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KARYOTYPES OF THE BASILISCINE LIZARDS *CORYTOPHANES CRISTATUS* AND *CORYTOPHANES HERNANDESII*, WITH COMMENTS ON THE RELATIONSHIP BETWEEN CHROMOSOMAL AND MORPHOLOGICAL EVOLUTION IN LIZARDS

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ABSTRACT: We have analyzed the karyotypes of two species of the lizard genus *Corytophanes* of the family Iguanidae. The karyotypes of *C. cristatus* and *C. hernandesii* are very similar to each other and to the closely related *Basiliscus vittatus*. They consist of 2N = 36 chromosomes, including six pairs of metacentric macrochromosomes and 12 pairs of microchromosomes. Our karyological data are compared with those reported for other iguanids, and the significance of karyological change in the evolution of lizard morphology is discussed.

Key words: Reptilia; Lacertilia; Iguanidae; *Corytophanes*; Karyotype; Chromosomes; Morphology; Evolution

LIZARDS of the large family Iguanidae have been well studied karyologically. However, the karyotypes of many groups within the family are known for only one or a few species (Paull et al., 1976). This dearth of information has weakened phylogenetic inferences based upon karyological data. Karyotypes of additional species, particularly from poorly studied groups, are needed if a general understanding of chromosomal evolution is to emerge.

The genus *Corytophanes*, which includes three Central American species (Peters and Donoso-Barros, 1970), is thought to be most closely allied to *Basiliscus* (four species; Maturana, 1962), and *Laemanctus* (two species; McCoy, 1968), together referred to as "basiliscines" (Etheridge, 1964; Gorman, 1973). Basiliscines are morphologically unusual lizards and are unique among iguanids in possessing a cranial crest. The species of *Corytophanes* have a particularly derived morphology characterized by lateral compression of the body, a head casque, and an especially pronounced cranial crest supporting unusually elongated adductor musculature (Schwenk, 1980).

Gorman et al. (1967) described a karyotype of 12 bi-armed macrochromosomes and 24 microchromosomes for *Basiliscus vittatus*, the only basiliscine karyotyped to date. Here we describe the karyotypes of *Corytophanes cristatus* and *Corytophanes hernandesii*, and we comment on the relationship between chromosomal and morphological evolution in lizards.

MATERIALS AND METHODS

One female of each species was sacrificed for karyotypic analysis. The *C. cristatus*, purchased from a dealer, was thought to have originated from the north coast of Honduras. The *C. hernandesii* was collected by the senior author in coastal rainforest at La Playa Escondida, Sierra de Los Tuxtlas, Veracruz, Mexico. Animals will be deposited as osteological specimens in the Museum of Vertebrate Zoology, University of California, Berkeley.

Each female was given an intraperitoneal injection of 1.0% colchicine (0.3 cc per 10 g body weight) 5 h before killing with an overdose of sodium pentabarbitol. Cell suspensions of bone marrow, spleen and intestinal epithelium were prepared, but only bone marrow yielded usable cells in metaphase of mitosis. These cells were prepared by flushing the

