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PHYLOGENY AND BIOGEOGRAPHY OF THE LIZARD FAMILY XANTUSIIDAE

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Abstract.—The intergeneric relationships of the lizard family Xantusiidae were reevaluated against a cladistic synthesis of morphological (squamation and osteology) and karyological data. The two data sets were analyzed independently and examined for congruent patterns with each other and against biogeographic-geologic data. Patterns indicated by morphological, karyological, and biogeographic-geologic data suggest two sister groups: (1) *Klauberina-Xantusia*; and (2) *Cricosaura-Lepidophyma*. Our phylogeny differs from the accepted view of xantusiid relationships in suggesting that *Lepidophyma* should be transferred from the subfamily Xantusiinae (currently consisting of *Klauberina, Lepidophyma,* and *Xantusia*) to the Cricosaurinae. We propose a vicariance model for the distribution of the *Xantusia-Klauberina* clade. [Xantusiidae; morphology; karyology; biogeography; cladistic synthesis.]

The lizard family Xantusiidae includes four extant genera currently divided into two subfamilies (Savage, 1963): (1) Xantusiinae which includes *Klauberina* (1 species, Channel Islands off southern California), *Xantusia* (3 species, southwestern United States, Baja California, northern Sonora, and Durango, Mexico), and *Lepidophyma* (18 species, southern Mexico and Central America); and (2) Cricosaurinae, consisting of the monotypic genus *Cricosaura* (known only from Cabo Cruz, Granma Province, Cuba).

In this paper we reevaluate intergeneric relationships of the Xantusiidae based on a cladistic analysis of previously published morphological (Savage, 1955, 1963) and karyologic (Bezy, 1972) data. This reassessment was undertaken for three reasons: (1) the currently accepted hypotheses are based on phenetics (i.e., those of Savage [1963] and Schatzinger [1980]); (2) Savage's (1955) phylogenetic hypothesis is limited in scope; (3) Bezy's (1972) karyologic work covered only three of the relevant taxa.

Hypotheses of phylogenetic relationships within the family have been proposed by Savage (1955, 1963), Bezy (1972), and Schatzinger (1980). Savage (1955, 1963) used osteological and morphological data to suggest two phylogenies—one based on a phenetic analysis and the other on a phylogenetic analysis (Fig. 1). Our interpretation of the phenetic results suggests a *Xantusia-Klauberina* cluster united to *Lepidophyma*, with *Cricosaura* distantly related. In contrast, our interpretation of the phylogenetic results suggest *Klauberina* was the distantly related taxon to a cluster of the sister group *Cricosaura-Lepidophyma* and *Xantusia*.

Bezy (1972), using karyotypes, concluded that *Xantusia* and *Klauberina* were sister taxa, and *Lepidophyma* was related to this cluster. *Cricosaura* was unavailable and its karyotype remains unknown. Schatzinger (1980), in a study concerning the xantusiid fossil forms, published a "diagrammatic representation of xantusiid intrafamilial relationships" based on Savage's (1963) classification (Fig. 1A).

Phenetic hypotheses are based on overall similarity of characters among taxa, where specifying similarities as being apomorphic, plesiomorphic or homoplasious is not deemed important in determining relationships. Thus, no clear in-

A

XANTUSIA KLAUBERINA LEPIDOPHYMA CRICOSAURA

B

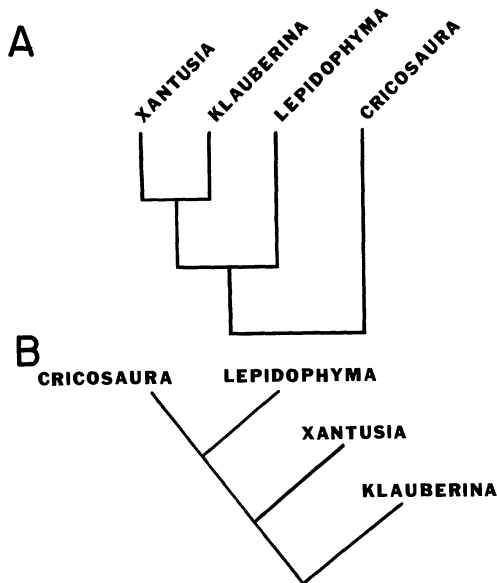CRICOSAURA LEPIDOPHYMA

XANTUSIA

KLAUBERINA

FIG. 1. Previously proposed xantusiid phylogenies not directly incorporated into this study. (A) Schatzinger (1980) phenogram interpreted from Savage (1963). (B) Interpretation of Savage's (1955) phylogenetic hypothesis.

