

A PHYLOGENETIC ANALYSIS OF LIZARDS OF THE *LIOLAEMUS CHILIENSIS* GROUP (IGUANIA: TROPIDURIDAE)

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The lizard genus *Liolaemus* includes over 160 species of which almost half are in the *chiliensis* group. Although some researchers have attempted to define smaller species groups within this large clade, the relationships among the taxa within the group as a whole remain enigmatic. The objectives of this study were to (1) identify characters that will be useful for present and future phylogenetic studies of this group, and (2) generate preliminary phylogenetic hypotheses for taxa within this large clade of lizards. I examined more than 800 specimens of 73 taxa belonging to the *chiliensis* group from which I identified 55 phylogenetically informative morphological characters. Additional characters (6) were derived from published and unpublished data on chromosomes, life history, and ecology. Four species considered basal for the genus were taken as outgroups. A tree-building program (PAUP 4.0b2) recovered three trees of length 11.516 (Retention index: 0.59). Differences found among these topologies were restricted to the relationships of species of the *elongatus* group, in which monophyly was recovered in only one tree. Results from PAUP's analysis support the monophyly of several previously proposed species groups: *alticolor*, *altissimus*, *gravenhorstii*, *hellmichi*, *kriegi*, *leopardinus*, *monticola*, *nigromaculatus*, *nigroviridis*, *pictus* and *tenuis*. Interestingly, most of the groups indicated above are endemic to areas that have recently been described as areas of high endemism for southern South America.

Key words: phylogeny, cladistics, iguanids, South American lizards

INTRODUCTION

Liolaemus is one of the most species-rich genera of lizards. Currently, more than 160 taxa have been described and many others await description (Etheridge & Espinoza, in review). Species belonging to *Liolaemus* are distributed primarily throughout South America's southern portion, from the southern tip of the continent in Tierra del Fuego to central Perú. They are found on both the east and west sides of the Andes and are important vertebrate components of the Patagonian steppe, and the Monte, Prepuna, Puna and Andean ecosystems (Cabrera & Willink, 1980). Perhaps as a consequence of their high species diversity, the intrageneric relationships are largely unresolved.

The first comprehensive taxonomic treatments of *Liolaemus* were conducted by Ortiz (1981) and Laurent (1983, 1984, 1985). Ortiz (1981) divided the species then included in *Liolaemus* into 25 groups, (17 of which are included in the *chiliensis* group [sensu Etheridge 1995]; see Table 1), but he did not propose any hypothesis concerning the relationships among these groups. Ortiz (1981) also performed the first cladistic analysis of members of the genus (the *nigromaculatus* group). Based on morphometric analyses, and through examination of additional characters, Laurent (1983a) defined two main groups which he considered distinct subgenera: the "chileno group" (*Liolaemus sensu stricto*) and the "argentino group"

(*Eulaemus*) distributed on the western and eastern sides of the Cordillera de los Andes, respectively. Laurent (1983a) also recognized the basal position of *L. archeoforus*, *L. kingii*, *L. lineomaculatus*, and *L. magellanicus* – and the relationship between the latter two species – with species described under the genus *Vilcunia* (Donoso-Barros & Cei, 1971). Laurent (1983) considered valid the subgenus *Ortholaemus* (Cei, 1979). Laurent's (1983a) proposal was amplified in a subsequent publication (Laurent, 1985) which also included a hypothesis concerning the main *Liolaemus* species groups. Despite the lack of a cladistic analysis, Laurent's (1985) paper provided an important first step toward understanding the evolutionary history of the genus.

Other subdivisions of the genus have been proposed by Cei (1986, 1993): 28 species groups, 12 of which are subsets of the *chiliensis* group (sensu Etheridge, 1995; Table 1). These proposed groupings were based on combinations of characters used for identification purposes (not apomorphies). Hence they may or may not represent natural groups.

Laurent (1992) added to his previous morphometric studies (Laurent, 1983a) other differences between the subgenera *Liolaemus* and *Eulaemus*: the position of the nasal openings (lateral in the chileno group and latero-dorsal in the argentino group), and the shape of the supralabials – longer and flattened with the fourth one turned upward in the chileno group. According to Etheridge (1995), the upturned fourth supralabial is shared with *magellanicus* and the members of the *lineomaculatus* group. Laurent (1992) also provided a

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list of the species of both subgenera, *Liolaemus* and *Eulaemus*. In this list, the chileno group included 68 taxa.

