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(GENUS SAUROMALUS) IN THE GULF OF CALIFORNIA,
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CHROMOSOMES, PROTEIN POLYMORPHISM, AND
SYSTEMATICS OF INSULAR CHUCKWALLA LIZARDS (GENUS
SAUROMALUS) IN THE GULF OF CALIFORNIA, MEXICO

by

Michael David Robinson

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF BIOLOGICAL SCIENCES

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN ZOOLOGY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my
direction by Michael David Robinson
entitled Chromosomes, protein polymorphism, and systematics
of insular chuckwalla lizards (genus Sauromalus)
in the Gulf of California, Mexico
be accepted as fulfilling the dissertation requirement of the
degree of Doctor of Philosophy

Collins
Dissertation Director

March 27, 1972
Date

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allowed me the use of his laboratory facilities at the University of Texas during August of 1971.

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ABSTRACT

Four species and six subspecies of chuckwalla lizards (genus Sauromalus) from Baja California and islands in the Gulf of California, Mexico were analyzed for karyotype, serum protein polymorphism, and five external morphological characters. These data were used to determine species levels in the genus and to analyze the systematic and biogeographical relationships of the taxa.

All the populations examined have a diploid number of 36 chromosomes, consisting of 12 macrochromosomes and 24 microchromosomes. No pericentric inversions were detected in the chromosomes.

In the populations of lizards sampled, the serum albumin locus had two alleles (Alb-1 and Alb-2). S. a. klauberi and S. a. slevini were the only taxa that have the less common Alb-2 allele. Three esterase systems (Est-1, Est-2, Est-3) were consistently present, but not always scorable. One locus (Est-2) is polymorphic, and the other two (Est-1 and Est-3) appear monomorphic. The serum proteins of Sauromalus require additional investigation before indices of genic heterozygosity can be determined.

Meristic characters exhibit considerable overlap in their values and have little value for defining species levels in the genus Sauromalus.

Insular populations formerly considered as species (S. ater, S. klauberi, S. shawi, and S. slevini) are regarded as subspecies of S. ater. Future analyses may warrant combining S. a. ater, S. a. shawi, and S. australis with S. obesus. Sauromalus hispidus and S. varius, the insular giants in the genus, evolved independently from mainland ancestors but are not the most recently derived species. The formation of the Gulf of California was instrumental in the speciation and radiation of these lizards during the last 10-15 million years.

INTRODUCTION

The chuckwallas (genus Sauromalus) are a diverse group of herbivorous lizards occurring primarily in the arid and semi-arid regions of the southwestern United States, northwestern Mexico, and on 17 desert islands in the Gulf of California.

Shaw's (1945) monograph was the last revision of the genus Sauromalus, and since then the systematic relationships of the insular taxa have been largely ignored. The purpose of this investigation was (1) to re-evaluate the "species" of chuckwallas in the Gulf of California region, with emphasis on the island taxa, and (2) to determine the relationships of these island populations to each other, and to those on the mainland in terms of their derivation, speciation, and biogeography.

In attempting to understand the evolution of these lizards, I have incorporated chromosomal (karyotype) and serum protein data with ecological observations and previous morphological analyses.

The evolutionary biology and biogeography of Sauromalus are discussed in terms of recent geological studies of the Gulf's formation. These data provide a reasonable historical framework for such investigations.

The results of this study have helped to answer some basic questions, but they have also left many unanswered. Additional work is needed before the evolution of these lizards is fully understood.

MATERIALS AND METHODS

Field Work

Boat transportation to the islands in the Gulf of California where chuckwallas were collected (Fig. 1) was arranged through local Mexican fishermen, primarily at Bahia Kino, Sonora, and at La Paz, Loreto, Santa Rosalia, and Bahia Los Angeles, Baja California, Mexico. Field work on the islands was carried out during the summer months of 1970 and 1971. All lizards were captured by hand and then transported to the laboratory at Tucson, Arizona as soon as possible.

Karyotypes

Chromosomes of cells from both bone marrow and testicular tissue were prepared by a modification of Patton's (1967) colchicine-hypotonic citrate technique for small mammals (Lowe and Wright, 1966; Lowe, Wright, and Cole, 1966).

A minimum of 20 cells was counted for each species from each island or mainland sample. The number of macrochromosomes and microchromosomes was recorded for each cell examined, and the centromeric position of the large chromosomes was noted. Chromosomes were classified by their centromeric position according to the four-class

Fig. 1. Collection localities of chuckwalla lizards
(genus Sauromalus) in the Gulf of California, Mexico.

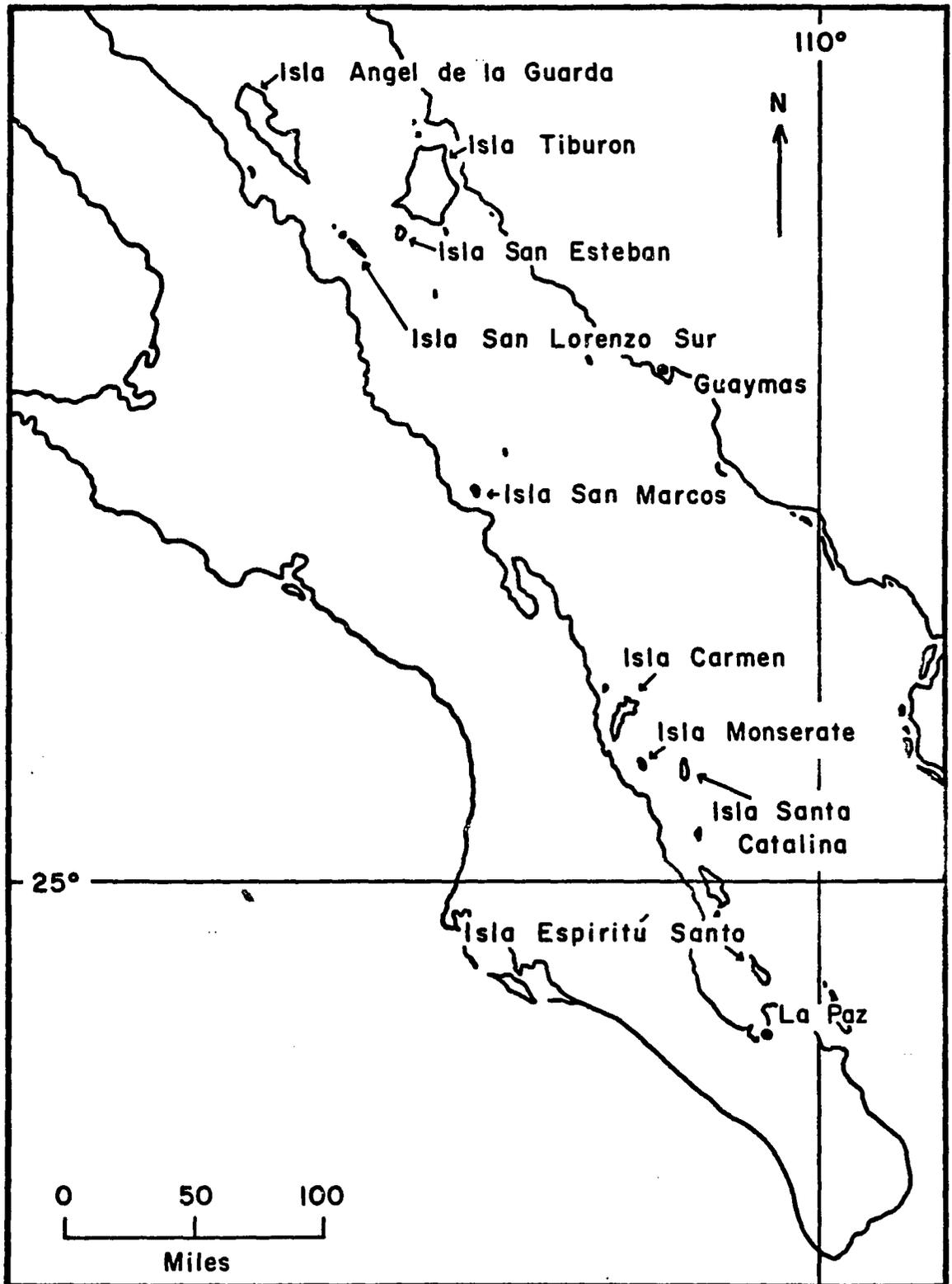


Fig. 1. Collection localities.

system used by Cole (1970). Chromosomes were classified and "paired" by both visual estimate and ocular measurement. In lizards, and in reptiles in general, the former technique is clearly as accurate as the latter. The karyotype of each species was then determined by the modal number.

Serum Proteins

Blood was removed from the lizards by cardiac puncture. Samples were then processed by the following procedure: (1) separation of the hemolysate and plasma fractions by centrifugation; (2) the hemolysates were washed three times with .85% NaCl solution and stored with the serum at -10°C . Temperatures evidently increased in the refrigerated storage area during power shortages, and most of the hemolysates denatured and could not be used for the analysis.

Serum proteins were separated by starch-gel electrophoresis in the laboratory of Dr. Robert K. Selander at the University of Texas. Samples were run for $3\frac{1}{2}$ hours at 350 volts in a lithium hydroxide gel and buffer system. The gels were sliced and stained specifically for leucine aminopeptidase, phosphoglucose isomerase, esterase, and lactate dehydrogenase. One slice was stained with a general protein stain. Details of these operations and other electrophoretic techniques are described by Selander

et al. (1971). Gels were photographed and enzyme systems scored for the presence or absence of polymorphisms. Relative mobilities of the proteins on the gels were measured and calculated from the photographs.

Morphology

Where morphological comparisons were made, I have utilized the same method of scale counting and compared the same characters as Shaw (1945).

Specimens Examined

The following specimens were used in the karyotypic, morphological, and serum protein analyses and are deposited in the Herpetological Collection, Department of Biological Sciences, University of Arizona (UAZ).

Sauromalus ater ater Dumeril. MEXICO: Baja California del Sur; Isla Espiritu Santo, Punta Dispensa (UAZ 32761-32763).

Sauromalus ater klauberi Shaw. MEXICO: Baja California del Sur; Isla Santa Catalina, Arroyo Blanco, west side of the island (UAZ 32768-32769; 32797-32800; 32900-32902; 33077-33078).

Sauromalus ater shawi Cliff. MEXICO: Baja California del Sur; Isla San Marcos, Southwest corner (UAZ 32502-32504).

