

Species Limits in the Genus Gerrhonotus (Squamata: Anguidae)

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SPECIES LIMITS IN THE GENUS GERRHONOTUS (SQUAMATA: ANGUIDAE)

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ABSTRACT: Gerrhonotus liocephalus is demonstrated to consist of at least three species rather than the single polytypic species currently recognized. Of the seven currently recognized subspecies, G. l. aguayoi, G. l. infernalis and G. l. taylori become G. infernalis; G. l. ophiurus and G. l. loweryi become G. ophiurus; and G. l. austrinus and G. l. liocephalus retain the name G. liocephalus. No subspecies are recognized within any of these three species. Certain populations from western Mexico (Durango, Sinaloa, Jalisco, and Colima) remain of uncertain identity, but are tentatively referred to as G. cf. liocephalus. Evidence for these conclusions is derived from an analysis of scalation, coloration, and morphometric variation. The taxonomic history in Gerrhonotus also is discussed.

Key words: Alligator lizard; Anguidae; Gerrhonotus; Mexico; Species; Systematics; Texas

THE genus *Gerrhonotus* at present contains two recognized species. *Gerrhonotus lugoi* is a poorly known form restricted to the vicinity of Cuatro Ciénegas, Coahuila, Mexico. *Gerrhonotus liocephalus*, on the other hand, is among the most widely distributed alligator lizards (Anguidae: Gerrhonontinae). Geographic variation in the latter taxon has led to the description of seven subspecies: *aguayoi*, *austrinus*, *in*- fernalis, liocephalus, loweryi, ophiurus, and *taylori*, with another suggested but not formally described (Smith, 1984). Several workers have discussed differences in scalation, body proportions, and color pattern among these forms, but since 1900 this discussion has been restricted to the context of a single polytypic species. In this paper, I will discuss the history of intraspecific taxonomy in the broadly defined G. liocephalus in order to provide a background for the currently accepted specific and subspecific limits. I will then re-analyze the patterns of variation in scalation, morphometrics, and color pattern within and among the currently recognized subspecies, and provide evidence for the division of G. liocephalus into multiple species

In discussing the results of this analysis, I will use the first six subspecies names listed above for ease of comparison with previous papers, although I will conclude later in the paper that some of them should be synonymized. The description of aguayoi (Contreras Arquieta, 1989) appeared only in an abstract from a scientific meeting and hence is of questionable validity. Because no type specimen was designated, the populations referable to it are unclear and I cannot include it in the character analysis below. I will refer to three unnamed western groups of populations as "western isolates" in presenting the results and then hypothesize possible species placement in the Discussion.

Intraspecific Taxonomy in Gerrhonotus liocephalus (sensu lato)

In 1828, A. F. A. Wiegmann described six species of gerrhonotine lizards on the basis of a set of specimens collected by F. Deppe and donated to the Berlin Museum. Among the specimens described by Wiegmann was a single juvenile he named *Gerrhonotus liocephalus*. Wiegmann provided no type locality, although the holotype was clearly from Mexico (as suggested by its inclusion by Wiegmann, 1834, in his *Herpetologia Mexicana*).

Soon after the appearance of Wiegmann's work, Peale and Green (1830) described *Scincus ventralis* from the "mining districts of Mexico." Peale and Green apparently were unaware of the description of G. liocephalus by Wiegmann and did not compare the two taxa. Wiegmann (1834), however, recognized that his G. *liocephalus* was identical to S. ventralis. Because he decided that the name "liocephalus" ("smooth head") was appropriate for the juvenile he had originally described but not for adult specimens such as those examined by Peale and Green, Wiegmann (1834) changed the name of the species to G. tessellatus. This latter name was in common use (e.g., Cope, 1866, 1878; Duméril and Bibron, 1839; Duméril and Duméril, 1851; Gray, 1838, 1845; O'Shaughnessy, 1873) until Bocourt (1878) resurrected *liocephalus*.

The first Texan specimen, from the canyon of the Devil's River, was described by Baird (1858) as *G. infernalis*. Baird did not compare his new species with either *G. liocephalus/G. tessellatus* or *Scincus* ventralis.

Cope (1866) described G. ophiurus from Orizaba, Veracruz, as differing from G. tessellatus by having a longer tail, shorter limbs, and a different arrangement of the head scales. Cope (p. 321) summarized what was then known about variation in Gerrhonotus as follows (with terminology modified to match that used in the present paper):

- One preocular; canthal/loreal series consisting of an anterior canthal, an anterior loreal, and a posterior cantholoreal; adpressed limbs separated by the length of the hind leg; venter immaculate; tail relatively shortG. ventralis
- No preoculars; canthal/loreal series consisting of an anterior canthal, an anterior loreal, and a posterior cantholoreal; adpressed limbs separated by length of the forearm; dorsum brown with ten crossbands; venter black-spotted;
- Three loreals present, no cantholoreal; anterior internasal not in contact with anterior supralabial; dorsum light olive, with

seven or eight dark crossbands; venter yellowish, marbled with olive; tail length twice snout-vent length G. infernalis

Bocourt (1871) described G. lemniscatus from Veracruz. He compared it only to G. multifasciatus (a synonym of Elgaria kingii), and not to any of the other forms of Gerrhonotus as here circumscribed.

O'Shaughnessy (1873) and Cope (1878) accepted tessellatus, ophiurus, infernalis, and *lemniscatus* as distinct species. Cope also accepted ventralis although O'Shaughnessy considered it to be a synonym of tessellatus. Because of their similarity to each other, all of these taxa were combined into the single species G. lio*cephalus* by Bocourt (1878) and generally have been considered to be synonymous since that time, although certain American authors (e.g., Burt, 1935; Murray, 1939; Stejneger and Barbour, 1939; Strecker, 1926) continued to accept G. infernalis for the Texan populations until Smith (1946) synonymized them.

Cope (1900) was the first to relegate some of these taxa (liocephalus, ventralis, ophiurus, and infernalis) to subspecific status, although he suggested that all but infernalis were "well marked subspecies, which may yet come to be regarded as true species." Cope provided no new characters differentiating the forms; in fact the key he provided in 1900 was lifted wordfor-word from his 1866 paper. Cope's subspecific system was accepted by most, but not all (see previous paragraph), subsequent authors, except that *ventralis* generally has been considered to be a synonym of liocephalus. Gerrhonotus lemniscatus was listed as a synonym of G. l. liocephalus by Cope and as a synonym of G. l. ophiurus since Smith and Taylor (1950).

Hartweg and Tihen (1946) described the subspecies *austrinus* from Cerro Malé, Chiapas. They considered this form (of which they had only a single juvenile specimen available for examination) to be more closely related to *liocephalus* than to the *"infernalis/ophiurus* complex," because *austrinus* and *liocephalus* possess only three canthal/loreal elements, a single preocular, and an immaculate venter, and lack prominent dorsal crossbands. On the other hand, they saw *austrinus* as differing from *liocephalus* in the absence of supranasals, the presence of a long rather than broad frontonasal ("azygous prefrontal" in their terminology), the lack of contact between the frontal and the interparietal, and contact between the second primary temporal and the posterior lateral supraocular. They also reported that the number of transverse dorsal scale rows in austrinus is at the lower limit for liocephalus. Tihen (1954) and Smith and Alvarez del Toro (1963) described the second and third known specimens of G. liocephalus from Chiapas (AMNH 71396 and UIMNH 52087, respectively). These specimens were both from the vicinity of Tuxtla Gutiérrez and agreed with liocephalus rather than *austrinus* in all of the diagnostic characters listed by Hartweg and Tihen. Tihen (1954) suggested that the subspecies *liocephalus* "is in fact a complex of two different races," but he did not elaborate.

Tihen (1948) described G. l. loweryi from the Xilitla region of San Luis Potosí. In his discussion, Tihen suggested that several characters vary clinally within infer*nalis* between its northern limit in Texas and its southern limit in San Luis Potosí: he cited southern populations as having increased tail length and caudal scale whorl number, decreased extent-though not necessarily distinctness—of the transverse dorsal crossbands, and stronger ventral patterning. Tihen saw the Veracruz subspecies ophiurus as a continuation of this cline. The southern Mexican *liocephalus* he saw as differing in having a smaller number of supralabials and canthal/loreal elements, a longer tail, and less distinct dorsal crossbands, and in lacking markings on the venter. Tihen considered *loweryi* to be intermediate between the *infernal*is/ophiurus complex and liocephalus. He noted that *loweryi* agrees with *infernalis* and ophiurus, but not with liocephalus, in having more than three canthal/loreal scales and 24 or more combined supralabials, but that in tail length, number of transverse dorsal scale rows, and number of caudal scale whorls, *loweryi* resembles

liocephalus and not the northern forms. Tihen also noted that contact of the second primary temporal with the supraoculars usually distinguishes loweryi from all three of these other subspecies (but not from the Chiapan form *austrinus*). Because of this hypothesized morphocline from infernalis /ophiurus to loweryi to liocephalus, Tihen decided that these forms are best recognized as subspecies of a single species. However, he pointed out that *loweryi* occurs geographically between infernalis and ophiurus rather than between infernalis/ ophiurus and liocephalus, and thereby tacitly hinted that this single species hypothesis might be oversimplified.

Gerrhonotus l. taylori was described from the vicinity of Santa Barbara, Chihuahua, by Tihen (1954). Tihen saw taylori as most closely allied with infernalis, to which it is similar in all respects except in having an increased number of dorsal scale rows. The other major diagnostic feature of taylori, 14 rather than 12 longitudinal ventral scale rows, was uncommon but not unknown in the samples of *infernalis* available to Tihen; he cited a population from Alvarez, San Luis Potosí (population sample 6 in the analysis below), in which approximately 50% of the individuals showed this character. Of color pattern, Tihen (p. 10) stated that:

"The color pattern in these two specimens [the holotype and paratype of *taylori*] is almost certainly not the adult pattern, but differs somewhat from the pattern in any *infernalis* of comparable size. The proportion of "white" to dark brown in the dorsal cross bands is greater here than in comparable *infernalis*, and the ventral lines are more prominent, with less tendency to break down into a mottled pattern."