Most recently, Etheridge (1995) re-examined the taxonomy of *Liolaemus* from a cladistic perspective. He rejected or questioned the validity of the subgenera *Liolaemus*, *Eulaemus* and *Ortholaemus*, as well as the genera *Rhytidodeira* Girard 1858 (resurrected by Laurent, 1985), *Phrynosaura* Werner 1907, *Vilcunia* Donoso-Barros & Cei 1971, *Pelusaurus* Donoso-Barros 1973b (previously assigned to subgenus *Ortholaemus* by Laurent [1983b]), *Velosaura* and *Abas* Núñez & Yáñez 1984, and *Ceiolema* Laurent 1984, because each of these taxa exhibit the synapomorphies of *Liolaemus* and/or their monophyly was uncertain at that time. Etheridge (1995) renamed the chileno group (*Liolaemus* sensu stricto, Laurent [1983a]) the *chiliensis* group, which he defined as those *Liolaemus* with a lower number of precloacal pores (four or fewer) and a fused Meckel's groove. Etheridge (1995) also provided an indented taxonomy of currently valid *Liolaemus* species and subspecies. The composition of his *chiliensis* group is coincident with that of the *chileno* group of Laurent (1992), with additions for newly described species. However, Etheridge (1995) considered as valid or taxonomically uncertain *L. lativittatus* (considered a synonym of *L. alticolor* by Donoso-Barros [1966]), and *L. modestus* (considered as *Stenocercus* by Laurent [1984], and later confirmed by Ortiz [1989a]). Also included in his *chiliensis* group is the problematic species *L. chacoensis*. According to Etheridge (in litt.), *isabelae* should have been placed in the *chiliensis* group, and not in the *montanus* group. According to this last list (Etheridge; op.cit.), the *chiliensis* group has 74 species and subspecies. Two thirds of these taxa are distributed in Chile, whilst the remaining third are from Argentina, Bolivia and Perú.

As a first attempt to resolve the phylogenetic relationships among members of the *chiliensis* group, I assembled data on most of the known species and subspecies of this group. Data were taken from external morphology and anatomy, as well as ecological and cytogenetic data from the literature for use in this preliminary phylogenetic analysis.

MATERIAL AND METHODS

Approximately 800 specimens were examined, representing 77 species and subspecies of *Liolaemus*. The majority of the species studied (73) was from the *chiliensis* group, (Etheridge, 1995). Most of the morphological characters were taken from specimens preserved in alcohol. Some characters were examined with the aid of a hand lens (x 10) or a binocular dissecting microscope (x 10-40). Measurements were taken with electronic vernier calipers to ± 0.01 mm. Neck-fold terminology follows Frost (1992). Hemipenes were everted and studied following Bohme (1988). Tooth morphology characters were taken from Richard

Etheridge's skeleton collection and from alcohol preserved specimens.

The majority of the characters used in this analysis were taken from the external morphology, including 24 characters associated with squamation; 18 body pattern; two coloration; two neck-fold morphology; one neck fat pouches; two precloacal pores; one hemipenes, three size and ratios; two tooth morphology; one osteology; one karyotype; and five physiology and ecology. Apomorphic characters of the *nitidus*, *lineomaculatus* and *chiliensis* groups identified by Etheridge (1995) were included in this analysis. Character states 58 to 61 were kindly provided by Robert Espinoza (unpubl. data), taken mainly from dissections.

Although the taxonomic status of several members of the *chiliensis* group has been controversial, I included each taxon (species and subspecies) belonging to the group (following Etheridge, 1995) as a terminal OTU. Indeed, this analysis may provide reasons for revisiting the taxonomic status of many forms. *L. kingii*, *archeforus*, *sarmientoi* and *lineomaculatus* were included as outgroups (following Etheridge, 1995). *Liolaemus kingii*, *L. archeforus* and *L. sarmientoi* were recently recognized as full species by Cei & Sclaro (1996). Twelve taxa were represented by only one or two specimens (*L. cristiani*, *L. curicensis*, *L. cyanogaster brattstroemi*, *L. monticola chillanensis*, *L. neuquensis*, *L. nigroviridis nigroroseus*, *L. pictus argentinus*, *L. pictus talcanensis*, *L. sanjuanensis*, *L. tacnae*, *L. tenuis punctatissimus*, *L. variegatus*). The following members of the *chiliensis* group were not included in this study: *Liolaemus ceii*, *L. petrophilus*, *L. lativittatus*, *L. modestus*, *L. nigroviridis minor*, *L. pictus major*. Most of the above were excluded because of lack of specimens for this study, and others because their validity was uncertain (e.g. *L. lativittatus* and *L. modestus*).

