct member of the genus *Uma*, most closely related to *Uma scoparia*. Of the members of the genus it is the closest to *Holbrookia* and *Callisaurus*. A dorsal pattern of reticulated black lines emphasized at intervals to form diagonal chevrons when viewed from above. Internasal scales usually four. A prominent black shoulder blotch. No small subdigital scales intercalated between the toe fringes and lamellae.

DESCRIPTION: Dorsal pattern, "reticulating black lines, emphasized at intervals to form diagonal lines or chevrons when viewed from above, enclose lighter colored areas that may be round or elongate, without a dark spot in the center" (Schmidt and Bogert, 1947). Ventrolateral blotch present, produced dorsally and becoming connected with a dorsal chevron. Ratio of snout to vent length to blotch width ranging from 20.3 to 26.3, mean 22.9 ± 0.82 . Gular fold marked with thin black chevrons, absent or faint at mid-gular region. Internasal scales usually four. Festoons of lower eyelid ranging from 11 to 14, mean 12.6. Interparietal scale subtriangular or rounded, bordered posteriorly by slightly differentiated post-parietal scales, separated from the interparietal scale by one to two rows of smaller scales, or in contact with it. Auricular lobules usually two. Ratio of snout to vent length to humerus length ranging from 3.57 to 4.06, mean 3.77 ± 0.05 . Round black shoulder blotches always present, very conspicuous. Groin blotches three, continuous with dorsal chevrons. Third groin blotch extending onto prefemoral scales. Femoral pores ranging from 19 to 28, mean 24.8. Doubling of pore rows not noted to occur. Post-femoral gray bars (yellow-orange in life) present in 100 per cent of specimens. Precloacal or lateral cloacal spots not noted to occur. Fringes on posterior edge of fourth toe of hind foot ranging from 31 to 40, mean 37.0. Fringes and

lamellae not intercalated with small subdigital scales. Sexual pattern dimorphism not evidenced. Post-cloacal scales enlarged in both sexes. Caudal whorls of enlarged scales indistinct, most evident caudad.

Dr. Richard Zweifel has supplied me with the following color description taken from a series of *Uma exsul* obtained on June 24–25, 1957, 7 and 13 miles east of Matamoros, Coahuila, Mexico: Dorsal color brown with a yellowish tint. Yellow-orange markings on femora and down midline of tail. Ventrolateral bar, groin blotches, and subcaudal bars jet black. Throat white, with radiating black lines. Venter white except for region around ventrolateral bars, where a yellow to yellow-orange tint crosses the belly. Sometimes this color suffuses over much of the ventral surface. Superciliaries, upper eyelids, and rostral scales bright reddish orange.

HABITAT: Zweifel supplied the following information on the Matamoros specimens: Restricted to small sand dunes vegetated mostly with creosote bush or mesquite. *Cnemidophorus tigris*, *Sceloporus* sp., *Masticophis flagellum*, *Arizona elegans*, and *Rhinocheilus lecontei* were taken at or near these localities. The area seems associated with drainage into the Laguna Viesca and not with the Laguna Mayrán, in which the type locality occurs.

LOCALITY RECORDS: Type locality: dunes 12 miles north of San Pedro de Las Colonias, Coahuila, Mexico. One and four-tenths miles southeast of Matamoros, Coahuila, Mexico, 7 miles east of Matamoros, Coahuila, Mexico, and 13 miles east of Matamoros, Coahuila, Mexico.

I have examined specimens from the type locality.

Uma scoparia Cope

MOJAVE FRINGE-TOED LIZARD

Uma notata COPE, 1866, Proc. Acad. Nat. Sci. Philadelphia, vol. 18, p. 310. MEEK, 1905, Field Columbian Mus., zool. ser., vol. 7, p. 4, pl. 1. CAMP, 1916, Univ. California Publ. Zool., vol. 12, p. 516, figs. 6, 7, pl. 12. VAN DENBURGH, 1922, Occas. Papers California Acad. Sci., no. 10, p. 132 (part). SCHMIDT, 1922, Bull. Amer. Mus. Nat. Hist., vol. 46, p. 651, fig. 7, pl. 53 (part). STEJ-

NEGER AND BARBOUR, 1939, A check list of North American amphibians and reptiles, ed. 4, p. 58 (part). SCHMIDT, 1953, A check list of North American amphibians and reptiles, ed. 6, p. 119 (part).

Uma scoparia COPE, 1894, Amer. Nat., vol. 28, p. 435, figs. 3, 4; type locality, "Fort Buchanan, Arizona" (*in errore*, from Inyo, Los Angeles, San Bernardino or Riverside County, California); type, U.S.N.M. No. 6063. COPE, 1895, Amer. Nat., vol. 29, p. 939. COPE, 1898 (1900), Rept. U. S. Natl. Mus., p. 282, fig. 29. HEIFETZ, 1941, Copeia, no. 2, p. 106, p. 108, figs. 1, 2, 4. H. M. SMITH, 1946, Handbook of lizards, p. 156, fig. 66, pl. 29.

Callisaurus notatus, BURT, 1935, Trans. Kansas Acad. Sci., vol. 38, p. 272, fig. 22 (part).

Callisaurus scoparius, COPE, 1896, Amer. Nat., vol. 30, p. 1049. STEJNEGER AND BARBOUR, 1917, A check list of North American amphibians and reptiles, ed. 1, p. 48.

DIAGNOSIS: A species most closely related to the *notata* group. A dorsal pattern of ocelli, not forming broken longitudinal lines over the shoulder. Ventrolateral blotch present. Internasal scales usually five. Breeding coloration ephemeral, consisting of a yellow-green ventral wash, becoming pink along the lateral abdominal fold.

DESCRIPTION: Dorsal pattern of ocelli never lineate in adults. Occasionally in juveniles a chevron dorsal pattern similar to that of *exsul* is present. Ventrolateral blotch present. Ratio of snout to vent length to blotch width, mean 17.9 ± 0.20 . Gular fold marked by one to three black gular crescents, widest medially, and one to three diagonal black lines directed medioposteriorly, not fused at middle of throat, anterior to the crescents. Internasal scales predominantly five, mean 4.63. Fестоons of lower eyelid 11 to 16, mean 13.3 ± 0.19 . Interparietal scale flask-shaped, bordered lateroposteriorly by a pair of enlarged post-parietal scales, separated from the interparietal scale by one to five smaller scales. Auricular lobules usually five. Ratio of snout to vent length to humerus length, mean, 3.97 ± 0.11 . Black shoulder blotches prominent, one to five, often colored at edges by an indefinite border of lemon yellow or greenish yellow scales. Femoral pores 25 to 35, mean 29.6 ± 0.31 . Pore rows doubled in 56 per cent of individuals. Precloacal or lateral cloacal black spots present in 42.5 per cent of individuals. Post-femoral bars or spots

present in 10 per cent of specimens. Fringes of posterior edge of fourth toe of hind foot ranging from 26 to 40, mean 31.9 ± 0.15 . Fringes and lamellae intercalated with small subdigital scales. Sexually mature males range from approximately 70 mm. to 116.4 mm. in snout to vent length. Sexually mature females range from approximately 65 mm. to 87.8 mm. in snout to vent length. Sexual pattern dimorphism evidenced by adult females as a diffuse starring of the dorsal ocelli on the lateroposterior portion of the abdomen. Tail ringed with whorls of enlarged scales separated by four rows of smaller scales. Breeding coloration in both males and females consisting of a pinkish suffusion along the ventral edge of the lateral fold (more prominent in females than males) and a distinct greenish yellow wash (more evident in males than females) covering the ventral surfaces of the tail, hind legs, abdomen (lightest midventrally), and the lower surfaces of the front legs. Also a bright orange wash covering the anterior supralabial scales, infra-labials, the canthal ridge, and the posterior festoons of the eyes. All these colors are ephemeral and are not present outside the breeding and egg-laying season.

LOCALITY RECORDS: Restricted to the desert portions of Inyo, San Bernardino, Los Angeles, and Riverside counties, California. *Inyo County:* One and one-half miles southeast of Saratoga Springs. *San Bernardino County:* El Mirage Dry Lake, Harper's Dry Lake, Daggett, 2 miles south of Yermo, Newberry School, west slope of Alvord Mountains, Cronise Lake, Crucero, Sands Siding, Devil's Playground, Kelso Dunes, Silver Lake, west slope of Kingston Mountains, Sperry Canyon, Pisgah Crater, Ludlow, Bristol Dry Lake, Cadiz Dry Lake, Rice (Blythe Junction), and Dale Dry Lake. *Los Angeles County:* Peck's Butte (Piute Butte), Wilsona Butte. *Riverside County:* Pinto Basin, Palen Dry Lake, Ford Dry Lake, 10 miles east of Ford Dry Lake, Blythe Escarpment.

I have examined specimens from all the localities listed above except El Mirage Dry Lake, west slope of the Kingston Mountains, and the Blythe Escarpment.

VARIATION WITHIN *Uma scoparia*: The species *Uma scoparia* is now known to occur at 27 different localities, each of small areal

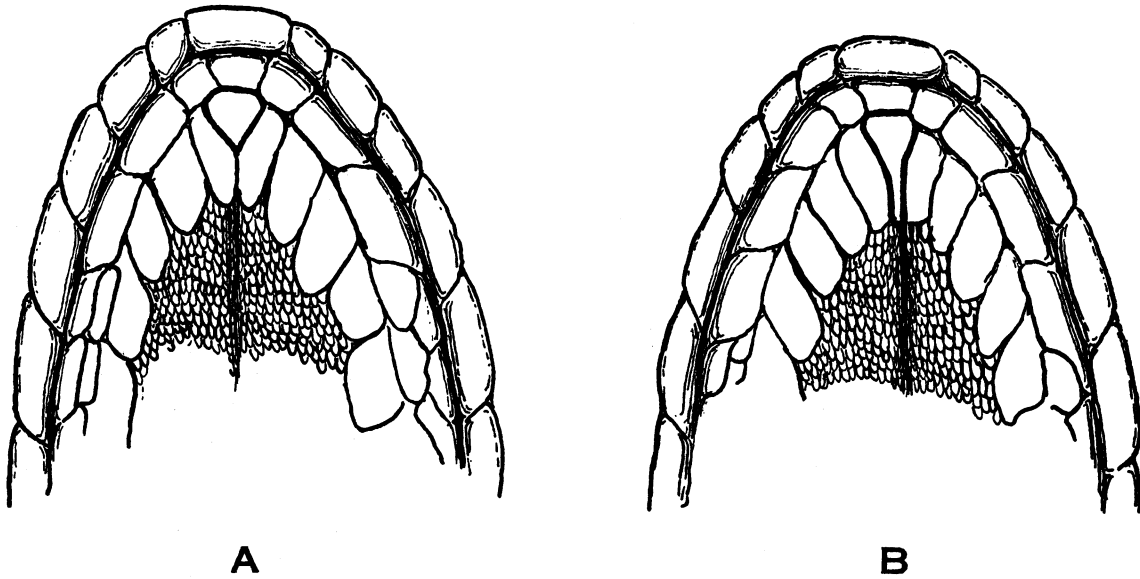


FIG. 8. Confluence of the post-mental scale. A. Occluded posteriorly. *Uma scoparia*, Sperry Canyon, San Bernardino County, California. B. Not occluded posteriorly. *Uma scoparia*, Wilsona Butte, Los Angeles County, California.

extent, and most of which are completely isolated. It is not surprising, therefore, to find considerable variation within the species. In fact, it is surprising that trends can be traced through the species, when the isolated nature of its populations is considered. The extreme recency of these disjunctions probably accounts for the degree of homogeneity seen today in *scoparia*.

On the basis of invasion routes,³ the species has been divided into three units: (1) southeastern populations, (2) intermediate populations, and (3) northwestern populations. The first division is composed of animals from these localities: Blythe Escarpment, Ford Dry Lake, Palen Dry Lake, Rice (Blythe Junction), Cadiz Dry Lake, and Bristol Dry Lake. Intermediate populations are Pinto Basin, Dale Dry Lake, Kelso, Devil's Playground, and Lavic Dry Lake-Pisgah Crater. These populations do not represent an inter-gradient group but are merely segregate populations from the first group, some of which

have formed the source of animals which have invaded the northwestern area. The third group is composed of these populations: Silver Lake, Sperry Canyon, the two Saratoga Springs populations, Cronise Dry Lake, Alvord Mountains, Newberry Dunes, Daggett, Harper's Dry Lake, El Mirage Dry Lake, Wilsona Butte, and Peck's Butte.

In this analysis three variable morphologic characters within *scoparia* have been found. They are (1) the confluence of the post-mental scale between the adjacent two lateral sublabial scales (see fig. 8), (2) the incidence of precloacal spots, and (3) the number of scales separating the interparietal and post-parietal scales.

CONFLUENCE OF POST-MENTAL SCALE: The small median post-mental scale either extends between the two lateral sublabial scales and touches the granular gular scale rows or is truncated posteriorly by these two lateral scales and fails to pass between them. At times the post-mental scale is fragmented posteriorly into a variable number of smaller scales which separate the lateral scales. This condition is considered as being "not occluded posteriorly" (fig. 8).

The differences between the three groups are highly significant. One hundred and

³ The term "invasion route" probably presents an erroneous picture for the movements of most animals and plants through geologic time. It seems apt for *Uma*, because the genus must have moved with its habitat along drainage courses and over divides, along what are good "routes."

twelve specimens were examined. Southeastern populations showed 73.2 per cent of the post-mental scales to be occluded posteriorly, while intermediate populations have 53.1 per cent of the animals showing a similar condition. The figure for the northwestern group is 13.9 per cent. There were no excessively variant populations noted; the characteristic seems to occur as a definite cline from southeast to northwest.

INCIDENCE OF PRECLOACAL SPOTS: Precloacal spots are absent in 73 per cent of the individuals of the southeastern populations, absent in 66.23 per cent of the intermediate specimens, and absent in 37.2 per cent of the northwestern specimens (see fig. 10). Unlike those of the post-mental configuration these figures are an average of variable populations. Kelso animals show a very low incidence of spotting as do Cronise Dry Lake animals, while a high percentage of Sperry Canyon animals possesses spots.

SEPARATION OF POST-PARIETAL AND INTER-PARIETAL SCALES: Two small, shield-shaped scales are situated posterior to the inter-parietal scale in *Uma scoparia*. It was noted that these scales are separated from the inter-parietal scale by a variable number of smaller scales (figs. 11, 12). The mean number of scales separating the two larger scales in southeastern populations is 3.34; in intermediates, 2.85; and in the northwestern populations, 2.69. As with the incidence of precloacal spots, this separation varies radically from population to population. Ten animals from Cronise and Alvord Dry lakes have a mean separation of 1.7 scale rows, 70 per cent are separated by two scales. Furthermore, the post-parietals of the Alvord animals are larger and flatter (being formed by fusion of surrounding scales) than those of any other population of *scoparia*.

These characteristics give separations between the extreme northwestern and south-

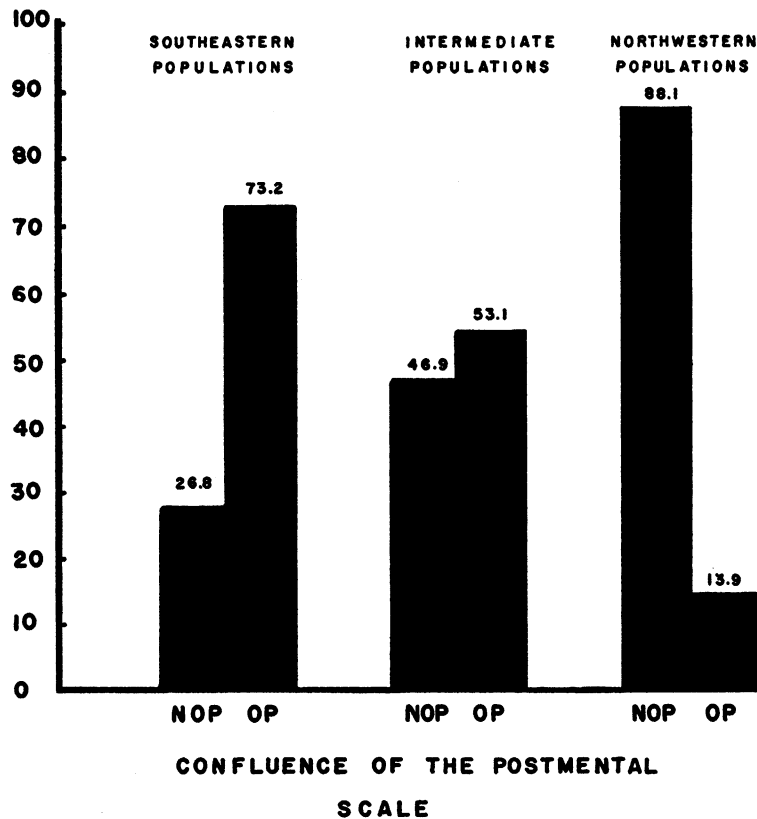


FIG. 9. Intraspecific variation in *Uma scoparia*. Confluence of the postmental scale. Abbreviations: NOP, not occluded posteriorly; OP, occluded posteriorly.

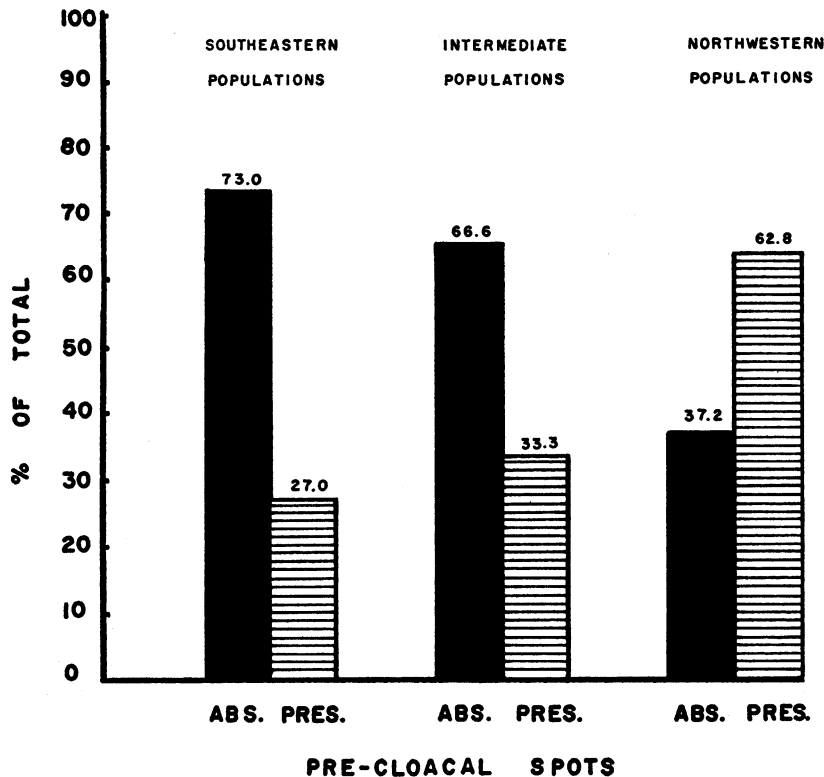


FIG. 10. Intraspecific variation in *Uma scoparia*, pre-cloacal spots. See text.

eastern groups of sufficient magnitude that they could be considered subspecies (Ginsburg, 1937). There are, however, reasons why this is not considered a good policy in this case. First, with the exception of the "confluence of the post-mental scale" the variation is not truly clinal but is an average of conditions obtaining in a series of disjunct populations. In naming such variation one would be faced with the dilemma of small populations as distinct from all others as the two geographic groups are from each other. For example, the post-parietal arrangement in the very small Alvord population is more distinctive than the northwest group is from the southeast group.

The variable characters are of an extremely insignificant nature. As is explained below, many of the now disjunct populations of *Uma scoparia* have reached their present locations by migration along the edges of stream courses and up stringers of wind-blown sand concentrated in barrancas and ravines. The animals that made these migrations must

have been few in number, as their routes were often tenuous and highly transitory. The group that formed the invading population represented a small segment of the parent population. Individual differences could have been magnified by this mechanism and by subsequent inbreeding.

Intermediate populations probably have resulted from repeated invasion from adjacent populations which has tended to make them more like their source populations. The configuration of the post-parietal scales in Alvord animals is unique in *scoparia*, and mutation or inbreeding may have been its cause.

