KARYOTYPIC VARIATION AND EVOLUTION OF THE LIZARDS IN THE FAMILY XANTUSIIDAE

By ROBERT L. BEZY[1]

ABSTRACT: Diploid chromosome numbers of ten species of the family Xantusiidae range from 36 to 40 with 16 to 18 macrochromosomes, 18 to 22 microchromosomes, and 50 to 58 chromosome arms. Seven pericentric inversions, the loss of two pairs of microchromosomes, two centric fusions, and the formation of satellites on one pair of chromosomes explain the variation observed. Intraspecific karyotypic variation occurs in *Xantusia vigilis* and *Xantusia henshawi*. Chromosomal differences suggest that *Lepidophyma smithi* and *Lepidophyma occulor* are specifically distinct. Chromosomal similarities are consistent with the inclusion of (1) *Klauberina riversiana* in the genus *Xantusia*, and (2) *Gaigeia gaigeae* in the genus *Lepidophyma*. Of the several groups of lizards that have been considered related to xantusiids, the microteiids have the most similar karyotypes. At present, there is no evidence to indicate that hybridization preceded the evolution of unisexuality in *Lepidophyma flavimaculatum* from Panama and Costa Rica, in that (1) the karyotype is primarily diploid and homomorphic; and (2) there are no plausible parental species known to occur in the area.

INTRODUCTION

In Camp's (1923) monumental classification of lizards, the species of the family Xantusiidae bridged the morphological gap between the two divisions (Ascalabota and Autarchoglossa) of the suborder Sauria, a systematic dilemma which he resolved by arbitrarily depositing them in the Autarchoglossa. Subsequent workers have also found this morphologically ambivalent family annoying and have shifted it between these divisions. In actuality, these lizards may well be relicts of the departure point of the two major lines of saurian evolution and thus might reasonably be placed in a third division, a taxonomic honor which many systematists might be hesitant to bestow on this small family.

Not only have xantusiid lizards been troublesome to students of "higher classification," but those unforutnate taxonomists who have been lured into extensive studies of the systematics of the family have suffered greater torments. Within this handful of species there occurs nearly every conceivable degree of morphological divergence. Many problems are encountered by a systematist attempting to define subspecies, species, and genera in

[1]Associate Curator of Herpetology, Natural History Museum of Los Angeles County, Los Angeles, Calif. 90007.

this small family because the morphological differences between populations do not tend to fall into discrete sizes that can be easily assigned rank. In partitioning this array of only about 14 species into genera, one must steer between the Scylla of monotypic genera and the Charybdis of a monotypic family. Cope (1895) recognized five Recent genera, all of which were monotypic except *Xantusia*, and one of which (*Amoebopsis gilberti*) contained what is currently recognized as only a subspecies (*Xantusia vigilis gilberti*). Savage (1963) recognized four Recent genera of which two (*Xantusia* and *Lepidophyma*) were polytypic and two (*Cricosaura* and *Klauberina*) were monotypic. In this study, these lizards are treated as two groups: *Xantusia* (inclusive of *Klauberina*) and *Lepidophyma* (inclusive of *Gaigeia*); *Cricosaura typica* has not yet been studied karyotypically.

Xantusiids have extremely disjunct distributions, a characteristic generally attributed to primitive, receding groups. Ranges of most of the species are extremely fragmented and populations are often isolated by hundreds of miles. Particularly spectacular examples are the occurrence of *Xantusia vigilis* and *Xantusia henshawi* in Durango, Mexico, ca. 400 to 800 air-line miles southeast of the nearest known populations of these species (Webb, 1965, 1970) and the insular isolation of *Xantusia riversiana* and *Cricosaura typica*. The occurrence of the Eocene fossil, *Paleoxantusia fera* (Hecht, 1956), in Wyoming, ca. 300 miles north of the present northern limit of the family, adds a time dimension to the receding of xantusiids.

Sympatric contacts have been reported for only two pairs of currently recognized species in the family Xantusiidae: *Xantusia henshawi* and *X. vigilis* in southern California (Klauber, 1931) and Durango, Mexico (Webb, 1970) and *Lepidophyma tuxtlae* and *L. pajapanensis* in southern Veracruz (Werler, 1957). When the lack of sympatry in this family is combined with extreme variability in morphological divergence at the population level, the task of defining evolutionarily meaningful (or even morphologically consistent) species becomes difficult (Bezy, 1967b). Further, strong selective pressure for saxicolous adaptations in highly isolated populations of xantusiids has led to morphological convergence at the subspecies level (*Xantusia vigilis arizonae* and *X. v. sierrae*, Bezy, 1967a, b), at the species level (*Xantusia vigilis arizonae* and *X. henshawi*, Klauber, 1931), and at the near-generic level (*Xantusia* and *Gaigeia*, Smith, 1939).

This analysis of karyotypic variation has been undertaken in the hope of finding new data to help establish meaningful phylogenetic relationships in this small but puzzling family. Karyotypes of ten species of xantusiids are reported and discussed herein: *Xantusia henshawi* Stejneger, *X. vigilis* Baird, *X. riversiana* Cope, *Lepidophyma flavimaculatum* A. Dumeril, *L. gaigeae* Mosauer, *L. micropholis* Walker, *L. occulor* Smith, *L. pajapanensis* Werler, *L. smithi* Bocourt, and *L. tuxtlae* Werler and Shannon. The biogeographical, morphological, and karyotypic information indicates that these are all valid species as will be discussed in a separate paper on the systematics of the genus

Lepidophyma. Karyotypic data are not yet available for five rare forms of uncertain status: *Cricosaura typica* Gundlach and Peters, *Lepidophyma dontomasi* (Smith), *L. radula* (Smith), *L. sylvaticum* Taylor, and an undescribed species of *Lepidophyma* from Guatemala.

I wish to emphasize that the karyotype data can be meaningfully interpreted only by comparison with information from other sources, that is, by the process which Hennig (1966) dignified with the term "reciprocal illumination." I consider the comparison of patterns emerging from data of radically different sources to be a vital step in the establishment of meaningful phylogenetic relationships, and do not accept Sokal and Sneath's (1963) view that this is merely circular reasoning. Convergence, for example, can occur in morphology and in karyotypes, but, because of the radically different factors governing morphological and karyotypic evolution, the probability is quite low that convergence between two taxa will occur in both parameters. For these reasons data on morphological variation are discussed in this paper where the major focus is on karyotypic evolution. Moreover, the phylogenetic relationships suggested herein are based not only on an appraisal of data from both of these sources, but also on biogeographical and ecological field impressions.

MATERIALS AND METHODS

Chromosomes of cells from bone marrow, spleen, and testicular tissue were prepared in vivo by Patton's (1967) modification of the colchicine-hypotonic citrate technique of Ford and Hamerton (1956) as has been adapted for lizards by Lowe and Wright (1966) and by Lowe, Wright, and Cole (1966). The karyotype of *Lepidophyma flavimaculatum* was also determined in vitro from lung tissue culture by Dr. T. C. Hsu of the M. D. Anderson Hospital and Tumor Institute of Houston.

Good karyotype preparations were especially difficult to obtain from xantusiid lizards due, in part, to an unusually low level of mitotic activity in the bone marrow. By increasing the stressing of the peripheral circulatory system, mitotic activity was increased; unfortunately, this also increased the mortality among the lizards. The limbs of *Xantusia vigilis* and *Lepidophyma gaigeae* are quite small, and the bone marrow is consequently difficult to "flush out." Pooling of the bone marrow from several individuals was necessary to obtain the somatic karyotype of *L. gaigeae*, while the karyotype of populations of *X. vigilis* was derived primarily from study of testicular tissue.

Whenever possible, a minimum of at least ten cells was studied from each specimen "run." For each cell, the permanent slide number, the cell coordinates, the diploid chromosome number ($2n$), the number of macrochromosomes (macros) and microchromosomes (micros), the occurrence of secondary constrictions, and the numbers and relative sizes of metacentric (M), submetacentric (SM), subtelocentric (ST) and telocentric (T) macro-

chromosomes were recorded. The karyotype of the specimen was then determined on a modal basis.

For the family Xantusiidae the following classification of chromosomes was found to be the most useful and was employed throughout the study: metacentric S/L (= ratio of short to long arm of chromosome), 0.76-1.00; submetacentric S/L, 0.51-0.75; subtelocentric S/L, 0.01-0.50; and telocentric S/L, 0.00. Both pairing and classifying the chromosomes, however, was done "by eye" rather than by actual measurement. In counting chromosome arms (CA), metacentric to subtelocentric macrochromosomes were considered bi-armed, while telocentric macrochromosomes were considered uni-armed. Because I could not consistently distinguish their centromere positions, all microchromosomes were considered uni-armed.

KARYOTYPE DESCRIPTIONS

Xantusia vigilis. Study of 525 cells from 30 individuals (29 ♂, 1 ♀) representing eleven populations (including *X. v. arizonae*, *X. v. extorris*, *X. v. sierrae*, and *X. v. vigilis*) indicates that the 2*n* of this species is 40, with 18 macros and 22 micros (Tables 1 and 2, Fig. 1). The macro pairs were numbered from largest to smallest (Fig. 1); the micro pairs were not numbered as their small size precluded recognition of individual pairs. Pair 1 is by far