Sauromalus ater slevini Van Denburgh. MEXICO:

Baja California del Sur; Isla Carmen, West side of island (UAZ 32770). Isla Monserate, Ensenada de las Galletas (UAZ 32766-32767; 32793-32796; 32903-32905; 33072-33076).

Sauromalus hispidus Stejneger. MEXICO: Baja

California del Sur; Isla Angel de la Guarda, Bahía Los Machos (UAZ 34496-34502). Isla San Lorenzo-South, North-east corner (UAZ 34344-34349).

Sauromalus obesus (Baird). MEXICO: Baja California

del Norte; 4.5 mi N. Las Arrastras (UAZ 34508). 1.6 mi N. Las Arrastras (UAZ 34509-34510). 2 mi S. Las Arrastras (UAZ 34511-34513).

Sauromalus obesus townsendi Dickerson. MEXICO:

Sonora; Isla Tiburon, Ensenada del Perro (32505; 32784-32785; 33071).

Sauromalus varius Dickerson. MEXICO: Sonora;

Isla San Esteban, Southeast corner (UAZ 34350-34356).

RESULTS

Karyotypes

A total of 240 cells from 45 individuals (19 ♂, 26 ♀) representing four species and six subspecies were studied from islands in the Gulf of California, Arizona, and Baja California (see Fig. 1 and Specimens Examined, p. 6).

The diploid chromosome number of all the populations of chuckwallas studied is 36, consisting of 12 macrochromosomes and 24 microchromosomes. In the following discussion, the macrochromosome pairs are numbered from the largest to smallest (left to right in Figs. 2 and 3). The small microchromosomes are not numbered.

Chromosome pair number 1 is the largest and is metacentric. Occasionally one member of this chromosome pair will appear nearly submetacentric. This apparent centromeric shift results from differential contraction of the individual chromosome arms, or from twisting of the chromosome arm(s) during slide preparation. The "normal" centromeric position can be determined by examining other unaltered cells (i.e., those where the chromosomal arms are in similar stages of contraction and in the same viewing plane). Pair number 2 is clearly submetacentric

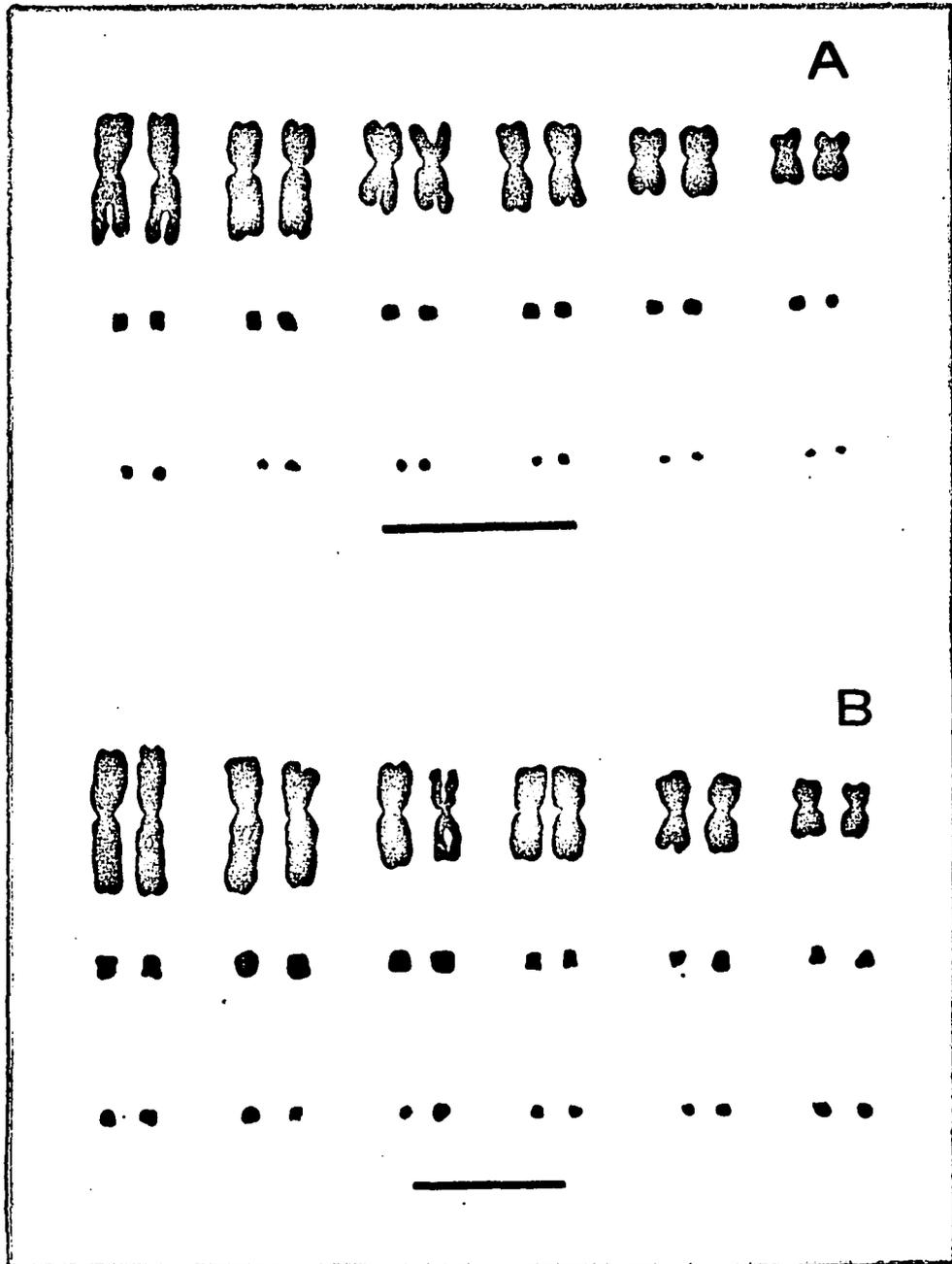


Fig. 2. Karyotype of Sauromalus varius (A), Isla San Esteban, and S. obesus (B), Isla Tiburon, Gulf of California, Mexico. -- Horizontal line equals 10 micra.

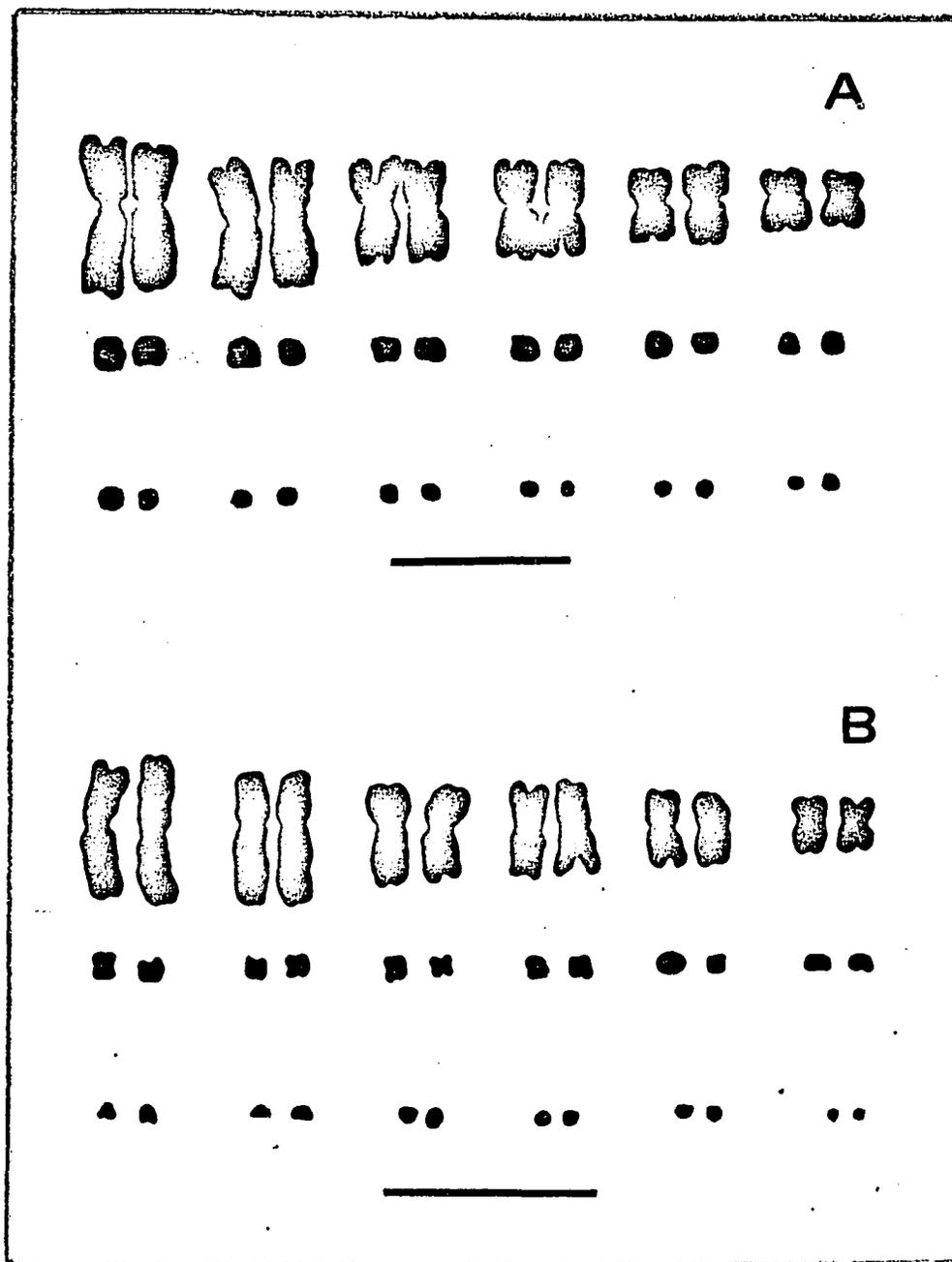


Fig. 3. Karyotype of *Sauromalus hispidus* (A), Isla San Lorenzo (South), and *S. ater slevini* (B), Isla Carmen, Gulf of California, Mexico. -- Horizontal line equals 10 micra.

and is slightly smaller than pair number 1. Pairs 3 and 4 are similar in size but definitely smaller than pairs 1 and 2; both are consistently metacentric. Pair number 5 is metacentric and intermediate in size between pairs 4 and 6. Pair number 6 is the smallest of the macrochromosome series and is submetacentric.

No pericentric inversional differences were detected in the macrochromosomes of these geographically isolated samples.