Binary characters that exhibited polymorphism were coded using the frequency bins method (Wiens, 1993, 1995), with 25 character states (a-y). These characters were numbers 1, 3, 5-8, 12-13, 16, 18, 24, 28 and 31. The gap weighting method of Thiele (1993) was applied for characters 2, 4, 9, 14, 19, 22-23, 47-48 and 50-52, which represent continuous characters with overlapping ranges – morphometrics or multistate polymorphics. The number of states were 25 (a-y) for maintaining parity with the rest of the characters. Binary characters not polymorphic were: 15, 21, 26-27, 29-30, 32-39, 41-43, 46, 49, 54-55 and 58. Multistate characters not polymorphic were: 17, 25, 40, 44-45, 53, 56-57 and 59-61. Only characters 17, 20, 53 and 59 were analysed as being unordered because no evident series of change were observable. The other characters not coded using frequency bins or the gap weighting method were weighted by 24. The analysis was performed using PAUP* Version 4.0b2 for 32-bit Microsoft Windows (Swofford, 1999), applying an

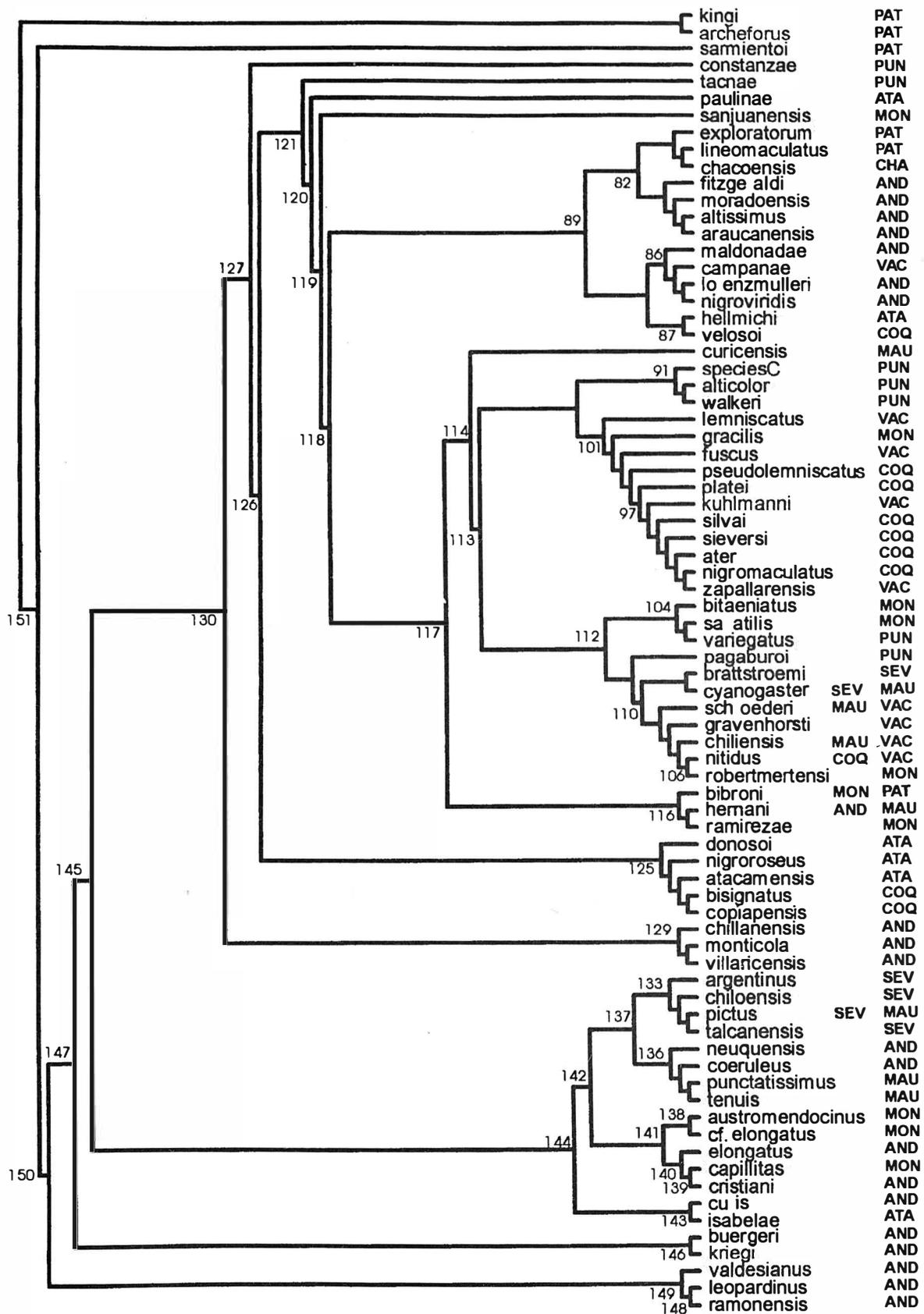


FIG. 1. Cladogram of the *chiliensis* group, the result of a parsimony analysis using PAUP* Version 4.0b2. Considering *Liolaemus kingii*, *archeforus*, *sarmientoi* and *lineomaculatus* as outgroups (note the inclusion of *lineomaculatus* within the *chiliensis* group). Congruence values: Consistency index = 0.20; Retention index = 0.59. Abbreviations for species distribution are: AND- Andina; ATA- Atacama; CHA- Chaco; COQ- Coquimbo; MAU- Maulina; MON- Monte (western Argentina); PAT- Patagonia; PUN- Puna; SEV- Selva Valdiviana; VAC- Valle Central. For more comments see the text.