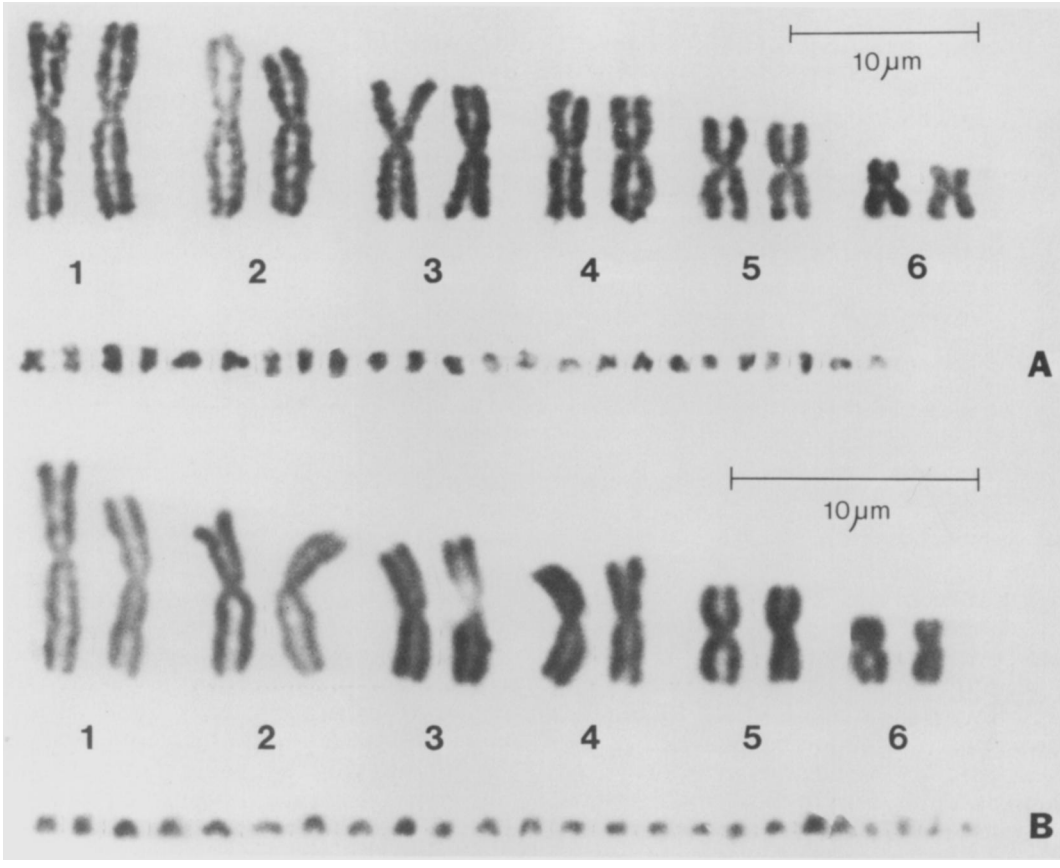

FIG. 1.—Karyotypes of female *Corytophanes*. (A) *C. cristatus*, catalogue number KS 8; (B) *C. hernandesii*, catalogue number KS 9. Karyotypes are to different scales due to differential states of contraction in the chromosomes figured.

contents of the long bones with 0.075 M KCl. The suspension was incubated at 37 C for 5 min and then centrifuged for 5 min. The supernatant was disposed of and cells were fixed in methanol-acetic acid (3:1). After gentle mixing, the suspension was centrifuged again. Centrifuging and mixing were repeated twice more using fresh fixative each time. Three drops of the resulting cell suspension were dropped onto slides taken from a bath of chilled distilled water. The slides were placed at a steep angle so that the suspension would spread across their surfaces. After three days of air drying, slides were stained with Giemsa.

Hundreds of cells were examined, and 114 were photographed. Measurements of chromosome arms were made on seven of the best spreads from *C. cristatus* and 11 from *C. hernandesii*. Relative lengths of the chromosomes were calculated for three and four cells, respectively. Karyotypes were prepared from photographs, and an idiogram was constructed. Terminology for centromere position is that of Levan et al. (1964), as modified by Green et al. (1980), except where noted.

RESULTS

In both *C. cristatus* and *C. hernandesii*, the diploid number of chromosomes is 36, with 12 metacentric macrochromosomes and 24 microchromosomes (Fig. 1).