Finally, color variation within *scoparia* is of considerable magnitude. As do other forms of *Uma*, the different populations of *Uma scoparia* tend to match closely the color of their sand habitat. This variation is dependent upon the factors determining sand color and shows no correlation with the trends of morphologic change demonstrated above.

It is thought that pointing to these varia-

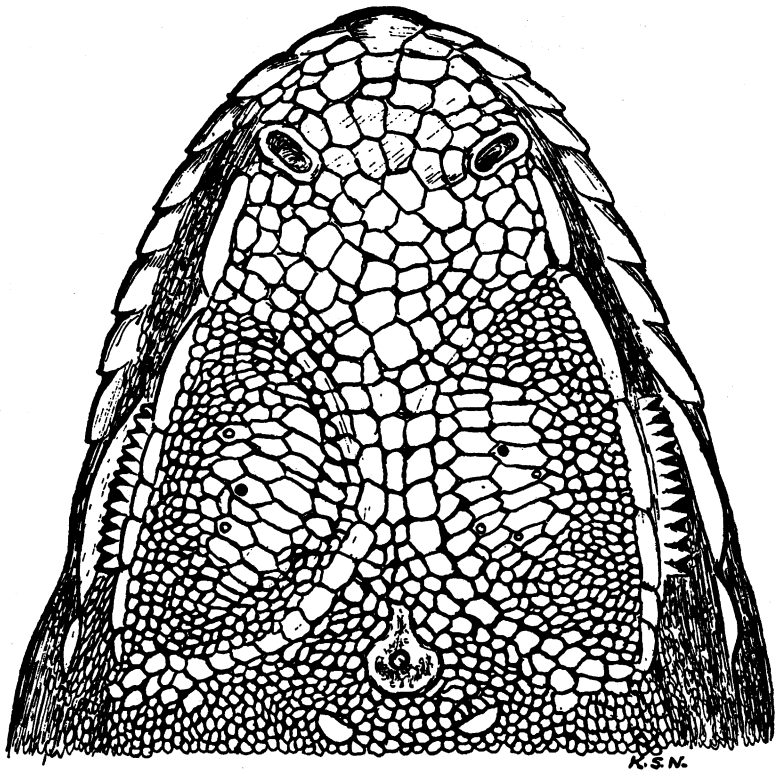


FIG. 11. Head of *Uma scoparia*, a male from Palen Dry Lake, Riverside County, California. Note the large, flask-shaped, interparietal scale and the two enlarged post-parietal scales bordering it posteriorly. These enlarged scales are typical of *Uma scoparia*. See text.

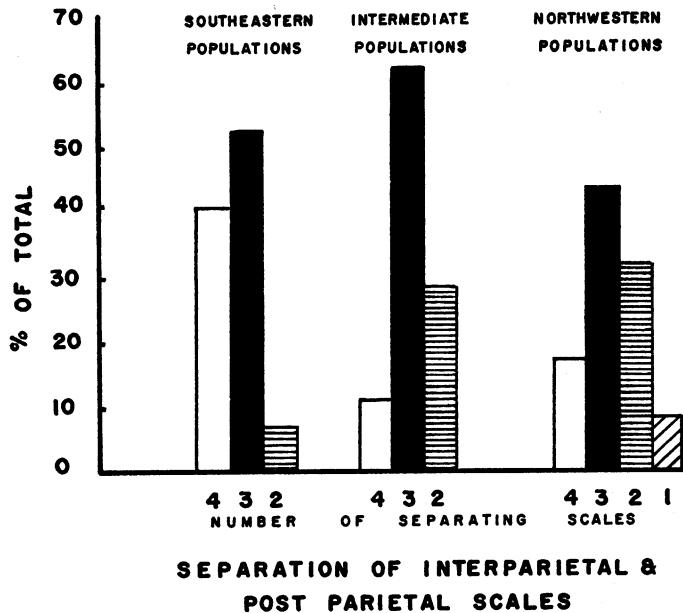


FIG. 12. Intraspecific variation in *Uma scoparia*. Separation of interparietal and post-parietal scales. See text.

tions by naming them would not present a true picture of their importance with respect to the other named groups of the genus and would necessarily obscure other, equally striking, variation.

Uma notata inornata Cope

COACHELLA VALLEY FRINGE-TOED LIZARD

Uma notata, VAN DENBURGH, 1922, Occas. Papers California Acad. Sci., no. 10, p. 132 (part). SCHMIDT, 1922, Bull. Amer. Mus. Nat. Hist., vol. 46, p. 651, fig. 7, pl. 53 (part). STEJNEGER AND BARBOUR, 1939, A check list of North American amphibians and reptiles, ed. 4, p. 58 (part). SCHMIDT, 1953, A check list of North American amphibians and reptiles, ed. 6, p. 119.

Uma inornata COPE, 1895, Amer. Nat., vol. 29, p. 939; type locality, "Colorado Desert, San Diego County, California" (*in errore*, doubtless from Riverside County, California). COPE, 1898 (1900), Rept. U. S. Natl. Mus., p. 281. HEIFETZ, 1941, Copeia, no. 2, p. 106, figs. 1, 2. H. M. SMITH, 1946, Handbook of lizards, p. 149, pl. 27.

Callisaurus notatus, STEJNEGER AND BARBOUR, 1917, A check list of North American amphibians and reptiles, ed. 1, p. 47 (part). BURT, 1935, Trans Kansas Acad. Sci., vol. 38, p. 272, fig. 22 (part).

Callisaurus inornatus COPE, 1896, Amer. Nat., vol. 30, p. 1049.

DIAGNOSIS: A subspecies most closely related to *Uma n. notata*. A dorsal pattern of ocelli, forming broken longitudinal lines over the shoulder. Ventrolateral blotch absent or evident as a minute cluster of black dots. Internasal scales nearly always three.

DESCRIPTION: Dorsal pattern of ocelli fused into broken diagonal lines over the shoulder. Abdomen immaculate or nearly so. Ventrolateral blotch evident in 50 per cent of specimens as a minute cluster of small black dots. Gular fold marked with thin black chevrons, absent or faint at mid-gular region. Internasal scales usually three. Fестоons of lower eyelid 12 to 15, mean 13.75 ± 0.28 . Interparietal scale usually rounded, not bordered posteriorly by enlarged post-parietal scales. Auricular lobules usually five. Ratio of snout to vent length to humerus length ranging from 3.3 to 4.3, mean 3.85 ± 0.17 . Shoulder blotches absent or indistinct. Groin blotches present in 2.5 per cent of individuals. Femoral pores 20 to 27, mean 22.9 ± 0.25 . Pore rows doubled in 6.2 per cent of individuals. Precloacal or

lateral-cloacal spots absent. Fringes of posterior edge of fourth toe of hind foot ranging from 23 to 32, mean 26.5 ± 0.30 . Fringes and lamellae intercalated with small subdigital scales. Sexually mature males range from approximately 70 mm. to 105.7 mm. in snout to vent length. Sexually mature females range from approximately 65 mm. to 85 mm. in snout to vent length. Sexual dimorphism evidenced occasionally by adult females as a diffuse starring of the dorsal ocelli on the latero-posterior portion of the abdomen. Tail ringed with whorls of enlarged scales separated by four rows of smaller scales. Sexual coloration consisting of a pinkish lateroventral suffusion between the axilla and groin along the lateral fold and orange washes over the anterior supralabials and infralabials and the posterior festoons of the eye. These markings are present only during nuptial and post-nuptial periods.

LOCALITY RECORDS: Restricted to the Coachella Valley and San Geronio Pass, Riverside County, California. *Riverside County:* Mouth of Snow Creek, Whitewater Wash, Garnet, Palm Springs, Thousand Palms Junction, La Quinta, Indian Wells, Cathedral City, and 2 miles east of Indio. I have examined specimens from all the localities listed above.

Uma notata notata Baird

COLORADO DESERT FRINGE-TOED LIZARD

Uma notata BAIRD, 1858, Proc. Acad. Nat. Sci. Philadelphia, vol. 10, p. 253; type locality, "Mojave Desert" (*in errore*, doubtless from the Sonoran Desert of California or northern Baja California); type U.S.N.M. No. 4124. YARROW, 1883, Bull. U. S. Natl. Mus., vol. 24, p. 9. COPE, 1894, Amer. Nat., vol. 28, p. 435. COPE, 1895, Amer. Nat., vol. 29, p. 939. COPE, 1898 (1900), Rept. U. S. Natl. Mus., p. 277, fig. 27. VAN DENBURGH, 1922, Occas. Papers California Acad. Sci., no. 10, p. 132 (part). SCHMIDT, 1922, Bull. Amer. Mus. Nat. Hist., vol. 46, p. 651, fig. 7, pl. 53 (part). STEJNEGER AND BARBOUR, 1939, A check list of North American amphibians and reptiles, ed. 4, p. 58 (part). HEIFETZ, 1941, Copeia, no. 2, pp. 101-104, figs. 1-3. H. M. SMITH, 1946, Handbook of lizards, pp. 154-155, pl. 28. SCHMIDT, 1953, A check list of North American amphibians and reptiles, ed. 6, p. 119.

Callisaurus notatus, COPE, 1896, Amer. Nat., vol. 30, p. 1049. STEJNEGER AND BARBOUR, 1917, A check list of North American amphibians and

reptiles, ed. 1, p. 47 (part). BURT, 1935, Trans. Kansas Acad. Sci., vol. 38, p. 272, fig. 22 (part).

DIAGNOSIS: A subspecies most closely related to *Uma n. inornata*. A dorsal pattern of ocelli, forming broken longitudinal lines over the shoulder. Ventrolateral blotch present. Internasal scales nearly always three. Distinguished from all other members of the genus by the presence of a permanent, bright orange, ventrolateral stripe (fading rapidly in preservative).

DESCRIPTION: Dorsal pattern of ocelli fused into diagonal lines over the shoulder. Ventrolateral blotch present, sometimes produced onto the dorsum as a thin line, connected or not with dorsal striping. Ratio of snout to vent length to blotch width, mean 16.1 ± 0.54 . Gular fold marked with thin, V-shaped, black lines, absent or indistinct at mid-gular area. Internasal scales usually three. Festoons of lower eyelid 11 to 15, mean 13.6 ± 0.12 . Interparietal scale usually rounded, not bordered posteriorly by enlarged post-parietal scales. Auricular scales usually five. Ratio of snout to vent length to humerus length ranging from 3.26 to 5.1, mean 3.9 ± 0.01 . Shoulder blotches absent or indistinct. Groin blotches present in 1 per cent of individuals. Femoral pores 19 to 32, mean 24.3 ± 0.24 . Pore rows doubled in 5.2 per cent of individuals. Postfemoral bars or blotches present in 32.0 per cent of specimens. Precloacal or lateral-cloacal black spots present in 6.9 per cent of individuals. Fringes of posterior edge of fourth toe of hind foot ranging from 22 to 34, mean 27.6 ± 0.36 . Fringes and lamellae intercalated with small subdigital scales. Sexual dimorphism evidenced occasionally by adult females as a diffuse "starring" of the dorsal ocelli on the lateroposterior portion of the abdomen. Tail ringed with whorls of enlarged scales, separated by four rows of smaller scales. Maximum snout to vent length (of specimens examined), 118.7 mm. Sexually mature males range from approximately 70 mm. to 118.7 mm. in snout to vent length. Sexually mature females range from approximately 64 mm. to 84 mm. in snout to vent length. Sexual coloration consisting of a lateroventral orange band extending from axilla to groin, slightly wider than the lateroventral blotch at its widest point. The color

is not greatly developed in immature animals. The color is permanent, becoming intensified during breeding season. During breeding season, orange suffusions cover the posterior eye festoons, the canthal ridge, and the anterior supralabial and infralabial scales.

LOCALITY RECORDS: *Uma n. notata* is restricted to the Colorado Desert of California and northeastern Baja California, Mexico. *San Diego County:* Clark Dry Lake and east base of Borego Mountain. *Imperial County:* McCain Spring, Squeaky Spring, Sandy Beach, Kane Spring, New River near Salton Sea, Coyote Wells, Dixieland, north slope of Signal Mountain, Tinhorn, Jaspard District, East Mesa, Algodones Dunes at various localities from Amos to Gray's Well and Midway Well. *Baja California:* Cerro Pinto, southwest slope of Signal Mountain, Pattie Basin, south entrance to Pattie Basin, Algodones Dunes between Algodones and Dieguenos. I have examined specimens from all the localities listed above.

***Uma notata rufopunctata* Cope**

COWLES'S FRINGE-TOED LIZARD

Uma rufopunctata COPE, 1895, Amer. Nat., vol. 29, p. 939; type locality, "Yuma Desert, Arizona," cotypes U.S.N.M. Nos. 21846-21852. COPE, 1898 (1900), Rept. U. S. Natl. Mus., p. 279, fig. 28.

Uma notata, VAN DENBURGH, 1922, Occas. Papers California Acad. Sci., no. 10, p. 132 (part). STEJNEGER AND BARBOUR, 1939, A check list of North American amphibians and reptiles, ed. 4, p. 58 (part). SCHMIDT, 1953, A check list of North American amphibians and reptiles, ed. 6, p. 119.

Uma notata cowlesi HEIFETZ, 1941, Copeia, no. 2, pp. 104-106; type C.A.S. No. 53370, Tepoca Bay, Sonora, Mexico.

Callisaurus rufopunctatus, COPE, 1896, Amer. Nat., vol. 30, p. 1049.

Callisaurus notatus, BURT, 1935, Trans. Kansas Acad. Sci., vol. 38, p. 272 (part).

DIAGNOSIS: A subspecies most closely related to *Uma n. notata*. Of the subspecies of *Uma notata* it is the form most closely related to *Uma scoparia*. A dorsal pattern of ocelli, forming broken longitudinal lines over the shoulder. Ventrolateral blotch present. Internasal scales nearly always three. Abdomen white except during breeding season, then colored along the lateral fold by a pink wash.

DESCRIPTION: Dorsal pattern of ocelli fused into broken diagonal lines over the shoulder.

Ventrolateral blotch present. Width of blotch highly variable within the subspecies. Ratio of snout to vent length to blotch width, mean 19.3 ± 0.9 . Gular fold marked with thin chevrons, absent or faint at mid-gular area. Internasal scales usually three. Festoons of lower eyelid 11 to 14, mean 12.2 ± 0.19 . Interparietal scale usually rounded, not bordered posteriorly by enlarged post-parietal scales. Auricular lobules usually five. Ratio of snout to vent length to humerus length, mean 4.03 ± 0.02 . Shoulder blotches absent or indistinct. Groin blotches present in 3 per cent of individuals. Femoral pores 22 to 32, mean 27.1 ± 0.37 . Pore rows very rarely doubled. Precloacal or lateral-cloacal black spots rarely present. Fringes of posterior edge of fourth toe of hind foot ranging from 23 to 31, mean 27.7 ± 0.27 . Fringes and lamellae intercalated with small subdigital scales. Sexually mature males range from approximately

70 mm. to 112 mm. in snout to vent length. Sexually mature females range from approximately 65 mm. to 89.5 mm. in snout to vent length. Sexual coloration consisting of a pinkish suffusion along the ventral border of the lateral abdominal fold and an orange wash over the canthal ridge, anterior labial scales, and the posterior festoons of the eye. These colors are present only during nuptial and post-nuptial periods.

LOCALITY RECORDS: Restricted to the Sonoran Desert of northwestern Sonora, Mexico, and southwestern Arizona, United States. *Arizona*: Yuma County: West slope of Mohawk Mountains (near Pembroke), Wellton Mesa, Yuma Mesa, vicinity of Yuma. *Sonora*: Fifteen miles south of San Luis, El Papalóte, Punta Peñasco, Cerro Prieto, mouth of Altar River (Rio de la Concepcion), Tepoca Bay. I have examined specimens from all the localities listed above.

COMPARISONS

Heifetz (1941) has analyzed the differences between the forms of *Uma* on a statistical basis. New differences have been uncovered and the extent of the known ranges of the component forms have been clarified since that time. *Uma exsul* has been discovered since Heifetz' analysis. Before variation in the genus can be utilized to interpret distributional history it must be reworked in light of these new findings.

PATTERN

The different types of pattern are noted in detail under the discussion of each form. Briefly the differences are as follows:

Uma exsul: A dorsal pattern consisting of a black reticulum and diagonal black chevrons, best developed caudad, forming three black blotches at the groin and the base of the femur. A prominent black shoulder blotch, much more conspicuous than that of *scoparia*. The lateroventral blotch continued onto the dorsum as a chevron. This characteristic is only slightly developed in other forms.

Uma scoparia: A dorsal reticulum of black superimposed over a brown reticulum, forming ocelli which are never lineate. Gular pattern of distinctive chevrons, thickest medially. Shoulder and groin blotches much

smaller than those of *exsul* but more prominent than those of the *notata* group. A high incidence of precloacal spotting. Breeding color differs from all others in that a pale yellow-green wash covers all ventral surfaces but the gular area.

Notata GROUP: A dorsal reticulum of black superimposed over a brown reticulum, fused in the shoulder region to form broken diagonal longitudinal lines passing ventrally to the lateral fold posteriorly. Groin blotches rarely present and then poorly developed. Shoulder blotches indistinct. Gular pattern similar to that of *exsul*, being composed of thin diagonal black lines absent at mid-gular area. A very low incidence of precloacal spotting.

Within the *notata* group the three forms are separated from one another by the following pattern characteristics: *Uma n. notata*: Breeding color consisting of an intensification of a permanent lateroventral orange stripe (adults only). *Uma n. inornata*: Breeding color consisting of a pinkish lateroventral wash, usually present only during the breeding season. Lateroventral black blotch present as a minute cluster of black dots in 50 per cent of individuals. Completely absent in the other 50 per cent. *Uma n. rufopunctata*: Breeding color the same as that of *Uma n.*

inornata. Blotch present, somewhat narrower on the average than that of *notata*.

VENTROLATERAL BLOTCH

One of the chief criteria used by Heifetz in naming the subspecies *cowlesi* [= *U. n. rufopunctata*] was the ratio of blotch width to snout-vent length. The greatest part of the difference noted by him seems to be a local population effect. The animals from Tepoca Bay, Sonora, Mexico, have a very narrow blotch compared to specimens from other localities within the range of the subspecies. This reduction is possibly a response to a white sand habitat. The ultimate in such reduction is shown by *Uma n. inornata* in which the blotch reaches its greatest expression as a very small cluster of black dots. In Heifetz' analysis, the animals from Arizona were considered as members of *U. n. notata* and not *U. n. rufopunctata* as they are considered here. The breeding color of the Arizona animals is typical of *rufopunctata* and not of *n. notata*. This probably further obscured Heifetz' picture. These blotch-width relationships are shown in figure 13. Whether the difference shown by the Tepoca Bay animals is worthy of a name is a matter best left undecided

until more specimens are available and more is known of the range of the narrow-blotched form. The presence or absence of *Uma* at La Libertad and Kino Bay, Sonora, Mexico, should be demonstrated in connection with this problem.

GROIN BLOTCH FREQUENCY

The three black blotches of the groin and femur are greatly developed in *Uma exsul*, less well developed, though nearly always present, in *Uma scoparia*, and nearly absent in the *notata* group.

	NO. OF SPECIMENS	PERCENTAGE PRESENT
<i>Uma exsul</i>	8	100.0
<i>Uma scoparia</i>	111	99.2
<i>Uma n. rufopunctata</i>	68	3.0
<i>Uma n. notata</i>	95	1.0
<i>Uma n. inornata</i>	41	2.5

POST-FEMORAL BARS

Schmidt and Bogert (1947) report the presence of post-femoral bars in *Uma exsul*. They suggest that this characteristic links *exsul* to *Callisaurus* rather than to other members of the genus *Uma*. Even though perfectly

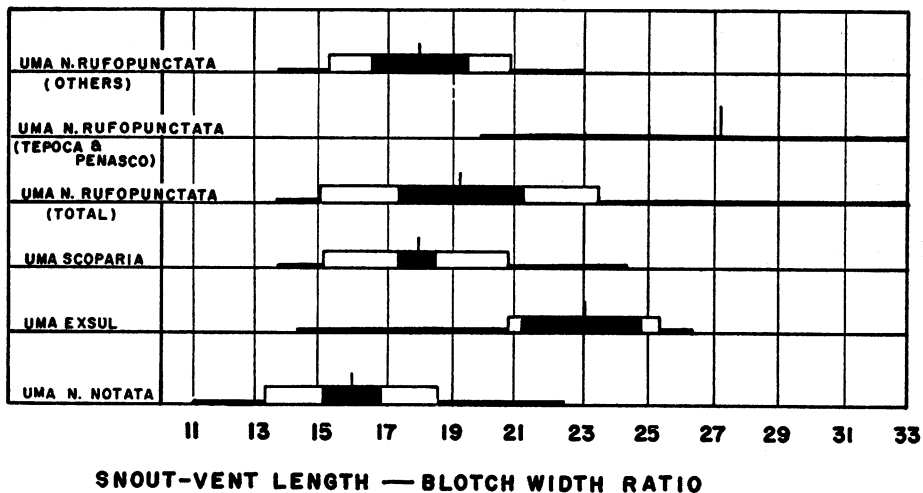


FIG. 13. Variation in ventrolateral blotch width, ratio of snout to vent length to blotch width. Graphic method after Hubbs and Hubbs, 1953. Horizontal black line indicates range of variation. One-half of each black box plus the white box at each end outlines one standard deviation on each side of the mean. The dark box represents two times the standard error of the mean on each side of the mean, and the vertical line is the mean.