Smith (1984) provided the most recent key to the subspecies of *G. liocephalus* and suggested that another should be erected for populations in Sinaloa and Durango. Smith incorporated most of the characters discussed by previous workers, and in addition pointed out that *liocephalus* has 14 longitudinal dorsal scale rows while all other forms have 16 or more.

Contreras Arquieta (1989) suggested that populations in the vicinity of Cuatro Ciénegas, Coahuila, should be considered to be a distinct subspecies (*aguayoi*) because they differ from *infernalis* in having a cantholoreal scale and in having dorsal crossbands with black margins and black flecks on the venter. His brief description appeared only in an abstract for a scientific meeting and no type specimen was designated.

In summary, seven subspecific names have been proposed for *G. liocephalus* (aguayoi, austrinus, infernalis, liocephalus, loweryi, ophiurus, and taylori), and the possibility of an eighth was suggested by Smith (1984). The characters that have been discussed by the describers of these subspecies and in published keys to *Ger*rhonotus taxa (Smith, 1942; 1984; Smith and Taylor, 1950) are summarized in Table 1.

MATERIALS AND METHODS

A total of 509 preserved specimens from 29 collections (listed in Acknowledgments) was examined (see Appendix I). Each specimen was coded for the characters listed in Table 1 and differences in color pattern were noted. Sex was determined by the presence of testes or ovaries in specimens bearing the appropriate incision or by the presence or absence of hemipenes. Scale terminology follows Good (1988).

To test for significant heterogeneity among samples in scale counts, ANOVA's were run using the Statview computer package. Post hoc Scheffé F-tests were conducted to test for pairwise differences among samples for those characters that showed significant ($P \leq 0.05$) heterogeneity.

Morphometric measurements were made to the nearest mm using either a ruler or digital calipers. A dissecting microscope was used for examination of small specimens. The following ten measurements were taken on each specimen, except where certain measurements were impossible due to damage: snout-vent length (hereafter abbreviated SVL), tail length, trunk length, trunk width, head length, head width, snout length, arm length, leg length, and longest hind toe length.

1.	Contact of nasal with anterior supralabials	Cope (1866, 1900)
2.	Supranasal presence	Hartweg and Tihen (1946); Smith and Tay- lor (1950); Smith (1984)
3.	Canthal/loreal series made up of three scales or more than three scales	Cope (1866, 1900); Smith (1942, 1984); Hart- weg and Tihen (1946); Tihen (1948); Smith and Taylor (1950); Contreras-Ar- quieta (1989)
4.	Supralabial number	Tihen (1948)
5.	Frontonasal shape	Hartweg and Tihen (1946); Smith and Tay- lor (1950)
6.	Frontal-interparietal contact	Hartweg and Tihen (1946); Smith and Tay- lor (1950)
7.	Preocular number	Cope (1866, 1900); Smith (1942); Hartweg and Tihen (1946)
8.	Second primary temporal-posterior lateral supra- ocular contact	Hartweg and Tihen (1946); Tihen (1948); Smith and Taylor (1950); Smith (1984)
9.	Transverse dorsal scale row number	Smith (1942); Hartweg and Tihen (1946); Tihen (1954); Smith and Taylor (1950)
10.	Longitudinal dorsal scale row number	Smith (1984)
11.	Longitudinal ventral scale row number	Tihen (1954); Smith (1984)
12.	Caudal tail whorl number	Tihen (1948); Smith and Taylor (1950); Smith (1984)
13.	Distance between adpressed limbs	Cope (1866, 1900)

TABLE 1.—Geographically variable characters in G. liocephalus (sensu lato).

To eliminate the confounding effects of ontogenetic and sexual differentiation, the specimens were divided into three classes: juveniles (those less than 90 mm SVL), adult males (males greater than 90 mm SVL), and adult females (females greater than 90 mm SVL). The cutoff at 90 mm for iuveniles vs. adults was chosen because at 90 mm males and females begin to diverge in certain characters, notably head width and length. Because of insufficient sample sizes for most populations, juveniles will not be discussed in this paper.

14. Tail length

15. Dorsal color pattern

16. Ventral color pattern

Character

Most of the variance observed either among adult males or among adult females resulted from size variation within populations (e.g., SVL in adult males in this survey varied from 90 mm to 180 mm) and not from among-population variation. Two approaches were taken to try to minimize this effect. In both of these approaches, SVL was assumed to provide a reasonably accurate reflection of overall size.

Günther (1885); Cope (1866); Tihen (1948): Smith and Taylor (1950); Smith (1984)

Cope (1866, 1900); Smith (1942); Hartweg and Tihen (1946); Tihen (1948); Tihen (1954); Smith and Taylor (1950); Contre-

Cope (1866, 1900); Smith (1942); Hartweg

and Tihen (1946); Tihen (1948); Tihen (1954); Smith and Taylor (1950); Contre-

ras Arquieta (1989)

ras Arquieta (1989)

References

The first of these approaches was a multivariate analysis in which each variable was first regressed against SVL and a covariance matrix of the resulting residuals was subjected to principal components analysis using the SAS computer package. Tail length was not considered because the majority of specimens lacked complete, unregenerated tails.

The second approach to examining morphometric differentiation was a simple univariate analysis in which each character was divided by SVL (to adjust for overall size) for adult males and adult females. Because ratios cannot be assumed to be normally distributed, a nonparametric Kruskal-Wallis analysis (SAS) was conducted in order to test for within-sex het-



FIG. 1.—The 20 population samples used for comparative purposes within G. liocephalus sensu lato. The currently recognized subspecies are as follows: *infernalis* = samples 1–6, *loweryi* = sample 7, *ophiurus* = sample 8, *liocephalus* = samples 9–15, *austrinus* = sample 16, *taylori* = sample 17. Isolated samples 18–20 have not been identified to subspecies, although Smith (1984) suggested that sample 19 should be accorded distinct subspecies status.

erogeneity among the population samples for each of the 10 morphometric characters. I wrote a computer program to conduct post hoc tests for significance ($P \leq$ 0.05) in all pairwise comparisons for those characters showing significant heterogeneity.

Phylogenetic analysis was conducted us-



specimens per unit area, but also so that no sample crossed currently recognized subspecies boundaries. The populations incorporated in these samples are referenced in Appendix I. Grouping localities was done because, in all but a very few instances, too few specimens were available from single localities to allow analyses of variance to be calculated. Unfortunately, specimens from some areas are so rare that some of the samples necessarily contain very few specimens. Sample sizes for each of the analyses below vary because not all characters were discernible on all specimens.

Scale Characters

Contact of the nasal with the supralabials.—Cope (1900) stated that the nasal contacts the first supralabial in all forms except *infernalis*, in which contact is with the second supranasal only. Cope examined only two specimens of *infernalis* and illustrated the head scale pattern of one of them. Contrary to his assertion in the text, the nasal was illustrated as contacting the first supralabial in the figure (Cope, 1900; Fig. 91); reexamination of the specimens examined by Cope (USNM 3060 and 13636) shows that both exhibit nasal-first supralabial contact. Such contact was essentially universal among the specimens examined in the present study.

Supranasal presence.—The absence of supranasals is supposed to distinguish G. l. austrinus from all other Gerrhonotus (Hartweg and Tihen, 1946). Supranasals were present in all specimens examined except the holotype of austrinus, in which they are fused with the posterior internasals.

Canthal/loreal series.—The condition of the canthals and loreals has been often cited as differentiating the subspecies of *Gerrhonotus*. The subspecies *infernalis*, *loweryi*, and *ophiurus* are generally thought to have a four- or five-scale pattern (two canthals, two or three loreals, and no cantholoreal; Fig. 2a) and *liocephalus* and *austrinus* to have a three-scale pattern (an anterior canthal, an anterior loreal, and a posterior cantholoreal; Fig. 2b). The relative frequencies of the three-scale pattern among the population samples illustrated



FIG. 2.—Variation in canthal/loreal scales and in the preocular series in *Gerrhonotus*. See text for discussion. c = canthal, l = loreal, cl = cantholoreal, p = preocular.

ing the PAUP computer package (Swofford, 1991). Characters were polarized using the clade containing *Elgaria*, *Barisia*, *Mesaspis*, and *Abronia* as the first outgroup (Good, 1988), *Coloptychon* as the second (Good, 1988), and the Diploglossinae and Anguinae as subsequent outgroups (Gauthier, 1982; Good, 1988). Polarity was determined using the global parsimony approach of Maddison et al. (1984). All of the possible phylogenies were examined for length using the PAUP exhaustive search algorithm.

RESULTS

For this study, specimens were segregated into 20 population samples as illustrated in Fig. 1. These samples were chosen in order to maximize number of HERPETOLOGICAL MONOGRAPHS

in Fig. 1 are as follows: *infernalis*: sample 1 = 0, sample 2 = 0, sample 3 = 0, sample 4 = 0.06 (one specimen), sample 5 = 0.10 (two specimens), sample 6 = 0.06 (one specimen); *loweryi*: sample 7 = 0.09 (three specimens); *ophiurus*: sample 8 = 0.08 (one specimen); *liocephalus*: sample 9 = 1.00, sample 10 = 1.00, sample 11 = 1.00, sample 12 = 0.95 (all but four specimens), sample 13 = 1.00, sample 14 = 1.00, sample 15 = 1.00; *austrinus*: sample 16 = 1.00; *taylori*: sample 17 = 0; other western isolates: sample 18 = 0, sample 19 = 1.00, and sample 20 = 0.67 (two specimens).