The microchromosomes comprise a graded series from the largest pair, which often appears metacentric, to the very small last pair of "dot" chromosomes. No attempt was made to classify the microchromosomes because their morphology is rarely distinguishable. Representative karyotypes from four species of chuckwallas are given in Figs. 2 and 3.

A definitive statement regarding the lack of karyotypic variation within the genus can not be made until samples from throughout the mainland and the Baja peninsula range have been examined. However, 8 of the 11 described taxa were analyzed in the present study, including the most morphologically and ecologically differentiated species in the genus (S. varius, S. hispidus, S. ater, and S. obesus). It is probable that the karyotype in the genus Sauromalus is invariant at the gross morphological level.

Serum Proteins

Blood samples were analyzed from 39 individuals representing seven taxa from Baja and the Gulf of California, Mexico. Because the hemolysate fractions denatured from improper refrigeration, only the serum proteins were used for this analysis.

The results obtained are preliminary and stress the need for a more detailed investigation. Since only serum proteins were used, several useful enzyme systems found primarily in tissues were unavailable for study (see Selander et al., 1971). The mobilities and relationships of the enzymes analyzed are shown in Fig. 4.

Albumins characteristically constitute the fastest migrating enzyme system of the serum proteins. In reptiles the molecular weight of the plasma protein considered the analog of mammalian albumin is approximately 65-75,000 (Masat and Dessauer, 1968). The populations examined have two alleles (Alb-1 and Alb-2) at the albumin locus. The fastest migrating band (Alb-1) is present in S. hispidus, S. obesus, S. varius, S. ater shawi, and S. a. ater. A slower albumin (Alb-2) is characteristic of S. a. klauberi and S. a. slevini (Fig. 4).

Three esterase loci were scorable in the samples examined. The most anodal migrating band, Est-1, is monomorphic. The Est-2 system is polymorphic but stained

Fig. 4. Variation in esterases and albumins in chuckwalla lizards (genus Sauromalus) from Baja California and the Gulf of California, Mexico. -- Species and locality are indicated by numbers below the origin as follows: S. hispidus, Isla Angel de la Guarda (1,2,3,14), Isla San Lorenzo-South (13) | S. a. klauberi, Isla Santa Catalina (4,10); S. o. townsendi, Isla Tiburon (5); S. obesus, Baja California Norte (6); S. varius, Isla San Esteban (7); S. a. shawi, Isla San Marcos (8); S. a. ater, Isla Espiritu Santo (9); S. a. slevini, Isla Monserate (11), Isla Carmen (12). Missing bands (e.g., Est-2) indicate proteins stained too poorly to be scored.

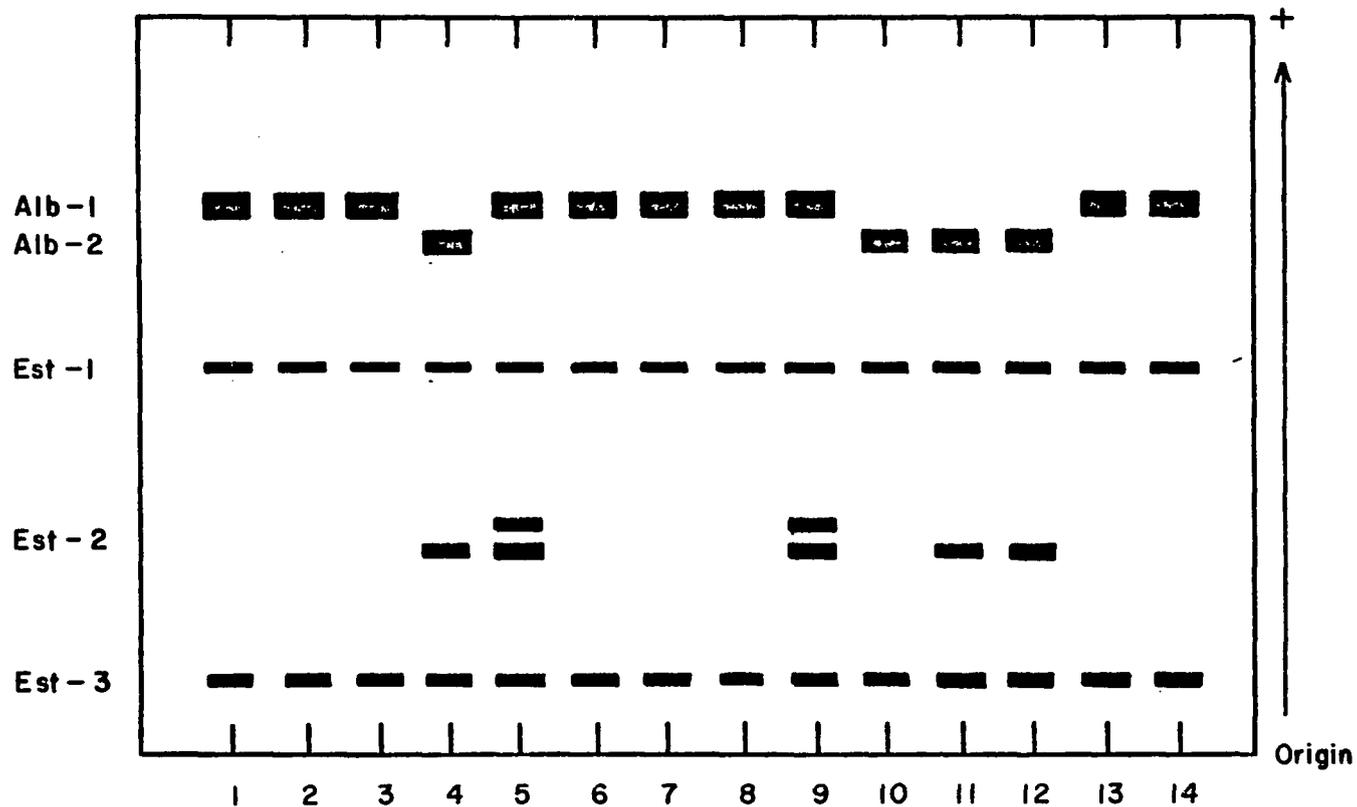


Fig. 4. Variation in esterases and albumins in chuckwalla lizards (genus Sauromalus) from Baja California and the Gulf of California, Mexico.

inconsistently. Several individuals of S. obesus and S. ater were scored at two-banded heterozygotes (Fig. 4). The third esterase (Est-3) also appears to be monomorphic. Allelic variation in the esterases of chuckwallas, and its applicability for defining evolutionary relationships within the genus will require further study.

More individuals from additional localities throughout the range of Sauromalus must be sampled before any meaningful indices of genic heterozygosity or allelic frequencies can be estimated.

Morphology

Data (Table 1) from the present study and previous morphological analyses were used to evaluate the variation of external characters in populations of Sauromalus. The countable scale characters previously used to define species of Sauromalus exhibit wide variability. This point was emphasized by Shaw (1945) and statistically verified by Gates (1968). Scale counts of mainland chuckwallas (S. obesus) are more variable than insular ones (Table 1). For example, the number of ventral scales in the mainland subspecies of S. obesus has a wider range (122-202) than do the five insular "species" S. hispidus, S. ater, S. klauberi, S. shawi, and S. slevini (107-151). Both mainland and island chuckwallas exhibit extreme variation in this and other scale characters (Table 1). Accordingly,

Table 1. Means and ranges of five characters from 11 taxa of Sauromalus. -- Ranges are in parenthesis. Spaces are blank where data are not available. These data have been compiled from Shaw (1945), Gates (1968), Cliff (1958), and Tanner and Avery (1964).

Species	N	Ventrals	Caudals	Humeral	Dorsal Scales	Femoral Pores
<u>S. o. multiforminatus</u> ^a	23	131.3 (122-141)	34.0 (27-45)	48.0 (34-60)		22.7 (17-31)
<u>S. o. obesus</u> (North) ^a	39	167.1 (140-204)	34.0 (27-40)	54.0 (40-66)		16.0 (10-21)
<u>S. o. obesus</u> (South) ^a	40	189.3 (165-215)	36.9 (30-41)	54.5 (50-60)		
<u>S. o. tumidus</u> ^a	21	156.6 (132-185)	32.5 (29-36)	44.0 (39-49)		17.2 (14-21)
<u>S. o. townsendi</u> ^a	11	148.7 (138-152)	28.5 (27-30)	40.4 (37-45)		15.4 (13-18)
<u>S. o.</u> (Baja Calif) ^a	27	172.6 (155-202)	34.4 (31-38)	48.6 (43-53)		180.0 (14-24)

^aValues are from Gates (1968) who summarized data from Tanner and Avery (1964) and Shaw (1945). S. o. obesus (North) are specimens from southwestern Utah, southern Nevada, and adjacent California. S. o. obesus (South) specimens from Imperial and San Diego Co., California. S. o. tumidus are from Yuma Co., Arizona and S. o. townsendi from Sonora, Mexico. S. obesus (Baja) from Gates (1968).

Table 1. (Continued)

Species	N	Ventrals	Caudals	Humeral	Dorsal Scales	Femoral Pores
<u>S. australis</u> ^b	6	163.5 (151-186)	34.7 (32-37)	49.0 (46-55)	31.3 (29-33)	17.6 (15-20)
<u>S. varius</u> ^b	11	158.5 (150-165)	32.0 (30-35)	54.3 (52-58)	32.0 (30-35)	16.1 (15-18)
<u>S. hispidus</u> ^b	11	121.4 (108-129)	25.5 (23-28)	35.6 (31-38)	18.2 (16-21)	14.9 (13-17)
<u>S. a. ater</u> ^b	18	139.8 (130-151)	28.3 (24-33)	40.2 (35-45)	28.0 (24-32)	18.7 (17-21)
<u>S. a. slevini</u> ^b	17	115.8 (107-123)	22.3 (22-23)	33.8 (30-37)	23.5 (20-28)	14.5 (12-18)
<u>S. a. klauberi</u> ^c	11	122.4 (114-133)	25.3 (21-29)	36.3 (32-42)	26.4 (24-32)	15.4 (14-16)
<u>S. a. shawi</u> ^d	5	129.0 (125-132)	30.0	37.6 (36-41)	27.6 (25-29)	

^bData from Shaw (1945). The six specimens of Sauromalus australis are from San Fransquito Bay, Loreto, 33 mi N. Canipole, Aqua Verde Bay, Comondu, and La Paz, Baja California. Data for S. a. ater include one specimen of S. a. shawi from San Marcos Island.

^cData from present study. Values for femoral pores are from 8 specimens.