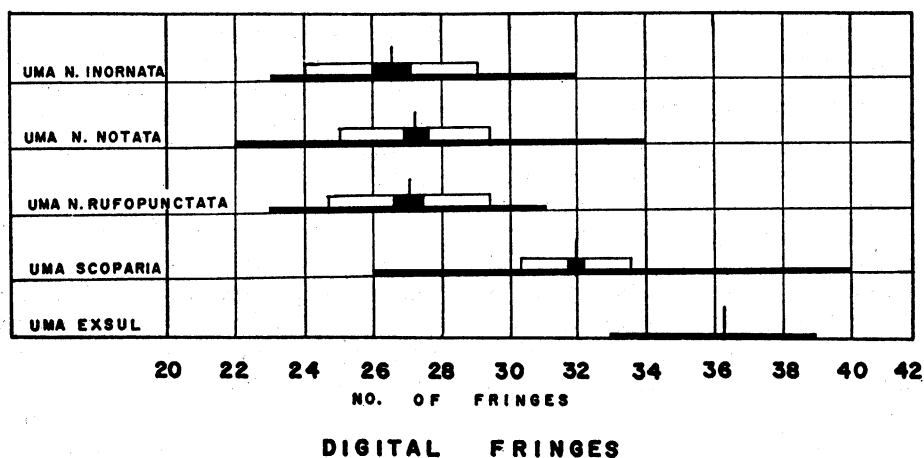


FIG. 14. Variation in digital fringe counts. For explanation of symbols, see figure 13.

comparable markings have been found in a few cases in western *Uma* and modified markings in many cases, their conclusion seems perfectly valid. The usual form of the bars in *scoparia* and the *notata* group is a variable number of gray blotches along the posterior edge of the thigh. The incidence of these blotches or of complete bars is:

	NO. OF SPECIMENS	PERCENTAGE PRESENT
<i>Uma exsul</i>	8	100.0
<i>Uma scoparia</i>	111	10.0
<i>Uma n. rufopunctata</i>	68	6.2
<i>Uma n. notata</i>	95	32.0
<i>Uma n. inornata</i>	41	13.2

SCUTELLATION: INTERNASAL SCALES

The author's conclusions are the same as those of Heifetz (1941) for the western forms. Forms of the *notata* group have predominantly three internasal scales, *scoparia* has predominantly five, and *exsul* four.

DIGITAL FRINGES

Again the relationships demonstrated for the western forms are the same as those determined by Heifetz (1941). Counts for the *notata* group are again rather uniform. Means are: *notata*, 27.6; *inornata*, 26.5; *rufopunctata*, 27.7; *scoparia*, 31.9; and *exsul*, 37.0 (see fig.

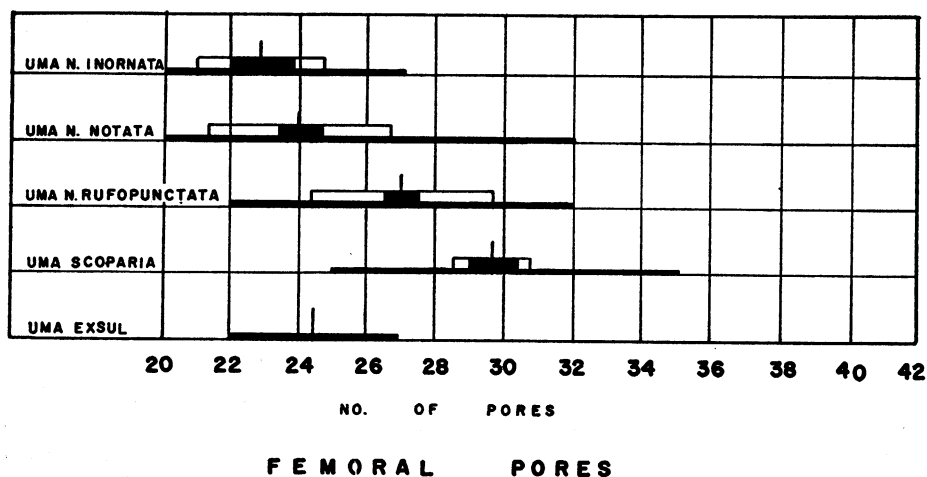


FIG. 15. Variation in femoral pore counts. For explanation of symbols, see figure 13.

14). All forms but *exsul* possess subdigital scales intercalated between the fringes and the lamellae, as noted by Schmidt and Bogert (1947).

FEMORAL PORES

Though each of the forms overlaps the counts of at least one other form, all the differences but the difference between *exsul* and *notata rufopunctata* and possibly between *exsul* and *n. notata* are statistically significant (fig. 15). Rather striking differences in the incidence of doubling of the femoral pore rows were noted.

NO. OF SPECIMENS PERCENTAGE DOUBLED

<i>Uma exsul</i>	8	0.0
<i>Uma scoparia</i>	111	56.0
<i>Uma n. rufopunctata</i>	68	0.0
<i>Uma n. notata</i>	95	5.2
<i>Uma n. inornata</i>	41	6.3

PROPORTIONS

As Schmidt and Bogert (1947) point out, the ratio of the length of the hind leg to the snout to vent length of *exsul* is significantly less than that of other species of *Uma*. All other proportions calculated in this report

TABLE 2
RELATIONSHIPS WITHIN THE GENUS *Uma*^a

	1 <i>Uma exsul</i>	2 <i>Uma scoparia</i>	3 <i>Uma n. rufopunctata</i>	4 <i>Uma n. notata</i>	5 <i>Uma n. inornata</i>
Dorsal pattern	2	3, 4, 5	4, 5	3, 5	3, 4
Gular pattern	3, 4, 5	—	1, 4, 5	1, 3, 5	1, 3, 4
Ventrolateral blotch	3	3, 4	1, 2, 4	1, 2, 3	—
Internasal scales	2	1	4, 5	3, 5	3, 4
Interparietal shape	2	1	4, 5	3, 5	3, 4
Post-parietal scales	2	1	4, 5	3, 5	3, 4
Auricular scales	—	3, 4, 5	2, 4, 5	2, 3, 5	2, 3, 4
Shoulder blotches	2	1	4, 5	3, 5	3, 4
Groin blotches	2	1	4, 5	3, 5	3, 4
Femoral pores	4	3	2	1, 5	1, 4
Eyelid festoons	3	4, 5	1	2, 5	2, 4
Post-femoral bars	4	3, 5	2	5	2
Digital fringes	2	1	4, 5	3, 5	3, 4
Breeding color	—	3, 5	5	2, 3, 5	3
Tail whorls	—	3, 4, 5	2, 4, 5	2, 3, 5	2, 3, 4
Doubling of femoral pore row	3	4, 5	1	5	4
Gular-mental length/anterior canthal width	3, 4, 5	3, 4, 5	1, 4, 5	1, 3, 5	1, 4, 3
Habitus	—	3, 4, 5	2, 4, 5	2, 3, 5	2, 3, 4
Groin blotches	2	1	4, 5	3, 5	3, 4
Snout-vent length/tail base width	4, 5	3	2	1, 5	1, 4
Sub-digital scales	—	3, 4, 5	2, 4, 5	2, 3, 5	2, 3, 4
<i>Uma exsul</i>	—	—	7 33%	5 24%	4 19%
<i>Uma scoparia</i>	8 38%	—	8 38	7 33	6 29
<i>Uma n. rufopunctata</i>	5 24	11 52	—	16 76	15 71
<i>Uma n. notata</i>	5 24	9 43	15 71	—	18 86
<i>Uma n. inornata</i>	3 14	9 43	15 71	20 95	—

^a Each of 21 variable characteristics within the genus *Uma* are listed. For every species or subspecies the form or forms most closely related to it on the basis of this characteristic are noted. For example, on the basis of dorsal pattern, *Uma exsul* is most closely related to *Uma scoparia* (2), but *Uma scoparia* is most closely related to the *notata* group (3,4,5) on the basis of this same characteristic.

The lower portion of the table summarizes this information. Between each of the forms the number of most closely related characteristics are noted and also converted to per cent of the total 21 variables considered. For example, eight of the 21 characters, or 38 per cent, link *U. exsul* most closely to *U. scoparia*. *Uma n. inornata* is closest to *U. n. notata* in 20 of the 21 characters, or 95 per cent. See text.

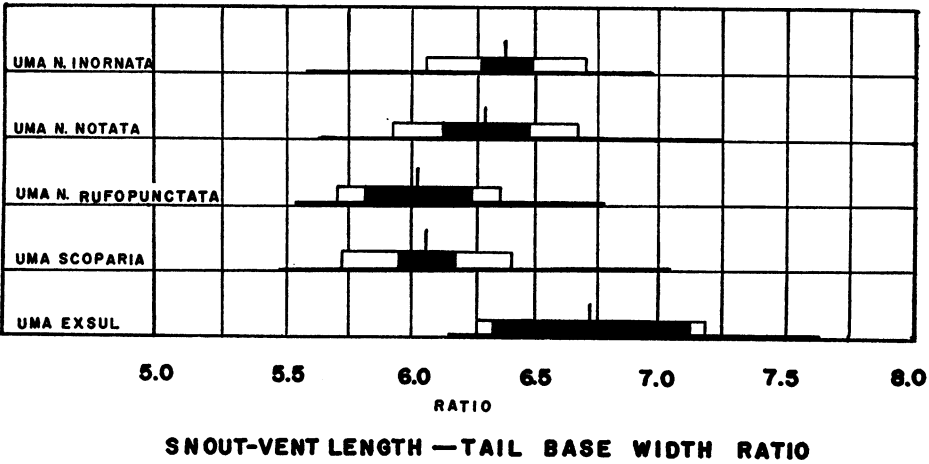


FIG. 16. Variation in tail base width, ratio of snout to vent length to width at base of tail. Only adult females used. See figure 13 for explanation of symbols.

overlapped, every form with every other form. However, the differences proved to be statistically significant in certain cases. The pointedness of the head is expressed in the ratio of the gular-mental length to the anterior canthal width. *Scoparia* has the bluntest head of the group, while no significant difference is shown among the other forms. The relative width of the tail base was tested by use of the ratio of the snout to vent length to the width at base of tail. Adult female animals were used in the testing of this

characteristic. *Uma n. rufopunctata* and *Uma scoparia* are linked by this proportion, both having relatively broad tails, while *exsul*, *n. notata*, and *n. inornata* form a homogeneous group having relatively narrower tails (see fig. 16). The ratio of the snout to vent length to the humerus length places the western forms close to one another, with *scoparia* and *n. rufopunctata* being closely allied and *exsul* rather distinct. A summary of the differences and relationships within the genus is presented in table 2.

PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHY

No FOSSILS are known of *Uma*. Tihen (1954) has described a single maxilla which he considers possibly represents *Holbrookia*. It was recovered, along with a rather large assemblage of reptile remains, from the Pleistocene (Sangamon interglacial) Kingsdown formation of Meade County, Kansas. The total fauna, with the possible exception of this maxilla, represents animals found at the site

at the present time. No paleogeographic conclusions regarding *Uma* can be drawn from fossil history. The phylogenetic and distributional history of *Uma* must therefore rest on inference from present-day relationships and habitat history. Some appraisals of the phylogenetic position of the *Callisaurus-Holbrookia-Uma* group within the family Iguanidae have been made.

PHYLOGENY

It is probable that true lizards have been in existence since Triassic time. The discovery in Africa of a pre-iguanid lacertilian type (*Paliguana*) has been interpreted as establishing the presence of the suborder Lacertilia in that period. Late Cretaceous representatives of the families Anguidae and Varanidae are known from North America (Gilmore, 1928). The modern genera *Cnemidophorus*, *Eumeces*, *Crotaphytus*, *Sceloporus*, *Ophisaurus*, and *Phrynosoma* are known from the Pliocene of North America (see Gilmore, 1928; Auffenberg, 1955; Oelrich, 1954; Twente, 1952; Brattstrom, 1955b).

Divergent views of phylogeny within the Iguanidae have been proposed. Camp (1923) states that "*Holbrookia* and other North American Iguanids" are considered primitive types (thus including the genus *Uma*). Camp's central group includes the large iguanids such as *Iguana*, *Cyclura*, *Sauromalus*, *Dipsosaurus*, and *Amblyrhynchus*. The two genera *Basiliscus* and *Anolis* are considered as offshoots of the latter group. The other viewpoint is that of H. M. Smith (1946) and Mittleman (1942) who consider the *Iguana*-like iguanids as primitive forms (their group includes such genera as *Ctenosaura*, *Dipsosaurus*, and *Sauromalus*). The group to which *Uma* belongs is considered derivative from this early stock.

Stebbins (1948) has analyzed the nasal structures in a considerable number of iguanid lizards. He has concluded that the types of structures represented are associated above the generic level. That is to say, certain groups of genera have similar nasal structures. Furthermore, he is able to say that cer-

tain types of structure are more advanced than others. He has shown that the nasal structure of *Uma* type (present in *Callisaurus*, *Holbrookia*, *Uta*, *Uma*, *Sceloporus*, and *Phrynosoma*) is more advanced than that of *Dipsosaurus* type (present in *Dipsosaurus*, *Crotaphytus*, *Sauromalus*, *Ctenosaura*, and *Iguana*).

Savage (in press) has presented another view of phylogeny within the Iguanidae, based largely on a careful examination of skeletal characteristics and the characteristics of nasal structure demonstrated by Stebbins (cited above). He concludes that Nearctic iguanids are divisible into two major groups that are distantly related to each other. No intermediate forms have been discerned. The first group, called the iguanine group, is composed of such large lizards as *Amblyrhynchus*, *Ctenosaura*, *Cyclura*, *Iguana*, *Sauromalus*, *Dipsosaurus*, and *Crotaphytus*. The second group is called the sceloporine group and contains all the remaining iguanids except *Anolis* found in the United States. Its distribution is largely northern compared to that of the iguanine group, though much overlap occurs in the faunas of Mexico and Central America. Included are these genera: *Sator*, *Sceloporus*, *Urosaurus*, *Callisaurus*, *Holbrookia*, *Phrynosoma*, *Uma*, and *Uta*. Within this group Savage says: "It seems likely that *Urosaurus* is best understood as a specialized off-shoot of *Sceloporus* from which it differs primarily in having a fully developed gular fold and in lacking a scapular foramen (no gular fold and a scapular foramen present in *Sceloporus*). *Uta* appears to be a specialized genus related to the highly adapted, but apparently more primitive, *Callisaurus-Hol-*

brookia-Uma series. *Uta* is probably best considered as a recent derivative of this stock and as such can only be distantly allied to *Urosaurus*."

The interpretations of Savage and Stebbins concerning the phylogenetic placement of the *Callisaurus-Holbrookia-Uma* group appear valid to me. I cannot agree with Smith and Mittleman that *Petrosaurus*, *Streptosaurus*, and *Crotaphytus* are derived forms from a pre-*Callisaurus-Holbrookia-Uma* stock as their diagrams imply.

Perhaps the precursor of *Callisaurus*, *Holbrookia*, and *Uma* was a small form developed from the stem stock of Savage's (cited above) sceloporine group. This prototype possibly lived in subtropical North America during Eocene or Oligocene times, or both.

The phylogeny of the *Callisaurus-Holbrookia-Uma* group is interpreted as follows. The ancestral stock of the three present genera first divided, possibly in Miocene

time, into two stocks: a *Callisaurus-Holbrookia* form and a pre-*Uma*. Both of these forms have since been divided in two by mountain building of the Rocky Mountains and the Sierra Madre Occidental of Mexico. This division has allowed *Holbrookia* to develop on the Mesa Central of Mexico and *Callisaurus* in the western area. *Holbrookia* has since been able to cross the barrier in Arizona and New Mexico (Bogert and Oliver, 1945). Pre-*Uma* developed into *exsul* in the Chihuahuan Desert and *notata* and *scoparia* in the western deserts. Both divisions of pre-*Uma* were probably channeled into newly developed sandy habitats, possibly through competition with the ubiquitous *Callisaurus* and *Holbrookia* types, finally becoming restricted completely to dunes. Differentiation on a specific and subspecific level has taken place since that time. These hypotheses are documented in the pages that follow.

BIOGEOGRAPHY

Historical distribution of reptiles has undoubtedly shifted in response to climatic change, as activity of cold-blooded animals is, to a considerable extent, directly controlled by environmental temperatures (Cowles and Bogert, 1944). However, the development of certain behavior patterns and morphologic adaptations has undoubtedly allowed reptiles to maintain themselves in some areas and to invade unoccupied regions in opposition to climatic controls. For example, characteristics that aid reptiles in "controlling" their body temperatures in spite of shifting environmental temperatures have probably extended distributions in opposition to primary climatic controls.

Thus even reptilian distributions can be traced only in the most general sense by a study of the record of climatic change through geologic time. The general nature of the distributional inferences that may be drawn from climatic history proves to be of greatest interest when it is seen that distributions of large numbers of types of desert reptiles can be interpreted on the basis of these inferences. Epling (1944) says: "Apart from the tropical biota of Mexico and Central America, the

biota of western North America has been derived from two sources, namely, a mesophytic temperate biota which was holarctic during the Eocene, and a relatively xerophytic temperate or subtropical biota which developed prior to the Miocene in what is now north Mexican plateau. The history of temperate western North America since the Eocene is the history of the interactions of these two communities. Both became widespread and, in their earlier stages, were seemingly more generalized in the sense that species were then associated which have since become restricted to more depleted and specialized communities, now geographically and ecologically segregated. The differentiation and segregation is interpreted as a response to a continued trend toward a cooler and drier climate and a more pronounced physiographic differentiation which began during the Oligocene."

The flora associated with Epling's (*ibid.*), "mesophytic temperate biota" has been termed the Arcto-Tertiary Flora. This flora was characterized by temperate, hardwood-deciduous and conifer-forest species, and, during the Tertiary, dominated the lowland areas

largely north of the thirty-eighth parallel and the highland areas south of that latitude (Axelrod, 1949). Lowe (1950) has interpreted salamander distributions on the basis of Cenozoic history of the Arcto-Tertiary flora. Zweifel (1955) has interpreted the evolution of frogs of the *Rana boylei* group and spadefoot toads (1956) in the light of climatic history.

The flora that formed the floral portion of Epling's (1941) "xerophytic temperate or subtropical biota" has been termed the Madro-Tertiary Flora. This flora was a greatly different assemblage than the northern Arcto-Tertiary vegetation. It was composed of small-leaved, drought-resistant plants. Plants of the type that composed this flora are now found in live oak and conifer woodland, chaparral, sage, thorn forest, and desert border vegetation of western North America (Axelrod, 1949).

The Madro-Tertiary Flora and its associated biota are of primary concern in this study.

The differences in distribution shown by many desert reptile groups of North America seem to be the result of adaptation to divergent ecologic niches during an evolution of all desert types in response to climatic changes on a continental scale. Therefore, to interpret the distributional history of *Uma* one must first look to the history of large-scale climatic shifts and, second, to the adaptations and specializations of the genus.

Historical climatic shifts seem to be the result of two primary causes: (1) geologic changes (i.e., orogeny, peneplanation, and so on) and (2) variations in energy received from the sun. At present, knowledge of changes in solar radiation through geologic time is too meager to be used as a basis for interpretation. Interpretations of past climates extracted from physiographic history are often arbitrary because of the large number of variables that determine the climate at each locality.

Of the various subdivisions of the paleontologic record, floral history most directly reflects climatic history and affords the best available basis for climatic interpretation. In order to use paleobotanical evidence, one major assumption must be made; namely, modern plants respond to climates in the same

way as the same or closely similar plants did in the past. The danger inherent in this assumption can be largely avoided if plant communities, rather than individual species or genera, are used for interpretation. This method has been used by most paleobotanists who have contributed to the knowledge of plant history in western United States in recent years.