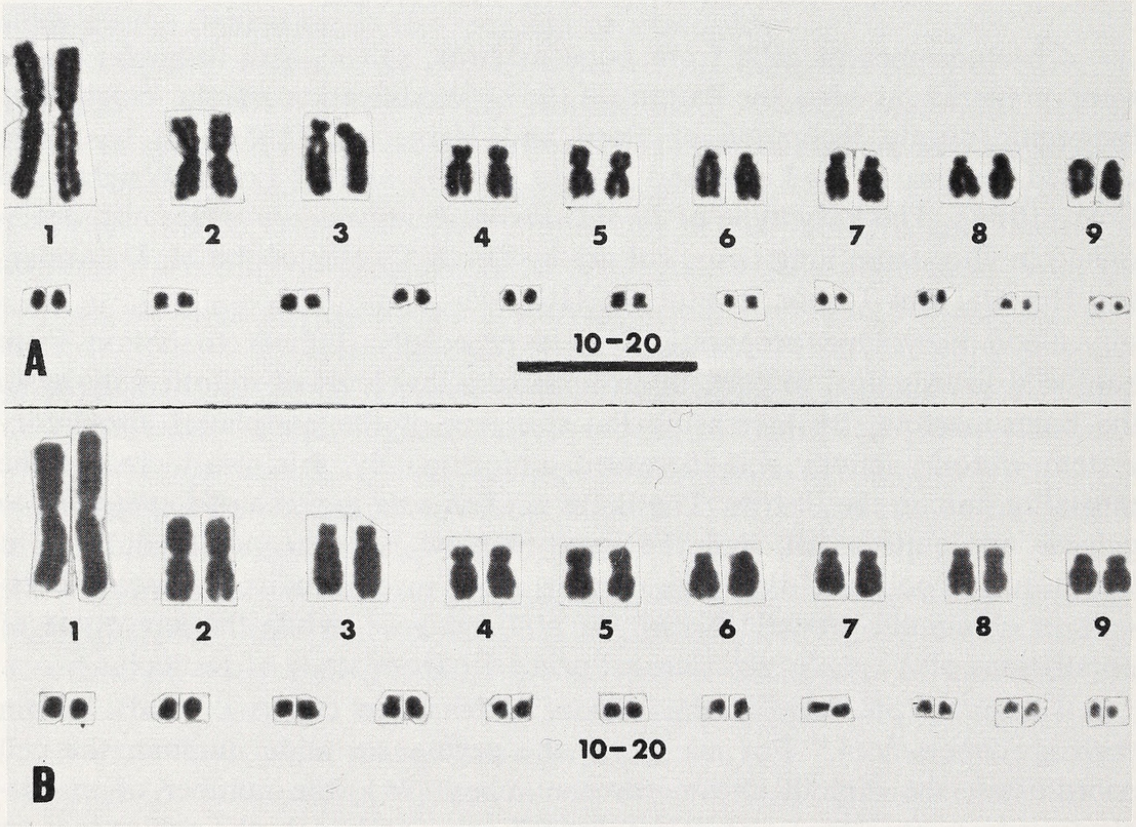

FIGURE 1. Karyotypes of *Xantusia vigilis*. A. Karyotype α; UAZ 24216, ♂, 11.3 mi (by Hwy 93) SE Burro Creek, 3200 ft, Yavapai Co., Arizona. Line represents 10 μ. B. Karyotype β; UAZ 24861, ♂, vic. Yarnell, 4750 ft, Yavapai Co., Arizona.

the largest in the complement and is metacentric to submetacentric. Pair 2 is about half the size of pair 1 and is consistently metacentric. Pair 3 is only very slightly smaller than pair 2 and is consistently subtelocentric. On the basis of size and centromere position these first three pairs are always clearly distinguishable from one another and are distinctly larger than the remaining six pairs. Pairs 4 and 5 are larger and more distinctly bi-armed than the last four pairs (6-9). Pair 4 is subtelocentric and pair 5 is submetacentric. Pairs 6, 7 and 8 are nearly identical in size and are subtelocentric; the largest (6), however, has only minute short-arms and thus occasionally appears telocentric.

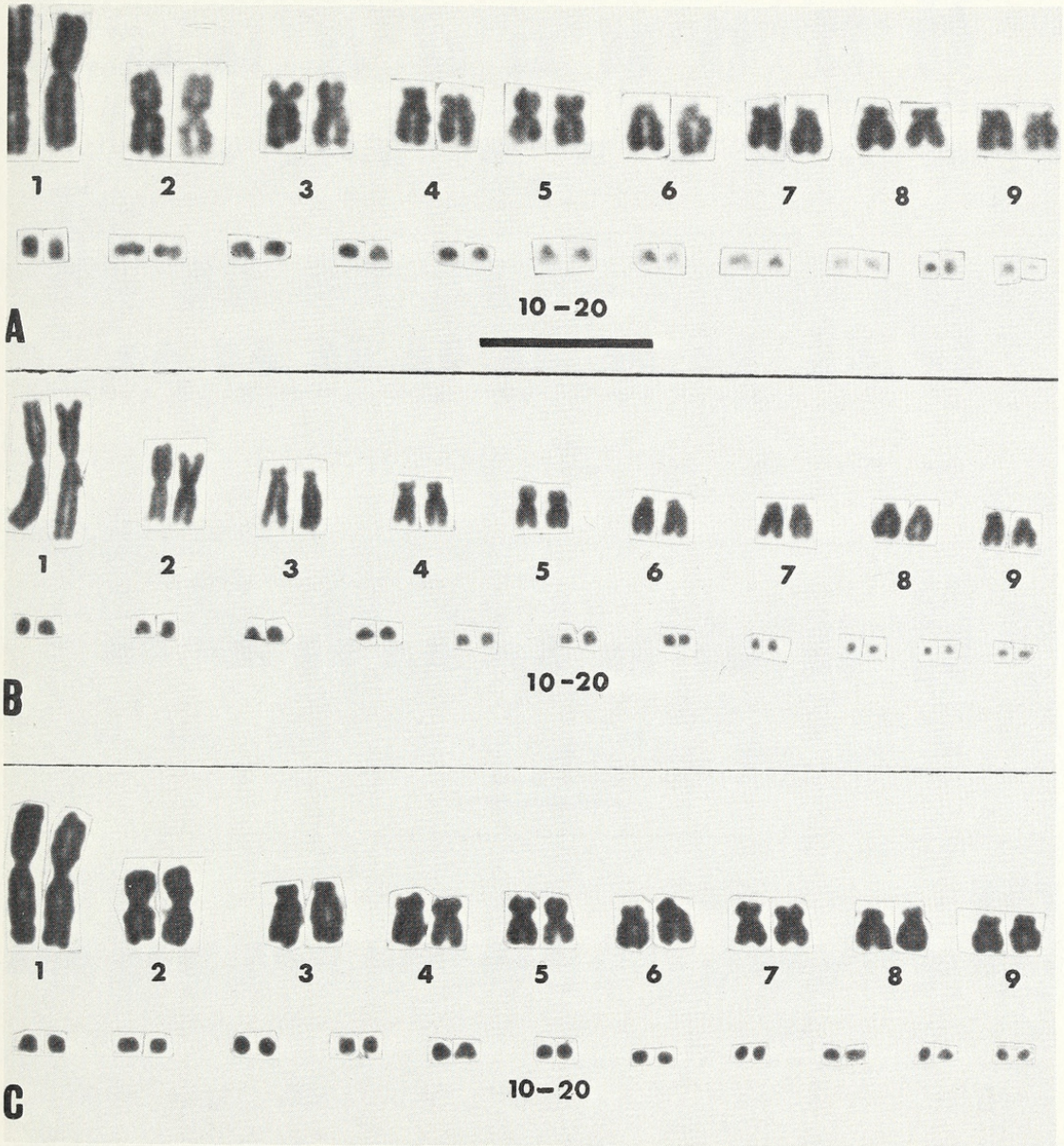

FIGURE 2. Karyotypes of two species of *Xantusia*. A. *X. riversiana*; UAZ 21688, ♀, N end of San Clemente Island, Los Angeles Co., California. Line represents 10 μ. B. *X. henshawi;* karyotype α; LACM 72325, ♀, 6.5 mi NE Pedricena, Durango, Mexico. C. *X. henshawi*; karyotype β; UAZ 21694, ♂, 2 mi (by rd to Idyllwild) S Banning, San Jacinto Mts., Riverside Co., California.

The smallest pair (9) varies among the populations of *Xantusia vigilis* studied. It appears telocentric (karyotype α, Fig. 1) in individuals from eight populations (*X. v. sierrae; X. v. vigilis* from the Mohave and Sonoran Deserts in Arizona, California, and Baja California), and subtelocentric (karyotype β) in three populations (*X. v. arizonae*; *X. v. extorris*; and *X. v. vigilis* from Desemboque, Sonora).

Xantusia henshawi. Study of 117 cells from 8 individuals (6♂, 2♀)

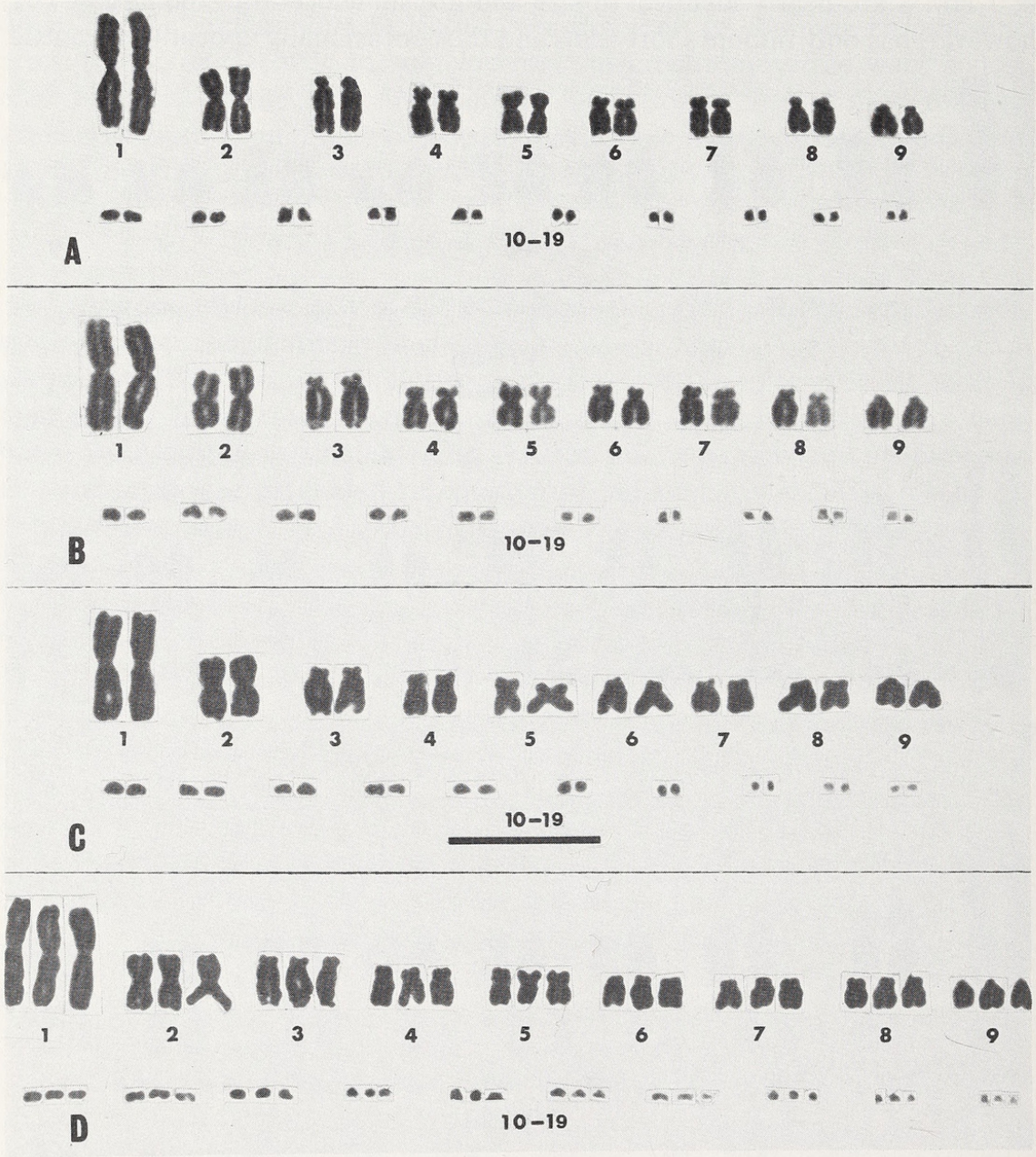

FIGURE 3. Karyotypes of *Lepidophyma flavimaculatum*. A. Bisexual population; UAZ 28805, ♀, 25 mi (by rd to Malpaso) NW Ocozocoautla, Chiapas, Mexico. B. Unisexual population; UAZ 27642, ♀, 3 mi (air line) SE Achiote, Canal Zone, Panama. C. Unisexual population. Diploid cell from UAZ 27640, ♀, same locality as UAZ 27642, above; line represents 10 μ. D. Unisexual population. Triploid cell from UAZ 27640.

from two populations (*X. h. henshawi* and *X. h. bolsonae*) indicates that the 2*n* of this species is 40, with 18 macros and 22 micros (Tables 1 and 2, Fig. 2). The karyotype of *X. h. bolsonae* (= α) appears identical to the β karyotype of *X. vigilis*, while that of *X. h. henshawi* (= β) differs in that pair 7 has longer short-arms and is submetacentric. Matthey (1931) reported that *Xantusia henshawi* has a 2*n* of 42 with 18 macros and 24 micros. Until his count can be verified, I prefer to disregard it.