TABLE 1. Basic character matrix of morphological data (characters and states defined in Appendix). Unresolved characters in the outgroup are represented by a 9.

Character	Outgroup	Crico-saura	Klauber-ina	Lepido-phyma	Xantusia
1	0	1	0	0	0
2	9	0	1	2	0
3	0	1	0	1	0
4	0	1	0	0	0
5	0	1	0	1	1
6	0	0	1	1	0
7	0	1	0	0	0
8	0	1	0	0	0
9	9	0	0	1	·0
10	0	1	0	0	0
11	0	0	1	0	1
12	0	2	1	0	2
13	9	0	1	0	1
14	0	0	1	1	1
15	9	0	0	1	0
16	0	1	0	1	0
17	0	1	0	0	0
18	0	1	0	0	0
19	0	0	0	1	0
20	0	0	0	1	0
21	9	0	1	0	0
22	9	1	1	0	1
23	9	1	0	0	0
24	9	0	1	1	1
25	9	0	1	1	1
26	0	0	0	2	1
27	9	0	2	1	0
28	0	2	1	1	0
29	9	2	0	2	1
30	9	0	1	1	1

formation of biological history is present in a phenogram. Therefore, the phenetic results of Savage (1955) are relevant to this study only because they are the currently accepted notion of xantusiid generic relationships and form the basis for the Linnean classification. Savage's (1955) suggested phylogeny resulted from a para-cladistic analysis and is limited in that only characters for which polarities could be determined were used, so characters potentially useful in the analysis were omitted. Bezy (1972) employed a better-developed cladistic methodology and was, therefore, able to construct a robust, if incomplete, cladistic phylogeny using karyotypes.

We reanalyzed Savage's (1955, 1963) morphological data set, including the characters previously omitted because their polarities could not be established, and compared the results to Bezy's (1972) cladistic hypothesis based on karyotypes. Thus, we test both of Savage's (1955, 1963) hypotheses, in addition to the one by Schatzinger (1980), and compare the phe-netic classification currently in use to the cladistic one summarizing all available data. In addition, biogeographic patterns of other taxa and geologic information are used to corroborate the cladistic synthesis.

MATERIALS AND METHODS

Thirty characters of squamation ($n = 10$) and osteology ($n = 20$) were obtained for the four xantusiid genera from Savage (1955, 1963) (see Appendix). These characters were considered useful for determining relationships at the generic level because little intrageneric variation occurs (Savage, 1955, 1963). Character states were arranged into morphoclines following Savage's (1955) transformation series (Mickevich, 1982). Outgroup comparisons with other lizard groups (Smith, 1946;

Savage, 1955; Romer, 1956; Jollie, 1960) were performed on a character-by-character basis (Kluge and Farris, 1969; Kluge, 1976). Character states deduced from these outgroup comparisons were assigned to a hypothetical taxon (see Table 1) included in the phylogenetic analysis for rooting purposes (Farris, 1972, 1982a; Lundberg, 1972). Values of 9 were assigned in the hypothetical taxon to those characters which could not be resolved by outgroup comparison due to extensive variation in the latter. The inability to resolve all characters of the hypothetical taxon does not limit its use as an outgroup, as long as it shares sufficient similarities with the study group to define a single rooting point (Miyamoto, 1983).

The small number of taxa ($n = 4$) allowed us to test all possible dichotomous cladograms ($n = 15$) for their fit to the available data (Felsenstein, 1979). Polychotomous cladograms were not individually assessed because by testing the dichotomous patterns, the polychotomous patterns are also inevitably tested (i.e., polychotomies are merely unresolved dichotomies). Each cladogram was individually optimized to the morphological data by Farris (1970) optimization using the diagnose procedure of the PHYSYS computer package (Farris, 1982b). Cladograms with the set of shortest overall-interval lengths (fewest steps) and greatest consistency (highest consistency-index value) were retained as the most-parsimonious cladograms (Farris, 1983; Miyamoto, 1984).