The paleontologic history of reptiles and amphibians offers comparatively little evidence from which climatic inferences can be drawn. Taylor (1936, 1939, 1941a, 1941b, and 1942) has analyzed amphibian and reptilian faunas from two upper Pliocene deposits in Kansas. Brattstrom (1955a, 1955b, 1955c) has analyzed reptile and amphibian faunas of the Pliocene and Pleistocene from Arizona, and the Pleistocene of California and Mexico. He has made climatic interpretations which are in accord with those postulated here. The monographs of Gilmore (1928, 1938) summarize the findings of fossil lizards and snakes. Hay (1908) has summarized the fossil turtles. In general, reptile and amphibian faunas represent such limited assemblages that they are of slight use for interpretation of paleoclimates.

Fossil mammals are known from many localities in western North America. Summaries of parts of this information are found in papers by Cope (1884), Hay (1902, 1927, 1929), Matthew (1901), Osborn (1909), Scott (1937), and Camp *et alii* (1940, 1942). The climatic interpretations that may be drawn from studies of fossil mammals are very general. Many warm-blooded animals are only moderately restricted in distribution by the direct effects of the climate. Food supplies, nesting sites, and competition often form barriers as effective as those of temperature and moisture. Climatic inferences can sometimes be made indirectly by use of knowledge of these barriers. For example, the rapid increase of grazing mammals during the Miocene and Pliocene in western North America has been used as an indication of extensive grasslands and hence grassland climates (Clements, 1936).

The fossil bird fauna of California has been summarized by L. H. Miller and DeMay (1942). Climatic inferences have been drawn from avian fossils in this paper and others

such as L. H. Miller (1930) and A. H. Miller (1937, 1939). In general, climatic information based on fossil birds is useful to supplement other evidence.

Wherever possible, the climatic history presented in the present report is based on

paleobotanical studies, in particular those of Axelrod (1939, 1940a, 1940b, 1940c, 1948, 1949, 1950), which have been directed at the problem of Tertiary climates in the arid regions of western North America and the evolution of desert plant communities.

EARLY TERTIARY HISTORY

Arid floral elements (cacti and microphyllous species) of Eocene age have been found in central United States in the Green River formation (R. W. Brown, 1934; Wodehouse, 1933; MacGinitie, 1953). By the Oligocene, a considerable belt of drought-resistant plants, derived from the Sierra Madre of northern Mexico and adjacent regions, had become established on the northern Mexican plateau and near-by interior regions of southwestern United States. This derivative flora has been termed the Madro-Tertiary Flora.

The present southern deserts are covered almost entirely with floral elements derived and segregated from the Madro-Tertiary Flora. Axelrod (1950) considers the Mojave Desert of today as an ecotone. Many of the plants common to the Great Basin and the Mojave Desert have been derived from the northern Arcto-Tertiary Flora. He states: "Since the climate was sufficiently mild for the persistence of arid subtropical scrub in the Mojave Region into middle Pliocene time, it would appear that many of the Great Basin plants may have invaded the Mojave lowlands only in latest Pliocene and Pleistocene."

The physiography of North America in the Oligocene is poorly known. However, some statements may be made. The central area of Mexico was part of the Cordilleran peneplain and stood at a much lower elevation than the Mesa Central of today (Schuchert, 1935). Little orogeny is indicated for the epoch, but coarse sedimentary deposits in some regions of western United States suggest moderate topography (Reed, 1933).

The subtropical precursor to *Callisaurus*, *Holbrookia*, and *Uma* living in this region must have responded to the changing environment by adaptive shifts towards greater tolerance of aridity, possibly by the formation of regionally adapted races (Moore, 1949). Similar changes must have been taking place in other reptilian stocks inhabiting the area. Logically, some forms would be expected not to adapt to the climatic shift, and these would ultimately be excluded from the region. Some of the reptile types that were able to keep pace with the changing environment were the precursors of present North American desert species.

MIOCENE HISTORY

Miocene floral studies (Tehachapi Flora, Axelrod, 1939; Mint Canyon Flora, Axelrod, 1940a) indicate that the Madro-Tertiary Flora covered much of southern California at that time. The flora had also spread northward in the Great Basin and had established a broad ecotone with the northern Arcto-Tertiary Flora (composed of temperate, hardwood-deciduous and conifer forest species) across central Nevada. The Madro-Tertiary Flora of Miocene time was composed of a mixture of vegetative types, each occupying ecologic situations suited to its own require-

ments. There were woodland types, chaparral, sage, thorn forest, grassland, and semi-desert types. Axelrod (1949) suggests that the Madro-Tertiary Flora of Miocene time: "... lived under a climate of 15 to 25 inches of yearly rainfall, distributed as winter rains and summer showers. Temperatures were high in summer, but winters were mild, with frosts rare or absent." The increasing aridity indicated by the floral history is supported by the rapid spread of grazing animals at this time. Merriam and Sinclair (1907) suggest that increasing aridity instituted a wide-

spread development of grassland conditions, thus fostering the development of grazers.

The geologic history of western North America during the Miocene epoch is much more completely known than that of the Oligocene. Lower Miocene deposits suggest a continuation of the seemingly uneventful Oligocene history. In middle and late Miocene, extensive volcanism occurred in western North America. The entire western and southern borders of the Mesa Central of Mexico were subjected to large and repeated outpourings of lava (Schuchert, 1935). The Sierra Madre Occidental of western Mexico was built to a considerable height by these flows. Similar and probably contemporaneous volcanism occurred in the northern Sierra Nevada, the Cascades, and on the Columbia Plateau (W. J. Miller, 1942). Uplift along the Sierra Nevada axis may have raised parts of this range to 7000 feet (Matthes, 1930).

The differential expression of the Madro-Tertiary Flora in various ecologic situations must have resulted in the development of numbers of ecological types within the reptile groups differentiating with the flora. Thus the *Sceloporus* prototype may have sent offshoots into the semi-desert vegetative life-form and the Sierra Madrean Woodland life-form and probably into other segregates of the Madro-Tertiary Flora. The semi-desert ecological type of *Sceloporus* is probably represented today by the *Sceloporus magister-clarki* complex. The Sierra Madrean representative of today may be the *Sceloporus undulatus-occidentalis* complex, a group that has spread far beyond the boundaries of Madro-Tertiary derivative floras.

The *Callisaurus-Holbrookia-Uma* prototype may have been associated originally with arid subtropical scrub, if one may judge from the present-day habitats occupied by subtropical representatives of the group. Secondly the members of the group became associated with the semi-desert vegetation as it developed and expanded in later Tertiary time.

Possibly during early or middle Miocene time the generalized ancestor of *Callisaurus*, *Uma*, and *Holbrookia* became divided into two or more forms, the ancestral *Callisaurus-Holbrookia* and the pre-*Uma*, because volcanism during late Miocene time completed a

continuous barrier of inhospitable terrain along the axis of the Sierra Madre Occidental. This probably isolated the Chihuahuan Basin effectively from the west for the first time in the Cenozoic. The barrier would thus have split each precursor into two segments. A limited contact may have been maintained through Arizona and New Mexico or through gaps in the volcanic barrier farther south.

Complete isolation in the southern Mesa Central may not have been achieved until the Antillean Revolution raised the Sierra Madre Occidental in late Pliocene and early Pleistocene time.

At any rate, late Miocene volcanism may have been the event that separated the fauna of the coast from that of the central plateau effectively from an evolutionary standpoint even if limited contact by some or all members was maintained.

The pre-*Holbrookia* of the Mesa Central (Chihuahuan Desert) probably developed "earlessness" after this division, and a radiation, forming a wide range of adaptive types, followed. Some of these types have since crossed the barrier and invaded the west coast of Mexico and parts of Arizona, presumably through the lowland areas of southern New Mexico and Arizona (for distributions see Schmidt, 1922; Smith, 1935). Axtell (personal communication) has pointed out that "earlessness" probably has developed twice in this evolution: once within the *Holbrookia* group, and again within the *Callisaurus* group, forming the *Callisaurus*-like but earless *Holbrookia texana*. I subscribe to this view and feel that detailed study will show that *Holbrookia texana* should be properly allocated to *Callisaurus*.

The pre-*Uma* at the time of the postulated division must have been close to *Callisaurus* and *Holbrookia* in many respects, as *Uma exsul* of the Chihuahuan Desert retains several similarities that have been lost in the western group.

It seems unlikely that the Miocene prototype of *Uma* could have been restricted completely to habitats of aeolian sand. Several facts support this contention. First, it would be difficult to explain how *Uma* could have spread over such a wide range if it had initially been developed directly in adaptive re-

sponse to a wind-blown sand habitat. The present species are restricted closely to sand and do not spread except on such a substratum. One would necessarily have to postulate a sand connection, either continuous or intermittent, between Coahuila and Sonora, and there is no evidence for such a connection. The climatic regime of the Miocene was nowhere typical in the region vegetated by the Madre-Tertiary Flora of the type now associated with the development of large inland sand deposits. Conditions of aridity, intermittency of streams, and sparse, low, open vegetation, usually associated with large-scale inland sand accumulation, did not develop until the Pliocene (Flint, 1947, p. 463). Second, and most significant in this discussion, is an analysis of the modifications that now restrict *Uma* to dune situations. One of the most striking of these adaptations is the behavior pattern "sand swimming." The chief difference between the "sand swimming" of *Uma* and the sand burrowing of such diverse forms as *Uta*, *Sceloporus*, *Callisaurus*, *Holbrookia*, and *Phrynosoma* lies in the use of the habit. *Uma* uses sand swimming as an escape pattern. [Escape by this means was not noted by Schmidt and Bogert (1947) for *Uma exsul*. However, Axtell (personal communication) states that while collecting *U. exsul* at the type locality he observed the lizard to run swiftly over the dunes and bury itself quickly beneath the surface of the sand.

It could then be picked up by hand. This account differs in no respect from the behavior of western forms of the genus.] *Uma* also burrows to reach shelter during daily and seasonal periods of inactivity. The other genera mentioned employ burrowing behavior only to obtain shelter during inactivity periods (with the exception of *Callisaurus crinitis* and possibly *Phrynosoma m'calli*; see K. S. Norris, 1949). Thus sand swimming in *Uma* is a relatively slight modification of a widespread saurian behavior pattern.

The body form of *Uma* is, as is discussed at length above, closely adapted to sand dwelling. Yet the body form of *Uma exsul* shows several characteristics that link it with the more generalized *Callisaurus-Holbrookia* habitus. Its comparatively blunt snout, long hind legs, and moderately broad abdomen exemplify this relationship. Possibly the pre-*Uma* of early Miocene was adapted to living on sandy soils such as stream washes and flood plains.

The present complete restriction of the genus to aeolian sand habitats is taken to indicate parallel evolution in the Mesa Central and western desert stocks since their isolation. Not enough is known of the habits of *Uma exsul* to state whether this form is completely restricted to sand dunes. From the evidence now at hand it seems probable that it is totally restricted.

PLIOCENE HISTORY

The Madro-Tertiary Flora continued to expand in early Pliocene time in response to increasing aridity. The once continuous Arcto-Tertiary Flora of the northern Great Basin area had become impoverished and reduced (Chaney, Condit, and Axelrod, 1944; Axelrod, 1949). Further, the components of the invading Madro-Tertiary vegetation were waxing and waning in different portions of the area covered by the flora as a whole. In the northern Great Basin woodland types expanded, while in the southern Great Basin they became somewhat restricted. Over the entire Great Basin, grassland was increasing in importance. The semi-desert vegetative type was not widespread in the southern

Great Basin but was expanding (Axelrod, 1949). Thorn-scrub was being restricted southward from the Mojave Desert and Great Basin regions but may have been an important vegetative type in the Mesa Central area (Axelrod, 1949). Undoubtedly it was an important component of the Sonoran lowland regions.

L. H. Miller (1930) has summarized the climatic data drawn from fossil birds and mammals of the Ricardo beds (early Pliocene) on the border of the Mojave Desert and concludes that the area was more humid than it is at the present time and the site of grassland and broad-leafed trees. Plant remains support this view. It is desert today. Bratt-

strom (1955b) has interpreted the small reptile fauna (four species) of the late Pliocene Benson deposit of southeastern Arizona in the light of paleoclimates. It is an assemblage typical of a fresh-water bog or pond of the general area today, including the modern genera *Ambystoma*, *Bufo*, *Crotaphytus*, and *Kinosternon*.

Geologically the early Pliocene seems to have been rather uneventful. Volcanism was less prevalent than during the upper Miocene (Reed, 1933).

The climate, interpreted from botanical evidence, was mild, with hot summers and winters somewhat cooler than those of the late Miocene. Precipitation occurred as summer and winter rains, averaging about 15 inches annually in the Mojave area and 18 inches in the southern Great Basin lowlands (Axelrod, 1949).

The expansion of semi-desert vegetation during lower Pliocene time was probably widespread enough for the first time so that reptilian stocks in these regions began major adaptation to this most arid portion of the Madro-Tertiary Flora.

Middle Pliocene vegetation and climates were of the utmost importance in the development of present-day plant and animal groups. The Madro-Tertiary components continued to shift in importance within the flora in response to a continued trend towards aridity. Woodland vegetation became markedly restricted in the Mojave-Great Basin region, while in central California this type became dominant, replacing much of the Arcto-Tertiary forest (Chaney, Condit, and Axelrod, 1944). In the pre-desert regions, semi-desert vegetation reached its greatest development of the Tertiary, though it was still subordinate to the dominant grassland. The more mesic chaparral and woodland types were forced into more moist situations as aridity increased. Axelrod (1948) says: "Middle Pliocene climate is inferred to have had an important role in evolution for it apparently initiated grassland and sub-desert environments of sub-continental extent. Genetically variable populations of herbaceous and semi-woody plants probably spread into these areas from more restricted semi-arid habitats already existing on the borders of forest, woodland and scrub vegetation where

they have been evolving slowly during earlier parts of the Tertiary. Evolution in the newly expanded Middle Pliocene environment seems to have been rapid. . . . Middle Pliocene and succeeding climates are considered to have been a major factor in the final breakup and segregation of major continental Tertiary Floras into restricted areas and their evolution into modern plant communities."

Geologic changes were not of great magnitude during the middle Pliocene. The Sierra Nevada continued to rise, throwing the Mojave and Great Basin areas into an ever-increasing rain shadow, producing a much more arid type of vegetation than that to the windward of the range (Matthes, 1930). Block-faulting, which probably began in the Great Basin in late Oligocene time, continued to produce alternating north to south trending mountain masses and intervening isolated basins (Nolan, 1943). Probably during much of the Pliocene, the Gulf of California extended northward towards the bases of the rising, moderately high, peninsular ranges of southern California (Vaughan, 1917; Woodring, 1932). If one can judge from the climates adjacent to the head of the Gulf today, there seems to be no reason to interpret this extension during the Tertiary as having produced a significant modifying effect on the general aridity of the surrounding area.

Axelrod (1948) infers from paleobotanical studies a mild and warm climate in the Mojave area during middle Pliocene time, with little or no frost. Rainfall approximated 15 inches on the desert borders and 8 to 10 inches in the central Mojave area [cf. the Ricardo Flora (lower Pliocene), Axelrod, 1939, and the Anaverde Flora (Transition-lower-middle Pliocene), Axelrod, 1950]. A considerable shift towards aridity had occurred since Miocene time.

Thus paleobotanical studies of facies throughout the Tertiary indicate that only during the mid-Pliocene and later were climatic and floral conditions present that were conducive to large-scale adaptive radiations of desert-adapted forms. It is probable that during the mid-Pliocene, the first extensive inland sand habitats appeared.

Many of the specializations to sand-dwelling existence seen in members of the genus

Uma today were probably developed in mid-Pliocene and later time. Digital fringes were developed, and body form became somewhat modified. That during evolution of adaptations to an arenaceous habitat the *exsul* and *notata-scoparia* stocks have been separated is suggested by trenchant differences in the sand adaptations of the two groups. These consist, as is pointed out above, of such features as the *Callisaurus*-like snout of *exsul*, its long hind legs, and relatively slender body.

The possibility that digital fringes were developed independently in *exsul* and the western forms does not seem at all remote, when one considers that such structures are present in such diverse arenicolous forms as *Ptenopus*, a gekkonid from South Africa, *Aporosaura*, a lacertid from western Africa, and *Teratoscincus* of Turkestan and Persia. The common characteristics of *exsul* and the *notata-scoparia* group are largely not sand-adaptive characteristics. Most of the pattern and scutellation similarities do not appear to be sand adaptations.

The *Callisaurus-Holbrookia-Uma* group shows a distinct predilection towards sand habitats in general. On sand deposits within the North American deserts where *Uma* does not occur, some other member of the group is almost universally present. In the west, *Callisaurus* dominates such habitats.

Callisaurus crinitis, of the Vizcaino Desert and Magdalena Plain areas of Baja California, Mexico, has become closely adapted to sand dunes. The similarity of this animal to *Uma* is most striking. My impression, when I first located one of these lizards, was that it was a *Uma*. Once the animal was captured, however, its *Callisaurus* body form was immediately apparent. Aside from the fact that this species has developed digital fringes, it is a most remarkable case of convergent evolution. Its dorsal pattern is more uniform than that of most other forms of *Callisaurus*, and it is closely color-adapted to the unicolored sand that it occupies. Furthermore, two separate populations, each a different color, were observed within the confines of the Vizcaino Desert. One, a gray form, occupies a long series of beach dunes, the color of which is a uniform gray (Tevis, 1944). Farther inland, a pink form was taken from the extensive pink-colored inland sand

areas. It has been my observation that *Callisaurus* in general, with the exception of *Callisaurus crinitis*, is matched less closely to substrate color than *Uma*. Possibly this is a function of the uniform color of desert dunes in the habitat of *crinitis* as opposed to the varicolored substratum occupied by the other species of *Callisaurus*.

Callisaurus crinitis is very abundant on the dune sands of the Vizcaino Desert. It was an easy matter to collect six or eight specimens in 15 minutes on the dunes, but on the clay flats immediately adjacent to dune areas not one individual was seen after a careful half hour's search. Specimens of *Callisaurus draconoides carmenensis* were taken within a short distance of the dunes and showed no intergradient tendencies. Linsdale (1932) and Tevis (1944) have noted what appear to be intergrades between the two forms.

The habits of *Callisaurus crinitis* are similar to those of *Uma* in several respects. Its posture and escape reaction are reminiscent of *Uma*. The lizard usually seeks shelter by running into the nearest bush, whereas most members of the genus *Callisaurus* run among the bushes, making long dashes and hiding behind bushes. *Uma* usually seeks bushes for shelter when they are available. *Callisaurus crinitis* was never observed by me to burrow, though Mosauer (1936) reports such behavior. A common characteristic of *Callisaurus* and some species of *Holbrookia* is the curling of the tail just before and during flight. I did not note this habit in *crinitis*, although Charles H. Lowe, Jr., who accompanied me in Baja California, reported seeing two large males curl their tails. Tevis (1944) and Mosauer (1936) have previously reported that *crinitis* does not curl its tail. Charles M. Bogert (personal communication) reports that *Uma exsul*, while running, curls its tail.

Holbrookia maculata ruthveni is another example of the *Callisaurus*-like lizards that have become adapted to sand habitats. In this case, coloration is the outstanding adaptation. *Ruthveni* is restricted to the White Sands of the Tularosa Basin, New Mexico, an area of 3200 square miles of pure gypsum sand. This little *Holbrookia* tends to occupy the vegetated flats between the large barren dunes and has not developed digital fringes or any significant adaptations towards sand

burrowing. For refuge, it nearly always enters burrows of one sort or another.

The mean grain diameter of the white sands is 0.26 mm., which is within the range of grain size of other desert sands occupied by *Uma*. However, the White Sands offer a more firm footing than most desert sands because of two factors: (1) the water table is close to the surface of the dunes, and the level flats occupied by *Holbrookia* are often "crusty" as a result; and (2) the individual gypsum grains are crystalline and angular and do not seem to slide over one another as readily as most aeolian sands.

It is not surprising that *H. m. ruthveni* has not developed "sand-swimming" habits. The lizard is, however, remarkably color-adapted. It is exceedingly difficult to see on the glaring white sands. Sharply abutting the dune deposit is the reddish soil of the basin floor. This soil is occupied by *Holbrookia m. approximans*, a form rather closely matched to its substrate color and distinctly different from *H. m. ruthveni*.