^dData from Cliff (1958).

they have limited value and should be given relatively "low weight" as taxonomic characters at the species level (see Mayr, 1969).

However, scale counts can be used to broadly define what Shaw (1945) termed the "fine-scaled" (obesus group here) and the "coarse-scaled" (ater group here) groups. As indicated in Fig. 5, members of the ater group (S. ater, S. hispidus, S. slevini, and S. klauberi) generally have a mean number of ventral scales of 140 or less. Species in the obesus group (S. obesus and S. varius) have mean ventral scales of 140 or greater. The single exception to this is the northernmost subspecies of S. obesus (multiforaminatus) which has a mean of 131.3 (Table 1).

Two types of dorsal banding patterns were described by Shaw (1945). The first pattern-type has unicolor bands (obesus and townsendi); the second has bands in which the central area has been lightened by the ground color giving each band a "double-banded effect" (S. australis, S. ater, S. slevini, and S. hispidus). In the specimens that I have examined from both groups, the banding pattern, when present, is usually found only in juveniles or subadults, and the pattern is often intermediate and difficult to assign to one pattern-class or another. I consider the dorsal pattern-type and its

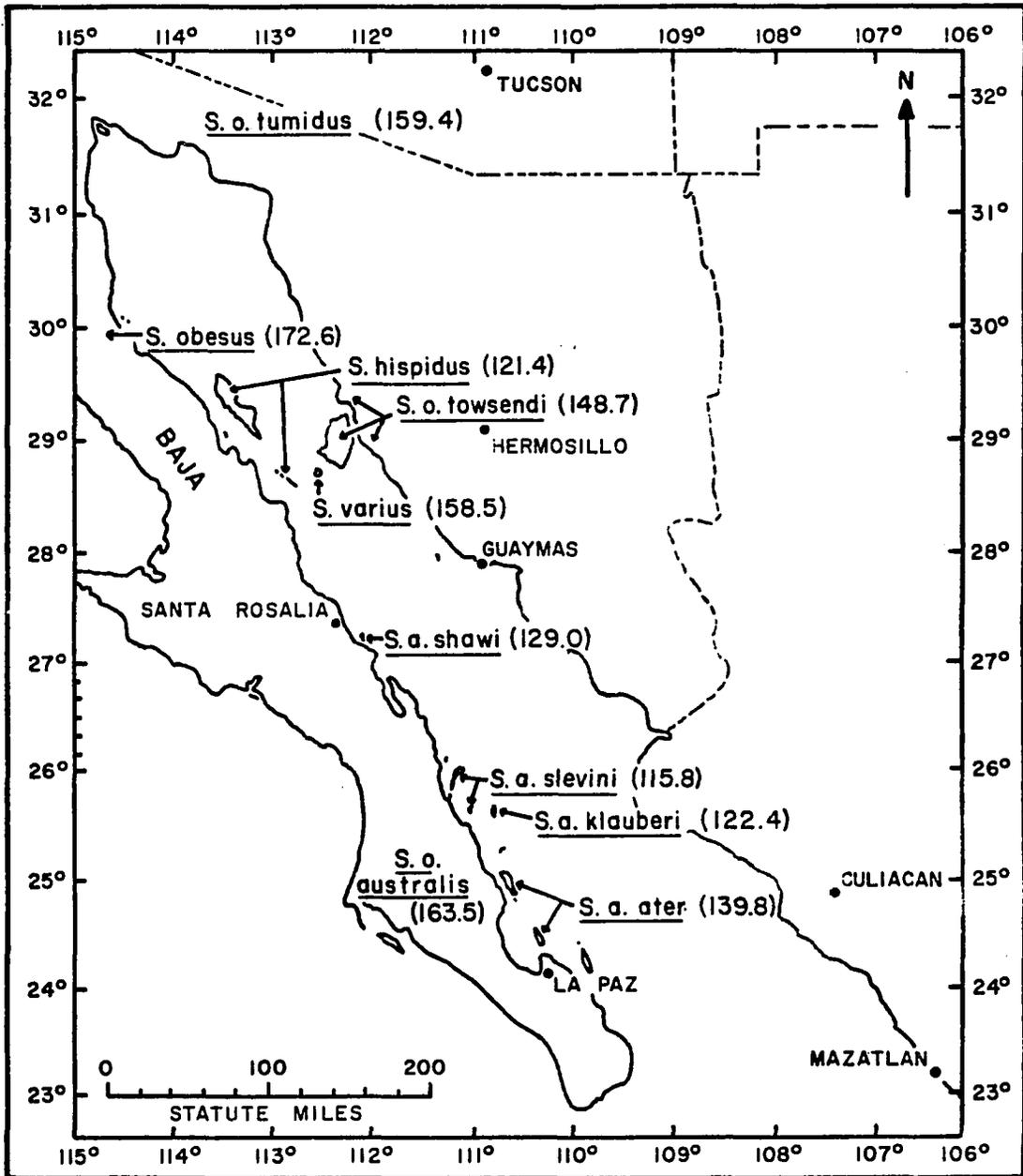


Fig. 5. Variation in the number of ventral scales of insular and mainland populations of chuckwalla lizards in northwestern Mexico. -- Data from Table 1.

occurrence in populations of chuckwallas too variable to be successfully used as a taxonomic character.

Several species can be distinguished by their size and/or color. Sauromalus varius and S. hispidus are easily identified by their large size, largest in the genus. Adults of these two species average 300 mm snout-vent length, or more. Both are so-called "island giants" and have attained this feature independently and convergently within the genus. The remaining species are smaller, similar to one another in size, and can not be identified by size alone.

The dorsal color and pattern are useful for identification of several taxa. Sauromalus klauberi has a unique pattern with black reticulate spotting on a lighter greyish background. On smaller individuals, some white flecking is also present on the dorsum. The other insular taxa related to S. klauberi (slevini, ater, and shawi) have dorsal color patterns that are all very similar. This color varies from light brown to dark brown and black. The piebald chuckwalla (S. varius) has a distinctive pattern of a yellow or straw-colored background with blotches of black or rust.

In summary, dorsal coloration and pattern are distinctive in the taxa indicated, but generally the

differences in color and pattern are too subtle to be diagnostic.

Taxonomic Changes

Soule and Sloan (1966) were first to regard the insular species, S. shawi, S. klauberi, and S. ater as subspecies of S. ater. They retained S. slevini as a species but gave no evidence for either of these changes.

I agree with Soule and Sloan's (1966) nomenclatorial changes, with one exception. I consider slevini to also be a subspecies of ater and propose the following arrangement:

Sauromalus ater ater Dumeril

Sauromalus ater klauberi Shaw

Sauromalus ater shawi Cliff

Sauromalus ater slevini Van Denburgh

Future study may show ater, shawi, and australis are subspecies of obesus, not ater, but until this information is available I will retain them as above. This and other species relationships are discussed in the synonymies of this section.

Several criteria are considered important and strongly support the proposed taxonomic changes. There is more variation in meristic characters, color, and pattern

of the polytypic species S. obesus than in the five "insular species" S. klauberi, S. shawi, S. slevini, S. hispidus, and S. ater (Table 1). No karyotypic differences were noted between these taxa, and only the serum albumins were polymorphic at the subspecies level.

In a recent study of a Gulf island hybrid swarm of chuckwallas on Isla Alcatraz, hybridization is reported involving S. hispidus, S. varius, and S. obesus (Lowe, Robinson, and Keasey, 1972). The results of this hybridization in nature between three distinctive species raise several questions on isolating mechanisms and speciation in Sauromalus.

The data available from these studies suggest that reproductive isolation in all taxa of Sauromalus is recent and is meaningful only in a spatial sense, and that gene exchange between these insular populations is presently restricted as such. The taxonomic arrangement presented here more correctly reflects the incipient speciation and/or accomplished speciation that has occurred in these lizards.

Sauromalus ater ater Dumeril

Sauromalus ater Dumeril, 1856; Arch. Mus. Hist. Nat. Paris, vol. 8:536 (Type locality not definitely known but probably one of the southern Gulf islands where it now occurs. Type specimen in the Museum d'Histoire Naturelle, Paris).
Sauromalus interbrachials Dickerson, 1919 (part); Bull. Amer. Mus. Nat. Hist., 41:463-464.

Sauromalus ater Shaw, 1945 (part);
 Trans. San Diego Soc. Nat. Hist.,
 10:284-286.
Sauromalus ater ater Soule and Sloan,
 1966; Trans. San Diego Soc. Nat.
 Hist., 14:141.

Diagnosis. -- Lower scale counts than S. australis which inhabits the adjacent Baja peninsula. A higher mean number of ventral scales (139.7) than a. shawi (129.0), a. slevini (115.8), or a. klauberi (122.4). Differs from a. klauberi by having 4 or 5 dark brown or black dorsal bands usually present in juveniles and smaller adults. When bands are lacking in ater, most specimens can be separated from a. slevini by the straw or tan ground color present in the former species. Ground colors of a. slevini are usually brown to dark brown and black. Banding is usually less apparent in a. slevini.

Remarks. -- Shaw (1945) has carefully described the scalation, color pattern, and variation in ater, and I will not repeat them here. Included in his description was a single specimen from San Marcos Island with a ventral scale count of 140. He referred the specimen to ater, but the biogeographic anomaly it imposed was disturbing to Shaw (1945:286). This population on San Marcos Island was later described by Cliff (1958) as S. shawi. I find the two populations extremely difficult to distinguish (see also S. a. shawi).

Distribution. -- Known from Espiritu Santo, Partida (South), San Francisco, San Jose, Santa Cruz, and San Diego islands, Gulf of California, Mexico.

Sauromalus ater klauberi Shaw

Sauromalus klauberi Shaw, 1941; Trans. San Diego Soc. Nat. Hist., 9:285 (Type locality Santa Catalina Island, Gulf of California, Mexico. Type specimen No. 6859 in the collection of L. M. Klauber).

Sauromalus klauberi Shaw, 1945; Trans. San Diego Soc. Nat. Hist., 10:282.
Sauromalus ater klauberi Soule and Sloan, 1966; Trans. San Diego Soc. Nat. Hist., 14:141.

Diagnosis. -- Scallation intermediate between a. slevini and between a. shawi and a. ater (Table 1). Dorsal pattern in juveniles and adults without bands, having a dark grey or light brown ground color covered with small black or dark brown spots. Some white maculations are present on the smaller juveniles. Spotting may become washed out in older individuals. This subspecies is most easily identified by the unique dorsal pattern and the intermediate texture and size of the body scales; that is, it is smoother than a. slevini but coarser than a. ater or a. shawi.