The karyologic data were originally presented as a Wagner ground-plan diagram drawn at the species level (Bezy, 1972). Because the present study is concerned with generic relationships, the diagram was collapsed and interpreted at the generic level. The reduced Wagner diagram was compared to the morphologic cladograms independently, as opposed to combining the karyologic with the morphologic data.

RESULTS AND DISCUSSION

The analysis resulted in tree lengths ranging from 45 to 49 steps, having consistency indices of 0.80 to 0.73, respectively (Fig. 2). Because the shortest tree length and highest consistency index indicate the most-parsimonious fit of the data (Kluge and Farris, 1969), trees with these characteristics represent the most-parsimonious hypotheses of xantusiid relationships. In this case, the high consistency indices may be accounted for by many ($n = 12$) autapomorphic characters. Regardless of the effect on the consistency index, the characters were included because our goal was to include all available data. We found three equally-parsimonious hypotheses (Fig. 2A, B, C): one hypothesis (2A) supports the two clusters *Cricosaura-Lepidophyma*, and *Xantusia-Klauberina*; a second (2B) supports a *Cricosaura-Lepidophyma* cluster united to *Xantusia*, with *Klauberina* as the most distantly related taxon; and the third (2C) is similar to the latter, except that the positions of *Xantusia* and *Klauberina* are reversed. Savage's (1955) phylogenetic hypothesis is identical to the second of the most-parsimonious hypotheses (Fig. 2B), but Savage's (1963) and Schatzinger's (1980) phenetic trees are identical to a tree one step longer (Fig. 2G). More significant, however, is that all three of the most-parsimonious cladograms show a *Cricosaura-Lepidophyma* sister-group relationship, thereby negating the phenetic hypotheses.

Bezy's (1972) cladogram collapsed to the generic level suggests a *Xantusia-Klauberina* cluster with *Lepidophyma* as the distantly related taxon among the three. The absence of *Cricosaura* does not lessen the usefulness of the cladogram, because congruence can be established from trees with missing data (Rosen, 1978; Miyamoto, 1981). The cladogram based on the karyologic data is congruent with only one of the three most-parsimonious cladograms supported by the morphological evidence (Fig. 3).