Supralabial number.—Tihen (1948) reported that liocephalus has fewer supralabial scales than *infernalis*, *loweryi*, or ophiurus. The distribution of supralabial counts for the 20 population samples in Fig. 1 is illustrated in Fig. 3. ANOVA demonstrated that there is significant heterogeneity among the population samples and that sample 9 is significantly different (P< 0.05) from samples 1, 2 and 8; sample 11 is significantly different from samples 1 and 4-8; sample 12 is significantly different from samples 1-8; and sample 13 is significantly different from samples 1, 2, 4-6, and 8 (Scheffé F-test). Although no other pairs of population groups show significant differences, *liocephalus* in general appears to have fewer supralabials than do infernalis, loweryi, or ophiurus, and there appears to be a cline in this character within *liocephalus* such that supralabial number increases from northwest to southeast. It is particularly noteworthy that *liocepha*lus samples 9 and 12 are significantly different from *ophiurus* sample 8 although they are in close geographic proximity to it; this is probably also true of *liocephalus* sample 10 (see Fig. 3), but small sample size precludes statistical verification. Among the small isolated populations, austrinus (sample 16) and sample 19 appear to have the *liocephalus* pattern, while taylori (sample 17), sample 18, and sample 20 appear to have the infernalis/loweryi/ ophiurus pattern. However, none of these determinations are statistically significant.

Frontonasal shape and contact.—Hartweg and Tihen (1946) suggested that a frontonasal that is longer than it is broad is diagnostic of *austrinus*. This is incorrect:



FIG. 3.—The distribution of supralabial numbers among 20 samples of *Gerrhonotus*. The vertical bar illustrates the mean and the horizontal bar one standard error. The horizontal line illustrates the range.

long frontonasals, though uncommon, occur in several populations. In the present analysis, such frontonasals were seen in 18 specimens from sample 1 (16%), two specimens from sample 5 (17%), and two specimens from sample 7 (6%). The presence of a long frontonasal is fairly well, though not strictly, correlated with contact between the frontonasal and the frontal, separating the prefrontals. This condition is seen occasionally in samples 1, 2, and 7, being particularly common in sample 1 (28% of specimens examined).

Frontal-interparietal contact.—Lack of contact between the frontal and interparietal was listed by Hartweg and Tihen (1946) as diagnostic of *austrinus*. In the present analysis, lack of contact was found also in one specimen each from samples 7 (3%), 8 (9%), 19 (33%), the single specimen from sample 18 (100%), two specimens from sample 6 (14%), six specimens from sample 1 (5%), and 11 specimens from sample 2 (15%). Its occurrence in the single known specimen of *austrinus* therefore is not diagnostic.

Preocular number.—According to Cope (1866, 1900), ventralis (a synonym of liocephalus) has one preocular, ophiurus has



FIG. 4.—The distribution of transverse dorsal scale row numbers among 20 samples of *Gerrhonotus*. The vertical bar illustrates the mean and the horizontal bar one standard error. The horizontal line illustrates the range.

two, and *liocephalus* has none. Hartweg and Tihen (1946) stated that *austrinus* and liocephalus have a single preocular but that infernalis and ophiurus have more than one. Divided preoculars (Fig. 2) are seen in the following percentages in the 20 population samples illustrated in Fig. 1: infernalis: sample 1 = 82, sample 2 = 86, sample 3 = 5, sample 4 = 40, sample 5 =10, sample 6 = 28; *loweryi*: sample 7 =40; ophiurus: sample 8 = 75; liocephalus: sample 9 = 0, sample 10 = 0, sample 11= 0, sample 12 = 0, sample 13 = 0, sample 14 = 0, sample 15 = 0; austrinus: sample 16 = 0; taylori: sample 17 = 50; other western isolates: sample 18 = 50, sample 19 = 0, sample 20 = 0.

Contact of the second primary temporal with the posterior supraocular.— Hartweg and Tihen (1946) listed this contact as a character of *austrinus* differentiating it from *liocephalus*. Tihen (1948) stated that *loweryi* is similar to *austrinus* in this regard and that all other taxa usually lack such contact. In the present analysis, contact was seen in at least a few specimens in most population groups. The percentages observed were: *infernalis*: sample 1 = 68, sample 2 = 57, sample 3 = 61, sample 4 = 74, sample 5 = 46, sample 6 = 13; loweryi: sample 7 = 92; ophiurus: sample 8 = 33; liocephalus: sample 9 = 25, sample 10 = 0, sample 11 = 31, sample 12 = 5, sample 13 = 0, sample 14 = 50, sample 15 = 0; austrinus: sample 16 = 0; taylori: sample 17 = 50; other western isolates: sample 18 = 50, sample 19 = 17, sample 20 = 50.

In addition, Martin (1958) reported contact in all six of the specimens he examined from the Gómez Farias region of southern Tamaulipas (sample 5). These specimens were not available for the present study.

Transverse dorsal scale row number.— Hartweg and Tihen (1946) suggested that austrinus has fewer dorsal scale rows than does liocephalus. Tihen (1948) suggested that *lowerui* and *liocephalus* have more than do ophiurus or infernalis, and Tihen (1954) suggested that *taylori* has more rows than does infernalis. The distribution of dorsal scale row counts for the 20 population samples are shown in Fig. 4. ANO-VA and Scheffé F-tests indicate that population samples 1-6 are significantly different from samples 7, 8, and 11-13 (except that sample 5 and sample 11 are not significantly different). No other sample comparisons were significant. It is clear that *infernalis* has fewer scale rows than do loweryi, ophiurus, or liocephalus. Note in particular that there is a significant difference between *loweryi* sample 7 and the adjacent *infernalis* sample 6. There is a tendency among the easternmost liocephalus populations (samples 14 and 15) to have intermediate numbers of scale rows. This trend is also seen in *austrinus* (sample 16) which, although it may have fewer scale rows than western liocephalus (samples 9-13) as suggested by Hartweg and Tihen, is indistinguishable from eastern populations. The loweryi/ophiurus/liocephalus condition appears to be characteristic of taylori (sample 17) and sample 18, while samples 19 and 20 tend toward the infernalis condition. These latter comparisons are not statistically significant.

Longitudinal dorsal scale row number.—Smith (1984) stated that liocephalus has 14 longitudinal rows of dorsal scales HERPETOLOGICAL MONOGRAPHS

while all other forms have 16 or more. The lateral dorsal scales (those in contact with the granular lateral fold scales) are variable in size. In some specimens there are 14 rows of full-sized scales with no reduced scales flanking them, in others reduced flanking scales are present, while in still others these scales are as large as any dorsal. In the latter case, 16 longitudinal rows of dorsals are present. Sixteen rows of dorsals or 14 rows with reduced lateral dorsals at least half the size of other dorsals are universally seen in population samples 1-8 (infernalis, loweryi, and ophiurus), the single *liocephalus* specimen from sample 10, sample 17 (taylori), and the western isolates samples 18-20. Fourteen longitudinal rows or 14 with reduced laterals less than half the size of the other dorsals are seen in *liocephalus* samples 9, 14, and 15, and *austrinus* sample 16. Most of the specimens of *liocephalus* from samples 11-13 are of the latter type, but some specimens (20%, 28%, and 22%, respectively) are of the former.

Longitudinal ventral scale row number.—Tihen (1954) pointed out that taylori has 14 longitudinal ventral scale rows while most other populations have 12. In this analysis, 14 rows were found also in both specimens of sample 18, 60% of the specimens from sample 4, 29% of the specimens from both samples 5 and 6, and a single specimen (ca. 1.5%) from sample 2. Sample 18 is a western isolate; the other samples are *infernalis*.

Caudal tail whorl number. — Tihen (1948) suggested that *loweryi* has more scale whorls in the tail than does infernalis. Very few tails were intact and unregenerated among the specimens examined. Tail whorl number is unknown for eight of the 20 population samples. The distribution of tail whorl numbers among the other 12 is illustrated in Fig. 5. ANOVA and Scheffé F-tests show that samples 1-4 are significantly different from samples 7-12. No other significant differences were observed. There appear to be fewer tail whorls in infernalis than in loweryi, ophiurus, and liocephalus. Population sample 20 also appears to have the latter type, although this is not statistically significant.



FIG. 5.—The distribution of caudal scale whorl numbers among 20 samples of *Gerrhonotus*. The vertical bar illustrates the mean and the horizontal bar one standard error. The horizontal line illustrates the range. Several samples lacked specimens with complete unregenerated tails.

Color Pattern

Color pattern varies geographically in Gerrhonotus (Fig. 6). In adults from lio*cephalus* samples 9–15, the dorsum is either an immaculate light tan or has scattered darker brown scales. The venter and lower surface of the tail are lighter, immaculate or with scattered darker scales in the lateral-most one or two rows. There are 10-12 very prominent dark bars, 1 or 2 dorsal scales in width, in the lateral fold that contrast strongly with the immaculate or nearly immaculate dorsum and venter. The limbs, head, and dorsal surface of the tail are similar to the dorsum in color except that the lips are lighter than the rest of the head, approaching the venter in color. There is often a dark line running posteroventrally from the eye separating the light lip and darker temporal areas. This line is prominent in smaller specimens and fades as the specimens get larger; it is, however, still found in some relatively large individuals. Occasionally, specimens from samples 9, 11, and 12 show 10 or 11 irregular dorsal crossbands consisting of a white band one scale wide flanked by scattered dark scales; these dark scales are reminiscent of the scattered dark scales sometimes seen in the absence of light crossbands (see above). Samples 13, 14, and 15 differ somewhat from other *liocephalus*



FIG. 6.—Color pattern variation in *Gerrhonotus*. The specimens are, from left to right: *G. infernalis* (KU 87742) from Nuevo León (SVL = 161 mm), *G. ophiurus* (MNHN 25005.1) from Veracruz (SVL = 144 mm), and *G. liocephalus* (UTA 6066) from Oaxaca (SVL = 140 mm). All are adult males.

in that they often show 10 or 11 faint dorsal crossbands, but these bands rarely contain white scales. The lateral fold bars in these southern specimens are also often less prominent than those in other *liocephalus*.