Remarks. -- Only three specimens were available to Shaw (1941) for his description of this subspecies. I have analyzed 11 recently collected adult and juvenile specimens and find the mean scale counts agree closely with those given by Shaw (1945). The most notable exception is

the lower mean number of ventral scales in the larger sample which I studied (122.4 compared to 130.3). This taxon and a. slevini appear to share the same allele for the albumin protein as previously reported on page 12 (Fig. 4).

Distribution. -- Known only from the type locality, Santa Catalina island, Gulf of California, Mexico.

Sauromalus ater shawi Cliff

Sauromalus ater Shaw, 1945 (part);
Trans. San Diego Soc. Nat. Hist.,
10:286.

Sauromalus shawi Cliff, 1958; Copeia
1958:259-261. (Type locality San
Marcos Island, Gulf of California,
Mexico. Type specimen No. 16120
Stanford University Nat. Hist.
Museum).

Sauromalus ater shawi Soule and Sloan,
1966; Trans. San Diego Soc. Nat. Hist.,
14:141.

Diagnosis. -- Distinguished from S. a. ater by "having large, acutely pointed scales in the lateral neck fold . . . and by its especially pronounced lateral neck fold" (Cliff, 1958:259). This form has transverse dorsal bands which are lacking in a. klauberi, and a higher number of ventral scales than in a. slevini (Table 1).

Remarks. -- I examined only three specimens (2 ♀, 1 ♂) of this subspecies. They exhibit the type and amount of variation in the scale counts, dorsal coloration, and pattern that has been described for a. ater (Shaw, 1945). Cliff's (1958) description of these characters

from six specimens further emphasizes this point. The two characters considered by Cliff (1958) as diagnostic for this species, (1) the shape and size of the scales in the neck fold, and (2) the enlarged size of the lateral neck fold (this is evident only in adult males) is slightly different from specimens of a. ater from Isla Espiritu Santo, but this is certainly not pronounced enough to warrant recognition as a species character. Furthermore, when larger samples are analyzed it is likely that the apparent difference in the mean number of ventral scales between ater and shawi (Table 1) will be reduced.

I have retained shawi as a subspecies of S. ater until more specimens are available and the amount of variation present in this population can be assessed. Moreover, the relationship of the subspecies shawi and ater to S. australis on the Baja peninsula is indeed close (see also page 35).

Distribution. -- Known only from the type locality, San Marcos Island, Gulf of California, Mexico.

Sauromalus ater slevini Van Denburgh
New Combination

Sauromalus slevini Van Denburgh, 1922;
Occas. Papers Calif. Acad. Sci., No.
10, vol. 1:97. (Type locality south
end of Monserate Island, Gulf of
California, Mexico. Type specimen
No. 50503 in the California Academy
of Sciences).

Sauromalus slevini Shaw, 1945; Trans.
San Diego Soc. Nat. Hist., 10:280.

Sauromalus slevini Soule and Sloan,
1966; Trans. San Diego Soc. Nat.
Hist., 14:141.

Diagnosis. -- Distinguished from all other subspecies of ater by having a lower mean number of ventral scales (115.8), and from S. hispidus by the smaller adult size, the smaller nuchal scales, and the greater number of dorsal scales in one head's length (Table 1).

Remarks. -- Shaw (1945:281) stated that S. slevini was "intermediate in scalation between S. hispidus and S. ater." Re-examination of Shaw's data and analysis of 10 specimens that I have recently collected from Monserate Island indicate hispidus, not slevini, is the intermediate in all scale characters except the number of dorsal scales in one head's length (Table 1).

When larger adults of a. slevini are compared to smaller S. hispidus in the field or laboratory the close resemblance of their color and dorsal pattern is striking. Separation of the two is most easily accomplished by examination of the nuchal scales, which are quite enlarged in hispidus. It can be reasonably argued that the difference in the scale characters between hispidus and slevini are no greater than that between the subspecies of ater, and on this morphological basis it is inconsistent to maintain hispidus at the species level. My decision to retain hispidus at species rank follows examination

of the ecological and behavioral differences (see Discussion) that exist between S. hispidus and S. a. slevini.

Distribution. -- Known only from Monserate, Carmen, and Coronados islands, Gulf of California, Mexico.

DISCUSSION

Karyotypes

Diverse genera of iguanid lizards (Iguanidae) have been karyotypically surveyed, and although few of these genera have been examined in sufficient detail, two basic chromosome patterns are now apparent within the family. The first pattern (12 macrochromosomes and 24 microchromosomes; 12+24), a diploid number of 36 chromosomes, is present in the following "informal" subfamilial groups, the "basiliscines", "tropidurines", "anolines" (in part), "iguanines" (including Sauromalus), and several other genera of uncertain affinities (see Savage, 1958, and Etheridge, 1964 for the genera contained in these arbitrary subfamilial groups).

The second pattern (12+22 or less) is found in the "sceloporine" group where one pair of chromosomes has been lost, and all but one of the genera have 22 microchromosomes. The exception is the genus Sceloporus where the diploid microchromosome number varies from 12 to 22 (Cole, 1970; Cole, 1971a; Cole, 1971b; Lowe, Wright, and Cole, 1966; Lowe, Cole, and Patton, 1967).

Gorman, Atkins, and Holzinger (1967) described the 12 macrochromosomes in iguanids as metacentric. However,

it is clear from the karyotypes illustrated by them that the six macrochromosomes pairs definitely are not all metacentric. Pairs number 2 (second largest) and 6 (smallest) are often submetacentric, even when a liberal chromosome classification system is used (e.g., Cole, 1970). A careful analysis of the morphological changes (e.g., pericentric inversions) that have occurred in the macrochromosomes of these iguanid genera is necessary before the relationships of these karyotypically similar lizards can be more fully understood. Newly developed heterochromatic staining techniques may be useful in this regard (see Arrighi and Hsu, 1971).

Gorman et al. (1967) were first to indicate the diploid chromosome number of Sauromalus is 36. They correctly concluded S. obesus and three other "iguanine" genera (Ctenosaura, Cyclura, and Iguana) have 12 large and 24 smaller chromosomes.

The seven taxa of Sauromalus that I examined from Baja California and islands in the Gulf of California all have 36 chromosomes (see Figs. 1, 2 and 3). No pericentric inversions in the 12 macrochromosomes were detected among the insular and mainland populations analyzed. Though this does little to clarify species relationships in Sauromalus, it is not unexpected in view of the invariability of iguanid karyotypes. Considerable evolution has occurred in the morphology, behavior, and ecology

of this genus without any detectable gross structural changes in the chromosomes.

White (1954:195) has pointed out that once a mechanically stable arrangement of chromosomes (both in number and size) has evolved it is likely that such a karyotype will be retained. This appears to be the situation in the family Iguanidae. The attainment of such an arrangement could occur by repeated parallel evolution and stabilization within various hierarchical categories (e.g., family, genus, species), or more likely, it could have become established early in saurian phylogeny and was retained as the various lizard families evolved. This latter interpretation is supported by the presence of the basic "12-24" chromosome pattern in several widespread lizard families (Gorman and Gress, 1970).

This suggests that strong selective pressures are probably necessary to produce changes in the chromosome number once it becomes stabilized. The genera of "sceloporine" lizards, which for the most part have evolved in, or are associated with, the recent desert communities seem to have surpassed this threshold, and have lost one or more pairs of microchromosomes. Sceloporus, the most karyotypically and ecologically diverse genus in this group, has undergone an explosive radiation and speciation, filling a wide variety of niches in numerous

environments and communities throughout temperate and tropical North America. This radiation has been accompanied by considerable chromosomal evolution including sex determining mechanisms, loss of chromosomes, and Robertsonian fusion. An analogous situation exists in the diverse iguanid genus Anolis in the West Indies (see Gorman, 1965; Gorman and Atkins, 1966; Gorman and Atkins, 1967; Gorman, Thomas, and Atkins, 1968).

The radiation and speciation in Sauromalus in the Gulf of California has evidently occurred under selective pressures insufficient to produce any of the above types of chromosomal evolution.

Serum Proteins

Electrophoretic studies of hemoglobins and other tissue proteins have contributed important data toward understanding the evolutionary relationships and zoogeography of several lizard genera. Dessauer (1966) and others have indicated the taxonomic significance of electrophoretic patterns.

Neaves and Gerald (1968, 1969) and Neaves (1969) electrophoretically analyzed several enzyme systems of both bisexual and unisexual species of the complex lizard genus Cnemidophorus (Teiidae). These studies have confirmed the hybrid origin of the parthenogenetic (unisexual) species

in this genus, which was proposed earlier from karyotypic data (Lowe and Wright, 1966; Wright and Lowe, 1967). The adenosine deaminase phenotypes of five sexual and five unisexual species of Cnemidophorus enabled Neaves (1969) to identify the particular parental sexual species involved in the hybrid origin of a unisexual (parthenogenetic) species.

Dessauer, Fox, and Pough (1962) earlier demonstrated that individuals considered hybrids between Cnemidophorus tigris marmoratus and C. t. gracilis, on morphological criteria (Zweifel, 1962), contained enzymes characteristic of both parental types.

The species relationships and zoogeography of the roquet species group of Anolis in the Lesser Antilles are based largely on the comparative electrophoretic patterns of hemoglobins, transferrins, esterases, albumins, and lactate dehydrogenase (Gorman and Dessauer, 1965, 1966; Gorman and Atkins, 1969). In this group of lizards, as in Cnemidophorus, protein studies have supported and complemented previous morphological and chromosomal analyses.

Guttman (1970a, 1970b; 1971) examined the hemoglobin phenotypes of lizards from the New and Old World. From these data he concluded that hemoglobin electrophoretic patterns were inconsistent; some varied within a species, genus, or family, but others demonstrated no variability within these taxonomic categories.

Gorman and Dessauer (1966) compared the mobility of lactate dehydrogenase (LDH) in Sauromalus obesus to several other iguanid genera and found it compared closest to Anolis carolinensis. Guttman (1971) found hemoglobin mobilities differed between the "iguanine" species Ctenosaura pectinata, Iguana iguana, and Sauromalus obesus.

LDH and hemoglobin were not analyzed in the present investigation. Only the serum albumins and esterases stained well enough for analysis. Therefore, I will limit my comments to the patterns observed in these two proteins in Sauromalus.