Xantusia riversiana. Study of 135 cells from 9 individuals (4♂, 5♀) of one population indicates that the 2*n* of this species is 40 with 18 macros and 22 micros (Tables 1 and 2, Fig. 2). The karyotype appears identical to the β karyotype of *X. vigilis.*

Lepidophyma flavimaculation. Study of 276 cells from 10 individuals (0♂, 10♀) representing three populations (bisexual *L. f. flavimaculatum*

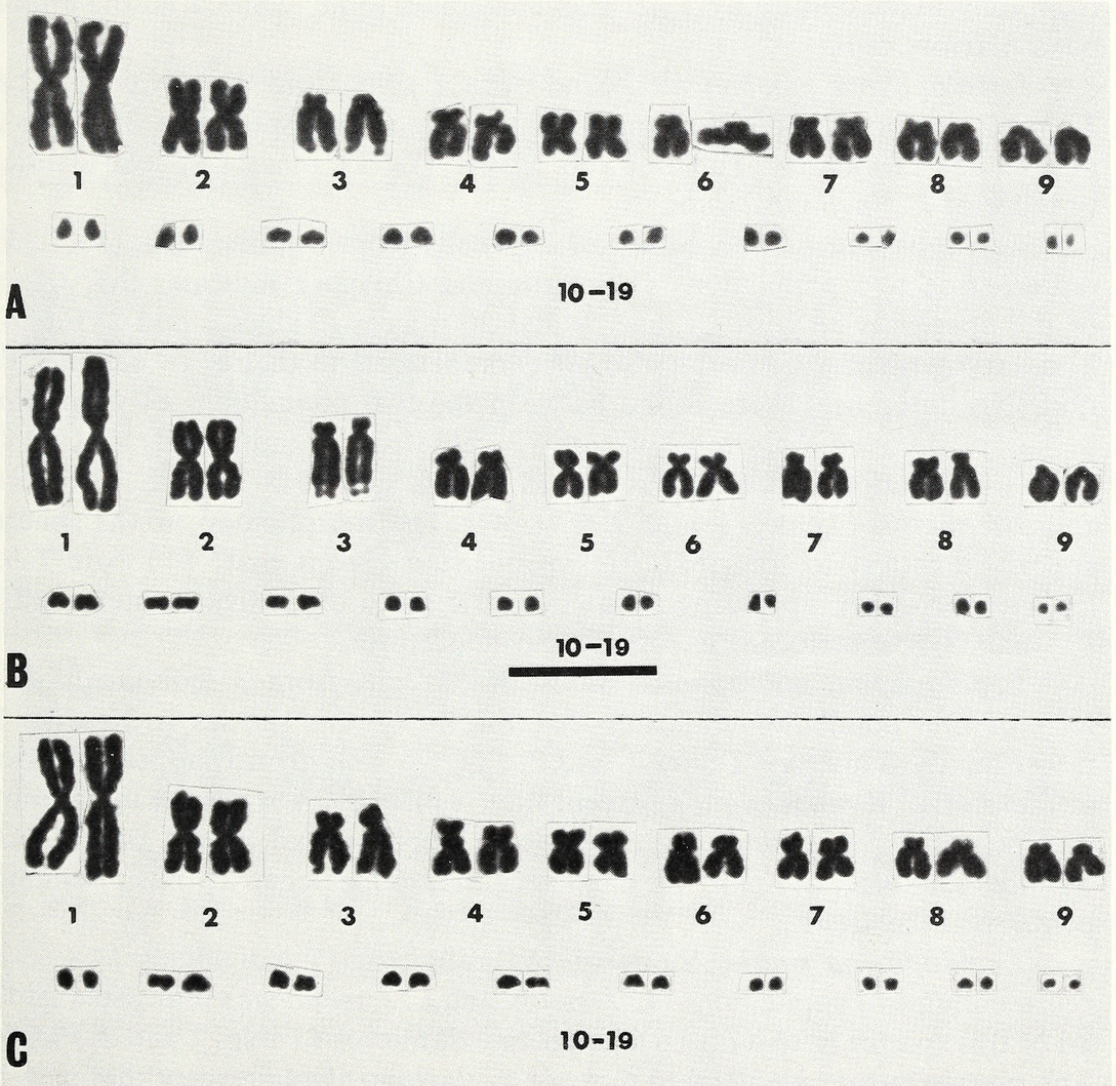

FIGURE 4. Karyotypes of three species of *Lepidophyma.* A. *L. tuxtlae.* UAZ 28770, ♂, 2 mi (by rd) SE Sontecomapan, Veracruz, Mexico. B. *L. pajapanensis.* UAZ 28810, ♂, same locality as *L. tuxtlae,* above. Line represents 10 μ. C. *L. gaigeae.* UAZ 28868-73, ♀, 2 mi N Durango, Hidalgo, Mexico.

from Chiapas and unisexual *L. f. obscurum* from Panama and Costa Rica) indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (rather than 22 as in *Xantusia*; Tables 1 and 2, Fig. 3). The macros in this species appear identical in morphology to those of the α karyotype of *Xantusia vigilis* except that pair 3 bears a distinct terminal satellite. The karyotypes of the unisexual populations appear to be homomorphic and identical to those of the bisexual population. However, bone marrow tissue of one individual from the all-female population in Panama appears to be composed of both diploid ($2n = 38$) and triploid ($3n = 57$) cells (Fig. 3). Eighty-two diploid and 25 triploid cells were examined from one bone marrow preparation, yielding a ratio of 3.28 diploid to 1 triploid. This condition was observed in only one of the 8 individuals studied from this all-female population. The karyotype of another individual from this same population was also determined in vitro from lung tissue culture by T. C. Hsu and found to be identical to the diploid bone marrow cells.

Lepidophyma pajapanensis. Study of 87 cells from 4 individuals (1♂, 3♀) of one population indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (Tables 1 and 2, Fig. 4). The macros appear identical to those of *L. flavimaculatum.*

Lepidophyma tuxtlae. Study of 200 cells from 8 individuals (5♂, 3♀) representing two populations (Veracruz and Chiapas) indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (Tables 1 and 2, Fig. 4). The karyotype of this species also appears identical to that of *L. flavimaculatum.* No differences were found between the two populations of *L. tuxtlae.*

Lepidophyma gaigeae. Study of 77 cells from 4 individuals (2♂, 2♀) of one population indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (Tables 1 and 2, Fig. 4). The morphology of the macros appears identical to that in *L. flavimaculatum* except that: (1) pair 7 has longer short-arms, appearing submetacentric more often than subtelocentric; (2) pair 9 is subtelocentric rather than telocentric.

Lepidophyma micropholis. Study of 83 cells from 3 individuals (2♂, 1♀) of one population indicates that the 2*n* of this species is 36 with 16 macros and 20 micros (Tables 1 and 2, Fig. 5). The macros appear identical to those of *L. flavimaculatum*, except that: (1) pair 2A is a large metacentric that probably was formed by the fusion of pairs 6 and 8; (2) pair 3 lacks terminal satellites; (3) pair 7 is submetacentric to metacentric, thus resembling pair 7 of *L. gaigeae.*

Lepidophyma smithi. Study of 151 cells from 7 individuals (4♂, 3♀) representing two populations (*L. s. smithi* and *L. s. tehuanae*) indicates that the 2*n* of this species is 36 with 16 macros and 20 micros (Tables 1 and 2, Fig. 5). The macros appear identical to those of *L. flavimaculatum* except that pair 2A is a metacentric to submetacentric and probably was formed by centric fusion of pairs 6 and 9; thus only its long-arms are homologous with pair 2A of *L. micropholis.* That chromosome pair 2A is formed by fusion of pairs 6 and 8

in *L. micropholis* and pairs 6 and 9 in *L. smithi* is conjectured from the following: (1) pair 2A appears somewhat more submetacentric in *L. smithi* than in *L. micropholis*; (2) the smallest chromosome pair in *L. micropholis* usually appears slightly smaller than the smallest pair in *L. smithi*, and is telocentric in the former and subtelocentric in the latter. All of these differences could also be explained as resulting from inversions occurring after one centric fusion, except the difference in the size of the smallest chromosome pair. This could be made more concrete by comparing measurements from photomicrographs of the karyotypes of the two species, but the size