heuristic search with the tree bisection-reconnection (TBR) option for branch swapping. For each analysis, 1000 random addition sequence replicates were performed, saving 40 trees at each step. *Liolaemus kingii*, *archeforus*, *sarmientoi* and *lineomaculatus* were considered outgroups following Etheridge (1995). Bootstrap analysis (Felsenstein, 1985) was used to evaluate the support for internal nodes (100 replicates). The list of characters is shown in Appendix 1.

RESULTS

After PAUP analysis, three trees were obtained with a length of 11516 and RI=0.59 (retention index, Farris, 1989). One of these trees is shown in Fig. 1. Differences among the three trees are related to the placement of the clade including *elongatus*, *cristiani* and *capillitas* (nodes 141 and 139, Figs 2A and B respectively). In Fig. 2A this clade is the sister taxon of another containing the *pictus* group (node 133), the *temuis* group (node 136) and the pair *austromendocinus* c.f. *thermarum* (node 138). In Fig. 2B is shown other alternative relationship found, in this tree the *elongatus* clade (node 139) is sister taxon only of the group including *pictus* and *temuis* groups (node 137). The tree shown in Fig. 1 is the one in which the entire *elongatus* group is monophyletic.

Bootstrapping was performed on this data set, but found almost no support in the results. The asymmetry of this matrix – with more taxa than characters – probably makes the deletion/resampling methods for yielding consistent results problematical. The best supported nodes from 100 replicates are: *bisignatus* – *copiapensis* (94.9%); *punctatissimus* – *temuis* (52.2%); *chillanensis* – *monticola* – *villaricensis* (*monticola* group, 47.5%); *gravenhorstii* – *schroederi* (46.8%); *austromendocinus* – c.f. *thermarum* (46.7%); *lineomaculatus* – *chacoensis* (44.3%); *nitidus* group (*lineomaculatus* plus all *chiliensis* group species, 43.0%); *capillitas* – *cristiani* (42.1%) and *hellmichi* – *velosoi* (40.7%).