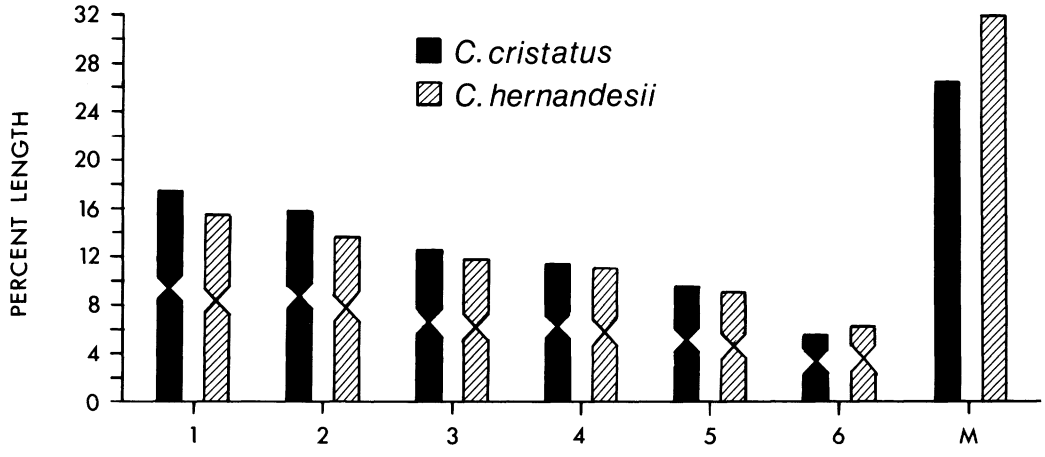

FIG. 2.—Idiogram of *Corytophanes* chromosomes based on data in Table 1. The vertical scale indicates the percentage length of the total haploid genome. 1–6 = number of macrochromosome (see Fig. 1); M = total contribution of microchromosomes.

Table 1 lists quantitative characteristics of the chromosomes and an idiogram made from these measurements compares the karyotypes directly (Fig. 2). Arm ratios of homologous chromosomes are remarkably similar in the two species. The relative contributions to the total haploid genome of homologous chromosomes are also seen to be very similar. However, with the exception of chromosome number 6, the macrochromosomes of *C. cristatus* are slightly larger. This results in a relatively greater contribution of the microchromosomal complement in *C. hernandesii*. While it is possible that these differences in length reflect real differences between the genomes, we believe them to be largely the result of artifact in measurement. Chromosome preparations of *C. hernandesii* were uniformly less sharp than those of *C. cristatus*. The poorly resolved edges of the chromosomes in these preparations would result in an overestimation of length during measurement. The resulting error would be greatest in the microchromosomes due to their small size, and hence would lead to an exaggeration of their relative contribution, with a concomitant reduction in the relative contribution of the macrochromosomes in *C. hernandesii*.

Resolution of the microchromosomes is not sufficient to allow detailed comparison; however, some interspecific differences are noticeable. In *C. cristatus*, at least five pairs of microchromosomes are bi-armed, whereas in *C. hernandesii*, only one pair is definitely so. Whatever the exact number of metacentric microchromosomes in each, it is clear that telocentrics are more numerous in *C. hernandesii*.

TABLE 1.—Quantitative characteristics of *Corytophanes* chromosomes. Arm ratio = length of long arm/length of short arm. Centromere position as defined by Levan et al. (1964); m = median (metacentric); *Cc* = *Corytophanes cristatus*; *Ch* = *Corytophanes hernandesii*.

Chromosome number	Percent length of haploid genome		Arm ratio		Centromere position	
	Cc	*Ch*	*Cc*	*Ch*	*Cc*	*Ch*
1	17.4	15.6	1.12	1.16	m	m
2	15.9	13.7	1.22	1.35	m	m
3	12.8	11.9	1.06	1.10	m	m
4	11.6	11.2	1.12	1.13	m	m
5	9.7	9.2	1.12	1.11	m	m
6	5.8	6.3	1.40	1.41	m	m
Microchromosomes (total)	26.7	32.1	—	—	—	—

Small differences between *C. cristatus* and *C. hernandesii* in relative lengths of homologous chromosomes are likely to be due to measurement artifact, hence we regard the karyotypes to be essentially identical in this respect. In contrast, it is possible that differences in microchromosome morphology represent species-level divergence, although their significance is unknown.