When the foregoing discussion of adaptation to sand habitats within the *Callisaurus*-like iguanids is considered, it is not surprising that parallel evolution may have taken place with *Uma*. The selectional stresses placed on a lizard by a sand habitat are apparently quite specific. Thus the sand-adaptive structures of *Uma* of the Chihuahuan Desert and those of the western desert forms may well have evolved separately, in isolation.

Late Pliocene vegetation reflects a change towards colder and more moist climates, with summer rainfall absent in the Great Basin near the end of the Tertiary (Axelrod, 1948). Semi-desert and grassland became restricted in the Great Basin and Mojave areas, while woodland and chaparral expanded somewhat. Late Pliocene fossil amphibians and reptiles of Kansas indicate a similar climatic change. Taylor (1942) suggests that a climate similar to that of the North Carolina lowlands may have prevailed—thus a much moister climate. This interpretation is based on the supposed large number of water-loving ranid frogs among the fossil forms. However, Ritland (1955) presents evidence indicating that Taylor's (1942) fauna was composed of only one species of *Scaphiopus* and possibly two species of *Rana*. In view of this drastic reduc-

tion of Taylor's proposed fauna it would seem improper to make estimates of the paleoclimate from this horizon.

The geologic changes that began in late Pliocene time were of great importance. The Mexican Plateau, which had been a lowland area until this time, began to rise as the Antillean Revolution got under way (Schuchert, 1935). The Sierra Nevada underwent renewed uplift at the end of the Pliocene. The whole Mojave Plateau may have been raised a thousand feet (Reed, 1933). Faulting and uplift were occurring in the San Gabriel and San Bernardino ranges at the close of the Tertiary. The Sierra Madre Occidental was the site of large-scale faulting and folding (Schuchert, 1935, p. 121). As the trend towards cooler, more continental climates through the Tertiary reached a climax, the additional impetus supplied by the great increase in mountain building of late Pliocene-early Pleistocene time may have been the factor that tipped the balance towards the development of continental ice sheets.

The effect of the climatic shift towards colder climates during the Late Pliocene must have been to restrict somewhat the semi-desert adapted forms southward. The effect must also have been differential. When the extreme range of habitat conditions occupied by *Callisaurus* today (northwestern Nevada southward at least to Mazatlán, Sinaloa, Mexico) is considered, this form might have been little affected in the Mojave and southern deserts.

It is difficult to assess the climatic tolerance of *Uma*, because the genus is so strictly limited in range by the limits of available sand habitats. Only one known distributional arrangement gives any possible clue to the climatic extremes that limit *Uma*. Along the edges of the San Geronio River Wash in San Geronio Pass, Riverside County, California, a series of nearly continuous sand dunes has been built from the point where the wash floods out into Upper Coachella (Cabazon) Valley upstream to the west of the western limiting spur of Snow Creek Wash. *Uma* is known to occur as far upstream as the mouth of Snow Creek Wash but has not been seen on the adequate habitat just upstream from this point. *Callisaurus*, however, ranges through the pass into the San Jacinto Valley

in the vicinity of Vallevista (Atsatt, 1913). If this apparent limitation of *Uma* is truly a climatic one, the example is important. It would imply that *Uma n. inornata*, at least, is intolerant of the climates of the Upper Pass. Climates of the pass change very rapidly as one descends from Banning into the Coachella Valley. The entire pass is subjected to strong winds much of the time. Vegetation is zoned abruptly in response to the rapid climatic shift. A band of *Yucca mohavensis*, 6 miles wide, crosses the pass at approximately

the altitude of the westernmost sand deposits. *Isomeris arborea* and *Larrea divaricata* are also common at this level. In other parts of the western range of *Uma* the most "climatically extreme" localities seem to be approximately in the same relation to the vegetation zones as the Snow Creek population. If these populations represent or approach closely the climatic limits of *Uma*, then the genus is far more climatically restricted than *Callisaurus* and would be expected to have retreated southward somewhat in the late Pliocene.

PLEISTOCENE HISTORY

The short glacial epoch was a period of great orogeny in western North America. The Sierra Nevada fault block was vigorously tilted and large-scale elevations occurred along its east face, producing present-day topography early in the Pleistocene (Matthes, 1930, 1933). The San Gabriel and San Bernardino Mountains were strongly elevated in early Pleistocene times (W. J. Miller, 1934). A large part of the rain shadow they now produce on the Mojave Desert is Pleistocene and recent in origin. Continued uplift was occurring in the Peninsular ranges.

Beal (1949) postulates great changes in sea level along the peninsula of Baja California, but there is reason to suspect that these changes were of more moderate magnitude. These changes resulted from sea level reductions due to the locking of sea water in the ice sheets and from orogeny. The sea level drops due to continental ice masses are given at about 75 meters by Daley (1934) and about 90 meters by Antevs (1928).

The Antillean Revolution, which was largely confined to the Pleistocene, continued to elevate the Mesa Centrál of Mexico. During this great upheaval, the central plain was elevated to heights of 4000 feet in the north and 7000 feet at its southern extreme (Schuchert, 1935). As recently as the beginning of late Pliocene time the area was probably a lowland not much elevated above the sea.

A large portion of the faulting and folding in the Sierra Madre Occidental of western Mexico which resulted in its present elevation probably took place in early Pleistocene time (Schuchert, 1935, p. 121).

In the Great Basin, considerable elevation of many of the fault-block ranges was occurring. Mature topography of Pliocene age has been noted on the high portions of several of these ranges. For example, orogenic movements of several thousand feet have raised this old surface far above the intervening valleys on the Panamint Mountains, Black Mountains, Coso Mountains, Argus Mountains, Inyo Mountains, and Ruby-East Humboldt Mountains (Hopper, 1947; Knopf and Kirk, 1918; Sharp, 1938).

The Colorado Plateau owes much of its altitude to Pleistocene elevations. W. J. Miller (1942) says: "The present cycle of erosion began in Early Quaternary. It was introduced by a profound general uplift of the whole Colorado Plateau region, accompanied by a general northeasterly uptilt. In the south the plateau was brought to an altitude of about 5000 feet, and in the north to more than 10,000 feet."

Blackwelder (1934) presents evidence that the Colorado River had its origin in early Pleistocene time. However, Longwell (1946) has presented good evidence indicating that the river existed as a through-flow drainage much earlier than the Pleistocene. Even so, it seems evident that most of the present physiography of the river channel and delta is Pleistocene in age. The uplift of the Colorado Plateau during the Quaternary has rejuvenated the river, causing great down-cutting in the channel and consequent transport of vast quantities of alluvium. The early delta was deposited across the trough of the Gulf of California in the vicinity of the International

Border. This blocked the sea completely from the north end of the trough. Subsequent down dropping of the northern valley floor has produced the sub-sea-level Cahuilla Basin. These geologic events have been of great significance in the evolution of the *notata* group of the genus *Uma*. The Colorado River divides the species into two segments today and probably has been the primary cause of their differentiation into two distinct subspecies, *rufopunctata* and *notata*. The drying of the Cahuilla Basin, caused in part by the Colorado delta, has allowed populations of *Uma notata* to become established in the northern parts of the basin, where subsequent isolation has allowed the evolution of another subspecies, *Uma n. inornata*.

The most remarkable feature of the Pleistocene epoch was its glaciation. Of the four major continental sheets in North America, the first is thought to have been the largest. Matthes (1930, 1933) has found a similar sequence in the alpine Sierra Nevada mass. Three times the Yosemite chasm has been invaded by a trunk glacier. The first of these invasions filled Yosemite to the top, while the last advance (Wisconsin) filled the valley to one-third of its depth. Blackwelder (1931) lists four glacial stages in the Sierra Nevada but does not correlate them with continental sheets.

Three relatively long interglacial periods intervened between glacial advances. Leverett (1929) says: "The studies of fauna and flora in interglacial beds are now sufficiently advanced, both in Europe and America, to bring out clear evidence that conditions at least as warm as the present were prevalent in each of the interglacial stages."

The history of Pleistocene climatic shifts is highly complex and extends to the present time. That the glacial epoch is not over is attested to by the large glacial masses that cover 10 per cent of the land surface of the globe today. At the maximum of the latest

(Wisconsin) advance, 27 per cent of the land was covered with ice (Flint, 1947).

Before beginning a discussion of the climatic history of the epoch, I wish to present four questions, the answers to which lie in Pleistocene climatology.

1. What has been the effect of glaciation and associated phenomena on the distribution of *Uma* and other desert reptile genera?

2. If restriction has occurred, has reoccupation taken place since the last retreat of the ice and, if so, how?

3. To what extent have the areas where *Uma* occurs been changed as a result of glaciation?

4. Can the development of any isolated or differentiated forms within *Uma* be attributed to Pleistocene phenomena?

The first question cannot be answered easily. First, an approximation of the range of *Uma* prior to the Pleistocene must be made. Then the climatic shifts in that area during the ice advances must be ascertained as closely as possible. This information must then be correlated with the available knowledge of the tolerances of the genus before the final estimate of restriction can be made.

In the absence of a fossil record, there is no way of determining with certainty the range of *Uma* at any time in its past history. It seems possible that the stocks that became sand-adapted in the middle Pliocene could have spread over considerable areas. Climatic conditions were favorable for the production of dune deposits (Flint, 1947, p. 463), and topography was less rugged than that of the present time; thus dispersal may have been relatively simple. Semi-desert environments extended into the northern Great Basin until late Pliocene time (Axelrod, 1949). Thus a climatic habitat was available which *Uma* and other desert reptiles could conceivably have occupied, prior to the onset of glaciation.

CLIMATIC SHIFTS DURING THE PLEISTOCENE

The evidence pertaining to Pleistocene climatic changes is considered under two headings for the sake of convenience—the physical evidence and the biological evidence.

THE PHYSICAL EVIDENCE

Within the present desert areas of western United States, 19 mountain masses supported glaciers at one time or another during

the Pleistocene epoch. These small glaciers have nearly all been correlated with the sub-stages of the last glaciation (Wisconsin). The evidence of previous glaciation has mostly been obliterated. The San Francisco Mountains of Arizona supported glaciers during the Wisconsin advance and during an earlier period (Sharp, 1942). These glaciers were the southernmost of the Great Basin region and, during the maximum expansion, reached the lowest elevation of 8000 feet. Glaciers of the northern Great Basin left terminal moraines as low as 6100 feet on the Ruby-East Humboldt Mountains in Nevada (Sharp, 1938).

No glaciers were recorded for the mountains within the Sonoran Desert except for those on the San Bernardino Mountains at the extreme northern border of the Coachella Valley (Vaughan, 1922). These glaciers reached a terminus at 8000 feet. W. J. Miller (1926) has produced evidence of glaciation, now interpreted as frost effect, from the near-by San Gabriel Mountains. He suggests the possibility of glaciation on Mt. San Jacinto, just south of the San Bernardino Mountains. It is not surprising that no other examples of glaciation have been found on the Sonoran Desert, as there are few peaks of sufficient height to support such features.

Surprisingly enough, glaciers occur today along the southern limits of the Mesa Central near Mexico City, on Mt. Ixtaccihuatl (17,425 feet), extending down to 15,000 feet in elevation. During the glacial periods these glaciers terminated at about 11,000 feet (Jaeger, 1925).

With regard to correlation, Antevs (1925) says: "From a climatologic point of view we can even expect a glaciation in the western mountains corresponding to each ice sheet. On the other hand, the idea that the glaciations in the two regions would be of different dates is absurd."

The effects of glacial climates must have extended southward from the continental ice sheets for considerable distances. Climate seems to have ameliorated fairly sharply as the southern latitudes or lower altitudes were approached.

In view of the widespread presence of periglacial effects, it is evident that Great Basin and Mojave Desert climates must have been markedly altered during glacial maxima. In

turn, the altered climates must have caused extinction of the more northern segments of the evolving desert biota, perhaps including northern salients of *Uma*.

Much more spectacular than the record of glaciation in the desert areas is the history of the numerous Pluvial lakes that occupied the lowland regions of the present deserts during glacial and post-glacial time. All the present desert regions supported some of these lakes. Within the Basin and Range Province, Free (1914) lists 126 closed basins. Nearly all of these supported permanent or ephemeral lakes which occupied one or more basins. Meinzer (1922) lists 68 Pluvial lakes occurring in these basins. Flint (1947) has added four lakes to this list, bringing the total to 72. Hubbs and Miller (1948) list 103 permanent Pluvial lakes or groups of lakes of Great Basin affinities occurring within the Great Basin today, or peripheral to it.

Lakes Bonneville and Lahontan of the northern Great Basin were huge lakes occupying a number of now isolated basins. Lake Bonneville was the largest, covering 19,750 square miles in Utah and Nevada. It had an extreme depth of 1050 feet (Flint, 1947). The remains of this lake are present today as the saline Provo, Sevier, and Great Salt lakes of Utah. Lake Lahontan had a surface of 8422 square miles and occupied the basins now filled by Pyramid, Winnemucca, Carson, and Walker lakes of Nevada.

In the south, the Pluvial lakes rarely occupied more than a single basin. Jaeger (1925) reports the presence of many Pluvial lakes in the Mesa Central area of Mexico. He has produced detailed information showing a considerable Pluvial expansion of Lake Texcoco, near Mexico City.

In general, the Sonoran Desert is devoid of closed basins that could have supported Pluvial lakes. Where these basins do occur, there is usually evidence of ephemeral or permanent bodies of water recorded in the basin. The ample evidence for the existence of a Pluvial lake in Cahuilla Basin (Lake LeConte) is discussed above. In addition, a few small lakes were located in southern Arizona and northern Sonora (Hubbs and Miller, 1948).

There was a sharp north-south gradient in the number and size of these Pluvial lakes.

Meinzer (1922) says: "The range in humidity (or aridity) among the various basins in the Pleistocene epoch was apparently as great as the difference, in a given basin, between the Pleistocene and the present. A considerable number of the closed basins in the province were too arid in the Pleistocene to contain lakes of any consequence, whereas a few are humid enough at present to contain perennial lakes of considerable size. The relatively humid parts of the province [Basin and Range] at the present time seem to be comparable to the most arid parts of the Pleistocene epoch. The region of southwestern New Mexico and southeastern Arizona in the Pleistocene is apparently comparable to southern Oregon at present, for the Pleistocene lakes near the Mexican border do not seem to amount to much more than do the present lakes of Oregon."

At present the southern arid basins differ from those of eastern Oregon by a mean annual temperature of about 15° F. Meinzer interprets this as meaning an approximately equal change in the southern basins during the height of the Pluvial period. However, no claim to accuracy is made for these figures. These widespread Pluvial lakes have been important in the history of sand dunes and of *Uma*. Many of these lakes have left shore-edge dunes, which have been reworked into the present-day dunes, which are found in nearly every basin. Particularly in the Mojave Desert ancient drainage channels, which ran from lake to lake during pluvial periods, seem to have served as routes in the spread of *Uma*.

There is still no unanimous agreement concerning the climates that have induced glaciation. Certain of the current views diametrically oppose one another. Cooler temperatures, warmer temperatures, and increased precipitation have all been used to explain glaciation. It would not be profitable to discuss the various explanations that have been offered for the production of these climatic changes. Some of the evidence pertaining to the suggested climatic changes of the North American deserts is summarized. The first view, that of cooler temperatures inducing glaciation, as Epling (1944) points out, has been based largely on studies of Alpine glaciation. There are, however, many other adher-

ents. The viewpoint is exemplified by Antevs (1925) who says: "The conclusion [that low temperatures caused glaciation] is drawn chiefly from the everywhere-existing indications of a lower temperature during the Ice Age than at present and from the dominating role played by the temperature also in the post-glacial climatic changes."

Adherents to the general theory that cold winters and cool summers have been the major cause of glaciation have been Croll (1875), Hitchcock (1891), Antevs (1925), Milankovitch (1930), Flint (1947), and many others. Both Antevs and Flint have pointed to a combination of temperature reduction and increased precipitation as the change that has induced glaciation. Antevs (1925) recalls that, whereas temperatures are and have been very low in Siberia, very scanty glaciation has been recorded in this region. This is owing, he says, to low precipitation in the area.

Huntington and Visser (1922) have emphasized the role of increased precipitation in the production of glaciers.

One of the most provocative hypotheses is that of Simpson (1934), who considers the cause of glaciation to have been fluctuations in solar radiation which produced higher temperatures. He thinks the glaciers advanced during periods of solar radiation maxima. His hypothesis is briefly as follows: Increased radiation at the Equator initiated greater atmospheric circulation; these winds plus the higher temperature increased the evaporation rate. Cloudiness was thus more prevalent, and therefore precipitation was also greater. In the equatorial regions pluvial periods would coincide with glacial maxima and interpluvial periods with interglacial times. In high latitudes, greater snowfall gave rise to glaciers, but, as the radiation increased melting and evaporation overbalanced the snowfall, recession of the ice sheet followed. Then a warm wet interglacial period began. When the radiation cycle reversed, the sequence was repeated in reverse. Thus two fluctuations of solar radiation could account for the four glaciations and the three interglacial periods. Epling (1944) states (*vide* Bjerknes) that the theory of slight mean temperature increase of the earth's surface during glacial advances finds general accept-

ance among meteorologists. Whether or not Simpson's hypothesis can be used to explain world-wide glaciation is not of concern here. There appear to be major objections to the association of a rise in temperature with the glacial climates of the deserts of North America. These objections may possibly be resolvable on the basis of topographic effect. Epling (1944) has pointed out that the increase in precipitation postulated by the theory should have produced much more humid conditions than seem to have occurred in the Great Basin during pluvial periods. Considerable aridity in the southern portions of the Great Basin has been postulated by Meinzer (1922).

The great expansion of Pluvial lakes in the Basin and Range Province seemingly could be explained by a reduction in evaporation during the summer months and a consequent accumulation of surface water plus a slight increase in rainfall. The tremendous effect of evaporation in the removal of water at present can be realized when one considers the figures presented by Meinzer (1922) who states: "The north basin of Big Smoky Valley, Nevada, may serve to illustrate the importance of ground water discharge. In this basin there is an area of 160 square miles in which ground water is discharged into the atmosphere. The average rate of discharge in this area has been roughly estimated to be six inches of water per year, which would amount to about 50,000 acre-feet a year, or 45 million gallons a day—about 8% of the water that falls on the basin as rain or snow."

Simpson's hypothesis postulates alternating pluvial and glacial periods in high latitudes. Evidence from Mono Lake and Lake Bonneville shows that maximum glacial advances and the high stages of the lakes were contemporaneous (Antevs, 1925; Putnam, 1938). Seven glaciers extended to the high shore line of Lake Bonneville.

The cause of temperature reduction in areas peripheral to a continental ice mass probably can be attributed to the system of anticyclonic winds which blow off such a mass. Simpson (1919), in a study of wind distribution over Antarctica, points out that cyclonic winds prevail in the higher levels of the atmosphere and settle onto the ice mass, become cooled, and pass off the ice as anticyclonic winds. These winds are strong and

cold. Brooks (1949) states that an ice mass must be of a certain minimum diameter before an anticyclone can develop. Greenland, which is about 650 miles in width, is not large enough to establish an anticyclone, because cyclonic storms are able to pass across the area and disrupt forming anticyclonic systems. Brooks (1949) says: "When the diameter [of the ice sheet] reaches, say, 1000 miles, a glacial anticyclone develops, with clear skies and intense cooling by radiation. The outwardly directed winds spread Arctic conditions in a broad zone round the margin of the ice, and may even result in the 'sympathetic' glaciation of a neighboring mountain range."

Thus when an ice sheet begins to shrink, the anticyclonic effect would continue until the critical diameter was reached, at which time periglacial climates would most likely become noticeably more temperate.

From the physical evidence at hand it is suggested that the climates of the deserts of North America were significantly colder during the maximum advances of the continental glaciers and that precipitation may have been somewhat greater than at present. It is suggested that "sympathetic glaciation" on various peaks in the Great Basin area was induced by periglacial effect during glacial maxima. This physical evidence makes probable the idea that warmth-loving desert animals and plants must have been excluded from the northern portions of what is now desert, during glacial maxima. I feel that many present-day inhabitants of the Mojave Desert must have been entirely absent from this area or restricted to the small, low-altitude segment at its southern fringe.

THE BIOLOGICAL EVIDENCE

The biological evidence relating to Pleistocene climates is both paleontological and distributional in nature. There is little paleobotanical evidence from desert regions. A considerable record is available from the west coasts of North America.