The color pattern of *infernalis* differs from that of *liocephalus* in several ways. There are usually 7 or 8 fairly prominent irregular dorsal crossbands consisting of white markings one scale in width or less flanked by darker scales. The venter is usually distinctly mottled rather than immaculate. There are no bars in the lateral fold. The dark temporal line seen in many *liocephalus* is present only in young specimens of *infernalis*. This color pattern is characteristic of samples 1-6. Although this is the general color pattern of infernalis, there is substantial individual variation. The patterning of both the dorsal and ventral surfaces can sometimes be lost almost entirely. This condition appears in many specimens in samples 2 and 3, as well as occasionally in other areas. In the vicinity of Cuatro Ciénegas, Coahuila (within sample 4), some specimens show a pattern in which the medial portion of each dorsal crossband is eliminated, although the crossbands are still visible along the flanks. The mottled venter is sometimes replaced by heavy spotting in these specimens.

Specimens of *loweryi* (sample 7) and ophiurus (sample 8) are similar in color pattern to the occasional specimens of *liocephalus* that show dorsal crossbands. There are 10 or 11 such bands, with an irregular white band flanked by darker scales. The lateral fold bars are prominent. The subspecies ophiurus differs from other *Gerrhonotus*, however, in that the dorsal crossbands extend onto the lateral three or four scale rows of the venter. As in some specimens of *infernalis* (see above), color pattern is subdued in much of the type series of *loweryi*.

Color pattern variation among the disjunct populations in western Mexico is unclear because of the small number of specimens available for study. KU 78904 from southern Sinaloa (sample 19) is most similar to ophiurus in that it has ten irregular dorsal crossbands consisting of both light and dark scales, which extend onto the lateral scales of the otherwise immaculate venter, MVZ 197549 from Colima and CM 65825 and MVZ 205566 from southwestern Jalisco (all sample 20) are similar to the Sinaloan specimen except that each has 7-9 dorsal crossbands that do not extend onto the venter (hence the venter is immaculate as in *liocephalus*). In the Coliman specimen, the dorsal crossbands are visible only on the flanks, reminiscent of the dorsal pattern seen in some infernalis from Cuatro Ciénegas, Coahuila. There is some tendency toward obscure longitudinal ventral stripes in all of the Jaliscan and Coliman specimens. The only three known specimens from Durango appear to be of two different types. The two UTEP specimens (4562 and 4563) from Municipios Durango and El Salto (sample 19) appear to be fairly similar to the specimens from Sinaloa discussed above, except that the crossbands do not extend onto the venter. TCWC 35499 from the eastern face of the Sierra Madre Occidental southwest of Torreón (sample 18) has no pattern on either the dorsum or the venter.

Too few specimens were available to allow for detailed observations of geographic variation of juvenile color pattern. However, the few specimens available suggest major differences. Neonate infernalis from Texas (samples 1 and 2) have a dorsal ground color of dark brown with 7 or 8 very prominent light crossbands creating a striking banded appearance. The crossbands extend onto the lateral scale rows of the much lighter venter, the remainder of which is heavily speckled and/or mottled. The arms and legs are also mottled. The top of the head is much lighter than the dark dorsal ground color, which extends onto the sides of the head as far anterior as the nasal. The lips are lighter, similar to the venter in color. This pattern is also seen in *taylori*; the differences cited by Tihen (1954) (see above) are well within the range of variation in *infernalis*. The only other small juvenile infernalis examined were from central Nuevo León. They were similar, except the top of the head was darker. Only two neonate liocephalus were available, and they differ markedly from infernalis. The striking crossbands of *infernalis* are entirely lacking. Instead, the dorsal coloration consists of a broad brown dorsal stripe between dark flanks. The head is marked with a dark stripe similar to that seen in *infer*nalis. The venter has longitudinal stripes along its margins and is otherwise immaculate. The holotype of *austrinus* is also a small juvenile which shows no hint of the prominent crossbands seen in infernalis. No small specimens of the other forms of Gerrhonotus were available.

Morphometric Variation

Only two morphometric characters have been discussed in previous analyses of *Gerrhonotus* systematics: Cope (1866, 1900)



FIG. 7.—The distribution of *Gerrhonotus* populations on the first three principal components using the covariance matrix of the residuals of each morphometric character (see text) in adult males regressed against SVL. Tail length was eliminated from consideration because of the high frequency of tail breaks among the specimens examined.

suggested that *ophiurus* has a greater distance between adpressed limbs than the other forms, and Cope (1866, 1900) and Tihen (1948) discussed variation among

	Principal component								
Character	1	2	3	4	5	6	7	8	
Trunk length	0.378	-0.102	-0.826	-0.140	0.105	0.346	0.073	0.091	
Trunk width	0.198	0.491	-0.089	0.037	0.693	-0.468	0.060	-0.086	
Head length	0.197	0.403	0.160	-0.099	-0.101	0.051	0.151	0.837	
Head width	0.240	0.534	-0.059	0.600	-0.361	0.219	-0.162	-0.297	
Snout length	0.341	0.283	0.272	-0.715	-0.125	0.217	-0.016	-0.393	
Arm length	0.350	-0.241	0.327	0.149	0.413	0.347	-0.608	0.171	
Leg length	0.397	-0.263	0.312	0.274	0.140	0.175	0.734	-0.105	
Toe length	0.570	-0.305	-0.033	0.007	-0.368	-0.642	-0.184	0.008	

 TABLE 2.—Character loadings (eigenvectors) on the principal component axes resulting from an analysis of the covariance matrix of residuals of eight morphometric characters regressed against SVL in 19 populations of Gerrhonotus.

the subspecies in tail length. In the present analysis, 10 morphometric characters (SVL, tail length, trunk length, trunk width, head length, head width, snout length, arm length, leg length, and longest hind toe length) were measured in each of the specimens examined.

Figure 7 illustrates the first three axes for adult males resulting from the principal components analysis described above; the pattern for adult females is similar. The first axis explains 63% of the variation, the second 12%, and the third 10% (totalling 85%). The population samples in Fig. 1 are not clearly distinguishable on any of these three axes except samples 7 and 8 (loweryi and ophiurus, respectively), which are indistinguishable from each other but showed relatively high scores on principal component 2. Loadings on all eight principal components are listed in Table 2. Head length, head width, and trunk width load particularly heavily on component 2.

Univariate analysis of each character adjusted for SVL was more informative. All of the characters were significantly heterogeneous (P < 0.02) within both sexes. The significant comparisons in the post hoc tests involve only population samples 1, 2, 3, 4, 6, 7, 8, 11, 12, and 13; all pairwise comparisons among the other eight samples that contain adult specimens are not significant. However, all of these other groups contain at most three specimens of each sex, and in at least some cases lack of significance is likely a result of insufficient sample sizes rather than similarities in character states.

Among the differences that are signifi-

cant at $P \leq 0.05$, only two occur within a single taxon: within *infernalis*, females in sample 6 (the southernmost sample) have significantly longer heads than those in samples 1 and 2 (the two northernmost samples), although the ranges of the latter two overlap that of the former considerably. All other significantly different comparisons are between samples in different taxa as follows:

There are no significant differences between *loweryi* and *ophiurus* (samples 7 and 8) in any of the nine characters.

Not surprisingly, most of the significant differences between *loweryi* (sample 7) and populations of *infernalis* (samples 1–6) involve samples 1 and 2, which contain far more specimens than any other sample (see Appendix I). Significant differences between *loweryi* and these two groups include male and female trunk width (wider in *infernalis*) and female snout length (longer in *infernalis*). There is no indication from the material available that loweryi differs from all infernalis samples in these characters; female snout length may even show a cline within infernalis such that populations geographically closest to *loweryi* are also most similar to *low*eryi, although, because sample sizes do not allow for the identification of significant differences within infernalis, this cannot be determined with statistical certainty. Samples 3 and 4 in *infernalis* also differ from *loweryi* in male head length, but again there is no indication that *loweryi* differs from all *infernalis* in this character, especially in view of the fact that it does not differ from the larger samples 1 and

2. Perhaps the most significant morphometric difference between *infernalis* and *loweryi* is the difference between *loweryi* and *infernalis* sample 6 in female head width (wider in sample 6). Sample 6 is the only *infernalis* sample that differs from *loweryi* in this character, and it is geographically the closest sample to it. The significant differences between sample 6 and samples 1 and 2 in this character (see above) suggest that there may be a cline within *infernalis* such that populations become less *loweryi*-like the closer they approach *loweryi* geographically (Fig. 8).

Female head width is also the only character that differentiates any *infernalis* population from *ophiurus* (sample 8). Females of *ophiurus*, which are indistinguishable from *loweryi* (sample 7) in this character, have narrower heads than do those in sample 6 (Fig. 8).