Discussion

The karyotypes of *C. cristatus* and *C. hernandesii* are very similar to that reported for *Basiliscus vittatus* by Gorman et al. (1967). Other than the slight variation in microchromosomal morphology noted above, the karyotypes are virtually indistinguishable. However, karyotypes of 12 metacentric macrochromosomes and 24 microchromosomes are extremely widespread among lizards and may be primitive for the family Iguanidae (Gorman et al., 1967, 1969; see also Paull et al., 1976); thus little phylogenetic information may be extracted from these data. Nonetheless, the presence of a primitive, or at least widespread, karyotype in such morphologically derived lizards as *C. cristatus, C. hernandesii* and *B. vittatus* suggested to us the possibility that morphological evolution may proceed independently of chromosomal change in these lizards. This is in contrast to statements in the literature, discussed below.

Wilson et al. (1974, 1975, 1977) suggested that morphological evolution and gene rearrangement are causally linked. Their conclusion was based upon a comparison of frogs and mammals, in which they demonstrated that chromosomal and morphological evolution had proceeded in mammals at 20 times the rate it had in frogs. They speculated that chromosomal rearrangements might disrupt regulatory systems controlling gene expression; an accumulation of such changes would promote morphological evolution. Wilson et al. (1974) predicted that the number of rearrangements should be correlated with the degree of morphological evolution within a lineage and that morphologically conservative forms should show less change from an ancestral karyotype than morphologically derived forms.

Lande (1979), however, concluded that chromosomal rearrangements are not a major cause of morphological change, contrary to the hypothesis of Wilson et al. (1974, 1975, 1977). Cherry (1980) showed that chromosomal and morphological evolution in frogs and primates are not correlated if one considers evolution within single lineages and suggested that karyotypic and morphological evolution proceed independently.

We believe that morphological evolution may be similarly uncoupled from chromosomal evolution in lizards. A consideration of the family Iguanidae yields two lines of circumstantial evidence that support this hypothesis. (1) Lizards of extremely different morphologies, including highly derived forms, share a common, possibly primitive, karyotype; and (2) lizards of more or less uniform morphology (as in a single genus) may vary widely in karyotype.

Appendices I and II list species that correspond to these categories. A large number of iguanid species share a karyotype with 2N = 36 chromosomes, essentially identical to those illustrated here for *Corytophanes* (Appendix I). This list will likely grow when additional species are karyotyped. Furthermore, if one wishes to include, as basically similar, a karyotype of 2N = 34 chromosomes (involving either the loss or the fusion of a single pair of microchromosomes), one could append an additional eight genera, including the remaining species of *Phrynosoma,* some *Sceloporus,* and the rest of the sceloporines. Even without such an addition, this list includes such morphologically disparate forms as *Corytophanes, Sauromalus* and *Phrynosoma.*

In contrast, the three genera listed in Appendix II are remarkably speciose; each is characterized by an equally re-

markable array of karyotypes. It is evident that this extensive chromosomal rearrangement has not been attended by similarly extensive morphological change.

While we have not attempted to quantify the degree of morphological difference alluded to, we believe that the relative divergence apparent among forms in Appendix I is sufficiently great relative to the intrageneric variation of *Anolis*, *Sceloporus* and *Liolaemus* (Appendix II) that such an assessment is unnecessary. Indeed, the taxonomy itself suggests that this is the case. Systematic analyses of the Iguanidae have traditionally been based upon morphology, particularly osteology (see Etheridge, 1960, 1964, 1967; Savage, 1958). Thus generic and species-level distinctions have been made largely or entirely on morphological grounds. As genera in such a taxonomy are aggregates of morphologically similar species, the high number of genera in Appendix I, encompassing, in total, fewer than 100 species (Gorman, 1973; Paull et al., 1976), reflects the presence of frequent, large morphological gaps among forms with nearly identical karyotypes. In contrast, *Anolis*, *Sceloporus* and *Liolaemus* are each very speciose, including well over 300 species among them (Paull et al., 1976). The inclusion of so many species within each karyologically diverse genus suggests relatively uniform morphology compared to the generic level gaps noted above.