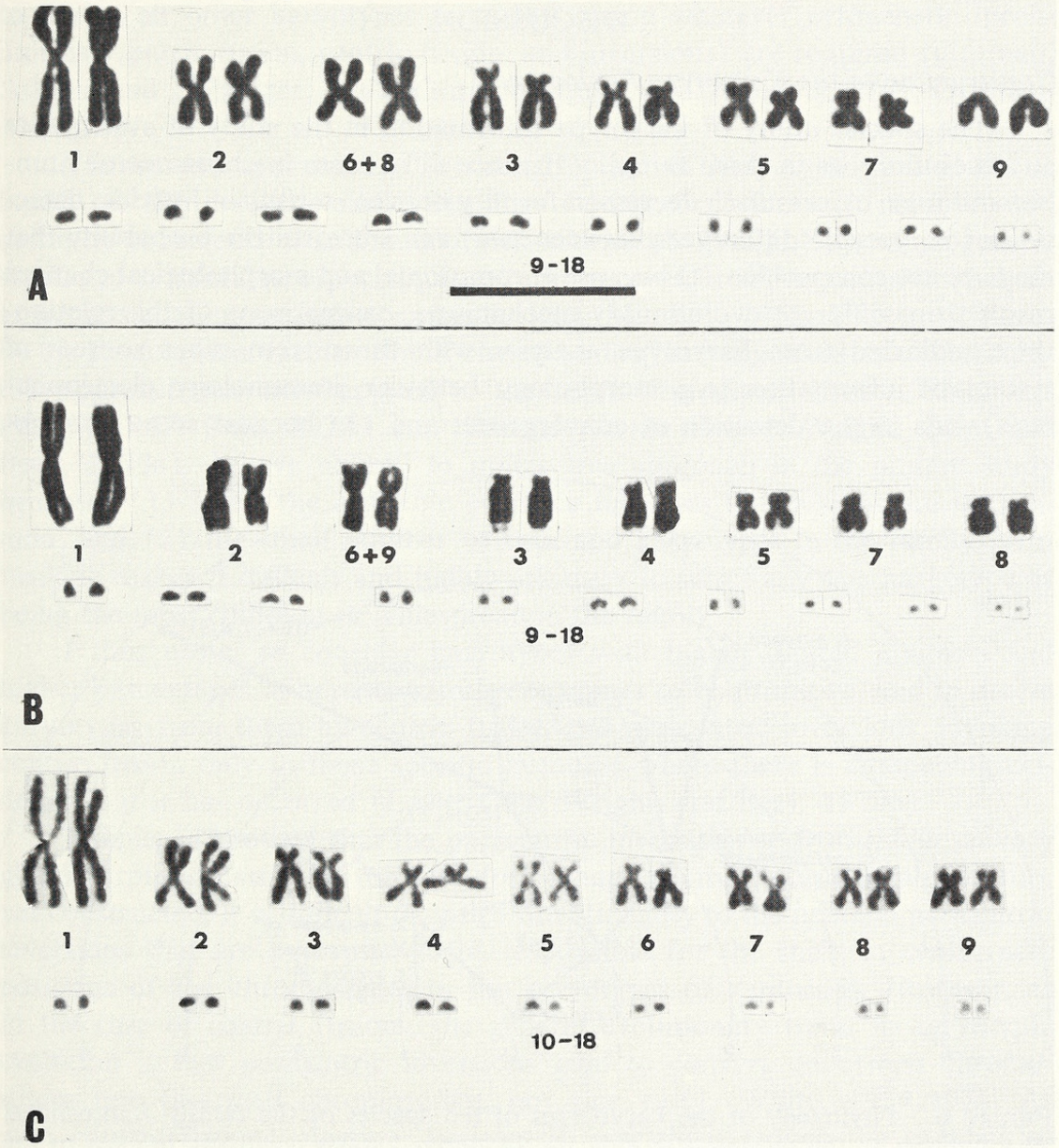

FIGURE 5. Karyotypes of three species of *Lepidophyma*. A. *L. micropholis*. UAZ 28762, ♀, cave at El Pachon, 8 km (by rd) NNE Antigua Morelos, Tamaulipas, Mexico. Line represents 10 μ. B. *L. smithi*. UAZ 28812, ♂, 4 mi NW Mapastepec, Chiapas, Mexico. C. *L. occulor*. TCWC 35605, ♂, 2.5 mi S Conca, 2000 ft, Queretaro, Mexico.

differences involved are so small that truly convincing identification of homologous chromosomes would probably require observation of synapsis in artificially produced hybrids.

Lepidophyma occulor. Study of 101 cells from one male indicates that the $2n$ of this species is 36 with 18 macros and 18 micros (Tables 1 and 2, Fig. 5). The macros are identical to those of *L. flavimaculatum*, except that (1) pair 3 lacks terminal satellites; (2) pairs 7 and 8 are submetacentric instead of subtelocentric; (3) pair 9 is submetacentric instead of telocentric.

DISCUSSION

Construction of the Karyotype Phylogeny:

The special utility of karyotype information in the study of systematics and evolution lies in three things: (1) since differences in chromosome number and form can result in decreased fertility or even sterility of hybrids, detection of karyotypic differences between two taxa increases the probability that they are not conspecific; (2) because chromosomal and morphological changes result from different evolutionary mechanisms, comparisons of the relationships indicated from karyotype analyses with those from other sources of systematic information (e.g. morphology, behavior, immunology, electrophoresis) aids in the detection of convergence; and (3) because some chromo-

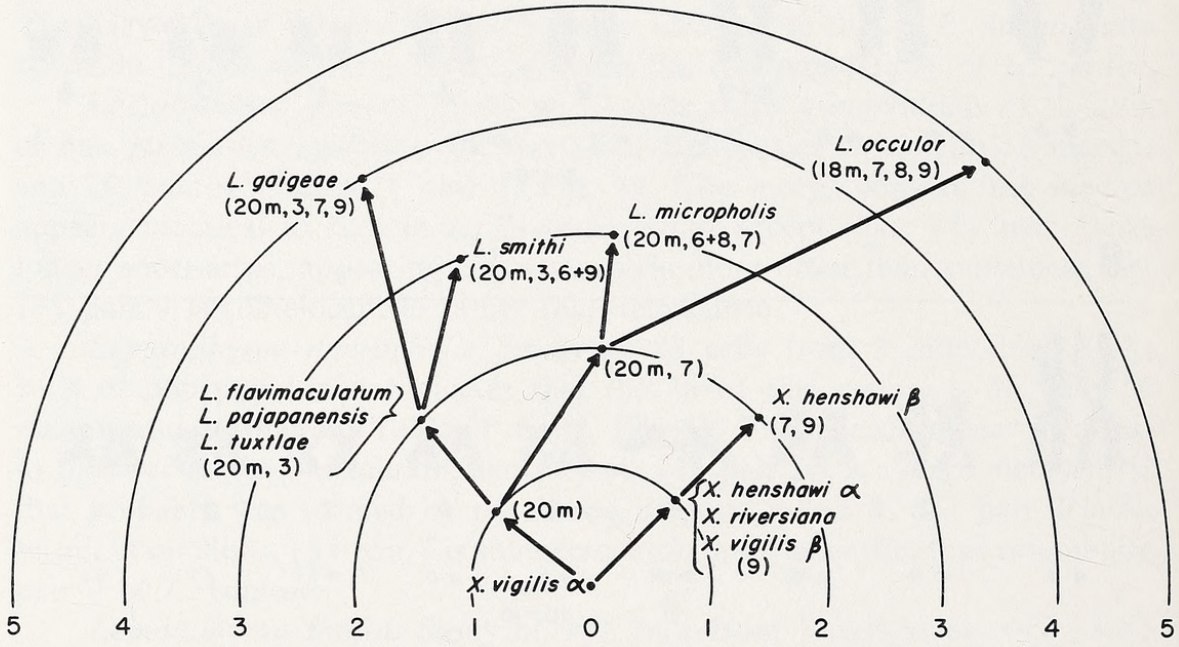

FIGURE 6. Phylogeny of the karyotypes of ten species of the family Xantusiidae. The symbols in the parentheses indicate the derived states occurring in each of the karyotypes: 18m and 20m = reductions in number of micros; 3 = formation of satellites on this pair; 6+8 and 6+9 = centric fusions of macros; 7, 8, 9 = pericentric inversions shifting the position of the centromeres on these macros. The numbers beneath the concentric half circles indicate the total number of derived states in each of the karyotypes. Data from Tables 1 and 2.

somal changes appear to be much more common than others, designation of primitive and derived character states is possible.

Although many cogent criticisms of Hennig's (1966) theory and methods have been presented (Darlington, 1970), he has, if nothing else, re-emphasized the necessity of identifying primitive (plesiomorphic) and advanced (apomorphic) character states before constructing phylogenies. In the formulation of karyotype phylogenies of lizards, two approaches have been taken to estimate the direction of evolution. One approach is to regard as primitive that karyotype which occurs most widely among the families of lizards and to derive all other karyotypes from this, using whatever cytogenetic mechanisms (centric fusion, centric fission, and inversions) are required (Gorman, Atkins, and Holzinger, 1967; Gorman, Huey, and Williams, 1969; Gorman, 1970).

The second approach to the construction of karyotype phylogenies is based on the evidence indicating that centric fusions are of much more common occurrence than fissions (Hsu and Mead, 1969). Earlier cytogenetic studies of vertebrates, especially lizards, have considered centric fusion (whole arm translocation or Robertsonian fusions; Matthey, 1951; White, 1954) to be the predominant mechanism of chromosomal rearrangement. More recently this approach has been applied to the genus *Sceloporus* (Lowe, Cole, and Patton, 1967; Cole, 1970) and *Cnemidophorus* (Lowe, Wright, Cole, and Bezy, 1970a). I have elected to utilize this approach in the present study because: (1) I feel the available evidence indicates that fissions are uncommon, and (2) the small number of taxa and karyotypes in the family Xantusiidae makes it difficult and highly arbitrary to select any one karyotype as being the most common or widespread in the family.

I thus prefer to consider karyotypes with higher diploid numbers and higher percentages of acrocentric chromosomes to be primitive, and to derive karyotypes from these by centric fusion and pericentric inversions, invoking centric fission only in those specific instances where there is compelling evidence that it has occurred (Lowe, Cole, Wright, and Bezy, 1970b).

In spite of the fact that the paracentric inversions of *Drosophila* salivary gland chromosomes form the basis for perhaps the most concrete phylogenies yet constructed, it is difficult to assign directionality to the unequal pericentric inversions that are presumed to be responsible for the shifts in centromere positions of the chromosomes in the karyotypes of xantusiids. However, as in the case of centric fusions, the general evolutionary trend in karyotypic evolution is that pericentric inversions tend to convert uni-armed chromosomes into bi-armed chromosomes, not vice versa (White, 1954:192). As with centric fusions, unequal pericentric inversions reduce the number of acrocentrics and increase the number of subtelocentric to metacentric chromosomes.

Thus, in constructing the karyotype phylogeny (Fig. 6) for each chromosome I have always considered the most nearly acrocentric condition observed

TABLE 1. Variation in the chromosomes of ten species in the family Xantusiidae. Centromere position (M = metacentric, SM = submetacentric, ST = subtelocentric, T = telocentric) and presence of satellites (*) for the macrochromosome pairs. Centromere positions in parentheses are those observed less frequently for the chromosome pair.