Population sample 12 contains far more specimens than any of the other samples in *liocephalus*, and, as with *infernalis* samples 1 and 2, most of the significant differences between *liocephalus* and other taxa involve this group. Sample 7 (loweryi) differs from sample 12 in female trunk length, and trunk width, arm length, leg length, and toe length in both sexes. Both sexes in ophiurus (sample 8) also differ from sample 12 in arm, leg, and toe lengths (sample 8 is also significantly different from *liocephalus* sample 11 in male arm length and female leg length). No clear trends are indicated in trunk length or width, but the patterns in Fig. 8 suggest that both sexes in all *liocephalus* population groups probably have shorter limbs than do *loweryi* and ophiurus. It should be noted that, except for sample 9 which contains only one male and three females and hence is unlikely to show significant differences from any other sample, sample 12 is geographically the closest population to sample 8.

Several characters significantly distinguish *infernalis* populations from *liocephalus* populations as follows: male trunk length (samples 1, 2, 4 vs. 12; 4 vs. 11), female trunk length (2 vs. 12), female head length (2 vs. 12), female head width (6 vs. 13), male snout length (1, 2, 3, 4 vs. 12; 1, 2, 4 vs. 13), female snout length (4 vs. 12), arm length in both sexes (1, 2 vs. 12), male



FIG. 8.—The three morphometric ratios that show definite patterns of differentiation among the subspecies of *G. liocephalus*. Subspecific designations for each population are listed in the caption for Fig. 1.

leg length (1, 4 vs. 12) female leg length (1, 2 vs. 12), male toe length (1, 6 vs. 12), and female toe length (1, 2 vs. 12). Again, most, though not all, of the significant comparisons involve the samples with the largest sample sizes, *infernalis* samples 1 and 2 and *liocephalus* sample 12. There is no indication of an overall difference between *infernalis* and *liocephalus* in trunk length, head length, head width, or snout length, but limb length generally appears to be less in *liocephalus* than in *infernalis* (Fig. 8).

The western isolate population samples 17–20 each contain at most three specimens and as a result no statistical differences were seen in any character when these groups were compared with other *Gerrhonotus* populations.

DISCUSSION

The recent resurgence of interest in species concepts has resulted in the segregation of systematists into a number of theoretical camps (reviewed recently by Cracraft [1989], Frost and Hillis [1990], McKitrick and Zink [1988] and Templeton [1989]. The most prominent of these camps include proponents of the biological species concept (BSC), the phylogenetic species concept (PSC), and the evolutionary species concept (ESC). Despite the extensive and sometimes polemical theoretical discussions emanating from these camps regarding how species should and should not be defined, species in Gerrhonotus (as in many, if not most, other taxa) continue to be delimited operationally without regard to any of them. Instead, the operational definition for Gerrhonotus species uses what might be termed an "inertial species concept" in which species limits are set solely by historical precedence: the taxa austrinus, infernalis, liocephalus, loweryi, ophiurus, and taylori are treated as conspecific because herpetologists are used to them being conspecific, and not because the evidence for or against conspecificity has been rigorously examined.

A "biological" species is a "group of interbreeding natural populations that [is] reproductively isolated from other such groups" (Mayr, 1969). An "evolutionary" species is "a single lineage of ancestraldescendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1978). A "phylogenetic" species is "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft, 1983). In the absence of direct knowledge of gene flow or of the history or future of population divergence, the evidence available for estimating conspecificity among contiguous populations is similar regardless of which of these species concepts is followed. One should expect clinal patterns of character distribution and/or overlapping character state distributions within groups of populations that are "interbreeding," within groups of populations that are members of a lineage with a common set of "evolutionary tendencies and historical fate," or within groups of populations that are members of a "smallest diagnosable cluster." Alternatively, if species divergences are old enough, coincident breaks in the distributions of multiple characters should be seen among species because they are not interbreeding (i.e., not sharing genes), they are on separate evolutionary trajectories, or they are members of distinct diagnosable clusters.

There are no discernable breaks in character distribution within any of the six currently recognized subspecies of "G. liocephalus," suggesting that none of them consists of multiple species, although both infernalis and liocephalus show geographic differentiation in some characters. Similarly, loweryi and ophiurus are indistinguishable from each other, suggesting that they should not be recognized as distinct taxa. The taxa austrinus and taylori are known from very few specimens (one and two, respectively), so levels of within-group variation are uninformative.

Of the four characters cited by Hartweg and Tihen (1946) as diagnostic of austrinus, all but one (absence of supranasals) also occur in other Gerrhonotus populations. In all other characters, *austrinus* is indistinguishable from liocephalus. Although the type of *austrinus* is unique in the absence of supranasals, supranasal absence occurs occasionally among anomalous individuals of other gerrhonotine species (Good, 1988), and the evidence for the specific distinction of austrinus and lio*cephalus* based on this single character in this single specimen is therefore weak. Admittedly, inclusion of austrinus and lio*cephalus* in the same species diverges from a strict phylogenetic species philosophy because austrinus, as it is now understood, is diagnosable. However, such an extreme adherence to a phylogenetic species concept is unrealistic; *austrinus* is known from only a single specimen and there is no way to determine if the distinctive feature of this specimen is due to population differentiation or simply to individual variation. Because the single diagnostic character of *austrinus* is known to be variable in other alligator lizards, I prefer a conservative approach in which *austrinus* and *liocephalus* are viewed as conspecific. This hypothesis is tentative, however; further specimens could easily demonstrate that separate species status is warranted.

Tihen (1954) listed a high number of longitudinal dorsals and juvenile color pattern as characters distinguishing *taylori* from *infernalis*. The *taylori* condition in both of these characters is within the range of variation in *infernalis*, and the two therefore should not be recognized as distinct taxa.

On the other hand, sample 6 (*infernalis*) differs from nearby sample 7 (*loweryi*) in transverse dorsal number, tail whorl number, dorsal crossbar number, ventral color pattern, the presence of lateral fold bars, and female head width, and sample 8 (*ophiurus*) differs from nearby samples 9, 10, and 12 (*liocephalus*) in canthal/loreal number, supralabial number, preocular number, longitudinal dorsal number, ventral pattern (usually), and limb length. In all of these characters, intra-taxon variation is either clinal or nonexistent.

None of these taxa are sympatric. Nor are the populations in question strictly parapatric (samples 6 and 7 are approximately 120 km apart and samples 8 and 9 are approximately 30 km apart), so it is possible that clines occur in all of the diagnostic characters. However, this seems unlikely in view of the broad areas of uniformity relative to the few kilometers between the populations in question. The coincident breaks in the distributions of six relatively independent characters in each case provides circumstantial evidence that multiple species are involved. In the face of a complete lack of evidence for conspecificity, the best working hypothesis therefore is that *infernalis/taylori*, ophiurus/loweryi, and liocephalus/austrinus are distinct biological, evolutionary, and/or phylogenetic species (G. infernalis, G. ophiurus, and G. liocephalus, respectively; Fig. 9). Examination of the type specimens of the two synonyms Scincus ventralis and G. lemniscatus indicates that the former is synonymous with G. liocephalus and the latter with G. ophiurus.

Population sample 18 from eastern Durango is indistinguishable from G. infer*nalis* and should be considered conspecific with it. The identity of the other two population samples in western Mexico (19 and 20) is more problematical. Among the 12 characters that differentiate G. infernalis, G. ophiurus, and G. liocephalus, the condition in samples 19 and 20 is unknown or unscorable for tail whorl number, female head width, leg length, and neonate color pattern. Among the remaining eight characters, sample 19 is most similar to G. infernalis and G. ophiurus in longitudinal dorsal number, to G. liocephalus and G. ophiurus in dorsal crossband number and the presence of lateral fold bars, to G. in*fernalis* alone in transverse dorsal number, and to G. liocephalus alone in canthal/ loreal number, supralabial number, and preocular number. Ventral color pattern in sample 19 may be more similar either to G. liocephalus or to G. ophiurus. Sample 20 is more similar to G. infernalis and G. ophiurus in supralabial number and longitudinal dorsal number, to G. ophiurus and G. *liocephalus* in lateral fold number, to G. infernalis in transverse dorsal number and dorsal crossband number, and to G. liocephalus in preocular number and ventral color pattern. Both the G. infernalis/G. ophiurus and G. liocephalus canthal/loreal states were seen among the three specimens available from sample 20 (one with the former and two with the latter). The two western isolates themselves appear to differ in supralabial number, transverse dorsal crossband number, ventral pattern, and perhaps canthal/loreal number.

Table 3 lists the character states for G. infernalis, G. ophiurus, G. liocephalus, and samples 19 and 20 for the 12 characters that distinguish among them. Gerrhonotus lugoi, a diminutive species from the Cuatro Ciénegas Basin of Coahuila (McCoy,



FIG. 9.—The distribution of Gerrhonotus species based on the specimens available for the present study.

1970), is also included. It is the only other member of the genus *Gerrhonotus* and its status as a species distinct from the sympatric *G. infernalis* has not been seriously questioned (although see Morafka, 1977). Cladistic (sensu Hennig, 1966) analysis yields two most parsimonious trees, the strict consensus of which is illustrated in Fig. 10. Of the 12 characters in this analysis, only one is homoplastic aside from those contributing to the trichotomy of G. *liocephalus*, sample 19, and sample 20: a low number of transverse dorsal scales occurs in parallel in G. *infernalis* and in samples 19 and 20.

Smith (1984) suggested that the western

TABLE 3.—The distribution of character states among the species of *Gerrhonotus*. 0 = ancestral state; 1, 2 = derived states (each derived independently from state 0); a, b = unpolarized character states. The character states are as follows (see text for specifics): 1: 2 canthals and 2-3 loreals (0) or 1 canthal, 1 loreal and a cantholoreal (1); 2: combined supralabial number high (0) or low (1); 3: preoculars divided (0) or single (1); 4: transverse dorsal number high (0) or low (1); 5: longitudinal dorsal number high (0) or low (1); 6: tail whorl number high (0) or low (1); 7: dorsal crossband number low (a) or high (b); 8: ventral pattern immaculate (0), mottled (1), or laterally barred (2); 9: lateral fold bars absent (0) or present (1); 10: neonate pattern with broad dorsal stripe (0) or strong crossbands (1); 11: female head width broad (a) or narrow (b); 12: limb length short (a) or long (b).