While some link between speciation and chromosomal rearrangement is likely (Bush et al., 1977; Paull et al., 1976), there appears to be no correlation between karyotypic and morphological divergence within the Iguanidae. The predictions of Wilson et al. (1974) are not supported by these observations. We conclude that chromosomal and morphological evolution proceed within this family as independent processes. Although other large lizard families remain less well known karyologically, a cursory examination of karyotypes and morphologies suggests that a similar lack of concordance exists. Hence it is possible that this conclusion can be generalized to the entire suborder.

Chromosomal banding studies in lizards may resolve rearrangements not now apparent, even in those forms with superficially identical karyotypes. For example, White (1973) suggested that the widespread 36-chromosome karyotype in iguanids might be the result of "karyotypic orthoselection," representing a particularly stable structural configuration, or "equilibrium karyotype" that has been repeatedly acquired in a number of lineages. Thus, any number of non-homologous rearrangements may have led to structurally similar karyotypes. It is also possible that identical-looking 2N = 36 karyotypes have been generated by changes in centromere position as a stochastic process, in the absence of any selection. If centromere position can change frequently or at random in a chromosome, then a karyotype of all bi-armed metacentric chromosomes is the expected configuration (Imai and Maruyama, 1978). Once again, numerous rearrangements could be obscured by apparently similar karyotypes. Although the observed patterns of chromosomal and morphological diversity within the Iguanidae remain convincing, these theoretical considerations are real possibilities and point to the need for more banding data.

Given information about the morphology of a lizard in a particular lineage (i.e., primitive vs. derived, generalized vs. specialized), one can make no prediction about its karyotype. The converse, of course, is also true. Additional evidence from other animal groups such as frogs (Bogert, 1970, 1981*a*,*b*), bats (Baker and Bickham, 1980) and muntjacs (Fredga, 1977) shows that extremely large chromosomal changes are frequently not reflected in morphological differences among closely related congeners. Data for lizards, frogs and mammals suggest that chromosomal rearrangement is not nec-

essarily a causal factor in morphological evolution.

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APPENDIX I

Species listed here share a nearly identical 2N = 36 (12V + 24m) karyotype yet embrace a wide range of morphologies, as reflected in the large number of genera included (see text for discussion). Based on data in Gorman's (1973) review, except where noted. 2N = diploid chromosome number; V = bi-armed macrochromosomes; m = microchromosomes.

Anolis allisoni, A. arenteolus, A. bartschi, A. blanquillanus[a], *A. bonairensis, A. carolinensis, A. chlorocyanus, A. coelestinus, A. cuvieri, A. cybotes, A. equestris, A. hendersoni, A. luciae, A. lucius, A. maynardi, A. occultus, A. olssoni, A. porcatus, A. richardi, A. ricordi, A. semilineatus, A. trinitatis, Basiliscus vittatus, Chamaeleolis porcus, Conolophus subcristatus*[b], *Corytophanes cristatus*[c], *C. hernandesii*[c], *Crotaphytus collaris, Ctenosaura pectinata, Cyclura cornuta, Dipsosaurus dorsalis, Enyalioides* sp.[b], *Gambelia* (*Crotaphytus*) *silus, G. wislizenii, Leiocephalus schreibersi, Oplurus sebae, Phenacosaurus heterodermus, Phrynosoma cornutum, Pristidactylus* (*Cupriguanas*) *achalensis, Sauromalus ater*[d], *S. hispidus*[d], *S. obesus, S. varius*[d], *Tropidurus albemarlensis*[b], *T. delanonis*[b], *T. duncanensis*[b], *T. torquatus*

[a] Gorman and Stamm (1975).
[b] Paull et al. (1976).
[c] This study.
[d] Robinson (1974).