Chromosome Pair No.	1	2	2A	3	4	5	6	7	8	9
Xantusia										
vigilis α	M(SM)	M	—	ST	ST	SM	ST(T)	ST	ST	T(ST)
vigilis β	M(SM)	M	—	ST	ST	SM	ST(T)	ST	ST	ST
riversiana	M(SM)	M	—	ST	ST	SM	ST(T)	ST(T)	ST	ST
henshawi α	M(SM)	M	—	ST	ST	SM	ST	ST	ST	ST
henshawi β	M(SM)	M	—	ST	ST	SM	ST	SM(ST)	ST	ST
Lepidophyma										
flavimaculatum	M(SM)	M	—	ST*	ST	SM	ST	ST	ST	T
pajapanensis	M(SM)	M	—	ST*	ST	SM	ST	ST	ST	T
tuxtlae	M(SM)	M	—	ST*	ST	SM	ST	ST	ST	T
gaigeae	M(SM)	M	—	ST*	ST	SM	ST	SM(ST)	ST	ST
micropholis	M(SM)	M	M	ST	ST	SM	–	SM(M)	—	T
smithi	M(SM)	M	M(SM)	ST*	ST	SM	–	ST	ST	—
occulor	M(SM)	M	—	ST	ST	SM	ST	SM(M)	SM	SM

TABLE 2. Summary of karyotypic variation in ten species of the family Xantusiidae. Diploid chromosome number ($2n$); number of macrochromosomes (macros); number of microchromosomes (micros); number of pairs of metacentric (M), submetacentric (SM), subtelocentric (ST), and telocentric (T) macrochromosomes; presence (+) or absence (−) of satellites (Sats) on macrochromosome pair 3; number of chromosome arms (CA); and total derived states (TDS).

	$2n$	Macros	Micros	M	SM	ST	T	Sats	CA	TDS
Xantusia										
vigilis α	40	18	22	2	1	5	1	−	56	0
vigilis β	40	18	22	2	1	6	0	−	58	1
riversiana	40	18	22	2	1	6	0	−	58	1
henshawi α	40	18	22	2	1	6	0	−	58	1
henshawi β	40	18	22	2	2	5	0	−	58	2
Lepidophyma										
flavimaculatum	38	18	20	2	1	5	1	+	54	2
pajapanensis	38	18	20	2	1	5	1	+	54	2
tuxtlae	38	18	20	2	1	5	1	+	54	2
gaigeae	38	18	20	2	2	5	0	+	56	4
micropholis	36	16	20	3	2	2	1	−	50	3
smithi	36	16	20	3	1	4	0	+	52	3
occulor	36	18	18	2	4	3	0	−	54	5

among the various forms to be the primitive condition for that chromosome and have considered fused chromosomes to be a derived condition. From this line of reasoning, primitive karyotypic states in the family are: (1) a $2n$ of 40; (2) 22 micros; (3) 18 macros; (4) pairs 1 and 2, metacentric; (5) pair 5, submetacentric; (6) pairs 3, 4, 6, 7, and 8, subtelocentric; (7) pair 9, telocentric; and (8) no satellites. All of these states are present in the α karyotype of *Xantusia vigilis*.

From this primitive condition, the observed karyotypes can be derived by centric fusions and pericentric inversions using those pathways that would require the minimum number of chromosomal rearrangements and yet produce the minimum amount of karyotypic convergence (Fig. 6). A total of seven pericentric inversions, two fusions of macros, two fusions or losses of micros, and one instance of satellite formation is required to account for the chromosomal evolution observed thus far in the family Xantusiidae; a total of four instances of chromosomal convergence result (chromosomal convergence occurs when a specific derived state of a given chromosome is independently evolved in separate lineages). The phylogeny (Fig. 6) is superimposed on a scale (total derived state or TDS) that is simply the total number of character states in each karyotype that can be considered to be derived.

Species:

Although recognized species were used to some extent as guides for the sampling of populations of xantusiids for chromosomal variation, I have attempted to study as many populations as possible of each of the species.

Two karyotypes (α and β) were observed among the eleven populations of *Xantusia vigilis*. The more primitive karyotype (α) occurred in seven populations of *X. v. vigilis* from the Mohave and Sonoran Deserts of California, Arizona, and extreme northern Baja California (for localities see *Specimens Examined*) and in *X. v. sierrae* from the foothills of the Sierra Nevada in the Central Valley of California. The derived karyotype (β) was found in the three most eastern populations sampled: *X. v. vigilis* from Desemboque, Sonora, Mexico; *X. v. arizonae* from Yarnell near the southern edge of the Colorado Plateau in Arizona; and *X. v. extorris* from Durango, Mexico.

The similarity of the karyotype of *X. v. sierrae* to *X. v. vigilis* rather than to *X. v. arizonae* tends to substantiate the hypothesis (Bezy, 1967a) that the two races specialized for living under granite spalls (*arizonae* and *sierrae*) were derived independently from the widespread yucca-dwelling race (*X. v. vigilis*). The apparent lack of correspondence of chromosomal races with morphological subspecies of *X. vigilis* is interesting, and karyotypic studies of the other subspecies (*gilberti, utahensis, wigginsi*) are planned.

The two populations of *Xantusia henshawi* studied also had karyotypic differences that would appear to involve one pericentric inversion. The more primitive karyotype (α) occurs in *X. h. bolsonae* from Durango, Mexico, while the more advanced karyotype (β) occurs in the morphologically more

specialized *X. h. henshawi* from southern California. Chromosomal differences of this magnitude have been found in a single population of *Sceloporus clarki* (Cole, 1970) and thus may not constitute an effective reproductive barrier.

Two forms that were considered by Walker (1955) to be subspecies of *L. flavimaculatum* have different chromosome numbers: *L. occulor* (2*n* of 36 with 18 macros and 18 micros) and *L. smithi* (2*n* of 36 with 16 macros and 20 micros). The three populations of *L. flavimaculatum* studied have a 2*n* of 38 with 18 macros and 20 micros. Such chromosomal differences rarely occur within species and may constitute genetic isolation mechanisms. Morphological and biographical data that also indicate these are distinct species will be presented in a separate paper on the systematics of the genus *Lepidophyma.*

Genera:

Mayr (1969:92-94) listed several criteria of an "ideal" genus: (1) monophyly; (2) separation from other genera by a morphological gap, the size of which is inversely proportional to the number of included species; (3) reasonable internal homogeneity; and (4) occupation of a distinctive adaptive zone. Application of these criteria to genera of xantusiids is made difficult by several factors. Convergence appears to be unusually common in the family, increasing the difficulty of accessment of monophyly. Because of the small number of xantusiid species, it is difficult to judge what size of a morphological gap should delineate a genus. Due to their secretive habits, little is known of the adaptive zones of xantusiids.

Comparisons of karyotypic phylogenies with those resulting from morphological analyses are quite useful in making decisions about monophyly and convergence, because radically different factors govern morphological and chromosomal evolution. However, for this same reason, caution must be employed in formulating generic classifications based entirely on homogeneity and gaps in chromosomal variation. For example, relying exclusively on the chromosomal data, the 10 species in this study would be partitioned into the following groupings: (1) *X. henshawi, X. riversiana, X. vigilis*; (2) *L. occulor*; (3) *L. micropholis*; (4) *L. flavimaculatum, L. tuxtlae, L. pajapanensis, L. smithi*; and (5) *L. gaigeae.* Although these groupings appear to be monophyletic on both karyological and morphological grounds, they do not entirely correspond to morphological clumps and gaps.

I feel that a more reasonable approach to the taxonomic interpretation of the chromosomal data is to consider the genera that have been proposed on morphological grounds as hypotheses which are, to varying degrees, testable by the chromosomal data.

During the last 50 years, a maximum of 5 Recent genera of xantusiids have been recognized (in parentheses are listed the Recent species that I consider valid): *Lepidophyma* A. Dumeril, 1851 (*flavimaculatum, micropholis, occulor, pajapanensis, smithi, tuxtlae,* species novum); *Xantusia* Baird,

1859 (*henshawi, vigilis*); *Cricosaura* Gundlach and Peters, 1863 (*typica*); *Gaigeia* Smith, 1939 (*dontomasi, gaigeae, radula*); and *Klauberina* Savage, 1957 (*riversiana*). In the most recent review of the genera of the family, Savage (1963) recognized 4 of these 5, placing the species formerly included in *Gaigeia* into the genus *Lepidophyma.*

No chromosomal data are yet available for *Cricosaura typica.* This is especially unfortunate because Savage (1963) considered this species to be morphologically the most distinctive in the family and placed it in a monotypic subfamily, Cricosaurinae, leaving all other species of the xantusiids in the Xantusiinae. The obtaining of chromosomal data for this species will allow further testing and comparisons of both the chromosomal and morphological phylogenetic hypotheses.

Among xantusiids the most primitive number of microchromosomes (22) is found in three of the ten species studied to date: *Xantusia henshawi, X. vigilis,* and *X. riversiana.* The similarity of the karyotypes of the three species of *Xantusia* and the consistently lower number of microchromosomes of the other 7 species xantusiids studied does not support Savage's (1957) partioning of *X. riversiana* into the monotypic genus *Klauberina.* The chromosomal evidence does not, however, unequivocably support the inclusion of *riversiana* in the genus *Xantusia* for two reasons: (1) the microchromosome number present in *X. henshawi, vigilis,* and *riversiana* is a shared *primitive* character state and this increases their phenetic similarity but does not necessarily indicate a close phylogenetic relationship; (2) as was discussed above, homogeneity and gaps in karyotypic variation do not always correspond with those of other data (morphological, ecological, behavioral, etc.). What can be said is simply that the chromosomal data lacks the pattern that Savage (1957) has reported for the morphological data, in that *X. henshawi* and *X. vigilis* do not share any chromosomal state that could be considered derived from a primitive state occurring in *X. riversiana.*

In addition to the pattern present in the chromosomal data, there are several other reasons why I prefer not to recognize the genus *Klauberina.* Genera are predictive hypotheses based on monophyly, similarities, and gaps. Monotypic genera are often the result of classifications in which there has been an overemphasis of differences. One increasingly popular solution to this problem is to use numerical techniques for quantifying species differences and then to compare these differences with standards for the minimum acceptable size of generic gaps. Short of such an analysis, I can argue against the partioning of the genus *Xantusia* only by pointing out the many similarities of the three species (*X. henshawi, riversiana,* and *vigilis*) and their differences from other xantusiids. This has already been done for the chromosomal data. The morphological evidence indicated that *Xantusia riversiana* (= *Klauberina*) is more closely related to *X. vigilis* and *X. henshawi* than any of these three species are to any of the other xantusiid (Savage, 1963). The Eocene Wyoming fossil *Paleoxantusia ferra* has been considered intermediate

between *X. riversiana* (*Klauberina*) on the one hand and *X. vigilis* and *henshawi* on the other (Savage, 1963:34), suggesting that these lines diverged later than did *Lepidophyma*, *Cricosaura*, and *Xantusia*. The distributions of the species of the family suggest that each of the above three genera also occupies a somewhat consistent and distinctive adaptive zone. Species of the genus *Lepidophyma* occur primarily in wet tropical forests; *Cricosaura typica* is isolated in the Cabo Cruz area of Cuba apparently occurring under rocks and decaying leaves in forest (Barbour and Ramsden, 1919:178); while the three species of *Xantusia* have largely allopatric ranges in the arid and semi-arid southwestern U.S. and northwestern Mexico. I am not trying to ignore such distinctive species ecologies as the montane limestone cap-rock habitat of *L. gaigeae* or the less restricted microhabitat enjoyed by *Xantusia riversiana* in its insular isolation, but wish simply to point out the biogeographical consistency of the three Recent genera that I feel should be recognized. Regal (1968) has recently pointed out that the pupils of some members of the genus *Lepidophyma* (perhaps exclusive of *L. gaigeae*) are round while those of other xantusiids are elliptical, an observation originally made by Cope (1900) but apparently overlooked by Savage (1963). This is a morphological observation that has broad ecological and evolutionary implications in that Regal (1968:85-86) presents the viewpoint that in xantusiids the elliptical pupil is a derived condition associated with the evolution of basking behavior. It may, then, be a derived character state shared by *Cricosaura typica*, *Xantusia henshawi*, *X. vigilis*, *X. riversiana*, and perhaps *L. gaigeae*. Further studies of pupil shape and retina structure in xantusiids are needed to determine the direction and degree of convergence in the evolution of eyes in this family.