This hypothesis recognizes two monophyletic groups: (1) *Cricosaura-Lepidophyma*; and (2) *Xantusia-Klauberina* (Fig. 4). The *Cricosaura-Lepidophyma* cluster is supported by three synapomorphies (heterogeneous caudal scale size, eight rows of ventrals, and absence of a parietal foramen),
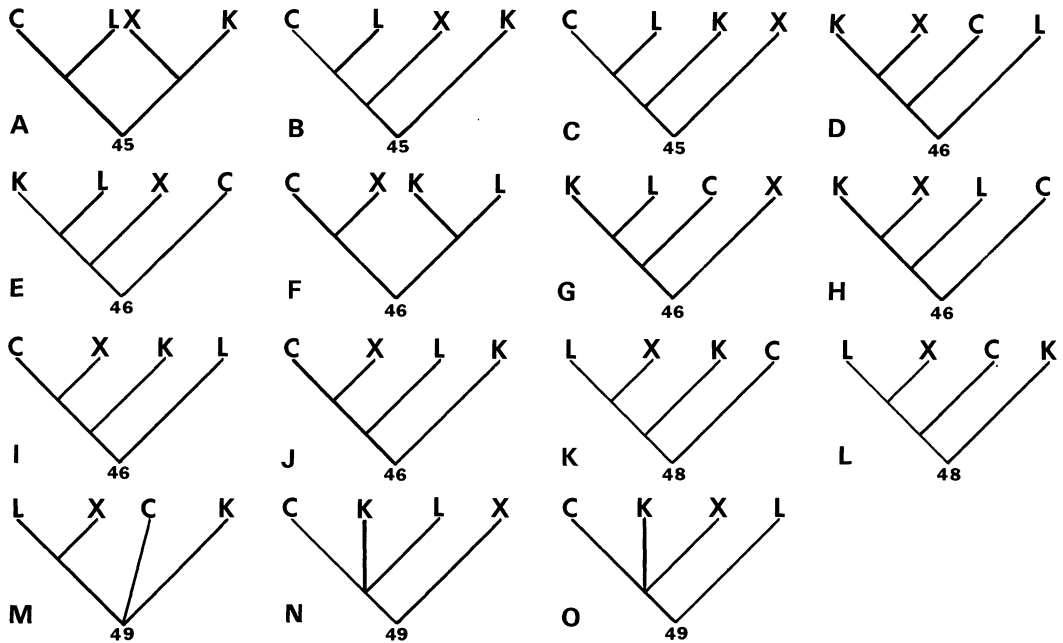
FIG. 2. All possible dichotomous cladograms fitted by optimization analysis to the character data of Table 1. Cladograms are rooted by outside reference to the hypothetical taxon (not shown). Tree lengths, which were from 45 to 49, are presented below each tree. Consistencies for trees are: 0.80, 0.78, 0.75, and 0.73 from the shortest tree to the longest trees, respectively. Abbreviations used: (C) *Cricosaura*, (K) *Klauberina*, (L) *Lepidophyma*, (X) *Xantusia*.
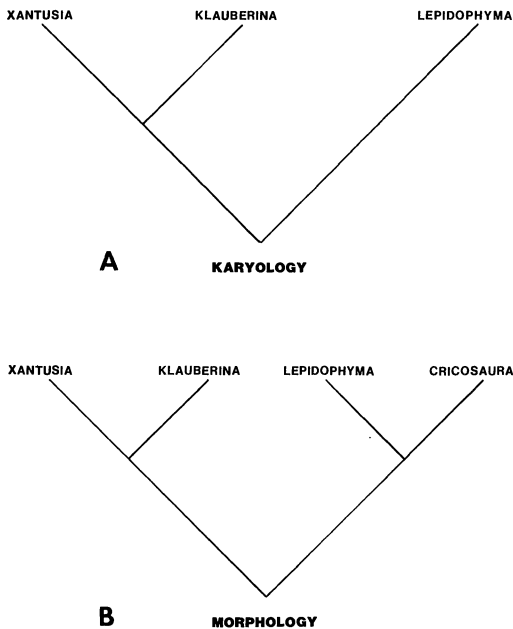

FIG. 3. (A) Bezy's (1972) hypothesis interpreted at the generic level. (B) The most-parsimonious cladogram based on morphology which is congruent with the karyologic tree of A.

whereas the *Xantusia-Klauberina* cluster is diagnosed by two synapomorphies (gulars larger than pregulars; and nasal opening at nasal, postnasal, rostral, and first supralabial junction). The latter synapomorphy of *Xantusia-Klauberina* and the ventrals synapomorphy for *Cricosaura-Lepidophyma* represent ambiguous assignments of the character states to the hypothetical taxonomic units due to missing data in the outgroup (HTUs; Farris, 1982b; D. L. Swofford and W. P. Maddison, pers. comm.). The existence of equally-parsimonious alternatives for this character is related to the missing data in the hypothetical outgroup (Fig. 5).