APPENDIX II

In contrast to the species listed in Appendix I, species of *Anolis, Sceloporus* and *Liolaemus* encompass a wide range of karyotypes, yet are intragenerically uniform in morphology (see text for discussion). For brevity, an older notation is used to describe karyotypes. Based on data in Gorman's (1973) review, except where noted. 2N = diploid chromosome number; V = bi-armed macrochromosomes; I = uni-armed macrochromosomes; M = unspecified macrochromosomes; m = microchromosomes; X,X_1,X_2,Y = sex chromosomes.

Species	Karyotype
Anolis acutus	2N = 31, 14V + 14m + X_1X_2Y (♂)
A. aeneus	2N = 34, 12V + 22m
A. auratus	2N = 30, 14V + 16m
A. bimaculatus	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
	2N = 30, 12V + 6I + 8m + $X_1X_1X_2X_2$ (♀)
A. biporcatus	2N = 29, 12V + 14m + X_1X_2Y (♂)
	2N = 30, 12V + 14m + $X_1X_1X_2X_2$ (♀)
A. capito	2N = 40, 24M + 16m
A. chrysolepis	2N = 30, 14V + 16m
A. conspersus	2N = 30, 13V + 1I + 16m (♂)
	2N = 30, 14V + 16m (♀)
A. cooki	2N = 29, 16V + 10m + X_1X_2Y (♂)
A. cristatellus	2N = 27, 16V + 8m + X_1X_2Y (♀)
A. cupreus	2N = 40, 24M + 16m
A. distichus	2N = 33, 14V + 16m + X_1X_1Y (♂)
	2N = 34, 14V + 16m + $X_1X_1X_2X_2$ (♀)
A. evermanni	2N = 26, 14V + 10m + XY/XX (♂/♀)
A. ferreus	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
	2N = 30, 12V + 6I + 8m + $X_1X_1X_2X_2$ (♀)

APPENDIX II.—Continued.

Species	Karyotype
A. fuscoauratus	2N = 40, 24M + 16m
A. garmani	2N = 30, 14V + 16m
A. gingivinus	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
	2N = 30, 12V + 6I + 8m + $X_1X_1X_2X_2$ (♀)
A. gracilipes	2N = 36, 8V + 12I + 16m
A. grahami	2N = 32, 12V + 4I + 16m
A. gundlachi	2N = 29, 16V + 10m + X_1X_2Y (♂)
A. homolechis	2N = 28, 14V + 14m
A. humilis	2N = 40, 24M + 16m
A. jacare	2N = 32, 12V + 20m
A. krugi	2N = 29, 16V + 10m + X_1X_2Y (♂)
A. leachi	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
	2N = 30, 12V + 6I + 8m + $X_1X_1X_2X_2$ (♀)
A. limnifrons	2N = 40, 24M + 16m
A. lineatopus	2N = 30, 14V + 16m
A. lineatus	2N = 30, 14V + 16m
A. lionotus	2N = 40, 24M + 16m
A. lividus	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
	2N = 30, 12V + 6I + 8m + $X_1X_1X_2X_2$ (♀)
A. luteosignifer	2N = 28, 14V + 14m
A. marmoratus	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
	2N = 30, 12V + 6I + 8m + $X_1X_1X_2X_2$ (♀)
A. mestrei	2N = 28, 14V + 14m
A. monensis[a]	2N = 29, 16V + 10m + X_1X_2Y (♂)
A. monticola	2N = 48, 24I + 24m
A. nebulosus	2N = 30, 13V + 17m
A. nubilus[a]	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
A. oculatus	2N = 31, 10V + 10I + 8m + X_1X_2Y (♂)
	2N = 32, 10V + 10I + 8m + $X_1X_1X_2X_2$ (♀)
A. opalinus	2N = 30, 14V + 16m
A. polylepis	2N = 40, 24M + 16m
A. poncensis	2N = 29, 16V + 10m + X_1X_2Y (♂)
A. pulchellus	2N = 29, 16V + 10m + X_1X_2Y (♀)
A. quadriocellifer	2N = 28, 14V + 14m
A. roquet	2N = 34, 12V + 22m
A. rubribarbus	2N = 28, 14V + 14m
A. sabanus	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
	2N = 30, 12V + 6I + 8m + $X_1X_1X_2X_2$ (♀)
A. sagrei	2N = 28, 14V + 14m
A. scriptus	2N = 27, 16V + 8m + X_1X_2Y (♂)
A. stratulus	2N = 29, 14V + 12m + X_1X_2Y (♂)
A. tropidogaster	2N = 40, 4V + 20I + 16m
A. tropidolepis	2N = 40, 24M + 16m
A. tropidonotus	2N = 40, 24M + 16m
A. valencienni	2N = 30, 14V + 16m
A. vermiculatus	2N = 34, 12V + 22m
A. wattsi	2N = 29, 12V + 6I + 8m + X_1X_2Y (♂)
Sceloporus chrysostictus	2N = 34, 12V + 22m
S. clarki	2N = 40, 4V + 16I + 20m
S. edwardtaylori	2N = 22, 12V + 22m
S. gadoviae	2N = 34, 12V + 22m
S. graciosus	2N = 30, 12V + 18m
S. horridus	2N = 22, 12V + 10m
S. jarrovi	2N = 31, 12V + 18m + Y (♂)
	2N = 32, 12V + 20m (♀)
S. lundelli	2N = 22, 12V + 10m
S. maculosus	2N = 33, 12V + 20m + Y (♂)
	2N = 34, 12V + 22m (♀)