Problems of correlation make the interpretation of all paleontologic evidence of Pleistocene age very uncertain (Ray, 1949). Correlation is rendered extremely difficult by the climatic complexity and the short duration of the epoch. Faunal and floral changes

within the Pleistocene are becoming increasingly useful to establish stratigraphy but their application is, as yet, limited. Archeologic dating is useful where it can be applied, but it has contributed little to the Pleistocene climatic chronology of our deserts.

Some excellent climatic inferences have been drawn from distributional data, but these interpretations are generally limited to the latest ice advance, or are of indeterminate age.

The bulkiness of the literature pertaining to the Pleistocene precludes the possibility of a thorough review. Only a small segment, illustrative of the conclusions, can be mentioned.

THE BOTANICAL EVIDENCE

Some of the pertinent fossil plant localities are considered briefly.

Fairbanks Flora, Alaska (Chaney and Mason, 1936): These fossil plants reflect a climate somewhat like that of the region today, possibly somewhat warmer. The ground, now frozen, could not have been frozen at the time of deposition. The flora is associated with camel, horse, and mastodont remains.

Puget Sound Pollen, Washington (Hansen and Macken, 1949): This "interglacial" flora reflects a climate like that found in coastal Washington today.

Punta Arena Flora, northern California (Mason, 1934): This flora also indicates a climate similar to that found in the region today.

Tomales Flora, central California (Mason, 1934): This fossil locality has produced a large assemblage of fossil plant species. These plants indicate a climate possibly somewhat colder than occurs in the region today. Associated with this flora is a considerable marine invertebrate fauna which has been studied by Dickerson (1922). He concludes that the fauna lived in warm seas such as those now found near San Diego, California. Thus the climatic data suggested by the fauna and flora are at complete variance with one another. The fauna and flora have been interpreted as interglacial. The presence of a warm ocean would have had a marked modifying effect on the climate of maritime areas. Thus the small change indicated by the Tomales Flora could have represented a much greater change in continental situations.

San Bruno Flora, central California (Potbury, 1932): This flora seems to indicate climatic conditions that obtain in hills about 1500 feet above the site of deposition today. The difference suggested by the flora may be the result of different exposure conditions during deposition than occur at the site today.

Willow Creek Flora, Santa Cruz Island, southern California (Chaney and Mason, 1930): This flora has been interpreted as indicating conditions at the time of deposition similar to those now found at Fort Bragg, 450 miles north of the site. A. H. Miller (1937) and Epling (1944) suggest that a perfectly adequate representation of the fossil floral types may be found today at Monterey, approximately 200 miles north.

Carpinteria Flora, southern California (Chaney and Mason, 1933): This fossil assemblage seems to be contemporaneous with the Willow Creek Flora and gives similar evidence of climatic change. Both floras are tentatively classified as glacial.

McKittrick Flora, southern Great Valley, California (Mason, 1944): A flora indicating moister climates than occur at the locality today. Piñon and juniper, two forms largely restricted to areas peripheral to deserts today, were associated in the flora, suggesting inland affinities. The elevation of the coast ranges since the time of deposition may have accounted for the climatic change that the flora indicates.

Southern Louisiana (C. A. Brown, 1938): This flora represents a peculiar combination of such elements as persimmon, *Magnolia*, and other mesic, broad-leaved species, plus larch, white spruce, and northern white cedar. These latter forms are represented in present floras 700 miles north of the fossil locality. Brown considers the assemblage to be contemporaneous with the maximum extent of ice. Possibly during maximum ice advance, zonation was much accentuated, with the northern conifer forests occupying highlands, and the present flora, protected lowland situations.

Dallas Pollen, Texas (Antevs, 1948): Such forms as white spruce and fir are interpreted as indicating a cool climate, approximately like that along the present 70° F. July isotherm. The 84° F. July isotherm crosses the locality today.

In addition to these floras, Davis (1946) has reported *Picea* and *Abies* from pollens of peat bogs in Florida. A similar flora to that now found in northern Wisconsin has been reported from the Pleistocene of North Carolina (Buell, 1945).

From this botanical evidence it seems logical to conclude that the west coast of California underwent extension of forest elements from higher altitudes and from the north during glacial advances, the southward shift being approximately 200 to 300 miles for the most severely affected elements. The restricted nature of this shift was probably the result of the maritime environment and the relative freedom from periglacial effects, as a consequence of topography and the distant location of the Cordilleran Ice Sheet.

In the Middle West and East, the glacial effects seem to have been greater during the height of glaciation than those on the west coast, consisting of a differential movement of vegetation southward from the glacial front and a sharply increased zonation in southern areas. Because of the low terrain in these regions, periglacial climates were effective for considerable distances in advance of the ice sheet. These conclusions are at variance with those of Gleason (1922) who, using present-day plant distributions in Illinois, postulates that all these floral distributions can be explained on the basis of glacial climates drier than those of the present time and of about the same temperatures. Gleason's conclusions do not now seem tenable because of the fossil evidence which has been brought to light since the publication of his work.

If the factors that controlled the expression of glacial climates were the presence or absence of topographic barriers and maritime conditions, what sort of climates might be interpreted as having occurred in the Great Basin region during the glacial maxima?

The main Cordilleran Ice Sheet of Wisconsin age covered the northern half of eastern Washington and western Montana. This sheet covered territory comparable in altitude and relief to that separating it from the Great Basin. Large isolated glacial masses bordered the Great Basin on all sides but the south, on the Cascade Mountains, Sierra Nevada Mountains, Salmon River and Sawtooth Mountains, Absaroka Mountains, Wind

River Mountains, and the Uinta Mountains (Flint, 1947). These isolated glaciers must have been the result of glacial climates and probably contributed only local climatic effects of their own.

In the absence of a maritime situation and protected by a rather indefinite barrier from the continental ice mass, glacial climates of the Great Basin must have been slightly less extreme than those of the middle western United States. This conclusion, once again, supports the idea that warmth-loving desert types were probably excluded from northern desert areas during glacial maxima. The following discussion of faunal evidence seems to support this conclusion.

THE ZOOLOGICAL EVIDENCE

The Pleistocene marked a climax of climatic, geologic, and biologic gradients. Giant animals of various sorts made their appearance and vanished. Romer (1945) says: "In any region where the fauna is adequately known, we find, in the Pleistocene, representatives of all [present] types present. But in addition, there are invariably numerous animals now extinct, and most of these are of large size."

Pleistocene faunas of the arid Southwest are not numerous. The climatic inferences drawn from them are sharply divided into two classes, those that reflect conditions somewhat like those of the present and those that suggest decreased temperatures. In general, these logically represent interglacial and glacial deposits.

A number of large extinct forms have been reported from the Great Basin. For example, bovid bison, ground sloths, glyptodonts, elephants, horses, camels, and deer have been recovered in central Nevada and parts of Arizona (Hay, 1927).

Astor Pass Fauna, northern Nevada (Merriam, 1915): This fauna is a small one, composed of types that are 60 to 70 per cent extinct, possibly associated with an early stage of Lake Lahontan, in interglacial time.

Fossil Lake, central Oregon (Hay, 1927): A large array of fossil forms, many now extinct, reflect interglacial climates and rather extensive grasslands.

Rancho La Brea, southern California: This unique accumulation has produced over 180 types of fossil animals and plants. Stock

(1946) correlates the age of the main deposits with the third interglacial (Sangamon time), following the Illinoian glaciation. He says of the climate indicated by the biota: "It was essentially an interior climate featured perhaps by a slight increase in rainfall over the present, and with temperatures similar to or slightly higher than those of today in this region."

Hibbard (1949) has summarized a rather remarkable record of Pleistocene faunal shifts in Kansas. Five horizons in stratigraphic sequence from Meade and Seward counties have been studied. The oldest, the Deer Park fauna, reflects a cool climate. This conclusion is based on a dominance of microtine rodents in contrast to a dominance of cricetine rodents in the underlying upper Pliocene Rexroad fauna, which has been interpreted as warm and moist (Taylor, 1942).

The Cudahy fauna is found in strata overlying the Deer Park deposit. Hibbard (1949) says: "The fauna is definitely Boreal in its affinities to living forms which are now found from southern Canada north to Alaska We are not dealing in this case with locally stranded relics, but with a fauna of widespread distribution. At the close of glacial time and at the beginning of interglacial time forms intermingled along the periphery of their ranges, and all degrees of intermingling occurred within a region until a climatic climax was developed in that region. In distinct contrast to the Cudahy fauna is the Borchers fauna, a warm temperate fauna, which occurs in the silt and clay directly overlying the Pearlite ash [Cudahy horizon] in Meade County, Kansas. Here we are dealing with the same geographic locality and the same formation though later and under different climatic conditions."

The *operarius* group of microtine rodents, which is abundant in the Cudahy, now occurs only in Alaska and northern Canada.

The Borchers fauna is related to the present fauna of southwestern United States. The assemblage is interpreted as "optimum interglacial in character."

The younger, interglacial, Cragin Quarry fauna also reflects warm conditions.

Even more recent is the Jones fauna, the aspect of which is nearly modern, but it reflects cooler and slightly more humid conditions than prevail in this region today.

In addition to these indications of fluctuating climates, the location of a musk ox skull (probably *Symbos cavifrons*) near Salt Lake City, Utah, suggests tundra conditions in that region sometime during the Pleistocene (Hay, 1927). Fossil specimens of the marmot (*Marmota flaviventris*) have been found in late Wisconsin or recent deposits and indicate marked climatic shifts. Hall (1946) reports marmot remains in kitchen middens in northern Arizona and in cave deposits in the Providence Mountains, California, which indicates a rather recent southward extension of the genus. Stearns (1942) suggests that fossil marmot remains from the Guadalupe Mountains, New Mexico, indicate a lowering of life zones of 4000 feet during a Wisconsin substage. Murray (1957) has carefully reviewed this New Mexican fauna. He lists four forms, in addition to the marmot, that indicate conditions now found only on high mountain peaks, and six typically desert forms, plus a preponderance (16) of juniper-grassland and yellow-pine forest forms. He concludes that climatic fluctuations may have been sufficient to allow repeated dispersal of forest-dwelling forms across what are now moderately arid zones.

These isolated climatic interpretations all point to the conception that the climate of the Great Basin and the Great Plains fluctuated with the advancing and retreating ice. Maximum advances were correlated with climates cold enough to induce sympathetic glaciation on isolated mountain peaks. These climates caused marked shifts in the biota, bringing Canadian animals and plants onto the Great Plains and probably into the Great Basin area. The reptile faunas of these regions must have reacted with the rest of the biota.

ZOOGEOGRAPHY OF THE GREAT BASIN

There is a considerable body of distributional evidence relating to Pleistocene climates in the deserts. Many zoogeographers have correlated their findings with interpretations of glacial events. For example, Hall (1946) correlates the development of subspecies in each of five different species of rodents and one species of fox with the development of soils after the recession of Pleistocene Lake Lahontan. Grinnell (1943) has correlated discontinuous desert populations of gophers (*Thomomys*) with Pleistocene

events. Hubbs and Miller (1948) have correlated a large body of fish distributional evidence with the history of Pleistocene hydrography.

It is pertinent to review the climatic conclusions reached in two of these studies.

Hubbs and Miller (1948), who, from 1934 to 1942, investigated the discontinuous fish fauna and Pleistocene hydrography of the Great Basin, conclude: "Now disconnected waters within many of the basins of western North America may have been connected and their fish fauna made uniform not many centuries ago. From a consideration of the evidences on climatic changes reviewed by Huntington, it seems likely that such connections may have been established several times during the last three millennia. We believe, however, that most of the local differentiation and endemism among the fishes of the isolated desert waters dates from the end of the glacial period."

Some discontinuous organic distributions might reasonably be attributed to dispersal mechanisms such as wind transport or wandering. These would not require climatic changes for their explanation. It seems impossible that the highly localized but widespread fish fauna living in the meager waters of the Great Basin Desert could be explained by any other means than previous water connections.

Grinnell (1943) has come to conclusions which are in accord with those of Hubbs and Miller (1948). In his study of pocket gopher distribution, Grinnell says: "As a result of these special conditions of food supply, the general distribution of gophers on the deserts is conspicuously discontinuous; the animals exist only in colonies here and there because surrounded by unoccupied desert; and such colonies are often far isolated from one another . . . [Each of these isolates] may appropriately be looked upon as a relict form from earlier times when conditions of moisture much more generally prevailed in the Great Basin territory, and when the dependent fauna and flora were correspondingly widespread." It should be noted that these isolated desert populations are largely of subspecific rank and most probably arose during or after the Pleistocene.

The high mountains of the Great Basin support populations of moisture-loving rep-

tiles that are absolutely restricted by the surrounding desert in the same manner as desert fish populations. As with the fishes, it is unlikely that they came to occupy these isolated locations by any other means than through migration in a lowland habitat. Two forms are considered here: *Eumeces skiltonianus* and *Sceloporus occidentalis biseriatus*.

Eumeces skiltonianus, a skink, has been recorded from nine scattered localities in Nevada. All localities are in the mountains, the lowest at 6300 feet, 2 miles west of Smith Cave, White Pine County, Nevada. Rodgers and Fitch (1947) have studied the *skiltonianus* group and state: "The most wide-ranging species, *skiltonianus*, has been found in British Columbia, Washington, Oregon, Idaho, western Montana, California, Nevada, western Utah and northern Lower California. . . . In the Great Basin, *skiltonianus* is spotty in occurrence and is restricted to the cooler, higher areas of certain mountain ranges. In California, the range of *skiltonianus* is nearly continuous. The species attains its maximum abundance in the Transition Life-zone, but is also common in the Upper Sonoran and occurs in some of the lower parts of the Canadian Life-zone." The range limits of the species, within California, coincide quite closely with the 15-inch mean annual rainfall line, as plotted by Sprague (1941). This amount of rainfall probably approximates the minimum tolerated by the species. In Nevada between the southern known occurrence of the species (Charleston Peak, Clark County, 7500 feet) and the nearest northern locality (Scofield Canyon, Mt. Grant, Nye County, 8000 feet) the minimum mean annual rainfall line is 6 inches (Sager, 1941).

The primary distribution control seems to be humidity, when the wide range of temperature conditions within which the species lives is considered. For example, the temperature records of two skink localities are instructive. The Dalles, Wasco County, Oregon, has a 40-year January average of 32.7° F., with a minimum of -30° F.; San Jacinto, Riverside County, California, has a 38-year July average of 77.6° F., with a maximum of 120° F. (Sprague, 1941).

If the physiology of *Eumeces skiltonianus* has not changed greatly since Pluvial time, it is reasonable to suppose that at least the min-

imum amount of rainfall (15 inches) must have prevailed in the separating lowlands. There is no reason to believe that these skinks have changed significantly since isolation. The habitat requirements of the isolated populations are very similar, and their morphology is almost completely uniform. Lack of differentiation of the isolated populations points to a Pleistocene separation. The evidence presented by Hubbs and Miller (1948) suggests that this isolation could have taken place in the latest Pleistocene times.

Sceloporus occidentalis biseriatus, the fence lizard, has been taken at many places in the Great Basin. In the northern portion, the lizard occupies both lowland regions and mountains, while southern populations are restricted to mountain situations. Probably because of its greater tolerance to aridity, *Sceloporus occidentalis biseriatus* ranges farther south than *Eumeces skiltonianus*.

Sceloporus occidentalis biseriatus occurs across most of Nevada and apparently intergrades with *Sceloporus undulatus tristichus* in southeastern Nevada and northwestern Arizona (Shannon, 1950). It also may intergrade with *Sceloporus u. consobrinus* in Utah (Burt, 1933). In central Nevada and eastern California the isolated populations are nearly uniform except for random color variations (e.g., at Sweetwater Springs, San Bernardino County, California).

The fence lizard is of particular interest, as some of its discontinuous distribution definitely originated in the Pleistocene. Geologic evidence shows that some of the southern mountain ranges occupied by isolated populations of *Sceloporus occidentalis biseriatus* were elevated in Pleistocene time. For example, the Argus and Panamint ranges were elevated in Pleistocene time, probably since the first interglacial period (Hopper, 1947), as was the Inyo Range (Knopf and Kirk, 1918).

In summary, in consideration of the biological and physical evidence relating to Pleistocene glacial climates in the Great Basin, it is suggested that rainfall was somewhat greater than that of the present time, diminishing rather rapidly southward. In south-central Nevada an increase of at least 8 to 10 inches of average annual rainfall is indicated for periods of late Pleistocene ice

advance. Temperatures were considerably lower, especially in the north. Zonation effects were probably heightened; the climatic difference between mountain tops and valleys were more extreme than they are at the present time.

These climatic changes probably produced an expansion of piñon-juniper association onto the lowlands of the southern Great Basin and Mojave deserts, and possibly a considerable expansion of forest types in the north. Riparian habitats must have been greatly expanded.

The climatic shifts occurring in the Sonoran Desert during ice advances probably were fairly extensive.

The climatic evidence, which has just been reviewed, suggests that subdesert conditions prevailed over all or most of the Sonoran Desert region during glacial maxima. At this time vegetation was probably a great deal denser and composed both of plants that now occupy the desert region and components of the peripheral floras. Zonation and local diversification of the flora, and consequently the fauna, were most likely common phenomena.

These conclusions seem to be well in accord with those of Antevs (1925) who says: "The supposition of various students that the Pleistocene lakes in the Great Basin can be accounted for by a rather slight change in existing conditions is correct, in so far as no great actual increase in humidity is necessary, because the region now has so little precipitation. Relatively, the moist conditions must have been very much greater than at present."

Epling (1944) on the basis of studies of vegetation and fossils relating to the distributional history of *Drosophila pseudoobscura* seemingly postulates a slightly lesser degree of change: "The increase in rainfall which apparently characterized certain parts of the period [Pleistocene] apparently did not greatly affect the Pacific southwest, and although the presence of the ice sheet doubtless caused a shift in the storm track, there is reason to believe that even during the pluvial periods the biota of the Pacific coast was separated from that of the Rocky Mountains, as now, by a relatively arid Basin and Range Province."

Deevey (1949), on the other hand, seems to postulate a somewhat more dramatic shift than I feel is indicated by the data: "Pleistocene climatic changes in the Great Basin and further south were extensive and of the sort making it possible for northern species to penetrate into the subtropical zone of high atmospheric pressures."

Numerous studies of desert animals show that these creatures are not ubiquitous in their harsh habitats. All vertebrate animals occupy the desert regions by virtue of behavioral adaptations which allow them to escape the extremes of climate (Cowles and Bogert, 1944; K. S. Norris, 1953). The microclimates in which the fauna of the deserts survive are all more mesic than the deserts themselves. Thus it is quite conceivable that, as true desert climates contracted, and possibly disappeared during glacial maxima, desert animals could have remained within portions of their old ranges. If climates became excessively cold, exclusion of species would have occurred in the order of their susceptibility to cold. My opinion, from a distillation of available data, is that ranges of most desert species were altered, obliterated in some locations, and extended in others, by glacial advances, particularly in the Great Basin and Mojave deserts, but that a major shift of the entire biota towards the south outside its present range probably did not occur.

Pluvial climates of most of the Mojave Desert and all of the Great Basin Desert were probably too harsh for *Uma* to endure. Cer-

tainly they were more extreme than anything now tolerated by the genus.

The first restriction, which may have been the greatest, during late Pliocene and early Pleistocene (Nebraskan) time possibly initiated the species *scoparia*. The presence of *Uma n. notata*, which has seemingly been formed *in situ*, adjacent to the southern limit of *scoparia* seems to indicate that later population movements of *scoparia* south of its present southern border did not occur. Therefore, it is likely that *Uma scoparia* became restricted to the old southern dunes of the Mojave Desert during the later Pluvial periods (i.e., the dunes at Rice and Palen lakes or earlier equivalents). These dunes are 1500 feet or more below the average elevation of the Mojave Desert and probably were not subjected to the climatic changes that occurred on the higher portions of the desert.

Uma n. notata and *Uma n. rufopunctata* have most probably arisen as a result of the division of the parent stock into two segments by the Colorado River. The separation has remained slight, possibly because of occasional gene interchange allowed by changes in the course of the Colorado River over its broad delta. Thus populations of both forms could have crossed the river barrier.

Uma n. inornata has been isolated by one or more fillings of Lake LeConte in Pluvial times. If one may judge from the small degree of separation of *Uma n. inornata* from *Uma n. notata*, *inornata* may have arisen during the last Pluvial period.