Character		infernalis	ophiurus	liocephalus	Sample 19	Sample 20	lugoi
1.	Canthal/loreal series	0	0	1	1	0/1	0
2.	Supralabial number	0	0	1	1	0	0
З.	Preocular number	0	0	1	1	1	0
4.	Transverse dorsal number	1	0	0	1	1	0
5.	Longitudinal dorsal number	0	0	1	0	0	0
6.	Tail whorl number	1	0	0	?	?	1
7.	Dorsal crossband number	а	b	b	b	a	b
8.	Venter pattern	1	2	0	?	0	0
9.	Lateral fold bars	0	1	1	1	1	0
10.	Neonate pattern	1	?	0	?	?	?
11.	Female head width	a	b	b	?	?	?
12.	Limb length	а	b	а	?	?	?

Mexican populations should be recognized as a distinct subspecies within "G. liocephalus" (sensu lato), although he did not name it. Fig. 10 suggests a relationship of these populations (samples 19 and 20) to G. liocephalus (sensu stricto) on the basis of canthal/loreal number and preocular number. On the other hand, samples 19 and 20 differ from that taxon and from each other in several characters. It is impossible to determine with any certainty whether, on examination of further specimens, these populations will prove to be conspecific with G. liocephalus or to represent one or more distinct species. The best working hypothesis given the current state of knowledge of the distribution and variation in Gerrhonotus in western Mexico therefore is to tentatively assign them to G. liocephalus, but with the appropriate caveat.

Interestingly, Fig. 10 also suggests that "G. liocephalus" as recognized prior to this paper is paraphyletic: G. lugoi appears to be more closely related to the sympatric G. infernalis than G. infernalis is to G. ophiurus or G. liocephalus. This, however, is based on the single synapomorphy of a reduction in tail whorl number.

The inclusion of G. infernalis, G. ophiurus, and G. liocephalus into a single species dates to the work of Bocourt (1878), who provided no explicit reasons for combining them. This arrangement has been essentially unquestioned since Bocourt's time. The most detailed re-examination of the problem was by Tihen (1948) who concurred that conspecificity was the best arrangement. This was because, as discussed above, Tihen considered the subspecies *loweryi* to be morphologically intermediate between *infernalis* and *ophiurus* on the one hand and *liocephalus* and *austrinus* on the other. He also considered G.



FIG. 10.—The phylogenetic relationships among the species of *Gerrhonotus*. Samples 19 and 20 are included because of their uncertain specific affinities. Length = 16, CI = 0.70, RI = 0.70.

ophiurus to represent a continuation of a north-south cline seen in several characters in G. infernalis. Examination of a greater number of specimens than were available to Tihen demonstrates that both of these conclusions were incorrect. Tihen cited tail length, number of transverse dorsal scale whorls, and number of caudal scale whorls as characters in which loweryi agreed with liocephalus rather than with infernalis and ophiurus: in fact loweryi is indistinguishable from ophiurus in all of these characters. In addition, none of the characters Tihen listed as varying clinally from north to south in infernalis and ophiurus (tail length, caudal scale whorl number, dorsal crossband number, and ventral coloration) in fact can be shown to vary clinally.

Contreras Arquieta (1989) suggested that specimens from the Cuatro Ciénegas basin of Coahuila should be accorded subspecies status within "G. liocephalus" (sensu lato) because they have a cantholoreal scale and a distinctive color pattern. He coined the name aguayoi. Some (but not all) of the specimens from central Coahuila examined in the present study had a color pattern (see above) reminiscent of the brief description provided by Contreras Arquieta, but all of these had a canthal/loreal condition characteristic of G. infernalis. Without a more detailed examination of specimens from the Cuatro Ciénegas area, there does not appear to be sufficient evidence to warrant taxonomic recognition of aguayoi.

Further collecting will undoubtedly clarify relationships among populations of Gerrhonotus. However, the specimens available for this study suggest that the genus contains at least four species: G. lugoi, G. infernalis, G. ophiurus, and G. liocephalus. Western Mexican populations may or may not constitute additional species. Although there is no absolute evidence (such as a test of sympatry) of the genetic or evolutionary independence of these taxa, character distribution patterns suggest that they do not exchange genes and are on separate evolutionary trajectories. Therefore a multiple-species system is the best working hypothesis.

RESUMEN

En el presente artículo se demuestra que Gerrhonotus liocephalus debería separarse por lo menos en tres especies diferentes. Al presente, es considerada como especie polytípica. De las 7 subespecies que se reconocen con la nomenclatura actual, G. l. aguayoi, G. l. infernalis, y G. l. taylori emergen como G. infernalis; G. l. ophiurus y G. l. loweryi se emergen como G. ophiurus; y G. l. austrinus y G. l. liocephalus se mantienen en la misma taxonomía. No se reconoce ninguna subespecies dentro de los especies. Algunas poblaciones del oeste de México (Colima, Durango, Jalisco, y Sinaloa) siguen con una identidad insegura, pero provisionalmente se emergen como G. cf. liocephalus. Evidencia para esta conclusión es apovada por medio de un análisis del diseño de las escamas, coloración y variación morfométrica. También, se presenta una discución de la historia taxonómica del género Gerrhonotus.

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APPENDIX I

Specimens examined

Group 1 (G. infernalis): TEXAS: AMNH 8772, Guadalupe R., E San Antonio; AMNH 121170-71, New Braunfels, Comal Co. (may be questionable); ANSP 12875, Blanes?; ASU 8785, 2 mi E Kerrville at Legion, Kerr Co.; ASU 8786, 8788, 2.5 mi E Kerrville, Kerr Co.; ASU 8787, Echo Hills Ranch; ASU 23065-66, Dudley Johnson Dam, off Rte. 136, 0.4 mi from railway tressel, Hays Co.; ASU 23116, 23533-34, Rte. 136 at Dudley Johnson Dam, Kyle, Hays Co.; ASU 23117, 23121, 23127, 23274, River Rd. along Guadelupe R. N of New Braunfels, Comal Co.; ASU 23126, 23128, 23499, 23532, 26053-56, 16 mi S Kerrville off Rte. 16, Kerr/Bandera Co. line; ASU 26052, Red River Rd., Guadelupe R., Comal Co.; BMNH 89.7.3.24, 92.10.29.28, Duval Co.; CAS 74075-76, Helotes, Bexar Co.; CAS-SU 13919-20, 7 mi SW Austin, Travis Co.; CAS-SU 17725-26, Helotes, Bexar Co.; CM 6676, New Braunfels, Comal Co.; CM 36552, Comal Co.; CM 52194, Pedernales River, Travis Co.; EAL 437, 13 mi S Kerrville-Chaney Ranch, Kerr Co.; FMNH 37538, McNeil, Travis Co.; FMNH 106121, Helotes; FMNH 130990, Fern Bank Spring, Hays Co.; KU 9047: Helotes, Bexar Co.; LSUMZ 9304, Blanco Co. (probably Edwards Plateau); MCZ 43925, Georgetown; MCZ 43983, Austin; MVZ 39667, 12 mi N New Braunfels, Comal Co.; MVZ 75938, West Caves, Pedernales River, Hamilton's Pool, Travis Co.; MVZ 128079, Ley's Canyon, Travis Co.; MVZ 150322-24 Edwards Plateau region, W of Austin, Hays or Travis Co.; MVZ 198034, probably vicinity of Austin, Travis Co.; SDSNH 40957, San Antonio, Bexar Co.; SDSNH 66360, Fort Sam Houston, Salada Cr., Bexar Co.; SRSU 1222, 3 mi N Fredericksburg, Gillespie Co.; TCWC 168, 5 mi W Hunt,