I feel that the chromosomal, morphological, and biogeographical information summarized above indicates that the evolutionary relationships of the three species of *Xantusia* (*henshawi*, *riversiana*, and *vigilis*) are best reflected by their inclusion in one genus *Xantusia*, with two subgenera, *Xantusia* (*X. henshawi* and *X. vigilis*) and *Klauberina* (*X. riversiana*).

Smith (1939) proposed the monotypic genus *Gaigeia* in which he placed *Lepidophyma gaigeae*. He considered the genus to be intermediate between *Lepidophyma* and *Xantusia* in scale characters, having three of the distinctive character states of each of these genera, plus one unique scale character and a unique habitat. Because he felt that (1) three subsequently described species (*L. dontomasi*, *L. radula*, and *L. sylvaticum*, considered by Smith, 1942, as species of *Gaigeia*) bridged the gap in scalation between the two genera (*Lepidophyma* and *Gaigeia*) and (2) "the two supposed genera are practically identical in their skeletons," Savage (1963:33) placed all these species in *Lepidophyma*, a conclusion that was anticipated by Hecht (1956:2). Although I have karyotypic data for only one (*L. gaigeae*) of the four species that Smith (1942) considered to be in the genus *Gaigeia*, it is perhaps the most distinctive one of this group. The chromosomal information is

more conclusive in this instance than it is in the case of *Xantusia riversiana*, in that *L. gaigeae* shares one definitely derived chromosomal state (loss of one pair of microchromosomes) with all other species of *Lepidophyma* studied. It also shares one character state that is probably derived (the presence of secondary constrictions on chromosome pair 3) with four other species of *Lepidophyma* (*flavimaculatum*, *pajapanensis*, *smithi*, and *tuxtlae*). The karyotype of *L. gaigeae* is one of the most highly derived in the genus *Lepidophyma* (Tables 1 and 2, Fig. 6). Interestingly enough, the karyotype of *L. gaigeae* shares two derived chromosomal states with the β karyotype of *Xantusia henshawi* in that chromosome pair 7 is submetacentric and chromosome pair 9 is subtelocentric. However, the pattern existing in the number of microchromosomes and the occurrence of secondary constrictions on the third pair of chromosomes make the conclusion inescapable that these two derived karyotypic states shared by *Xantusia h. henshawi* and *Lepidophyma gaigeae* must be the result of a certain amount of chromosomal convergence that has accompanied their morphological convergence. In this case I feel that the chromosomal data largely agree with the osteological information (Savage, 1963:33), and that *L. gaigeae* (and thus perhaps the other three species of *Gaigeia* recognized by Smith, 1942) should be included in the genus *Lepidophyma*.

Two species, *L. micropholis* and *L. occulor*, share (1) the loss of at least one pair of micros, a derived state characteristic of other species of *Lepidophyma*; (2) the absence of satellites on pair 3, a primitive state characteristic of the species of the genus *Xantusia*; and (3) submetacentric pair 7, a derived state also present in *X. henshawi* and *L. gaigeae*. Chromosomally *L. occulor* and *L. micropholis* thus appear to form a distinct species group in the genus *Lepidophyma*, a hypothesis which is to be tested by morphological data.

Inter-familial Relationships:

The evolutionary relationships of the Xantusiidae remain obscure. Cope (1900) placed the xantusiids in the suborder Leptoglossa within which he considered them to be most closely allied to the lacertids. Camp (1923) pointed out the similarities of xantusiids to both (1) the gekkonids (of the division Ascalabota) and (2) the scincids, teiids, and especially the lacertids (all of the section Scincomorpha of the division Autarchoglossa). Although the family Xantusiidae bridged the morphological gap between his two major divisions of the Sauria, Camp (1923) placed it in the Autarchoglossa, of which he considered it to be the most primitive family. McDowell and Bogert (1954) anticipated that future workers would refer the Xantusiidae to the Gekkota. Underwood (1957) placed the xantusiids in the Ascalabota; Savage (1963) referred them to the Gekkota. More recent morphological evidence has been presented which ally the family with both Gekkota (St. Girons, 1967) and Scincomorpha (Miller, 1966; Etheridge, 1967).

Available karyotype data for xantusiids, scincids, lacertids, teiids, and gekkonids are summarized in Table 3. Although there is overlap in both chromosome number and number of chromosome arms, gekkonid karyotypes differ from those of xantusiids in (1) usually being composed entirely of telocentric chromosomes; and (2) having a smooth gradation in chromosome size, thus precluding a distinction between marcros and micros. Scincid karyotypes differ in having (1) usually fewer micros, and (2) fewer chromosome arms. Those of lacertids differ in having (1) fewer micros, (2) more macros, and (3) fewer chromosome arms. Teiid karyotypes overlap those of xantusiids in all regards (numbers of chromosomes, macros, micros, and chromosome arms).

Derivation of the primitive xantusiid karyotype from known gekkonid karyotypes would require the fusion of telocentric chromosomes to form longer bi-armed macrochromosomes and the retention of the centromeres (devested of most of their euchromatin) as microchromosomes, thus increasing the number of chromosome arms while chromosome number remains approximately constant. However, because they have many primitive states, the karyotypes of gekkonids could be considered ancestral to those of most families of lizards.

Among the lizard families thought by various workers to be closely related to xantusiids, teiids appear to be karyotypically the most similar. That these two families may be closely related is suggested by: (1) the existence of macroteiids having primitive (unfused) karyotypes with numbers of chromosome arms approximating those of xantusiids; and (2) the complementary geographical distribution and the similarities in macrochromosome configuration, external morphology, and ecology of microteiids and xantusiids. I must stress that I present this simply as a phylogenetic hypothesis that should be tested by further comparisons (anatomical, karyotypic, serological, etc.) between xantusiids and other lizards, especially microteiids.

TABLE 3. Diploid chromosome number ($2n$), numbers chromosome arms (CA), macrochromosomes (Macros), and microchromosomes (Micros), and literature source (Reference) for five families of lizards.

Family	$2n$	CA	Macros	Micros	Reference
Xantusiidae	36-40	50-58	16-18	18-22	This paper
Gekkonidae	32-63	32-63	32-63		Kluge and Eckardt, 1969
Scincidae	24-32	36-46	10-32	0-18	Dutt, 1969
Lacertidae	24-38	38	24-36	0-3	Gorman, 1969
Teiidae	34-56	46-66	12-32	22-26	Gorman, 1970

Origin of Unisexuality in the Genus Lepidophyma:

Telford and Campbell (1970) reported an all-female population of *Lepidophyma flavimaculatum* in the Canal Zone (3 miles SE Achiote, Colon Province) of Panama. To help elucidate the evolutionary origin of unisexual xantusiids, I have studied karyotypes of specimens from this population and have analysed variation in sex ratio in the genus *Lepidophyma.*

As was pointed out above (see *Karyotype Descriptions*) the karyotypes of specimens from this all-female population of *L. flavimaculatum* are, with one exception, diploid and appear identical to those of individuals of this species from a bisexual population in Chiapas. This same karyotype was also found in recently obtained material from a unisexual population of *L. flavimaculatum* in southeastern Costa Rica. Thus, this case of presumed parthenogensis appears generally not to involve polyploidy. The possibility that this population is allodiploid, however, cannot be ruled out by

TABLE 4. Sample size (N), number of males (♂), number of females (♀), and percent females (% ♀) for ten species samples of *Lepidophyma* and 13 populations of *L. flavimaculatum*. Asterisk (*) indicates a sex distribution that is significantly different (.05 level) from that of *L. gaigeae* (see text).

	N	♂	♀	% ♀
dontomasi	1	0	1	100
gaigeae	260	110	150	58
micropholis	10	6	4	40
occulor	6	3	3	50
pajapanensis	13	4	9	69
radula	1	0	1	100
smithi	144	63	81	56
tuxtlae	53	24	29	55
species novum	5	1	4	80
flavimaculatum	174	29	145	83*
Tamaulipas	15	2	13	87
Queretaro	9	0	9	100*
Nuevo Leon	2	1	1	50
San Luis Potosi	1	1	0	0
Veracruz	3	0	3	100
Oaxaca	3	1	2	67
Tobasco	3	1	2	67
Chiapas	12	5	7	58
Guatemala	18	5	13	72
Honduras	17	10	7	41
Nicaragua	5	1	4	80
Costa Rica	49	2	47	96*
Panama	37	0	37	100*

the evidence at hand, since at least two other species, *L. tuxtlae* and *L. pajapanensis*, have karyotypes identical to the one under consideration. Hybridization between any of these species could result in an allodiploid in which the two separate chromosomal complements, although not distinguishable morphologically, are sufficiently different genetically to reduce the efficiency of meiosis and thereby increase the selective advantage of parthenogenetic reproduction.

Both triploid ($3n = 57$) and diploid ($2n = 38$) cells were observed in the karyotype slides from one of the eight individuals that was analysed from the Panama population (see *Karyotype Descriptions* above). It is difficult to hypothesize a reasonable mechanism for the origin of these two levels of ploidy that were observed in this one bone marrow preparation. Although the triploid and diploid cells were found in a bone marrow preparation, some type of mosaic may be involved and the two levels of ploidy may represent different types of leukocytes derived from different embryonic tissue lines. I am not aware of any really comparable phenomena among vertebrates, except perhaps the tissue mosaics involving centric fusions in *Salmo irideus*, reported by Ohno, Stenius, Fiast, and Zenges (1965) and the exparabiotic diploid-triploid leukocyte chimeraras of *Rana pipiens* reported by Volpe and Gebhardt (1966).