OCCUPATION OF THE MOJAVE DESERT

I feel that the initial invasion of pre-*Uma scoparia* into the Mojave Desert may have come from the Gran Desierto region up along the old Colorado River channel to the vicinity of Blythe (see fig. 17). *Uma scoparia* seems to have its closest affinities with *U. n. rufopunctata* and not with the California members of the *notata* complex. If, however, *scoparia* was derived from these populations in the Cahuilla Basin, it may have reached the Mojave Desert by crossing broad gaps in the eastern mountain border of the basin. If *Uma scoparia* had been restricted to a few southern dunes during the last Pluvial pe-

riod, it must have reinvaded the northern Mojave in post-glacial times.

A brief examination of the distribution of *Uma* on the higher portions of the Mojave Desert reveals that nearly all its localities are directly associated with two drainage systems: the Mojave River and its Pleistocene discharge channel by way of Lavic, Bristol, Cadiz and Danby Dry Lakes, and the Rice dunes; and the Amargosa River. Dale Lake, Pinto Basin, and the Wilsona Buttes are either immediately adjacent to old pre-Pluvial localities or to the river systems.

Of great significance are the areas where

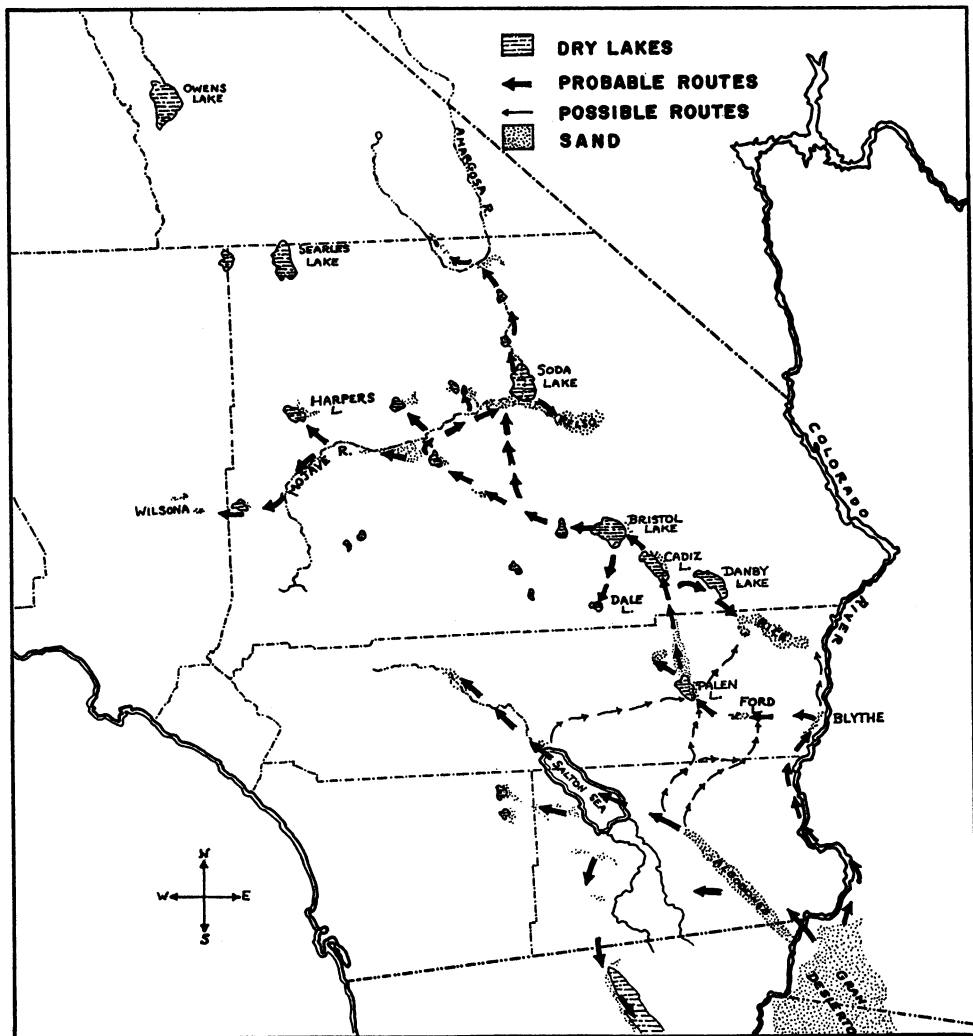


FIG. 17. Map of possible routes of movement followed by *Uma scoparia*, *Uma n. inornata*, *Uma n. notata*, and *Uma n. rufopunctata* during the climatic fluctuations of the Pleistocene.

Uma does not occur. It is not found on the Olancho Dunes, the Death Valley Dunes, or the Upper Amargosa River Dunes. It is not known from any of the small isolated basins of the northern Mojave Desert except those directly associated with the Mojave River. All the localities mentioned where *Uma* does not occur are isolated from the river drainages by rocky areas, coarse alluvial areas, or lacustrine deposits unsuitable for *Uma*.

The logical conclusion seems to be that *Uma scoparia* has usually followed stream courses in reinvading the Mojave Desert.

The probable mechanisms of invasion are simple. During the history of the Mojave and Amargosa rivers, their banks supported river-edge dunes along most of their length at one time or another. These dunes are conspicuous along these river banks today. Blow-ups and sand shadows have allowed population movement across divides.

The species crossed from the Bristol-Lanfair Basin into the Mojave drainage either through the Lavi-Pisgah area or through Broadwell Valley or possibly by both routes. The Mojave River may have flowed into the

Bristol-Lanfair Basin through the Broadwell Valley in Pluvial time (Thompson, 1929). The divide between the Mojave and Amargosa river drainages is covered with sand and occupied by *Uma* today.

The lizards have occupied all sand available to them and thus have followed sand movements from playa edges up mountain slopes and into other isolated situations.

The optimum period of sand production probably occurred in the past when desert streams carried more water but when they were still intermittent. Dune deposits were probably more often continuous then than they are today. Reworking and transport of old dunes have destroyed what continuity existed and isolated the sand deposits and the biota restricted to them.

SUMMARY AND CONCLUSIONS

1. THE GENUS *Uma* occurs on the Mojave and Sonoran deserts and on the Chihuahuan Desert of Mexico.

2. The genus is totally restricted to aeolian sand deposits, most of which are of recent origin.

3. Migration of present-day forms of *Uma* seems entirely limited by movements of occupied sand accumulations.

4. Dominant plant associates of the genus are quite uniform over its entire range.

5. *Uma* occurs on the most arid portions of the deserts. The genus endures habitat temperature extremes from about 0° F. to over 189° F. (black bulb, within the surface layer of the microclimate). By virtue of morphological and behavioral temperature-control adaptations, a small portion of this thermal range is selected (26° C. to 41° C. approximately) for activity.

6. Surface activity of *Uma* is often restricted to a small portion of the available daylight hours because of a narrow range of temperature tolerance.

7. The genus is found from 244 feet below sea level to about 3700 feet above sea level.

8. A study of variation within the genus shows:

A. Three major levels of differentiation are present. The most aberrant and primitive form is *exsul*, *scoparia* is intermediate, and the three subspecies *notata notata*, *notata rufopunctata*, and *notata inornata* form a homogeneous group which is closely related to *scoparia*.

B. *Uma n. rufopunctata* has been redefined on the basis of measurements, counts, and a distinctive breeding coloration. Its known range has been extended to include the Arizona populations, formerly thought to be part of the range of *Uma n. notata*.

C. The known ranges of all forms have been extended by the discovery of isolated populations.

D. Color variations in *Uma* are numerous. The individuals of nearly every population closely match the sand color of their habitat.

E. Intraspecific variation in pattern and scale configuration has been noted within *scoparia*.

9. The white ventral coloration of many

diurnal desert lizards, including *Uma*, may possibly have been produced by selection towards shadow reduction, background color matching, and temperature control (by reflection of radiated heat from the substratum).

10. Because a fossil record is lacking, any proposed evolutionary history of *Uma* must be based on environmental history. The conclusions drawn from this evidence are hypothetical and subject to considerable possible error.

11. The development of most North American desert reptiles appears to be correlated with the development of the Madro-Tertiary Flora. This flora originated in the Oligocene and Miocene in northern Mexico and southwestern United States in genetic response to increasing aridity.

12. Increasing aridity, reaching a climax in middle Pliocene, caused segregation of this flora into a number of vegetative types occupying separate ecological situations. Present desert vegetation has developed from the most xeric of these segregates.

13. *Uma* apparently arose as an offshoot of an early *Callisaurus-Holbrookia-Uma* stock as arid habitats developed, possibly in thorn forest or arid, subtropical, scrub associations.

14. It is postulated that the precursor of *Uma* was split into western and central Mexican populations by extensive volcanism along the axis of the Sierra Madre Occidental in middle or late Miocene time.

15. Since this separation, parallel evolution due to similar environmental stresses has kept the two groups closely allied morphologically. Middle Pliocene aridity most probably enhanced the development of widespread sand habitats. The pre-*Uma* of the two regions adapted to aeolian sand and, for the first time, developed the distinctive dune-adapted morphology associated today with the genus *Uma*.

16. Semi-desert vegetation underwent a widespread development in early and middle Pliocene times. Pre-*Uma* was probably associated with this vegetation as it developed. Many other desert reptile genera have probably followed a similar path of evolution.

17. Late Pliocene and Pleistocene climatic

extremes were such that *Uma* was restricted from part of its northern range as were other mesic desert reptiles. During the Pleistocene glacial advances, the Great Basin and most of the Mojave Desert were most likely uninhabitable to *Uma*.

18. *Uma scoparia* has differentiated in the north, probably as a result of isolation incurred during a pluvial period.

19. *Uma notata notata* and *Uma notata rufopunctata* have resulted from division of the Sonoran Desert populations by the rejuvenated Colorado River of Pleistocene time.

Gene exchange between the two subspecies may occur intermittently because of shifts in the course of the lower Colorado River.

20. *Uma n. inornata* has resulted from differentiation north of ancient Lake LeConte which has occupied the lower portions of the Cahuilla Basin during portions of the Ice Age.

21. *Uma scoparia* has reinvaded a considerable portion of the Mojave Desert since the last Pluvial age. The routes can be followed along stream courses and over low divides by a study of the present distribution of the species and the paths of Pluvial drainage.

BIBLIOGRAPHY

- ANTEVS, E. V.
 1925. On the Pleistocene history of the Great Basin. Publ. Carnegie Inst. Washington, no. 352, pp. 51-114.
 1928. The last glaciation, with special reference to the ice retreat in northeastern North America. Amer. Geogr. Soc., res. ser., no. 17, 292 pp.
 1948. *Review*: Pollen profile from a Texas bog, by J. E. Potzger and B. C. Tharp, Ecology, vol. 28, pp. 274-280, 1947. Jour. Geol., vol. 56, p. 83.
- ATSATT, SARAH R.
 1913. The reptiles of the San Jacinto area of southern California. Univ. California Publ. Zool., vol. 12, no. 3, pp. 31-50.
 1939. Color changes as controlled by temperature and light in the lizards of the desert regions of southern California. Publ. Univ. California at Los Angeles, Biol. Sci., vol. 1, no. 11, pp. 237-276.
- AUFFENBERG, WALTER
 1955. Glass lizards (*Ophisaurus*) in the Pleistocene and Pliocene of Florida. Herpetologica, vol. 11, pt. 2, pp. 133-136.
- AXELROD, D. I.
 1939. A Miocene flora from the western border of the Mojave Desert. Publ. Carnegie Inst. Washington, contrib. paleont., no. 516, 129 pp.
 1940a. Mint Canyon flora of southern California; a preliminary statement. Amer. Jour. Sci., vol. 238, no. 8, pp. 577-585.
 1940b. The Pliocene Esmeralda flora of west-central Nevada. Jour. Washington Acad. Sci., vol. 30, no. 4, pp. 163-174.
 1940c. Late Tertiary floras of the Great Basin and border areas. Bull. Torrey Bot. Club, vol. 67, no. 6, pp. 477-487.
 1948. Climate and evolution in western North America during middle Pliocene time. Evolution, vol. 2, no. 2, pp. 127-144.
 1949. Discussion. In Longwell, C. R. (chairman), Sedimentary facies in geologic history [symposium]. Mem. Geol. Soc. Amer., no. 39, pp. 155-164.
 1950. Evolution of desert vegetation in western North America. Publ. Carnegie Inst. Washington, contrib. paleont., no. 590, pp. 215-306.
- BAGNOLD, R. A.
 1941. The physics of blown sand and desert dunes. London, Methuen and Co., Ltd., xx+265 pp.
- BAKER, C. L.
 1911. Notes on the later Cenozoic history of the Mohave Desert region of southeastern California. Univ. California Publ. Bull. Dept. Geol. Sci., vol. 6, pp. 333-383.
- BEAL, C. H.
 1949. Reconnaissance of the geology and oil possibilities of Baja California, Mexico. Mem. Geol. Soc. Amer., no. 31, x+138 pp.
- BENFORD, F., G. P. LLOYD, AND S. SCHARZ
 1948. Coefficients of reflection of magnesium oxide and magnesium carbonate. Jour. Optical Soc. Amer., vol. 38, no. 5, pp. 445-447.
- BENSON, S.
 1933. Concealing coloration among some desert rodents of the southwestern United States. Publ. Univ. California, Zool., vol. 40, no. 1, pp. 1-70.
- BLACKWELDER, E.
 1931. Pleistocene glaciation in the Sierra Nevada and Basin ranges. Bull. Geol. Soc. Amer., vol. 42, no. 4, pp. 364-366.
 1933. Lake Manly: an extinct lake of Death Valley. Geogr. Rev., vol. 23, no. 3, pp. 464-471.
 1934. Origin of the Colorado River. Bull. Geol. Soc. Amer., vol. 45, no. 3, pp. 551-566.
- BLACKWELDER, E., AND E. W. ELLSWORTH
 1936. Pleistocene lakes of the Afton Basin, California. Amer. Jour. Sci., ser. 5, vol. 31, no. 186, pp. 453-463.
- BODE, F. D.
 1937. Geology of Lake Mohave outlet channel. In The archeology of Pleistocene Lake Mohave, a symposium. Southwest Mus. Papers, no. 11, pp. 108-118.
- BOGERT, C. M.
 1949. Thermoregulation in reptiles—a factor in evolution. Evolution, vol. 3, no. 3, pp. 195-211.
- BOGERT, C. M., AND J. A. OLIVER
 1945. A preliminary analysis of the herpetofauna of Sonora. Bull. Amer. Mus. Nat. Hist., vol. 83, art. 6, pp. 297-426.
- BRATTSTROM, B. H.
 1955a. New snakes and lizards from the Eocene of California. Jour. Paleont., vol. 29, pp. 145-149.
 1955b. Pliocene and Pleistocene amphibians and reptiles from southeastern Arizona. *Ibid.*, vol. 29, pp. 150-154.
 1955c. Pleistocene lizards from San Josecito Cavern, Mexico, with description of a new species. Copeia, no. 2, pp. 133-134.

- 1955d. Small herpetofauna from the Pleistocene of Carpinteria, California. *Ibid.*, no. 2, pp. 138-139.
- BROOKS, C. E. P.
1949. *Climate through the ages*. New York, McGraw-Hill, Inc., 395 pp.
- BROWN, C. A.
1938. The flora of Pleistocene deposits in the western Florida parishes, West Feliciana Parish and East Baton Rouge Parish, Louisiana. Louisiana Dept. Conserv., Geol. Surv., Geol. Bull., no. 12, pp. 59-96.
- BROWN, J. S.
1923. The Salton Sea region, California, a geographic, geologic and hydrologic reconnaissance, with a guide to desert watering places. Water-Supply Paper U. S. Geol. Surv., no. 497, 292 pp.
- BROWN, R. W.
1934. Recognizable species of the Green River formation. Prof. Paper U. S. Geol. Surv., no. 185c, pp. 45-77.
- BUELL, M. F.
1945. Late Pleistocene forests of southeastern North Carolina. *Torreya*, vol. 45, no. 4, pp. 117-118.
- BURT, C. E.
1933. Some lizards of the Great Basin of the west and adjacent areas with comments on the status of the various forms. *Amer. Midland Nat.*, vol. 14, pp. 228-250.
- BUWALDA, J. P.
1914. Pleistocene beds at Manix in the eastern Mohave Desert region. *Publ. Univ. California Bull. Dept. Geol. Sci.*, vol. 7, no. 24, pp. 443-461.
- CAMP, C. L.
1923. Classification of lizards. *Bull. Amer. Mus. Nat. Hist.*, vol. 48, art. 11, pp. 289-481.
- CAMP, C. L., D. N. TAYLOR, AND S. P. WELLES
1942. Bibliography of fossil vertebrates, 1934-1938. *Special Papers Geol. Soc. Amer.*, no. 42, 663 pp.
- CAMP, C. L., AND VERTESS L. VANDERHOOF
1940. Bibliography of fossil vertebrates, 1928-1933. *Special Papers Geol. Soc. Amer.*, no. 27, 503 pp.
- CAMPBELL, ELIZABETH WARDER CROZIER, AND W. H. CAMPBELL
1937. The Lake Mohave site. *In* The archeology of Pleistocene Lake Mohave, a symposium. *Southwest Mus. Papers*, no. 11, pp. 9-44.
- CHANEY, R. W.
1947. Tertiary centers and migration routes. *In* Origin and development of natural floristic areas, with special reference to North America. *Ecol. Monogr.*, vol. 17, no. 2, pp. 139-148.
- CHANEY, R. W., C. CONDIT, AND D. I. AXELROD
1944. Pliocene floras of California and Oregon. *Publ. Carnegie Inst. Washington, contrib. paleont.*, no. 553, vii+407 pp.
- CHANEY, R. W., AND H. L. MASON
1930. A Pleistocene flora from Santa Cruz Island, California. *Publ. Carnegie Inst. Washington, contrib. paleont.*, no. 415, pp. 1-24.
1933. A Pleistocene flora from the asphalt deposits at Carpinteria, California. *Ibid.*, contrib. paleont., no. 415, pp. 48-80.
1936. A Pleistocene flora from Fairbanks, Alaska. *Amer. Mus. Novitates*, no. 887, pp. 1-17.
- CHRAPLIWY, PETE S., AND CHARLES M. FUGLER
1955. Amphibians and reptiles collected in Mexico in the summer of 1953. *Herpetologica*, vol. 11, no. 2, pp. 121-128.
- CLEMENTS, F. E.
1936. The origin of the desert climax and climate. *In* Essays in honor of William Albert Setchell. Berkeley, University of California Press, pp. 87-140.
- COPE, E. D.
1884. The Vertebrata of the Tertiary formations of the west. *Rept. U. S. Geol. Surv., Territories*, no. 3, xxxv+1009 pp.
1900. The crocodilians, lizards and snakes of North America. *Ann. Rept. U. S. Natl. Mus.*, 1898, pt. 2, pp. 155-1294.
- CORNISH, VAUGHN
1897. On the formation of sand dunes. *Geogr. Jour.*, vol. 9, no. 3, pp. 278-309.
- COTT, H. B.
1940. *Adaptive coloration in animals*. New York, Oxford University Press, xxxii+508 pp.
- COWLES, R. B.
1941. Observations on the winter activities of desert reptiles. *Ecology*, vol. 22, no. 2, pp. 125-140.
- COWLES, R. B., AND C. M. BOGERT
1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Amer. Mus. Nat. Hist.*, vol. 83, art. 5, pp. 265-296.
- CROLL, JAMES
1875. Climate and time in their geological relations; a theory of secular changes in the earth's climate. New York, Appleton, xvi+577 pp.
- DALEY, R. A.
1934. The changing world of the ice age. New