The major discordance between the phylogeny based on this study and the currently accepted hypothesis about the relationships is the sister-group status of *Lepidophyma* and *Cricosaura*. This relationship is present in all the most-parsimonious cladograms, and is further supported by biogeographic information. The distribution of *Lepidophyma-Cricosaura* (Fig. 6)
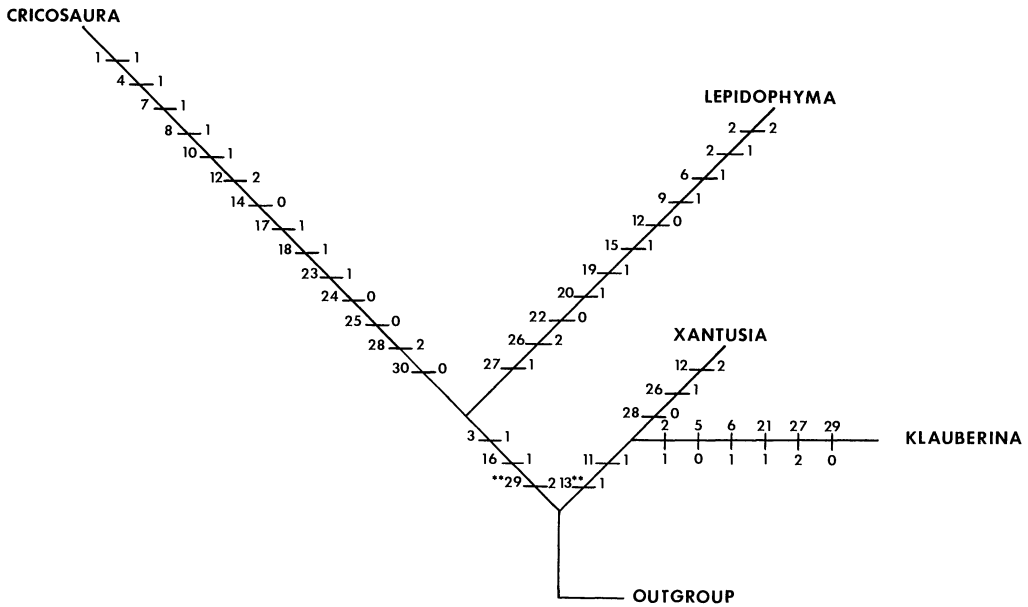
FIG. 4. The most-parsimonious cladogram based on the morphological data (Table 1) and the karyological tree of Figure 3. Character-state changes for morphological features (cross marks) are identified to character and character state (Appendix) by their associated numbers to the left and right of the branches, respectively. On the *Klauberina* branch, the numbers above are the characters and the numbers below are the character states. Branch lengths reflect patristic distances. Four steps are associated with the branch connecting the outgroup to the most recent common ancestor of the study group. These steps are not shown because they are unimportant in defining the relationships of the study group. Ambiguities associated with unresolved conditions of the outgroup are marked with two stars.

parallels the patterns (tracks) for a variety of monophyletic taxa (e.g., poeciliid, cichlid, and cyprinodontid fishes, gars, and synbranchid eels; Rosen, 1975). These groups not only have distributions similar to *Cricosaura* and *Lepidophyma*, but also exhibit phylogenetic relationships which suggest that lower Mexican–Nuclear Central American and Antillean taxa are more closely related to one another than either are to any other close relative occupying a third area.

Savage (1982) and Rosen (1975) both attributed the Central American–Antillean pattern of allopatric distributions to the tectonic history of a proto-Antillean archipelago, in which Cuba may have been adjacent to the Yucatan peninsula as late as the Eocene (Shields, 1979; Pindell and Dewey, 1982). The north–south split between the *Xantusia-Klauberina* and *Cricosaura-Lepidophyma* lineages can be attributed to historical physiographic events

(Sierra Madrean orogeny) and concomitant climatic changes (cooling and drying) through northern Mexico from the Eocene to the Pleistocene (Axelrod, 1975; Rosen, 1975; Morafka, 1977; Savage, 1982).

Bezy et al. (1980) proposed that the allopatry between *Xantusia* and *Klauberina* was the result of a dispersal event from the mainland to the three islands *Klauberina* now inhabits (Santa Barbara, San Nicolas, San Clemente; Fig. 7). They suggested that the colonization of San Clemente occurred about 15 million years ago with subsequent northward dispersal to the other islands (because only San Clemente does not have marine deposits over the entire island). The absence of *Klauberina* from Santa Catalina is intriguing, because it lies between the above three islands and the mainland, and has no record of Pleistocene submergence. *Klauberina's* absence from Santa Catalina suggests extinction on this island.
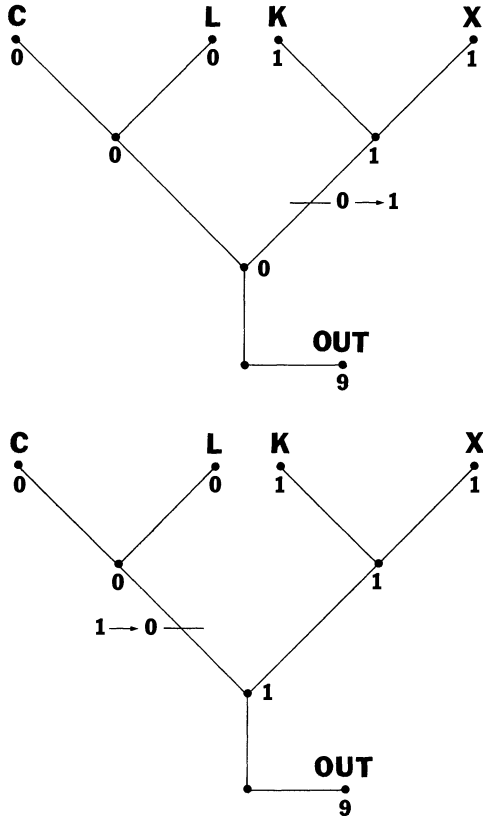
FIG. 5. An example illustrating the problem of ambiguous character-state assignments. The example corresponds to character 13 (nasal opening position). Character-state steps supported by Farris optimization and Figure 2 are shown above, whereas equally parsimonious changes are presented below. The alternative for fitting character 13 to the tree is associated with the unresolved condition (i.e., 9s) of the outgroup. Abbreviations used: (C) *Cricosaura*, (K) *Klauberina*, (L) *Lepidophyma*, (X) *Xantusia*.