To survey the genus *Lepidophyma* for the occurrence of unisexuality, the sex of 666 adult specimens of the 10 recognized species was determined by examination of gonads (Table 4). Because many of the samples are small and most have greater than 50 per cent female, statistical tests were used to determine which samples have significantly different sex ratios. Choice of the appropriate test was somewhat difficult because the per cent female is greater than 50 in 9 of the 10 species. These observed deviations from the 50 per cent female (that would be theoretically expected to occur at birth in a bisexual species) may be due to: (1) chance; (2) alteration of sex ratio by a basic genetic mechanism (*e.g.* meiotic deive); (3) differences in survivorship of the sexes; or (4) differences in the "collectability" of the sexes. Since chi-square analysis ordinarily requires the use of a theoretical value, it does not aid in the task of distinguishing between (1) sex ratio deviations resulting from a basic genetic mechanism and (2) those of non-genetic origin (differential sampling and survivorship). The other available statistical test, the contingency test (Simpson, Roe, and Lewontin, 1960:186-191), requires the selection of one of the samples as a standard with which the other samples are to be compared. Although this procedure has several pitfalls of its own, it does maximize the probability of making correct distinctions between genetic and non-genetic deviations in sex ratio, if it is accepted that the samples and the standard have a similar collecting bias.

The sample of *Lepidophyma gaigeae* was chosen as the standard because it (1) is the largest available species sample; (2) was drawn from a relatively small geographic area (mountains of Queretaro and Hidalgo, Mexico); and

(3) was collected throughout the year. Using a 2x2 contingency test, with Yates' correction where applicable (see Simpson, Roe, Lewontin, 1960:186-191), the number of males and females in each species sample was tested against that of *L. gaigeae*. For only *L. flavimaculatum* was the per cent female found to be statistically different (.05 level) from that of *L. gaigeae*. As this polytypic species ranges from Tamaulipas, Mexico, to Panama, the species sample was divided into 13 geographical samples (based on the states of Mexico and the countries of Central America). When the number of males and females in each of these geographical samples was compared with that in *L. gaigeae*, only Panama (100% female), Costa Rica (96% female), and Queretaro (100% female) were found to be significantly different; Tamaulipas (87% female) almost reached the accepted level of significance (.05). The only other geographical samples large enough to allow reasonable estimates of sex ratio (Chiapas, Guatemala, and Honduras) do not differ significantly from *L. gaigeae*. Twenty of the 29 known males of *L. flavimaculatum* occur among the samples of these apparently bisexual populations. Thus *L. flavimaculatum* appears to be a polytypic species composed of (1) a central diploid bisexual population, *L. f. flavimaculatum*, in Chiapas (58% female), Guatemala (72% female), and Honduras (41% female); (2) a northern all-female or nearly all-female population (of unknown level of ploidy), *L. f. tenebrarum*, in Tamaulipas (87% female) and Queretaro (100% female); and (3) a southern all-female or nearly all-female diploid population, *L. f. obscurum*, in Costa Rica (96% female) and Panama (100% female). Samples are inadequate to determine the sex ratios of the intervening populations with any degree of accuracy.

Analysis of large samples from local populations throughout the extensive range of the polytypic *L. flavimaculatum* is required to determine whether changes in sex ratio and morphology are gradual or abrupt, and to allow an appraisal of the taxonomic status of the included forms. The two known male specimens from Costa Rica are among the northernmost available from that country, suggesting that the occurrence of males in "highly female" populations in Costa Rica might be nothing more than an artifact resulting from the accidental grouping of samples from bisexual and unisexual populations. In Tamaulipas, on the other hand, there is better evidence that males may actually occur in quite low frequency in local populations, since among the 10 adult specimens available from the Gomez Farias region, only one male was found. Comparison of sex ratios in several age classes could help to determine the relative importance of pre- and post-natal mechanisms in altering the sexual composition of the population. Before any of these questions can be addressed, adequate samples must be collected. This task is made both difficult and urgent as the devastation of the lowland tropical forests of Middle America approaches completion.

Unisexuality in the genus *Lepidophyma* appears to be similar to that of the lizards of the *saxicola* group of *Lacerta* in that (a) all forms are diploids

with two identical sets of chromosomes, (b) there are forms intermediate between bisexual and unisexual; (c) the formation of small isolated populations appears to have been an important factor in the evolution of parthenogenesis (Darevsky, 1966). Known unisexual gekkos (Kluge and Eckardt, 1969) and agamids (Hall, 1970) are triploid rather than diploid. In the genus *Cnemidophorus* diploid unisexuality has been reported for *C. neomexicanus* and some *C. tesselatus,* but these, however, have been convincingly demonstrated to be allodiploids resulting from inter-specific hybridization (Lowe and Wright, 1966; Wright and Lowe, 1967), while karyotypic heteromorphism is not apparent in the unisexual *L. flavimaculatum* (Fig. 3). Vanzolini (1970) recently reported an apparently rapid shift from bisexuality to unisexuality in some Amazonian populations of *Cnemidophorus lemniscatus* and suggests that such a shift is probably not the result of inter-specific hybridization. However, Denise Peccinini (1971) reported that although these unisexual populations are diploid, they have one to three pairs of heteromorphic chromosomes and "it is possible, therefore, that the hybridization has been between subspecies of *C. lemniscatus* or even intraspecific polymorphic variants." For *Lepidophyma flavimaculatum* there is, at present, no morphological, cytogenetic, or biogeographical evidence that hybridization preceded the evolution of unisexuality. However, the paucity of the data leaves the question still open and it is certainly not unfeasible that the diploid unisexual population in Panama arose by hybridization between forms that are karyotypically similar but sufficiently different genetically to impair synapsis and thus add selective pressures for the evolution of unisexual reproduction.

During my approximately 10 years of experience with xantusiids, a number of field impressions have been formed about their ecology and probable evolutionary history. Although it is perhaps somewhat premature, I wish to here present those impressions that may help to explain the evolution of unisexuality in the family.

Xantusiids characteristically occur in localized but frequently dense populations. This distributional pattern is dictated by their narrow microenvironmental requirements. The ecological conditions to which the family is adapted were probably more widespread in the early Tertiary. This group of lizards appears to have responded to the increasingly arid continental climates of the middle and late Tertiary by becoming increasingly specialized for, and restricted to, specific limited ecological situations (e.g., under cap rocks of boulders, under bark, beneath yucca-like plants, in caves) in which their unaltered microenvironmental requirements could be met. These stresses have produced a disjunct relictual pattern of distribution. Moreover, the resulting isolated populations are frequently under tremendous pressure for colonization of new areas because of fluctuations in climate, vegetation, and habitat availability.

For example, the narrow ecological requirements of *Xantusia vigilis* result in a disjunct geographical range and in "clumped" distributions within

any given area. These local "clumps" appear to occur in areas having optimal edaphic and microclimatic conditions and relatively large numbers of yuccas or other suitable plants. Because of climatic and vegetational changes, the concurrence of all these conditions is not only a rare condition, but probably also an extremely transitory one.

Field experience with *Lepidophyma flavimaculatum* leads me to believe that these generalizations are particularly valid for this species. The population located by Telford and Campbell near Achiote appears highly localized and rather dense. To date approximately 50 individuals have been collected from this population while only ca. 20 are known from the rest of Panama. My efforts to locate other individuals of this species even short distances from this population were unsuccessful (see also Telford and Campbell, 1970). Optimal conditions of forest canopy, humidity, and soil, as well as the presence of a number of extremely large logs in the proper state of decay appear to be involved; all of these factors may be related to a particular stage in the succession of this nearly mature secondary forest. Judging from the large number of *Lepidophyma* found around them, each of these logs would appear to form a "colony." As forest maturation and log decay continue, the individuals of this population are under considerable selective pressure to establish new colonies, perhaps at great distances, where the soil, humidity, forest canopy, and logs are livable.

These selective pressures would favor the evolution of unisexuality, thereby facilitating colonization by allowing each individual to reproduce in isolation and by doubling the reproductive potential. The occurrence of unisexual populations at the northern and the southern periphery of the range of *L. flavimaculatum* is thus probably indicative of a continuing contraction rather than expansion of its range. This is in marked contrast to the situation in the genus *Cnemidophorus* in which the evolution of unisexuality appears to have resulted from interspecific hybridization and expansion into new habitats (Wright and Lowe, 1968).

SPECIMENS EXAMINED

The following specimens were used in the karyotypic analysis and are deposited in the Herpetological Collection, Department of Biological Sciences, the University of Arizona (UAZ); the Natural History Museum of Los Angeles County (LACM); and the Texas Cooperative Wildlife Collection (TCWC), Texas A & M University.

Lepidophyma flavimaculatum: MEXICO: *Chiapas*: 25 mi (by rd to Malpaso) NW Ocozocoautla (UAZ 28805-06). PANAMA: *Canal Zone*: 3 mi (air line) SE Achiote (8 mi NNW Escobal) (UAZ 27637-42, 27644, 28826). COSTA RICA: *Puntarenas Prov.*: 6 km S San Vito de Java (LACM 72323).

Lepidophyma gaigeae: MEXICO: *Hidalgo*: 2 mi N Durango, 13 mi

(by Hwy 85) S Jacala (UAZ 28868-72); Durango, 15 mi (by Hwy 85) S Jacala (UAZ 28880-84, 28895-905).

Lepidophyma micropholis: MEXICO: *Tamaulipas*: Cave at El Pachon, 8 km (by rd) NNE Antigua Morelos (UAZ 28762, 28767, 28769).

Lepidophyma occulor: MEXICO: *Queretaro*: 2.5 mi S Conca, 2000 ft (TCWC 35605).

Lepidophyma pajapanensis: MEXICO: *Veracruz*: Coyame, 9 mi SE Catemaco (UAZ 28804); 2 mi (by rd) SE Sontecomapan, 14 mi (by rd.) NE Catemaco (UAZ 28808-10).

Lepidophyma smithi: MEXICO: *Chiapas*: ca. ½ mi (by Hwy 200) NW Escuintla (UAZ 28788); 9 mi (by Hwy 200) NW Escuintla (UAZ 28797); 4 mi NW Mapastepec, 24 mi (by Hwy 200) NW Escuintla (UAZ 28812-15); *Oaxaca*: 1½ mi (by Hwy 190) E Tapanatepec (UAZ 28794).

Lepidophyma tuxtlae: MEXICO: *Chiapas*: 25 mi (by rd to Malpaso) NW Ocozocoautla (UAZ 28780, 28782); Veracruz: 2 mi (by rd) SE Sontecomapan, 14 mi (by rd) NE Catemaco (UAZ 28770-76).

Xantusia henshawi: MEXICO: *Durango*: 6.5 mi NE Pedricena (13.7 mi by rd SE Chocolate) (LACM 72324-25). UNITED STATES: *California*: Riverside Co.: 2 mi (by rd to Idyllwild) S Banning, San Jacinto Mts. (UAZ 21653, 21694, 21700); 3 mi (by rd to Idyllwild) S Banning, San Jacinto Mts. (UAZ 21690, 21692).

Xantusia riversiana: UNITED STATES: *California*: Los Angeles Co.: N end of San Clemente Island (UAZ 21679-81, 21683-84, 21686-89).