- Haven, Yale University Press, xxi+271 pp.
- DAVIS, J. H.
1946. The peat deposits of Florida, their occurrence, development and uses. Bull. Florida Dept. Conserv., Florida Geol. Surv., no. 30, xiii+247 pp.
- DEEVEY, E. S.
1949. Biogeography of the Pleistocene. Part 1, Europe and North America. Bull. Geol. Soc. Amer., vol. 60, no. 9, pp. 1315-1416.
- DICKERSON, R. E.
1922. Tertiary and Quaternary history of the Petaluma, Point Reyes and Santa Rosa Quadrangles. Proc. California Acad. Sci., ser. 4, vol. 11, no. 9, pp. 527-601.
- DIEREN, J. W. VAN
1934. Organogene dunenbildung, une geomorphologische analyse der dunenlandschaft methoden. The Hague, Nijhoff-Verlags, xx+304 pp.
- ELLSWORTH, E. W.
1933. Physiographic history of Afton Basin of Mojave Desert. [Abstract.] Pan-Amer. Geol., vol. 59, no. 4, pp. 308-309.
- EPLING, C.
1944. The historical background. *Part 3 in* Dobzhansky, T., and C. Epling, Contributions to the genetics, taxonomy, and ecology of *Drosophila pseudoobscura* and its relatives. Publ. Carnegie Inst. Washington, no. 554, pp. 145-183.
- FLINT, R. F.
1945. Glacial map of North America. Special Papers Geol. Soc. Amer., no. 60, viii+37 pp.
1947. Glacial geology and the Pleistocene epoch. New York, John Wiley and Sons, Inc., 589 pp.
- FREE, E. E.
1914. The topographic features of the desert basins of the United States with reference to the possible occurrence of potash. Bull. U. S. Dept. Agr., no. 54, pp. 1-65.
1916. An ancient lake basin on the Mohave River. Year Book Carnegie Inst. Washington, no. 15, pp. 90-91.
- FRY, F. E. J.
1947. Effects of the environment on animal activity. Publ. Ontario Fish. Res. Lab., vol. 68, no. 55, pp. 1-62.
- GILMORE, C. W.
1928. Fossil lizards of North America. Mem. Natl. Acad. Sci., vol. 22, no. 3, pp. 1-201.
1938. Fossil snakes of North America. Special Papers Geol. Soc. Amer., no. 9, vii+96 pp.
- GINSBURG, ISAAC
1937. The species and its subdivisions. Copeia, no. 3, pp. 184-188.
- GLEASON, H. A.
1922. The vegetational history of the Middle West. Ann. Assoc. Amer. Geogr., vol. 12, pp. 39-85.
- GRINNELL, JOSEPH
1924. A possible function of the whiteness of the breast in crevice-searching birds. Condor, vol. 26, pp. 32-33.
1943. Joseph Grinnell's philosophy of nature. Berkeley, University of California Press, 237 pp.
- HALL, E. R.
1946. Mammals of Nevada. Berkeley, University of California Press, 710 pp.
- HANSEN, H. P., AND J. H. MACKIN
1949. A pre-Wisconsin forest succession in the Puget lowland, Washington. Amer. Jour. Sci., vol. 247, no. 12, pp. 833-855.
- HAY, O. P.
1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U. S. Geol. Soc., no. 179, 868 pp.
1908. The fossil turtles of North America. Publ. Carnegie Inst. Washington, no. 75, iv+568 pp.
1927. The Pleistocene of the western region of North America and its vertebrate animals. *Ibid.*, no. 322B, vii+346 pp.
1929. Second bibliography and catalogue of fossil Vertebrata of North America. *Ibid.*, no. 390, vol. 1, 916 pp., vol. 2, xiv+1074 pp.
- HEIFETZ, WILLIAM
1941. A review of the lizards of the genus *Uma*. Copeia, no. 2, pp. 99-111.
- HIBBARD, C. W.
1949. Pleistocene vertebrate paleontology in North America. Bull. Geol. Soc. Amer., vol. 60, no. 9, pp. 1417-1428.
- HITCHCOCK, C. H.
1891. *Review*: The present standing of the several hypotheses of the cause of the glacial period, by T. C. Chamberlin. Amer. Geol., vol. 8, p. 237.
- HOLTENBERGER, M.
1913. On a genetic system of sand dunes, including two new types. Bull. Amer. Geogr. Soc., vol. 45, pp. 513-515.
- HOPPER, R. H.
1947. Geologic section from Sierra Nevada to Death Valley, California. Bull. Geol. Soc. Amer., vol. 58, no. 5, pp. 393-432.

- HUBBS, C. L., AND CLARK HUBBS
1953. An improved graphical analysis and comparison of series of samples. *Syst. Zool.*, vol. 2, no. 2, pp. 49-57.
- HUBBS, C. L., AND R. R. MILLER
1948. The Great Basin, with emphasis on glacial and postglacial times. II. The zoological evidence: Correlation between fish distribution and hydrographic history in the desert basins of western United States. *Bull. Univ. Utah*, vol. 38, no. 20, pp. 18-166.
- HUBBS, C. L., AND A. PERLMUTER
1942. Biometric comparison of several samples, with particular reference to racial investigations. *Amer. Nat.*, vol. 76, no. 767, pp. 582-592.
- HUNTINGTON, E., AND S. S. VISHER
1922. Climatic changes, their nature and causes. New Haven, Yale University Press, 329 pp.
- JAEGER, FRITZ
1925. Untersuchungen über das diluviale Klima in Mexiko. *Zeitschr. Gesell. Erdk.* Berlin, no. 9-10, pp. 366-373.
- KLAUBER, L. M.
1939. Studies of reptile life in the arid southwest. Part 1. Night collecting on the desert with ecological statistics. Part 2. Speculations on protective coloration and protective reflectivity. Part 3. Notes on some lizards of southwestern United States. *Bull. Zool. Soc. San Diego*, no. 14, pp. 1-100.
- KNOFF, ADOLPH, AND EDWIN KIRK
1918. A geologic reconnaissance of the Inyo Range and the eastern slope of the southern Sierra Nevada, California. *Prof. Paper U. S. Geol. Surv.*, no. 110, pp. 1-130.
- KRUMBEIN, W. C., AND F. J. PETTIJOHN
1938. Manual of sedimentary petrography. New York, Appleton-Century, xiv+549 pp.
- LEVERETT, FRANK
1929. Pleistocene glaciations of the Northern Hemisphere. *Bull. Geol. Soc. Amer.*, vol. 40, no. 4, pp. 745-760.
- LINSDALE, J. M.
1932. Amphibians and reptiles from Lower California. *Publ. Univ. California Zool.*, vol. 38, no. 6, pp. 345-386.
- LONGWELL, C. R.
1946. How old is the Colorado River? *Amer. Jour. Sci.*, vol. 244, no. 12, pp. 817-835.
- LOWE, C. H., JR.
1950. The systematic status of the salamander *Plethodon hardii*, with a discussion of biogeographical problems in *Aneides*. *Copeia*, no. 2, pp. 92-99.
- MACGINITIE, H. D.
1953. Fossil plants of the Florissant Beds, Colorado. *Publ. Carnegie Inst. Washington*, no. 599, iii+198 pp.
- MAERZ, A. J., AND M. R. PAUL
1930. A dictionary of color. New York, McGraw-Hill, vii+207 pp.
- MASON, H. L.
1934. Pleistocene flora of the Tomales formation. *Publ. Carnegie Inst. Washington*, contrib. paleont., no. 415, pp. 81-180.
1944. A Pleistocene flora from the McKittrick asphalt deposits of California. *Proc. California Acad. Sci.*, vol. 25, no. 8, pp. 221-233.
- MATTHES, F. E.
1930. Geologic history of Yosemite Valley. *Prof. Paper U. S. Geol. Soc.*, no. 160, pp. 1-137.
1933. Geography and geology of the Sierra Nevada. *Guidebook 16th Internatl. Geol. Congr.*, Washington, no. 16, pp. 26-40.
- MATTHEW, W. D.
1901. Fossil mammals of the Tertiary of northeastern Colorado. *Mem. Amer. Mus. Nat. Hist.*, vol. 1, no. 7, pp. 353-446.
- MEINZER, O. E.
1922. Map of the Pleistocene lakes of the Basin and Range Province and its significance. *Bull. Geol. Soc. Amer.*, vol. 33, no. 3, pp. 541-552.
- MELTON, F. A.
1940. A tentative classification of sand dunes; its applications to dune history in the southern high plains. *Jour. Geol.*, vol. 48, no. 2, pp. 113-174.
- MENDENHALL, W. C.
1909a. Some desert watering places in southeastern California and southwestern Nevada. *Water-Supply Paper U. S. Geol. Surv.*, no. 224, pp. 1-98.
1909b. Groundwaters of the Indio region, California. *Ibid.*, no. 225, pp. 1-56.
- MERRIAM, J. C.
1915. An occurrence of mammalian remains in a Pleistocene lake deposit at Astor Pass, near Pyramid Lake, Nevada. *Publ. Univ. California, Bull. Dept. Geol. Sci.*, vol. 8, no. 21, pp. 377-384.
- MERRIAM, J. C., AND W. C. SINCLAIR
1907. Tertiary faunas of the John Day region. *Publ. Univ. California, Bull. Dept. Geol. Sci.*, vol. 5, no. 11, pp. 171-205.

- MILANKOVITCH, M.
1930. Mathematische Klimalehre und astronomische Theorie der Klimaschwankungen. In Koppen, W., and R. Geiger, Handbuch der Klimatologie. Berlin, vol. 1, A, pp. 1-176.
- MILLER, A. H.
1937. Biotic associations and life zones in relation to the Pleistocene birds of California. Condor, vol. 39, no. 6, pp. 248-252.
1939. Climatic conditions of the Pleistocene reflected by the ecologic requirements of fossil birds. Proc. 6th Pacific Sci. Congr., Geophys. Geol., pp. 807-810.
- MILLER, L. H.
1930. A fossil goose from the Ricardo Pliocene. Condor, vol. 32, no. 4, pp. 208-209.
- MILLER, L. H., AND IDA S. DEMAY
1942. The fossil birds of California; an avifauna with bibliography with annotations. Publ. Univ. California Zool., vol. 47, no. 4, pp. 47-142.
- MILLER, R. R.
1946. Correlation between fish distribution and Pleistocene hydrography in eastern California and southwestern Nevada, with a map of Pleistocene waters. Jour. Geol., vol. 54, no. 1, pp. 43-53.
- MILLER, W. J.
1926. Glaciation in the San Gabriel Mountains, California. Jour. Geol., vol. 34, no. 1, pp. 74-82.
1934. Geology of the western San Gabriel Mountains of California. Publ. Univ. California at Los Angeles, Math., Phys. Sci., vol. 1, no. 1, pp. 1-114.
1942. An introduction to historical geology. New York, D. Van Nostrand Co., Inc., x+499 pp.
- MITTLEMAN, M. B.
1942. A summary of the iguanid genus *Urosaurus*. Bull. Mus. Comp. Zoöl., vol. 91, no. 2, pp. 106-176.
- MOORE, J. A.
1949. Patterns of evolution in the genus *Rana*. In Jepsen, G. L. Ernst Mayr, and G. G. Simpson (eds.), Genetics, paleontology and evolution. Princeton, Princeton University Press, pp. 315-338.
- MOSAUER, WALTER
1932. Adaptive convergence in the sand reptiles of the Sahara and of California. Copeia, no. 2, pp. 72-78.
1936. The reptilian fauna of sand dune areas of the Vizcaino Desert and of northwestern Lower California. Occas. Papers Mus. Zool., Univ. Michigan, no. 329, pp. 1-21.
- MUNZ, P. A.
1935. A manual of southern California botany. Claremont, California, Claremont College, xxxix+642 pp.
- MURRAY, K. F.
1957. Pleistocene climate and the fauna of Burnet Cave, New Mexico. Ecology, vol. 38, no. 1, pp. 129-132.
- MYERS, G. S.
1950. The systematic status of *Hyla septentrionalis*, a large tree frog of the Florida Keys, the Bahamas and Cuba. Copeia, no. 3, pp. 203-214.
- NOLAN, T. B.
1943. The Basin and Range Province in Utah, Nevada and California. Prof. Paper U. S. Geol. Surv., no. 197d, pp. 141-196.
- NORRIS, K. S.
1949. Observations on the habits of the horned lizard, *Phrynosoma m'callii*. Copeia, no. 3, pp. 176-180.
1953. The ecology of the desert iguana, *Dipsosaurus dorsalis*. Ecology, vol. 34, no. 2, pp. 265-287.
- NORRIS, R. M.
1956. Crescentic beach cusps and barkhan dunes. Bull. Amer. Assoc. Petrol. Geol., vol. 40, no. 7, pp. 1681-1686.
- OELRICH, T. M.
1954. A horned toad, *Phrynosoma cornutum*, from the upper Pliocene of Kansas. Copeia, no. 4, pp. 262-263.
- OSBORN, H. F.
1909. Cenozoic mammal horizons of western North America with faunal lists of Tertiary Mammalia of the west by W. D. Matthew. Bull. U. S. Geol. Surv., no. 361, 138 pp.
- POOLE, D. M., AND W. S. BUTCHER
1951. The use and accuracy of the Emery Settling Tube for sand analysis. Tech. Memorandum, Beach Erosion Board, Corps of Engineers, no. 23, 9 pp.
- POTBURY, SUSAN S.
1932. A Pleistocene flora from San Bruno, San Mateo County, California. Publ. Carnegie Inst. Washington, contrib. paleont., no. 415, pp. 25-44.
- PUTNAM, W. C.
1938. The Mono Craters, California. Geogr. Rev., vol. 28, no. 1, pp. 68-82.
- RAY, L. L.
1949. Problems of Pleistocene stratigraphy. Bull. Geol. Soc. Amer., vol. 60, no. 9, pp. 1463-1473.

- REED, R. D.
1933. Geology of California. Tulsa, Oklahoma, American Association of Petroleum Geologists, xxiv+355 pp.
- RIDGWAY, ROBERT
1912. Color standards and color nomenclature. Washington, D. C., iv+44 pp.
- RITLAND, R. M.
1955. Studies on the post-cranial morphology of *Ascaphus truei*. I. Skeleton and spinal nerves. Jour. Morph., vol. 97, no. 1, pp. 119-178.
- RODGERS, M. J.
1939. Early lithic industries of the lower basin of the Colorado River and adjacent desert areas. San Diego Mus. Papers, no. 3, 75 pp.
- RODGERS, T. L., AND H. S. FITCH
1947. Variation in the skinks (Reptilia: Lacerilia) of the *skiltonianus* group. Publ. Univ. California, Zool., vol. 48, no. 4, pp. 169-220.
- ROMER, A. S.
1945. Vertebrate paleontology. Chicago, the University of Chicago Press, ix+687 pp.
- SAGER, G. V.
1941. The climate of Nevada. In Climate and man. Yearbook U. S. Dept. Agr., pp. 979-988.
- SAVAGE, J. M.
[In press.] The iguanid lizard genera *Urosaurus* and *Uta*, with remarks on related groups. Zoologica.
- SCHMIDT, K. P.
1922. A review of the North American genus of lizards *Holbrookia*. Bull. Amer. Mus. Nat. Hist., vol. 46, art. 11, pp. 709-725.
- SCHMIDT, K. P., AND C. M. BOGERT
1947. A new fringe-footed sand lizard from Coahuilla, Mexico. Amer. Mus. Novitates, no. 1339, 9 pp.
- SCHMIDT, K. P., AND D. D. DAVIS
1941. Fieldbook of snakes of the United States and Canada. New York, G. P. Putnam's Sons, xiii+365 pp.
- SCHUCHERT, CHARLES
1935. Historical geology of the Antillean-Caribbean region, or lands bordering the Gulf of Mexico and the Caribbean Sea. New York, John Wiley and Sons, xxvi+811 pp.
- SCOTT, W. B.
1937. A history of land mammals in the Western Hemisphere. New York, Macmillan Co., xiv+786 pp.
- SHANNON, F. A.
1950. Some additional remarks on the status of the species *Sceloporus occidentalis*. Herpetologica, vol. 6, no. 2, pp. 31-32.
- SHARP, R. P.
1938. Pleistocene glaciation in the Ruby-East Humboldt Range, northeastern Nevada. Jour. Geomorph., vol. 1, no. 4, pp. 296-323.
1942. Multiple glaciation in San Francisco Mountain, Arizona. Jour. Geol., vol. 50, no. 5, pp. 481-503.
- SHREVE, FORREST
1942. Desert vegetation of North America. Bot. Rev., vol. 8, pp. 195-246.
- SIMPSON, G. C.
1919. Meteorology, volume 1, discussion. In British Antarctic Expedition, 1910-1913. Calcutta, Thacker, Spink and Co., x+326 pp.
1934. World climate during the Quaternary period. Quart. Jour. Roy. Met. Soc., no. 60, pp. 425-478.
- SMITH, H. M.
1935. Notes on some Mexican lizards of the genus *Holbrookia*, with the description of a new species. Bull. Univ. Kansas, vol. 36, no. 8, pp. 185-201.
1946. Handbook of lizards. Ithaca, Comstock Publ. Co., xi+557 pp.
- SMITH, H. T. U.
1949. Physical effects of Pleistocene climatic changes in nonglaciated areas: eolian phenomena, frost action and stream terracing. Bull. Geol. Soc. Amer., vol. 60, no. 9, pp. 1485-1515.
- SPRAGUE, MALCOLM
1941. Climate of California. In Climate and man. Yearbook U. S. Dept. Agr., pp. 783-797.
- STEARNS, C. E.
1942. A fossil marmot from New Mexico and its climatic significance. Amer. Jour. Sci., vol. 240, no. 12, pp. 867-878.
- STEBBINS, R. C.
1944. Some aspects of the ecology of the iguanid genus *Uma*. Ecol. Monogr., vol. 14, no. 3, pp. 311-332.
1948. Nasal structures in lizards with reference to olfaction and conditioning of inspired air. Amer. Jour. Anat., vol. 83, no. 2, pp. 183-222.
- STOCK, CHESTER
1946. Rancho La Brea, a record of Pleistocene life in California. Third edition. Los Angeles County Mus. Sci. Ser., no. 11, Paleont., no. 7, 74 pp.

- TAYLOR, E. H.
1936. Una nueva fauna de batracios anuros del Pliocene Medio de Kansas. *An. Inst. Biol., Mexico*, vol. 7, no. 4, pp. 513-529.
1939. A new anuran amphibian from the Pliocene deposits of Kansas. *Univ. Kansas Sci. Bull.*, vol. 25, no. 18, pp. 407-420.
1941a. Extinct lizards from the upper Pliocene deposits of Kansas. *Univ. Kansas Bull., Geol. Surv.*, no. 38, pt. 5, 165-176.
1941b. Extinct toads and salamanders from middle Pliocene beds of Wallace and Sherman counties. *Ibid.*, no. 38, pt. 6, pp. 177-196.
1942. Extinct toads and frogs from the upper Pliocene deposits of Meade County, Kansas. *Univ. Kansas Sci. Bull.*, vol. 28, pt. 2, pp. 199-235.
- TEVIS, LLOYD
1944. Herpetological notes from Lower California. *Copeia*, no. 1, pp. 6-18.
- THOMPSON, D. G.
1929. The Mohave Desert region, California. A geographic, geologic and hydrologic reconnaissance. *Water-Supply Paper U. S. Geol. Surv.*, no. 578, xi+759 pp.
- TIHEN, J. A.
1954. A Kansas Pleistocene herpetofauna. *Copeia*, no. 3, pp. 217-220.
- TWENTE, J. W.
1952. Pliocene lizards from Kansas. *Copeia*, no. 2, pp. 70-73.
- VAUGHAN, T. W.
1917. The reef-coral fauna of Carrizo Creek, Imperial Valley, California, and its significance. *Prof. Paper U. S. Geol. Surv.*, no. 98, pp. 355-395.
- VAUGHN, F. E.
1922. Geology of the San Bernardino Mountains north of San Geronio Pass, California. *Bull. Univ. California, Publ. Dept. Geol. Sci.*, vol. 13, no. 9, pp. 319-411.
- WARD, R. DEC., C. F. BROOKS, AND A. J. CONNER
1936. The climates of North America. *In Handbuch der Klimatologie*. Berlin, Gebrüder Borntraeger, vol. 2, pt. J, 325 pp.
- WOODRING, W. P.
1932. Distribution and age of marine Tertiary deposits of the Colorado Desert. *Publ. Carnegie Inst. Washington*, no. 418, pt. 1, pp. 1-25.
- WODEHOUSE, R. P., W. G. HARPER, JAMES THORP, AND M. R. ISAACSON
1933. Tertiary pollen, II. Oil shales of the Green River formation. *Bull. Torrey Bot. Club*, vol. 60, pp. 479-521.
- YOUNGS, F. C.
1929. Soil survey of the Yuma-Wellton area, Arizona-California. *Washington, D. C.*, 37 pp.
- ZWEIFEL, R. G.
1954. A new *Rana* from the Pliocene of California. *Copeia*, no. 2, pp. 85-87.
1955. Ecology, distribution and systematics of frogs of the *Rana boylei* group. *Publ. Univ. California, Zool.*, vol. 54, no. 4, pp. 207-292.
1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and recent forms. *Amer. Mus. Novitates*, no. 1762, 45 pp.