APPENDIX II.—Continued.

Species	Karyotype
S. magister	2N = 26, 12V + 14m
S. melanorhinus	2N = 40, 4V + 16I + 20m
S. merriami	2N = 46, 24I + 22m
S. nelsoni	2N = 34, 12V + 22m
S. occidentalis	2N = 22, 12V + 10m
S. olivaceus	2N = 22, 12V + 10m
S. orcutti	2N = 34, 12V + 22m
S. poinsetti	2N = 31, 12V + 18m + Y (♂)
S. pyrocephalus	2N = 34, 10V + 2I + 22m
S. scalaris	2N = 24, 12V + 12m
S. spinosus	2N = 22, 12V + 10m
S. utiformis	2N = 34, 12V + 22m
S. undulatus	2N = 22, 12V + 10m
S. virgatus	2N = 22, 12V + 10m
Liolaemus altissimus[b]	2N = 32, 12V + 20m
L. chilensis[b]	2N = 30(32?), 12V + 18(20?)m
L. fuscus[b]	2N = 32, 12V + 20m
L. gravenhorsti[b]	2N = 32, 12V + 20m
L. lemniscatus[b]	2N = 34, 12V + 22m
L. lutzae	2N = 34, 12V + 22m
L. monticola[b,d]	2N = 32, 12V + 20m
	2N = 38, 10V + 4I + 24m
	2N = 38, 9V + 5I + 24m
	2N = 39, 9V + 6I + 24m
	2N = 40, 8V + 8I + 24m
L. nigromaculatus[b]	2N = 40, 4V + 16I + 20m
L. nigroviridis[b]	2N = 34, 12V + 22m
L. nigroviridis[c]	2N = 30, 12V + 18m
L. tenuis	2N = 32, 12V + 20m

[a] Gorman and Stamm (1975).
[b] Lamborot et al. (1979).
[c] Valencia et al. (1971).
[d] Karyotypic variation in *L. monticola* is both intersubspecific and intrapopulation. *L. monticola chillanensis*, 2N = 32; *L. monticola monticola*, 2N = 38–40. See Lamborot et al. (1979) for further details.