Xantusia vigilis: MEXICO: *Baja California del Norte*: ca. 14 mi (by rd) E La Trinidad, Valle de La Trinidad (UAZ 28961-62); *Durango*: 6.5 mi NE Pedricena (13.7 mi SW Chocolate) (LACM 72326-331); *Sonora*: 1-2 mi (by rd) S Desemboque del Rio San Ignacio (UAZ 24858, 24860, 24868, 24894). UNITED STATES: *Arizona*: Yavapai Co.: 11.3 mi (by Hwy 93) SE Burro Creek, ca. 3200 ft (UAZ 24210, 24216, 24231); vic. Yarnell, 4750 ft (UAZ 24184, 24196, 24227, 24854, 24861); Yuma Co.: E end of Palm Canyon, Kofa Mts. (UAZ 24215, 24240); *California*: Kern Co.: 0.5 mi (by rd) E Granite Station (LACM 72332-33); 0.9 mi (by Hwy 178) SE of the summit of Walker Pass (LACM 72334); 6 mi W Mojave (LACM 72335); Los Angeles Co.: 1.8 mi (by Hwy 14) N Palmdale (LACM 72336); Riverside Co.: 1 mi S, ¾ mi W Whitewater (LACM 72337-338).

ACKNOWLEDGMENTS

This paper is an expansion and revision of a part of a dissertation submitted to the University of Arizona. During my graduate work, several individuals have been exceptionally generous with their time, ideas, and constructive criticisms. I am particularly grateful to my dissertation advisor, Dr. Charles H. Lowe, for imparting an ecophysioevolutionary perspective to my interest in reptiles and amphibians; to Dr. C. Jay Cole, for his patience in

helping me to find my way out of corn fields and in tutoring me in all aspects of cytotaxonomy including the art of making a pastie; to Dr. James L. Patton for discussing ideas and principles of cytogenetics; to Dr. Philip J. Regal for discussing with me his thoughts on the ecology and evolution of spectacled lizards; and to Dr. David S. Hinds for sparing me from the tragedy of the "double-nested do-loop." Dr. John Wright has helped greatly with the difficult task of revising and preparing the paper for publication, by offering encouragement, advice, and constructive criticism.

Xantusiid lizards are collected with crowbars and hard work; I am indebted to many blister-handed field friends: Kathryn Bolles, Eldon Braun, Duke Campbell, Jay Cole, Steven Goldberg, Charles Lowe, Roy McDiarmid, Philip Regal, Michael Robinson, Wade Sherbrooke, Sam Telford, David Whistler, and John, Brian, and Keith Wright. I am especially grateful to James Dixon for making available a live specimen of the rare *Lepidophyma occulor* for chromosomal analysis.

I express my thanks also to those who have read and criticized this manuscript: Drs. L. A. Carruth, L. A. Crowder, H. K. Gloyd, W. B. Heed, C. H. Lowe, J. L. Patton, F. G. Werner, and J. W. Wright. The skillful editorial efforts of Dr. Gloyd are especially appreciated.

The following persons permitted me to examine specimens under their care: Dr. James R. Dixon, Texas Cooperative Wildlife Collection, Texas A & M University; Dr. Charles L. Douglas, Texas Natural History Collection, University of Texas; Dr. William E. Duellman, University of Kansas Museum of Natural History; Dr. Donald F. Hoffmeister, University of Illinois Museum of Natural History; Dr. Charles H. Lowe, University of Arizona; Dr. James A. Peters, United States National Museum; Dr. William F. Pyburn, University of Texas, Arlington; Dr. Douglas H. Rossman, Louisana State University Museum of Zoology; Dr. Jay M. Savage, University of Southern California; Dr. Sam R. Telford, Florida State Museum; Dr. Charles F. Walker, University of Michigan Museum of Zoology; Dr. Richard G. Zweifel, American Museum of Natural History.

Dr. T. C. Hsu of the M. D. Anderson Hospital and Tumor Institute of Houston generously determined the karyotype of an individual of *Lepidophyma flavimaculatum* by lung tissue culture.

The Computer Center of the University of Arizona facilitated the data reduction.

This study was partially supported by a NASA traineeship at the University of Arizona.

LITERATURE CITED

BARBOUR, T., AND C. T. RAMSDEN. 1919. The herpetology of Cuba. Mem. Mus. Comp. Zool. 47(2): 77-166.

BEZY, R. L. 1967a. A new night lizard *(Xantusia vigilis sierrae)* from the southern Sierra Nevada in California. J. Ariz. Acad. Sci. 4:163-167.

_____. 1967b. Variation, distribution, and taxonomic status of the Arizona night lizard *(Xantusia arizonae)*. Copeia 1967:653-661.

CAMP, C. L. 1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist. 48: 289-481.

COLE, C. J. 1970. Karyotypes and evolution of the *spinosus* group of lizards in the genus *Sceloporus*. Amer. Mus. Nov. 2431:1-47.

COPE, 1895. The genera of Xantusiidae. Amer. Nat. 29:757-758.

COPE, E. D. 1900. The crocodilians, lizards, and snakes of North America. Ann. Rep. U. S. Nat. Mus. for 1898, part II:151-1294.

DAREVSKY, I. S. 1966. Natural parthenogenesis in a polymorphic group of Caucasian rock lizards related to *Lacerta saxicola* Eversmann. J. Ohio Herp. Soc. 5:115-152.

DARLINGTON, P. S. 1970. A practical criticism of Hennig-Brundin "Phylogenetic Systematics" and Antarctic biogeography. Syst. Zool. 19:1-18.

DUTT, K. 1969. Study of chromosomes in two species of Indian lizards. Microscope 17:213-218.

ETHERIDGE, R. 1967. Lizard caudal vertebrae. Copeia 1967:699-721.

FORD, C. E., AND J. L. HAMERTON. 1956. A colchicine, hypotonic citrate, squash sequence for mammalian chromosomes. Stain Tech. 31:247-254.

GORMAN, G. C. 1969. New chromosome data for 12 species of lacertid lizards. J. Herpetol. 3:49-54.

_____. 1970. Chromosomes and the systematics of the family Teiidae (Sauria, Reptilia). Copeia 1970:230-245.

GORMAN, G. C., L. ATKINS, AND T. HOLZINGER. 1967. New karyotypic data on 15 genera of lizards in the family Iguanidae, with a discussion of taxonomic and cytological implications. Cytogenetics 6:286-299.

GORMAN, G. C., R. B. HUEY, AND E. E. WILLIAMS. 1969. Cytotaxonomic studies on some unusual iguanid lizards assigned to the gerera *Chamaeleolis, Polychrus,* and *Phenacosaurus,* with behavioral notes. Breviora 316:1-17.

HALL, W. P. III. 1970. Three probable cases of parthenogenesis in lizards (Agamidae, Chamaeleontidae, Gekkonidae). Experientia 26:1271-73.

HECHT, M. K. 1956. A new xantusiid lizard from the Eocene of Wyoming. Amer. Mus. Nov. 1774:1-8.

HENNIG, W. 1966 Phylogenetic systematics. Univ. Ill. Press, Urbana.

HSU, T. C., AND R. A. MEAD. 1969. Mechanisms of chromosomal changes in mammalian speciation, p. 8-17. *In* Comparative Mammalian Cytogenetics (Kurt Benirschke, ed.). Springer-Verlag, N. Y.

KLAUBER, L. M. 1931. A new species of *Xantusia* from Arizona, with a synopsis of the genus. Trans. San Diego Soc. Nat. Hist. 7:1-16.

KLUGE, A. G., AND M. J. ECKARDT. 1969. *Hemidactylus garnoti* Dumeril and Bibron, a triploid all-female species of gekkonid lizard. Copeia 1969:651-664.

LOWE, C. H., AND J. W. WRIGHT. 1966. Evolution of parthenogenetic species of *Cnemidophorus* (whiptail lizards) in western North America. J. Ariz. Acad. Sci. 4:81-87.

LOWE, C. H., C. J. COLE, AND J. L. PATTON. 1967. Karyotype evolution and speciation in lizards (genus *Sceloporus*) during evolution of the North American Desert. Syst. Zool. 16:296-300.

LOWE, C. H., J. W. WRIGHT, AND C. J. COLE. 1966. Chromosomes and karyotypes of sceloporine iguanid lizards in the North American Southwest. Mamm. Chrom. Newsletter 22:201-203.

LOWE, C. H., J. W. WRIGHT, C. J. COLE, AND R. L. BEZY. 1970a. Chromosomes and evolution of the species groups of *Cnemidophorus* (Reptilia: Teiidae). Syst. Zool. 19:128-141.

———. 1970b. Natural hybridization between the teiid lizards *Cnemidophorus sonorae* (parthenogenetic) and *Cnemidophorus tigris* (bisexual). Syst. Zool. 19:114-127.

MATTHEY, R. 1931. Chromosomes de Reptiles Sauriens, Ophidiens et Cheloniens. L'evolution de la formule chromosomiale chez les Sauriens. Revue Suisse de Zoologie 38:117-184.

MATTHEY, R. 1951. The chromosomes of the vertebrates. Adv. Genet. 4:159-180.

MAYR, E. 1969. Principles of systematic zoology. McGraw-Hill, New York.

MCDOWELL, S. M., AND C. M. BOGERT. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Amer. Mus. Nat. Hist. 105:1-142.

MILLER, M. R. 1966. The cochlear duct of lizards. Proc. Calif. Acad. Sci. 23: 255-359.

OHNO, S., C. STENIUS, E. FAISST, AND M. T. ZENZES. 1965. Post-zygotic chromosomal rearrangements in rainbow trout (*Salmo irideus* Gibbons). Cytogenetics 4:117-129.

PATTON, J. L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). J. Mamm. 48:27-37.

PECCININI, D. 1971. Chromosome variation in populations of *Cnemidophorus lemniscatus* in the Amazon valley. Ciencia e Cultura 23(2):133-136.

REGAL, P. J. 1968. An analysis of heat-seeking in a lizard. Ph.D. dissertation, UCLA.

ST. GIRONS, H. 1967. Morphologie comparee de l'hypophyse chez les Squamata: Donnees complementaires et apport a la phylogenie des reptiles. Ann. des Sci. Nat. Zool. (Paris) 12:229-308.

SAVAGE, J. M. 1957. Studies on the lizard family Xantusiidae. III. A new genus for *Xantusia riversiana* Cope, 1883. Zoologica 42:83-86.

———. 1963. Studies of the lizard family Xantusiidae IV. The genera. Los Angeles Co. Mus., Contrib. Sci. 71:1-38.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative Zoology. Harcourt, Brace, New York.

SMITH, H. M. 1939. Notes on Mexican reptiles and amphibians. Zool. Ser., Field Mus. Nat. Hist. 24:15-35.

SMITH, H. M. 1942. Mexican herpetological misellany. Proc. U. S. Nat. Mus. 92: 349-395.