As illustrated in Fig. 4, three esterase loci were scored. Two of these loci (Est-1 and Est-3) appear to be monomorphic. There is some suggestion that S. a. slevini may have a slightly slower migrating esterase band at the Est-1 locus. If this is the case the Est-1 locus would also be polymorphic. The third locus (Est-2) is considered polymorphic. More esterase systems from tissue and serum should be analyzed before any phylogenetic affinities or estimates of esterase polymorphism in Sauromalus can be discussed.

The distribution of the serum albumin alleles in the populations of chuckwallas examined from the southern islands is rather confusing and requires some speculation. Sauromalus a. klauberi and S. a. slevini both have the

slower migrating albumin (Fig. 4). While this emphasizes the close relationship of these two subspecies, the absence of this allele from the other subspecies of ater (shawi and ater) was not expected. Furthermore, a. shawi and a. ater share the same albumin (Alb-1) with S. hispidus and two more distantly related species of the obesus group, S. obesus and S. varius. Models involving genetic drift (Selander et al., 1971) or selection (Gaines, Myers, and Krebs, 1971) can be used to explain this distribution of the two albumin alleles. A less likely possibility is that the small samples analyzed (six or fewer individuals) contained only homozygotes and the apparent distribution of these two alleles is therefore spurious due to sampling error.

Selection or genetic drift could have fixed the Alb-2 in klauberi after the population became isolated on Isla Santa Catalina. Independently the same events could have fixed this allele in a. slevini on Monserate Island. However, if all three island populations of a. slevini (Monserate, Carmen, and Coronados) contained only the Alb-2 allele, it would be very unlikely that this allele was independently fixed three different times. The single individual of a. slevini from Isla Carmen had the same albumin mobility as the Monserate sample (Fig. 4).

A more plausible explanation is that the ancestral stock, which became isolated on these islands, had the Alb-2 allele already fixed in the genotype. The remaining subspecies of ater (shawi and ater), which were more recently isolated on the near-shore islands during Pleistocene sea level changes, have retained the Alb-1 allele that was present in the Baja gene pool.

Scale counts and color patterns indicate that gene influences from the Baja peninsula are more prominent in subspecies shawi and ater than in subspecies klauberi or slevini. The relationship of a. shawi and a. ater to the Baja populations of chuckwallas (australis) is probably closer than has been assumed previously. Comparison of the enzyme patterns and allele frequencies between these taxa would be most instructive in this regard. Further study may warrant the combination of australis, ater, and shawi with S. obesus in one species.

Understanding the evolutionary significance of protein polymorphism is still in a nascent stage. From an adaptational point of view, it has been assumed that in natural populations a correlation exists between genetic and ecologic diversity (Manwell and Baker, 1970:305; Beardmore, 1970). Selander et al. (1971) have suggested that the degree of genic variability within a population may reflect the ecological amplitude or "niche-width" that

the population is adapted to exploit. From their analysis of protein polymorphism in populations of the old-field mouse (Peromyscus polionotus) they determined that the small isolated populations contained the lowest degree of heterozygosity. This suggested "that the level of heterozygosity may be directly related to extent of habitat distribution or to other related aspects of the ecological amplitude of populations". Powell (1971) recently demonstrated that in experimental populations of Drosophila willistoni some protein polymorphism is maintained by environmental heterogeneity.

Comparison of genic variability in esterases and albumins between the insular and mainland chuckwallas that I have analyzed implies that these proteins have low levels of molecular polymorphism. Again, more samples are needed before meaningful interpretations can be made regarding levels of proteins polymorphism and adaptability.

Geology of the Gulf of California

Understanding the geological history of the Gulf of California is fundamental to biogeographic studies in this region. The initial formation and subsequent spreading of the Gulf, and island formation during these processes was a major factor in the speciation of chuckwallas. Recent geological theories concerning the Gulf's formation are discussed below.

Anderson (1971) has emphasized that geological activities (earthquakes, tectonics, and mountain-building) in western North America are intimately related to the shifting of two huge lithospheric plates (the Pacific and North American plates) which are bordered by faults, oceanic rifts, and trenches. This dynamic concept of plate tectonics is fundamental to the theory of continental drift, and to the formation of the Gulf of California.

Separation of Baja California from mainland Mexico was probably initiated 25-30 million years ago when a section of the Eastern Pacific Rise collided with the continent (Anderson, 1971). Presumably the irregular profile of the shoreline at the time of contact created unequal stress features, causing one or more long pieces of the continent to be split off and welded to the northwesterly moving Pacific plate. Subsequent movement occurred by ocean-floor spreading as rifts appeared, were filled with magma, and then offset by fractures (Anderson, 1971).

The width, rate, and extent of this initial opening of the gulf is not known, but several authors (Rusnak and Fisher, 1964; Moore and Buffington, 1968) have suggested that a narrow and shallow protogulf existed in the late Miocene or early Pliocene. Apparently the rate of spreading in the Gulf has not always been constant. Moore and Buffington (1968) report a 6 million year period of

"quiescence" in the gulf-spreading, which ended about 4 million years ago.

The Gulf's history is further complicated by the lack of agreement among geologists as to the directionality and sequence of the gulf-forming events. For example, Normark and Curray (1968) and Rusnak and Fisher (1964) have proposed that the gulf was created by a series of offsets, starting in the north and working south to the tip of Baja. Assuming this sequence, the northern portion of the Gulf is older (late Miocene) than the southern portion (late Pliocene). Magnetic profiles and seismic-reflection studies (Moore and Buffington, 1968; Larson, Menard, and Smith, 1968) indicate the southern Gulf began an increased spreading rate about 4 million years ago. This agrees with the late Pliocene date postulated by Normark and Curray (1968) and Rusnak and Fisher (1964) for the opening of the southern Gulf.

The cyclic Pleistocene glacial events produced eustatic sea level changes in the Gulf of California, and elsewhere, of approximately 110 meters (Fairbridge, 1961; Russell, 1964). This would have repeatedly altered the shoreline by exposing the flooding landmasses and existing islands that were separated from the mainland by water less than 110 meters deep. These "shallow-water islands" include Islas Tiburon, Alcatraz, San Marcos, Coronados,

Carmen, San Jose, Espiritu Santo, and numerous other smaller islets. Presumably their last connection to the mainland was 15-17,000 years ago at the time of the last glacial retreat. Any evolutionary divergence which had occurred on these islands was then diluted by repeated genetic exchange with, or re-population from, the adjacent connecting landmass during the sea level changes.

The "deep-water islands" such as Angel de la Guarda, San Esteban, San Lorenzos, Monserate, Santa Catalina, Ceralvo, plus several smaller midrif islands have probably remained isolated since Pliocene times. These islands were relatively unaffected by Pleistocene flooding or land connections. It has been suggested that some of the "deep-water islands" (e.g., Monserate, Angel de la Guarda, and San Lorenzo) are younger (late Pliocene) and were exposed by uplifting (Shepard, 1950; Anderson, 1950; Wilson and Rocha, 1955).

From the preceding discussion it is apparent the Gulf of California's geology has been complicated by its activity during the past 15 million years. Several aspects of the Gulf's history are unclear but are important to biogeographic studies in the area. First, it is uncertain what regions of Baja became separated from the mainland as the early protogulf formed. Some approximation of which islands were formed first, and have been isolated the

longest, can be made from the relatively high percentage of biotic endemism of these islands (Table 2). Second, until an estimate of the width of the early gulf is available, it is difficult to determine the effectiveness this separation had upon the biotic exchange and colonizational events between the two landmasses. Nevertheless, enough is now known of the geology to provide a reasonable historical framework to discuss the evolution and biogeography of Sauromalus in this area.

Ecology of Island Gigantism in Reptiles

The average body size of adults in island vertebrate populations is often greater than their mainland counterparts. This phenomenon is referred to as insular gigantism. Cases of insular gigantism have been analyzed in birds and reptiles (e.g., Van Valen, 1965; Grant, 1965; Soule, 1966). Other less thoroughly studied examples of gigantism in plants and animals are summarized by Carlquist (1965).

The factors that enhance such size changes on islands are collectively referred to as "ecological release", which in turn evokes "character release" or "character displacement" (MacArthur and Wilson, 1967). This means that islands, compared to mainlands, are impoverished in the number of species present and the habitats available to them. Species that become established on these islands

Table 2. Percent endemism in the reptile faunae of selected deep-water and shallow-water islands in the Gulf of California, Mexico. -- Data from Soule and Sloan (1966).

Island	Total Number of Reptile Species	Number of Endemic Species or Subspecies	Percent Endemicity
DEEP-WATER ISLANDS			
San Esteban	8	6	75.0
Angel De La Guarda	13	7	53.8
Salsipuedes	3	2	66.6
San Lorenzo (North)	5	3	60.0
San Lorenzo (South)	5	3	60.0
San Pedro Martir	3	2	66.6
San Pedro Nolasco	5	3	60.0
Isla Tortuga	4	2	50.0
Santa Catalina	9	8	88.9
Isla Cerralvo	16	5	31.3
SHALLOW-WATER ISLANDS			
Tiburón	24	0	0
San Marcos	14	2	14.3
Coronados	10	2	20.0
Carmen	16	2	12.5
Espiritu Santo- Partida (South)	19	3	15.8
San Jose	20	3	15.0

have fewer food competitors and fewer predators. This allows the species to be "released" from its old and usually more restricted mainland niche to exploit new habitats and food resources. In turn new behavioral, morphological, and ecological features may evolve.

The ecological and evolutionary components that promote "ecological release" and their inter-relationships are poorly known and generally have been ignored. The data presented in Table 3 and the discussion that follows is an attempt (1) to analyze the manner in which the islands in the Gulf of California obtained their lizard fauna, and (2) to consider some of the factors that have canalized evolution toward gigantism in chuckwallas on several of these islands.

Islands receive their biota by two basic processes, or a combination of the two. The choice of which of these processes or their combinations is largely determined by the island's history, its distance from the mainland, the oceanographic and wind currents between island and mainland, and the size of river discharge on the mainland. Both processes will be discussed in terms of their contributions to the insular lizard faunas in the Gulf of California.

The first process occurs on islands that are geologically produced de novo. These islands may be oceanic islands (e.g., Hawaiian Islands) or continental islands.

Table 3. Some biotic and physical environmental parameters on several Gulf islands where giant (S. varius and S. hispidus) and small-sized (S. obesus) chuckwallas occur. -- See text for discussion of these parameters.