Because dispersal hypotheses may be untestable (Rosen, 1975) and, therefore, provide little explanatory power, we propose a testable alternative hypothesis for the distribution of *Klauberina*—a vicariance model based on tectonic evidence. The model is testable in that it can be falsified if other monophyletic groups do not conform to a track between central Baja California and the Channel Islands (San Clemente). If other monophyletic taxa do form such a track, their cladistic relationships should indicate that populations from the Channel Islands and central Baja
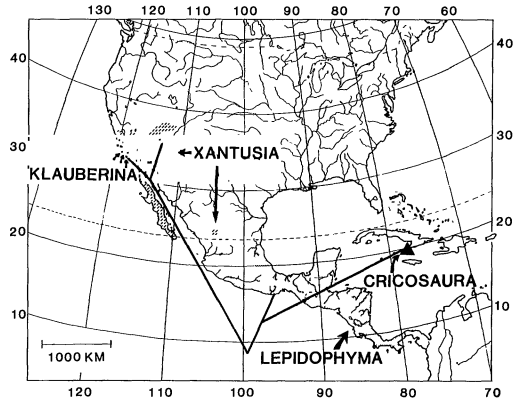

FIG. 6. Distribution of extant genera, on which is superimposed the supported cladogram from this study.

California are closer to one another than either are to the area of California adjacent to the Channel Islands.

Crouch (1979) suggested that based on geologic, geophysical, and paleomagnetic data, the outer Channel Islands and the northern islands associated with the Transverse Ranges were part of the Baja Peninsula up to about 18 million years ago. At that time, part of the Great Valley Belt (the tectonic element associated with the islands) began moving northward along a fault system similar to the present San Andreas fault and attained its current position about 5 to 8 million years ago. The absence of *Klauberina* from the northern Channel Islands associated with the Great Valley Belt may be explained by the occurrence of an early and mid-Pleistocene submergence, which was sufficient to eliminate the biota (Weaver and Doerner, 1967). However, Santa Catalina is not part of the Great Valley Belt, but belongs to the relatively stable Franciscan Belt that may have been stationary during the disruption of the Great Valley Belt.

This model suggests that xantusiids were distributed over Baja California in a fashion similar to their current distribution. This assumption is based on the current distribution of xantusiids on both sides of the Gulf of California. This distribution is an ancient one, since the Gulf is the result of a Miocene tectonic event. Thus, the vi-
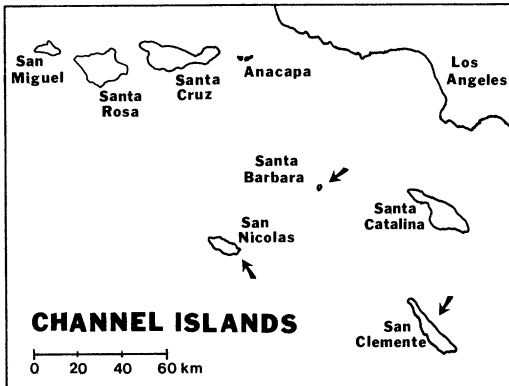
FIG. 7. Distribution of *Klauberina* on the California Channel Islands: Santa Barbara, San Nicolas, and San Clemente (indicated by arrows).

TABLE 2. Revised classification of the genera in Xantusiidae based on a cladistic synthesis of multiple character sets.