Kerr Co.; TCWC 391, 22 mi S Junction, Edwards Co.; TCWC 449, Kerrville, Kerr Co.; TCWC 450, 8 mi NW Ingram, Kerr Co.; TCWC 1082, S Fork Guadalupe R. 20 mi SW Kerrville, Kerr Co.; TCWC 18107, Barton Creek, 10 mi W Austin, Travis Co.; TCWC 25395, Fern Bank Springs, near Wimberly, Hays Co.; TCWC 33092, 2 mi NE Liberty Hill, Williamson Co.; TCWC 46494, Mountain View Ranch (29°48'30"N, 98°10'45"W), Comal Co.; TCWC 60532, 60534, 60536, 60538-39, 4.3 mi NE Vanderpool, Hwy. 407; TCWC 63498, W Austin, Travis Co.; TCWC 60535, 60771, 4.3 mi NE Vanderpool, Hwy. 407, Bandera Co.; TNHC 1439, 2686-87, Austin, at mouth of Bee Creek near W end of Tom Miller Dam, Travis Co.; TNHC 1440-42, 1445, 5 mi SW Austin on Barton Creek, Travis Co.; TNHC 1675-76, 1819, 1940, 4294, 5869, 5 mi SW Austin on Barton Creek, Gaines Ranch, Travis Co.; TNHC 4295, Bexar Co.; TNHC 4570, Marshall Ford Dam, Travis Co.; TNHC 4571-72, 17 mi W Medina on Sutton Ranch, Bandera Co.; TNHC 4574, 30 mi NW Austin near mouth of Pedernales River, Travis Co.; TNHC 4575, 25 mi NW Austin near mouth of Pedernales River, Travis Co.; TNHC 4576, 2 mi W Wimberley on Blanco River, Hays Co.; TNHC 4826, 4902-04, 18989-93, 5 mi SW Austin on Gaines Ranch, Travis Co.; TNHC 5948, 12 mi W Austin on Barton Creek, Travis Co.; TNHC 8883, Austin, Mt. Barker at Dry Creek, Travis Co.; TNHC 9223, 11909, 4 mi SSW Austin on Gaines Ranch, Travis Co.; TNHC 11929-30, 8.3 mi S and 2.5 mi W Kerrville on Ml. Pampbell Ranch [sic], Kerr Co.; TNHC 12285, 30 mi W Austin at Pedernales River, Travis Co.; TNHC 13258, Austin, Barton Creek, Travis Co.; TNHC 18987-88, 1 mi NW Austin, Travis Co.; TNHC 18994, 12 mi W Austin; TNHC 20543, 5 mi NW Helotes in cabin near Inactive Creek, Bexar Co.; TNHC 21192, near Dade City, Travis Co.; TNHC 21639, Real, Bonner Ranch, Real Co.; TNHC 23140, Austin, in town, Travis Co.; TNHC 28543, Elgin, in town, Bastrop Co. ("probably transported to this area"); TNHC 42613-19, Hammett's Crossing, Martin property, Travis Co.; TNHC 42775, Austin, Williamson Creek between IH35 and S Congress Ave., Travis Co.; TNHC 42971, Spicewood Springs Rd. near where Bull Creek crosses the 2nd time on way from Austin, Travis Co.; TNHC 50464: Barton Springs, Austin, Travis Co.; UCM 7902, 7 mi N New Braunfels, Guadelupe Co.; UF 4090-92, near Austin, Travis Co.; UF 55814, Austin, Travis Co.; USNM 13636, 37057, Helotes, Bexar Co.; USNM 33830, San Marcos, grounds of USFC, Hays Co.; USNM 58665, Travis Co.; USNM 59401, Georgetown, Williamson Co.; USNM 132044, San Antonio, Bexar Co.; UTA 1613, 6.3 mi NE Wimberly, Hays Co.; UTA 2070, Hamilton, Pedernales River near pool, Travis Co.; UTA 2141, Georgetown, Williamson Co.; UTA 2154, N shore Lake Austin, wooded hillside, Travis Co.; UTA 5592, 17.5 mi W Lampasas at Colorado River, Gorman Falls Camp, San Saba Co.; UTA 10290, "hill country"; UTA 10343, 3.0 mi S & 1.7 mi E Bend, Gorman Falls Camp, San Saba Co.; UTA 25905-06, FM 337, 9.0 km W jct. FM 187 (1.8 km W Jct West Sabinal River, Real Co.; UTA

25907–09, ca. 8 km NW Boerne, Kendall Co.; UTA 25910, N side Austin, near Decker Lake, Travis Co.; UTA 25911, Austin, jct. Rabb Rd. and Robert E. Lee Rd., Travis Co.; UTEP 2968, Near Austin, Travis Co.

Group 2 (G. infernalis): TEXAS: AMNH 62598, Chisos Mts., base of Emory Peak, Brewster Co.; AMNH 72638, 73556, Chisos, Pulliam Canyon, Brewster Co.; AMNH 112126, Chisos Basin, Big Bend National Park, Brewster Co.; AMNH 112127, Chisos Basin water tower, Big Bend National Park; FMNH 22992, 27699, 38172-73, Chisos Mts., Brewster Co.; FMNH 23788, 23803, State Park 33, Chisos Mts.; FMNH 26627, The Basin, Big Bend, Chisos Mts., 5200 ft.; FMNH 27481, probably Brewster Co.; FMNH 27482, Casa Grande, Chisos Mts., Brewster Co., 5500 ft.; FMNH 27483, 27487-89, 27490, Oak Creek, Chisos Mts., Brewster Co., 5200 ft.; FMNH 27484-85, 27491, The Basin, Chisos Mts., Brewster Co., 5200 ft.; KU 176653, Big Bend National Park, Chisos Mts., Brewster Co.; KU 176654, Big Bend National Park, 7.8 km S jct. Rte. 118 and Green Gulch Rd., Brewster Co.; MSB 6015, Upper Green Gulch, Chisos Mts., Brewster Co.; MSB 6391, south rim (western), Chisos Mts., Brewster Co., 7300 ft.; MSB 6392, slope SE Laguna, Chisos Mts., Brewster Co., 7000 ft.; MSB 6393, Green Gulch, Chisos Mts., Brewster Co., 5900 ft.; MSB 9310, wash just below hairpin turn, Green Gulch, Brewster Co., 5500 ft.; MSB 23644, Big Bend National Park, 0.25 mi N of campground, The Basin, Chisos Mts., Brewster Co., 5450 ft.; MSB 23645, Big Bend National Park, road junction to campground, The Basin, Chisos Mts., Brewster Co., 5400 ft.; MSB 23646, Big Bend National Park, Basin Rd. at Campground Jct., The Basin, Chisos Mts., Brewster Co., 5350 ft.; MSB 23647, Big Bend National Park, Upper Green Gulch, Chisos Mts., Brewster Co., 5250 ft.; MVZ 18942, Green Gulch, Chisos Mts., Brewster Co., 5500 ft.; MVZ 21227-29, head Oak Creek Canyon, Chisos Mts., Brewster Co., 5200 ft.; MVZ 24847, The Basin, Chisos Mts., Big Bend, Brewster Co., 5600 ft.; MVZ 25361, 2 mi N Rock Spring, Chisos Mts., Brewster Co.; SAM 457, Chisos Mts. near base of Emory Peak, Brewster Co.; SAM 460, Chisos Mts., Laguna Meadow, Brewster Co.; SRSU 345, Big Bend National Park at Boot Springs, Brewster Co.; SRSU 865, Big Bend National Park, The Basin, Brewster Co.; SRSU 867, Big Bend National Park, Window Trail, Brewster Co.; SRSU 1165, Big Bend National Park, Chisos Mts., Brewster Co.; SRSU 2548, Big Bend National Park, Upper Green Gulch, Brewster Co.; SRSU 3538, Big Bend National Park, South Rim Trail, Brewster Co.; SRSU 3896, Big Bend National Park, Emory Peak cut-off trail, Brewster Co.; SRSU 3918, Big Bend National Park, Lost Mine Trail, Brewster Co.; SRSU 5911, 12.5 mi SE Alpine, Del Norte Mts., Brewster Co.; TCWC 1166, 5601, The Basin, Chisos Mts., Brewster Co., 5600 ft.; TCWC 11684, The Basin, Chisos Mts., Big Bend National Park, Brewster Co.; TCWC 16110, 16112, Boot Spring Canyon, Chisos Mts., Brewster Co.; TCWC 16111, Lower Boot Canyon, Chisos Mts., Brewster Co.; TCWC 16114, South of Flat Top, Chisos Mts., Brewster Co.; TCWC 16116, Basin, Big Bend National Park, Brewster Co.; TCWC 33111, 0.5 mi S Boot Spring, Big Bend National Park, Brewster Co.; TCWC 35500, The Basin, Big Bend National Park; TNHC 28079-83, Big Bend National Park, Brewster Co.; UCM 14551, Big Bend National Park, Chisos Basin cabin area, Brewster Co.; UCM 14552-53, Big Bend National Park, Juniper Flat Rd. near cabin area, Chisos Mts., Brewster Co.; UIMNH 19522, Mount Emory, Chisos Mts., Brewster Co., 6000 ft.; USNM 32840, Chisos Mts., Brewster Co.; USNM 103636, Chisos Mts., Basin, Brewster Co., 5200 ft.; USNM 103660, Chisos Mts., Wade Canyon, Brewster Co., 6500 ft.; USNM 312861, Brewster Co.; UTA 401, 2024, Chisos Mts., Brewster Co.; UTA 910-12, between Laguna Meadow and Boot Springs, Chisos Mts., Brewster Co.; UTEP 10656, Big Bend National Park, Green Gulf Canyon at top of Chisos Basin Rd., Chisos Mts., Brewster Co.