	Isla San Esteban	Angel de la Guarda	San Lorenzo-Norte	San Lorenzo-Sur	Isla Tiburon
Island size (sq. km) ^a	43	632	8.5	44.5	1212
Island type	deep-water	deep-water	deep-water	deep-water	shallow-water
Relative predation pressure	weak	strong	strong	strong	weak
Number of plant species	88 ^b	97 ^c	6 ^c	22 ^c	260 ^b
MAMMALS					
Number of native mammal species ^a	1	3	2	2	12
Number of herbivorous mammals	0	0	0	0	4
LIZARDS					
Native chuckwalla species and mean size range (snout-vent length)	<u>S. varius</u> (450-550 mm)	<u>S. hispidus</u> (325-400 mm)	<u>S. hispidus</u> (325-400 mm)	<u>S. hispidus</u> (325-400 mm)	<u>S. obesus</u> (125-200 mm)
Number of lizard species ^a	5	8	4	4	12
Number of herbivorous lizards	2	2	1	1	1
Number of iguanid species	3	6	2	2	9

^aData taken from Soule and Sloan (1966).

^bData from Felger (1966).

^cData from Gentry (1949). The species number on these islands are probably too low, but the ratios between islands are similar (Felger, pers. comm.).

The important point here is that one must know that the island emerged from the sea, and thus could have received no fauna by overland emigration. Then providing marine isolation continued, one may unequivocally state that the fauna arrived by over water colonization (by rafting, flight, wind, etc.) or from introduction by man or other agents.

The number of species maintained on such an island's ecosystem fluctuates and has been described as an equilibrium point between the immigration of new species and the extinction (usually by extirpation) of resident species. This is the MacArthur and Wilson (1963) insular equilibrium model. In the West Indies, the islands initially received their lizard fauna by colonization from the mainland, but following this the radiation and differentiation of these lizards has been largely confined to inter- and intrainland events. In fact, several species, which evolved on the islands, have "colonized" the mainland from their native islands (Williams, 1969). In this island group the extinction and immigration events have not been continuous (as in the MacArthur and Wilson model) but have been largely limited to one major occurrence (Williams, 1969).

From what is known of the geological history of the Gulf of California (p. 36), only two islands (Islas Tortuga and Santa Lucia) were produced from the ocean floor de novo, and consequently the remaining islands did not acquire the

majority of their faunas by colonization from adjacent land areas. Isla Tortuga, a deep-water volcanic island, has a small reptile fauna (4 species) that contains both Baja and Sonoran elements, which apparently arrived by over water colonization.

The second manner that islands attain their biota is by isolation of the species present on a landmass at the time that it becomes an island. This system is predominant on continental islands (i.e., those formerly connected to the mainland). These insular faunas were isolated in situ as the Gulf and its islands formed. This does not, however, suggest colonizational events have not occurred on these islands. Certainly near-shore islands have received individuals from the mainland.

The contribution of new species to a Gulf island fauna by colonization is minor, if any, because (1) when colonizers arrive on one of these islands it is likely that a conspecific form would already be there, thus the influence of its arrival is slight other than possibly supplying some new genetic variability to the population, and (2) if a colonizer was a new faunal element (species), chances are that a balance between the number of animal species and the plant community diversity of a given island had previously been reached, and available niches would be filled. That is, each island quickly reduces the number

of species that are initially isolated to meet the demands of the new physical and biotic environment on each island. Moreover, colonization is physically an unlikely possibility in the Gulf because the major rivers (the Yaqui, Mayo and Fuerte) discharge into it on the Sonoran coast where nearby islands are lacking. The single exception is the Colorado, which has only one smaller island near its mouth. Also vegetational debris suitable for rafting lizards is sparse in adjacent desert communities, and the most suitable lizards for rafting (viz., gekkos) are terrestrial (Coleonyx) or live in rocks (Phyllodactylus). Chuckwallas preferentially live in rocky areas and would also be unsuitable rafters.

This strongly suggests that both the giant and small species of chuckwallas have evolved in situ on their respective islands as an integral part of the fauna and did not later colonize these islands from the mainland source areas.

A positive correlation and direct relationship exists in the number of animal species on an island and the size (surface area) of that island. This relationship has been demonstrated in many animal groups, many which are summarized by MacArthur and Wilson (1967). Lowe (1955) earlier expressed this same direct relationship between the number of land reptiles and land mammals and the island

size in the northern Gulf of California. He further showed that the percent of differentiation and island size are inversely related.

The surface area of the four islands on which the two gigantic species of chuckwallas (S. varius and S. hispidus) live varies considerably from 8.5 square km on Isla San Lorenzo Norte to 632 square km on Isla Angel de la Guarda (Table 3). The largest of these islands (Angel de la Guarda) is, however, only one-half as large as Isla Tiburon where the small (125-200 mm) chuckwalla (S. obesus) occurs. It should be noted that several smaller islands in the southern Gulf (e.g., Isla Santa Catalina, 43 sq. km, and Isla Monserate, 19.4 sq. km) have small chuckwallas (S. ater) in their faunas. Thus it is clear that the surface area of the islands where giant chuckwallas occur is indeed variable, to the extent that this factor alone seems meaningless. More important is the effect that the interaction of island history and island size have upon the biota. The most easily measured of these ecological parameters is the diversity of plant and animal species (Table 3).

The number of lizard species, which increases on larger islands, apparently affects the maximum body size attainable by competing species on the same island. Soule (1966) demonstrated that in the Gulf of California the body

size of island populations of the lizard genus Uta is inversely related to the square root of the number of iguanid species present on each island.

The number of iguanid species on islands supporting giant chuckwallas is highest on Angel de la Guarda (6 species) and lowest on the smaller islands of San Esteban (3 species) and the San Lorenzos (2 species). Isla Tiburon, where the small chuckwalla (S. obesus) occurs, is the largest island in the Gulf and contains nine iguanid species (Table 3).

Perhaps of greater importance than the total number of lizard species, or how many congeners exist on an island, is the number of taxa that compete on the same trophic level. Five herbivorous mammal and reptile species occur on Isla Tiburon; two of these are large mammals (Mule deer and Allen's Jackrabbit), and two are small largely herbivorous rodents (Rock squirrel and Pack Rat). The islands that have giant chuckwallas have no large herbivorous mammals (Table 3). The only land mammals on these islands are small granivorous rodents (Perognathus and Peromyscus).

Ctenosaura hemilopha, a herbivorous lizard, appears to be larger on islands that lack Sauromalus (e.g., San Pedro Nolasco) than it is on islands where the two species are sympatric (e.g., San Esteban). Although the ecological

interactions of these two species are unknown, it is possible that some type of competitive exclusion limiting the adult size of Ctenosaura may be operating.

Clearly an important factor that would favor evolution of larger body size in a reptile is reduction in number of mammalian and reptilian species that share a particular trophic level on a given island. The total lack of mammalian herbivores on many of the Gulf islands would permit increased utilization of this niche by the resident lizards.

Another ecological feature of most of the islands in the Gulf is the total lack of mammalian predators. Instances of avian predation on chuckwallas have been reported on Gulf islands (Van Denburgh, 1922) and on the mainland (Camp, 1916; Miller and Stebbins, 1964). Estimates of the effect of predatory birds or mammals upon a chuckwalla population are non-existent. During this study I recorded the number of eviscerated chuckwalla carcasses observed during collection periods on Gulf islands. Since predatory mammals are lacking on all islands in the northern Gulf except Isla Tiburon, I assume that those eviscerated bodies found on the ground as well as in osprey nests resulted from avian predation. From these data, I assigned values that describe the relative amount of predation that I noted on several Gulf islands (Table 3). On islands where predation is considered strong, 10 or more dead

chuckwallas were found in 2-3 hours, but islands where predation is regarded as weak, only 1-3 carcasses were found during the same time period. Apparently both strong and weak predation pressure exists on islands where gigantism occurs in chuckwallas. For example, predation on Isla San Esteban (S. varius) appears nearly non-existent, but numerous dead chuckwallas were found on the islands where S. hispidus lives.

Kramer (1949) suggested that the lack of typical mainland predators shifted the age distribution of island lizard populations in favor of older individuals. Soule (1966) noted a similar shift in insular populations of Uta in the Gulf of California. This aspect of the population structure of insular chuckwallas may be important with regard to gigantism and should be investigated.

One of the most obvious and different behavioral traits of the large chuckwallas (S. varius and S. hispidus) is their natural tameness and apparent lack of predator fear (see also Shallenberger, 1970). Presumably reduced predator fear has allowed one of the giant species (S. varius) to largely abandon the usual rock crevice-dwelling habit of chuckwallas, and instead the majority of the population chooses habitat sites among the debris in arroyos, or excavates large dens in arroyo banks or on hillsides. Juveniles are nearly always found farther up the

rocky slopes along with an occasional young adult (Lowe, pers. comm.). The movements of individuals in the population are not known, but it appears that most individuals spend only the first portion of their life cycle in the "old" rock crevice habitat. Gigantism in S. varius may result, in part, from a more rapid growth rate, which occurs in the less restrictive arroyo-bottom habitat.

These may be only a few of the factors that have contributed to the evolution of gigantism in chuckwallas, and they have resulted primarily from the different ecological structure and new selective pressures on several of the Gulf islands. This evidently provided the "ecological release" necessary that permitted the small mainland chuckwalla to exploit different ecological situations (i.e., more and different food resources), which in turn lead to morphological, behavioral, and ecological divergence.

The mosaic distribution of island gigantism in Sauromalus and Uta on the Gulf islands emphasizes the fact that each island differs in its physical and biotic environment. Equally important to the evolution of large body size is the length of uninterrupted isolation on an island. Preventing "dilution" from nearby gene pools is essential for maintaining the integrity of a changing genetic system. The higher percentage of endemism on deep-water (=longer

isolated) islands effectively illustrates this point (Table 2).

Phylogeny and Biogeography of Sauromalus

Before discussing the phylogeny of living chuckwallas it is necessary to briefly review the fossil record of these lizards and consider some historical aspects of the plant communities associated with them.

The fossil record of Sauromalus is extremely poor. Sauromalus obesus is known only from Gypsum and Rampart Caves, both are late Pleistocene sites in the Mohave desert (Brattstrom, 1954; Wilson, 1942).

Gilmore (1928) described Parasauromalus from the middle Eocene of Wyoming. He provisionally assigned the genus to the Iguanidae and remarked that it was similar to specimens of recent S. ater (= S. obesus). The relationship of Parasauromalus to Sauromalus, and to other genera of Eocene iguanids is still unclear. The scanty fossil record does not assist interpretation of the phylogeny of living Sauromalus.