Family Xantusiidae
  Subfamily Xantusiinae
    Genus *Xantusia*
    Genus *Klauberina*

  Subfamiy Cricosaurinae
    Genus *Cricosaura*
    Genus *Lepidophyma*

cariance model suggests that a continuous xantusiid distribution of north to central Baja was fragmented by the northward movement of the Great Valley Belt. The northern and southern Channel Islands were a part of the belt, but Santa Catalina was not. Only San Clemente was continuously emergent since that fragmentation, which explains the presence of *Klauberina* there. The presence of *Klauberina* on San Nicolas and Santa Barbara may be due to special dispersal because both seem to have undergone Pleistocene submergence.

The morphologic, karyologic, and biogeographic data we analyzed suggest that the generic classification within the Xantusiidae should be changed. Our revision would remove *Lepidophyma* from the subfamily Xantusiinae, placing it with *Cricosaura* in the Cricosaurinae (Table 2).

Our analysis does not support either the phylogenetic hypothesis of Savage (1955) or the phenetic trees of Savage (1963) and Schatzinger (1980). The phylogeny of Bezy (1972) was not reevaluated but incorporated into this study, although his study did raise the issue of the generic status of *Klauberina*. Savage (1957) created the monotypic genus based on scutellation, body proportions, coloration, life history, and osteology (characteristics which in his words were "so different from other members of the group that a new genus is required"). Bezy (1972) suggested that *riv-*

ersiana be kept in *Xantusia*, whereas we followed Savage's scheme in this paper.

In summary, this study provides best estimates of xantusiid relationships, but further phylogenetic study of this group is needed to test our hypotheses. Living *Cricosaura* are needed for complete biochemical, karyologic, and ontogenetic studies. A detailed study of fossil taxa would also provide a test for the biogeographic hypotheses. Analysis of fossil taxa by J. A. Gauthier (pers. comm.) is in preparation and will provide the opportunity for such a test.

ACKNOWLEDGMENTS

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APPENDIX

Morphological Characters and Character States

1. Anterior palate (0) fenestra vomeronasalis and fenestra exochoanalis connected, (1) separated. 2. Caudal scales (0) smooth, (1) weakly keeled, (2) strongly keeled. 3. Caudal scale size (0) homogeneous, (1) heterogeneous. 4. Clavicular foramen (0) present, (1) absent. 5. Cranial osteoderms (0) absent, (1) present. 6. Ectochoanal cartilage (0) greatly expanded, (1) moderately expanded. 7. Ectopterygoid and palatine (0) separated, (1) in contact. 8. Epipterygoid attachments to parietal and prootic processes (0) attached only to parietal, (1) attached to both parietal and prootic. 9. Frontal margin of orbit (0) concave, (1) not concave. 10. Frontals (0) paired, (1) single. 11. Gulars (0) same size as pregulars, (1) enlarged. 12. Jugal (0) greatly expanded, (1) moderately expanded, (2) narrow. 13. Nasal opening position (0) at nasal, postnasal junction, (1) at nasal, postnasal, rostral, and first supralabial junction. 14. Nasal size (0) large, (1) reduced. 15. Orbit roofed by frontal (0) partially, (1) completely. 16. Parietal foramen (0) present, (1) absent. 17. Parietals (0) paired, (1) single. 18. Phalangial formula (0) 2-3-4-5-3, (1) 2-3-4-4-3. 19. Postmental, infralabial (0) distinct, (1) fused. 20. Prefrontal (0) extends on top of cranium, (1) no covering on cranium. 21. Pretemporals (0) present, (1) absent. 22. Radials and femorals (0) not enlarged, (1) enlarged. 23. Scale texture (0) granular, (1) flat. 24. Squamosal and parietal contact (0) no contact, (1) in

contact. **25.** Sternum (0) posterior projection present, (1) absent. **26.** Supraoculars (0) two rows, (1) one row, (2) absent. **27.** Teeth (0) strongly tricuspid, (1) weakly tricuspid, (2) simple. **28.** Temporals (0) small plates in a series, (1) enlarged plates in series, (2) a few very large plates. **29.** Ventrals (0) 16 rows, (1) 12-14 rows, (2) 8 rows. **30.** Xiphisternal ribs (0) two pairs, (1) one pair.