- Group 3 (*G. infernalis*): COAHUILA: KU 39940, 5 mi N and 7 mi W Acebuches, Sierra del Pino; MSB 20078, 23642–43, ca 4 mi E and 1 mi N San Ysidro Mine, Sierra del Carmen, Frontereza Range; USNM 103700–05, Carbonero Canyon, Carmen Mts.
- Group 4 (G. infernalis): COAHUILA: ASU 22185, Canyon de la Hacienda, Sierra Madera, NW of Cuatro Ciénegas; CM 118619, Rio Churince, Cuatrocienegas Basin; FMNH 48528-30, 167099, Monclova, Sierra de la Gloria; JFBM 2683, 6.1 mi from Cuatro Ciénegas; KU 33588, 22 mi S and 5 mi W Ocampo, 6200 ft.; KU 37724, 6 mi E Hermanas; KU 39941-44, 4 mi N and 2 mi W Cuatro Cienegas; TCWC 57086, 13.5 mi S, 14.7 mi W Ocampo, ca. 6000 ft.
- Group 5 (G. infernalis): COAHUILA: USNM 248108, 13 km ESE Saltillo, 2300 m (25°22'N, 100°53'W). NUEVO LEON: CAS 87132, 12 mi SSE Galeana, 6400 ft.; EAL 4246, 4259-60, Cumbres de Monterrey, 2.6 mi NE La Ciénega; EAL 4249, Cumbres de Monterrey, 3.4 mi NE La Ciénega; EAL 4759, 4.9 mi SW Zaragosa; FMNH 30702, Horsetail Falls, Santiago; FMNH 30704, Ojo de Agua, near Galeana; KU 87742, 3 mi SW La Escondida, 6300 ft.; KU 92618, La Meseta de Chipinque; KU 92619, Chipinque (100°21'W, 25°37'N), 1356 m. TAMAU-LIPAS: SDSNH 52731, 19 mi N Tula; TCWC 49465, 3.5 mi WNW Gavilan, (24°44'N, 99°01'W); TCWC 52505, 52511, 52513, 52515-17, 52519-20, 9.1 mi (rd.) W Palmillas, on Hwy. 101, 5975-6000 ft.; TCWC 52510, 21 mi (rd.) W Palmillas, on Hwy. 101, 5975-6000 ft.
- Group 6 (*G. infernalis*): SAN LUIS POTOSI: ANSP 20045, Alvarez Mts. at Km. 42, Potosi–Rio Verde R.R.; ANSP 28778, Alvarez (formerly MCZ 24522); MCZ 8337–38, 19060, 19062–64, 24510–11, 24513, 24515–17, 24519–21, Alvarez.
- Group 7 (G. ophiurus): HIDALGO: FMNH 34396, Jacala. QUERETARO: TCWC 29618, 4 mi W El Madrono 5400-5600 ft.; TCWC 33091, 3.8 mi W El Lobo, 5900 ft.; TCWC 40688, 12.4 mi WSW San Joaquin. SAN LUIS POTOSI: CM 41517, Xilitla region (Paratype of G. l. loweryi, formerly LSUMZ 483); CM 41518, 6 mi W Ahuacatlán, 5400 ft. (formerly LSUMZ 4955); CM 65824, Xilitla region (formerly LSUMZ 612); KU 24063-66, Xilitla

region (Paratypes of G. l. loweryi, formerly LSUMZ 484, 476, 474, and 486); KU 24067, Xilitla region (formerly LSUMZ 613); LSUMZ 472-73, 475, 477-79, 481-82, 485, 485a, 487, Xilitla region (Paratypes of G. l. loweryi); LSUMZ 480, Xilitla region (Holotype of G. l. loweryi); LSUMZ 480, Xilitla region (Holotype of G. l. loweryi); LSUMZ 488, Ciudad del Maiz; LSUMZ 614, Xilitla region; LSUMZ 4953-54, 4956-57, 6 mi W Ahuacatlán, 5400 ft.; LSUMZ 4958, Birmania, 3 mi S of Valles, 300 ft.; TCWC 29617, 5 mi E El Lobo, 4500 ft.; TCWC 35604, 33.8 mi W Valles, 2500 ft.; UIMNH 51208, Tamazunchale.

- Group 8 (G. ophiurus): VERACRUZ: BMNH 56.4.17.6, Cordova; NMW 25005, Orizaba; SAM 878, 1.5 mi N Zapotalillo; USNM 12245, Mirador; USNM 30206, Orizaba (Holotype of G. ophiurus); USNM 113219, Cerro Gordo; USNM 224806, Cuautlapan; ZMH R03936, Jalapa.
- Group 9 (G. liocephalus): PUEBLA: UIMNH 19520,
 Km. 226, Tehuacan; USNM 113216, Cacaloapan;
 UTA 4715, 1 mi N Cacaloapan, 7400 ft. VERA-CRUZ: MVZ 76326, 2 mi S Acultzingo.
- Group 10 (G. liocephalus): VERACRUZ: UTA 3360, ca. 2 mi NE Catemaco, north side Lago Catemaco.
- Group 11 (G. liocephalus): GUERRERO: BMNH 1913.7.19.103, Amula; CM 52764, SW Amojileca, SW Chilpancingo; MCZ 33749, Chilpancingo; MCZ 42719, Omilteme, Sierra de Burros; MVZ 45006– 07, near Chilpancingo; TCWC 8585, 9896, Acahuizotla, 2800 ft.
- Group 12 (G. liocephalus): OAXACA: AMNH 93210, 2 mi E Ixtlan de Juarez, 7000 ft.; AMNH 93211, El Tejocote (ca. 30 mi NW Oaxaca de Juarez), 7600 ft.; AMNH 93212, 2 mi E Ixtlan de Juarez, 7200 ft.; AMNH 100723-27, Tejocotes, 7200 ft.; AMNH 100728, 1.5 mi E Ixtlan de Juarez (Vivero Rancho Teja), 7300 ft.; AMNH 102726-30, Disto. de Etla, Tejocotes, 7400-7700 ft.; AMNH 102731, near Tejocotes, Rio Negro, ca. 7000 ft.; AMNH 102732, Disto. de Etla, Tejocotes, 7900 ft.; AMNH 102733, Tejocotes; AMNH 106722-25: Tejocotes, 7500 ft.; AMNH 106726-29, ridge W Tejocotes, 8100 ft.; AMNH 106730-31, Tejocotes, 7200-8000 ft.; AMNH 106733, Tejocotes, 7400 ft.; AMNH 106734-39, 9 mi N San Juan del Estado, 8000 ft; AMNH 106740-41, 2 mi NE El Estudiante, 7200 ft.; AMNH 106742-47, 1.5 mi E Ixtlán de Juárez, 7400 ft.; AMNH 110618-19, 1.5 mi E Ixtlán de Juárez, 7300 ft.; AMNH 110620, Distrito de Ixtlán, 1.4 mi E Ixtlán de Juárez, 7300 ft.; MSB 41654-55, Distrito de Etla, Tejocotes, 7600-7900 ft.; USNM 46748, Valley of Oaxaca, 9000 ft.; UIMNH 63666, 63667-68, 73588-89, Cerro San Felipe; UTA 4232, 5644, 6064-69, 6104-05, 7626, 9858, 10276 (7400 ft), 12221-26, 13606-10, 19681-84, 22560-73, 27035-38, El Tejocote.
- Group 13 (G. liocephalus): OAXACA: AMNH 68125, Cerro Arenal, near Tenango; AMNH 102735–36,

Juquila, Mixes; MNHN 6135, Tehuantepec; MSB 22753, Distrito de Yautepec, 9 mi SW San Carlos Yautepec, 6500 ft.; UCM 44530, Tehuantepec, Lachiguiri, Cerro de Lachiguiri, 7000 ft.; UIMNH 8633, 10 mi SW Miahuatlan; UIMNH 8634, Tenango, near Tehuantepec; UIMNH 19521, Llano Ocotal; UIMNH 35527, Santo Domingo Chontecomatlan; UIMNH 46733–34, Cerro Jacal, San Bartolo, Yautepec, 5000 ft.; UIMNH 73590, Rio Sal, Lachao, Juquila; UIMNH 73594, Tres Cruces, Tehuantepec; USNM 113217, Tres Cruces; USNM 113218, La Concepcion.

- Group 14 (*G. liocephalus*): OAXACA: AMNH 66891, El Palmar, Cerro Atravesado; UCM 41063, Sierra Madre, NW Zanatepec; UIMNH 40928, between Cerro Atravesado and Cerro Azul; UIMNH 56865, Sierra Madre, N Zanatepec; UTA 8784, Cerro Baul, ca. 19 km NW Rizo de Oro, Chiapas.
- Group 15 (*G. liocephalus*): CHIAPAS: AMNH 71396, El Otatal, Tuxtla Gutierrez; UIMNH 52087, Cerro de Sumidero, Tuxtla Gutierrez, 1200 m.
- Group 16 (G. liocephalus): CHIAPAS: UMMZ 94921: Cerro Malé, 3200 m (Holotype of G. l. austrinus).
- Group 17 (G. infernalis): CHIHUAHUA: AMNH 67918, Clarines Mine, ca. 5 mi W Santa Barbara, 6800 ft. (Holotype of G. liocephalus taylori); AMNH 68235, Santa Barbara, 6300 ft. (Paratype of G. l. taylori).
- Group 18 (G. infernalis): DURANGO: ANSP 20129, Sierra Guadelupe, La Cuchilla Station, 7500 ft.; TCWC 35499, 74.4 mi SW Torreon, Hwy. 31.
- Group 19 (G. cf. liocephalus): DURANGO: UTEP 4562, 2 mi N Pueblo Nuevo, Municipio El Salto, 6000 ft.; UTEP 4563, 6 mi SE Llano Grande, Municipio Durango, 6800 ft. SINALOA: KU 78904, 19.2 km NE Santa Lucía, 1940 m.
- Group 20 (G. cf. liocephalus): COLIMA: MVZ 197549:
 vicinity of Colima. JALISCO: CM 65825, 40 mi N
 Hwy. 80 on Hwy. 200; MVZ 205566, 53 km NW
 (by Mexico Hwy. 200) of jct. Mexico Hwy. 80.
- Other specimens examined: Gerrhonotus infernalis: KU 33587, El Río Alamos en Cañon Mulato, Las Margaritas, 3500 ft.; MNHN 5140, 1888.277, Guanajuato; UOMZ 30391, Texas; USNM 3090, Devil's River, Texas (Holotype of G. infernalis); USNM 47136, Sierra Encarnacion; ZMB 1154, Texas. Gerrhonotus liocephalus: AMNH 106732, near summit Cerro Guirone, Disto. Tlacolula, 8100 ft.; ANSP 9026-27, mining districts of Mexico (Syntypes of Scincus ventralis); ZMB 1153 (Holotype of G. liocephalus); MVZ 10323, Oaxaca. Gerrhonotus lu-goi: ASU 8818, "rastro municipal," 2.7 km SW Cuatro Ciénegas de Carranza, Coahuila, 740 m (Paratype of G. lugoi); TCWC 55258, 4.2 mi W Ocampo, Coahuila. Gerrhonotus ophiurus: MNHN 1151; locality unknown (Syntype of G. lemniscatus).

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