Most of the modern genera of North American lizards first appear in the fossil record during the Miocene (Estes and Tihen, 1964; Holman, 1966). Sauromalus was probably present in western North America by the Miocene, but doubtfully before.

The North American deserts are commonly represented as relatively recent geographic features. The Sonoran and Mohave deserts, with which Sauromalus is most closely associated, were allegedly derived during the middle or upper Pliocene from the southern Madro-Tertiary thornscrub communities (Axelrod, 1948). The Pleistocene glacial advances and retreats and the concomitant sea level changes repeatedly altered the size and locality of the deserts, and presumably the distributions of Sauromalus. The overall effect of Pleistocene vegetational changes on the speciation of chuckwallas in the Gulf region was less than the spatial isolation imposed on these lizards by the formation of the Gulf and its islands.

The phylogeny of the genus Sauromalus was first discussed by Shaw (1945). He divided the genus into two groups consisting of the "fine-scaled" species (S. varius, S. o. townsendi, S. o. tumidus, and S. o. obesus) and the "coarse-scaled" species (S. hispidus, S. slevini, S. klauberi, S. ater, and S. australis). Shaw (1945) considered the formation of the Gulf instrumental to the division of the genus into these two groups, and to speciation within each group. I concur with Shaw on this important point. His interpretation of speciation in the genus is summarized below (Shaw, 1945:277).

S. hispidus and S. varius are the oldest species in the genus, ". . . their differentiation occurring before that of the other species" S. klauberi and S. slevini were next to evolve from the ancestral group that gave rise to hispidus. S. ater evolved last in this lineage and was considered most closely related to S. australis on Baja California. The "fine-scaled" species were derived from the Sonoran ancestral population in the following temporal sequence: S. varius, S. o. townsendi, S. o. tumidus, and S. o. obesus.

Several important differences exist between the phylogeny presented by Shaw (1945:278) and the one that I have proposed. These differences are discussed below.

In formulating a phylogeny of the insular chuckwallas, I consider the island forms to be derived from the mainland populations. An opposite view, the "island relict" hypothesis, would require a complete replacement of the mainland fauna during the past 5-10 million years, leaving the ancestral taxa isolated on the islands. Furthermore, islands offer new ecological situations not found on the mainland (see page 40). Under these circumstances it is expected new taxa will evolve in response to the different selective pressures encountered on the islands, and it is unlikely the ancestral species would remain unchanged on an island in a new environment. In fact, we would expect the opposite.

In chuckwallas, as in other Gulf island reptiles and mammals the degree of divergence from mainland ancestors is related to the time of isolation and the distance from the mainland source. The highest percent of biotic endemicity occurs on the deep-water islands, which have been isolated the longest (Table 2).

The genus Sauromalus as conceived here contains two groups of species that are similar in content to the "fine-scaled" and "coarse-scaled" groups proposed by Shaw (1945). These two groups are artificial and do not imply monophyly, and they are used only for convenience. I prefer to call the former the obesus group, and the latter the ater group. The evolutionary relationships of the taxa within each species group are discussed below.

The Obesus Group

This group presently contains the following taxa: S. obesus obesus, S. o. multiforminatus, S. o. tumidus, S. o. townsendi, S. o. australis, and S. varius. These species occur on the mainland of Mexico, Baja California, southwestern United States, and on San Esteban and Tiburon Islands.

The relationship of the obesus group taxa that surround the Gulf on coastal Sonora and Baja California are completely known at this time (viz. S. o. townsendi, S. o. tumidus, and S. o. australis, and a population of

obesus from northern Baja). These populations exhibit a clinal variation in the number of ventral scales that increases from south to north in Sonora and then decreases from north to south in Baja California (Fig. 5). Presumably the Gulf's formation was instrumental in effecting this subspeciation.

Shaw (1945) included S. australis in his "coarse-scaled" (= ater group) group. I consider australis a southern peninsular population of obesus and have included it in the nominant group. I expect intergrades between S. o. australis and S. obesus will be found in the northern third of the Baja peninsula. As previously discussed (page 35), recent gene exchange between S. o. australis (Baja) and the two insular forms, S. a. ater (Isla Espiritu Santo) and S. a. shawi (Isla San Marcos), is apparent from morphological characters. If further studies of serum proteins also indicate similar genotypes between these populations, then S. a. ater and S. a. shawi should also be included in the obesus group. Until this evidence is available, I have retained them as members of the ater group.

I consider S. varius an insular derivative of a mainland population of chuckwallas similar to S. o. townsendi, which occurs today on Tiburon Island and adjacent coastal Sonora. Shaw's view (1945) was that S. o. townsendi evolved after S. varius.

The Ater Group

Species in the ater group (S. hispidus, S. a. klauberi, S. a. slevini, S. a. shawi, and S. a. ater) were derived from a peninsular S. obesus ancestor and have evolved on their respective islands in the Gulf. Subspecies of ater that were isolated on the shallow-water islands (S. a. shawi and S. a. ater) were recently derived from the Baja populations of S. o. australis since the last Pleistocene sea level drop.

The relative ages between the deep-water species in the ater group (hispidus, a. klauberi, and a. slevini) are less certain, but I consider these taxa older (Pliocene) than ater or shawi.

Isla Santa Catalina was isolated early in the Gulf's history and contains a highly endemic herpetofauna (Table 2). The chuckwalla on this island, S. a. klauberi, is the ancestral species in the ater group. Several characters in S. a. klauberi (e.g., scale counts, pattern, and coloration) are intermediate between species in the obesus group, and those in the ater group. Thus a. klauberi is somewhat "transitional" between the two groups, but included in the latter group. It is most closely related to S. a. slevini.

The geological history of the islands (Islas Carmen, Monserate, and Coronados) inhabited by the Monserate

chuckwalla (S. a. slevini) has been complicated by recent tectonic activity (Anderson, 1950). Apparently these three islands have not been isolated as long as Isla Santa Catalina. This assumption is supported by the significant difference in the percent endemism of the herpetofaunas of the two island groups (Table 2).

Accordingly, S. a. slevini (Isla Carmen, Monserate, and Coronados) evolved after S. a. klauberi (Isla Santa Catalina). It is unclear if the former species was a direct descendent from a population of klauberi that was isolated as these islands formed, or if slevini was an insular derivative from a population of chuckwallas from the Baja peninsula (S. o. australis). It is clear, however, that both klauberi and slevini share the same allele at the albumin locus, a situation that is most easily explained by their common genetic ancestry, rather than the independent evolution and fixation of this allele in three different populations of S. a. slevini (on Islas Carmen, Monserate, and Coronados).

The morphological differences (Table 1) noted today between slevini and klauberi have evolved since their isolation in response to the different environments of these islands.

The spiny chuckwalla (S. hispidus) was apparently derived from a Baja California ancestor in the late

Pliocene or early Pleistocene. Anderson (1950) has suggested that the large deep-water islands, on which hispidus occurs (Angel de la Guarda, and the San Lorenzos), may not have originated until this time. On the basis of the relative ages of their respective islands, hispidus is older than ater or shawi, but younger than klauberi, and probably contemporaneous with slevini.

The disjunct distribution of hispidus is somewhat disturbing (Figs. 1 and 5). Approximately 25 miles of deep ocean separate the northern populations of hispidus on Isla Angel de la Guarda (and several satellite islands), from the southern populations on Isla San Lorenzo North (= Las Animas). A similar distribution is noted in the rodent genus Peromyscus. Banks (1967) and Lawlor (1971) contend that two species of Peromyscus have evolved independently on Angel de la Guarda (P. guardia) and on the San Lorenzos (P. interparietalis) from a Baja P. erimicus-like stock. They argue that the absence of either species on islands between the two groups is best explained by their separate mainland origin.

The distribution and differentiation of the herpetofauna on these two island groups tend to support the "separate-origin" hypothesis. For example, Cnemidophorus tigris canus is restricted to the southern group (Salsipuedes, and Islas San Lorenzos) of islands, and a different

subspecies, C. t. dickersonae is found only on the northern island (Angel de la Guarda). This same pattern occurs in the lizard genus Uta (Soule, 1966; Ballinger and Tinkle, 1968).

No morphological, karyotypic, or serum protein variation was noted between the northern island and southern island samples of S. hispidus (Figs. 2, 3, and 4). This is unexpected in view of the observed differences present in the other lizards of these disjunct island groups. If S. hispidus also had separate origins, then it is fair to assume the ancestral populations that became isolated on these islands was monomorphic at least at the albumin and esterase loci.

Another possibility is that the Seri Indians, who use chuckwallas as food, may have introduced them to the San Lorenzo islands, which they visited periodically (Moser, 1963; Lowell, 1970). This would provide a more convenient food source for the Seri than the more distant Isla Angel de la Guarda, where S. hispidus is native.

SUMMARY AND CONCLUSIONS

The Miocene-Pliocene formation of the Gulf of California was instrumental in the speciation of chuckwalla lizards (genus Sauromalus) in this area. These insular populations have undergone marked evolutionary changes since their initial isolation. This divergence is most apparent in their morphology, behavior, and ecology, and it has occurred without any presently detectable chromosomal evolution, such as Robertsonian fusion, centromeric fission, or pericentric inversions. Preliminary data on enzyme polymorphisms in serum proteins indicate that the level of molecular evolution is also quite low within the genus.

Two artificial groups of species are presently recognized in Sauromalus: the obesus, or fine-scaled group (S. obesus and S. varius) and the ater, or coarse-scaled group (S. ater and S. hispidus). Members of the ater group were derived on islands from obesus or an obesus-like Baja' ancestor. In the obesus group, S. varius, was derived from a Sonoran population of chuckwallas similar, if not identical, to S. o. townsendi, the only island population (Tiburon Island) of this species.

Island gigantism has independently evolved within the two groups of species in response to the new ecological opportunities encountered by the lizards on several of the Gulf islands. Sauromalus hispidus and S. varius, the two gigantic species, evolved from peninsular and mainland ancestral populations respectively.

Chuckwallas on the deep-water island (S. varius, S. hispidus, S. ater klauberi, and S. a. slevini) have been isolated longer than those species (S. a. shawi, S. a. ater, and S. o. townsendi) on shallow-water islands, which have periodically exchanged genes with the mainland populations during times of low sea level. This difference in the temporal isolation is reflected in the degree of similarity to their mainland congeners.

The data presented indicate that the insular members of the ater "complex", formerly considered distinct species (S. shawi, S. slevini, and S. klauberi), are subspecies of S. ater. This arrangement is consistent with "biological" species levels in the genus and emphasizes the degree of their divergence.

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