The topology of the recovered phylogeny is shown in Figs 1 and 2. The general structure of the trees show the *leopardinus* group as the sister taxon of all other species of the *chiliensis* group. This is a monophyletic group including *monticola*, *chillanensis* and *villaricensis*. Subsequently, the *kriegi* group is the most external to node 145, which includes a clade (node 144, containing *pictus*, *temuis* and *elongatus* groups) and the remaining species of the *chiliensis* group. Node 130 includes the *monticola* group as a sister taxon of the remaining species. The next sister taxon is *constanzae*, followed by the *copiapensis* group (5 spp.). Following the structure of the tree we have as subsequent sister taxa *tacnae*, *paulinae*, *sanjuanensis* and a node containing two big subclades (nodes 89 and 117). The first subclade (89), includes *altissimus*, *nigroviridis* and *hellmichi* groups, and a small group formed by *exploratorum*, *chacoensis* and *lineomaculatus*.

Subclade 117 includes as most external group that formed by *bibroni*, *hernani* and *ramirezae* (node 116); subsequent sister taxa are *curicensis*, node 112 (which includes *gravenhorstii* group, the pair *cyanogaster* – *brattstroemi*, and the group formed by *bitaeniatus*, *saxatilis* and *variegatus*) and finally, the terminal pair of sister taxa: the *alticolor* group (node 91) and node 101 (containing the *nigromaculatus* group at node 97). The content of different groups recovered in this analysis are shown in Table 1.

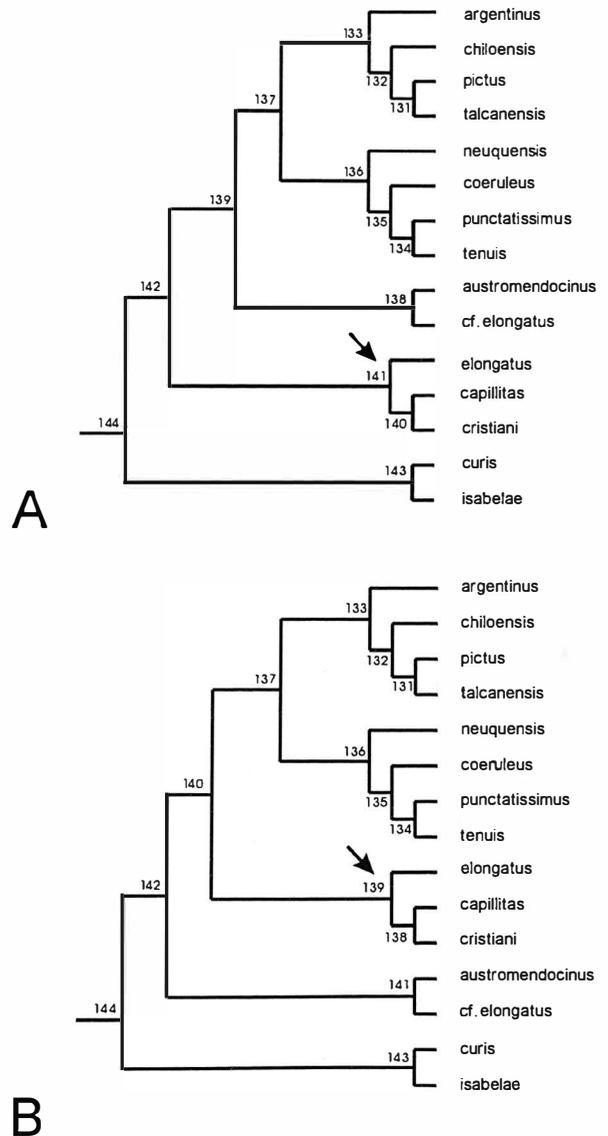


FIG. 2. Two equally parsimonious trees different to that shown in FIG. 1. A, clade including *elongatus*, *capillitas* and *cristiani* (node 141) is sister taxon of the group containing both the *temuis*-*pictus* groups and the species pair *austromendocinus* and c.f. *thermarum*. Cladogram of the *chiliensis* group based on a parsimony analysis considering all characters equally weighted (PAUP) rooting in *Liolaemus kingii*. B, same clade (node 139), exclusively sister taxon of the pair *temuis*-*pictus* groups.

TABLE 1. Comparisons of taxonomic arrangements proposed for species of the *chiliensis* group (sensu Etheridge, 1995). Groups in the third column are those recognized here, based on the results of the present analysis. Groups without equivalents in the third column did not have their monophyly supported in this analysis. Nine of the seventeen groups of Ortiz (1981) are monophyletic. *Groups proposed by Cei (1986, 1993) only included Argentine species, hence they may not contain all the species belonging to these groups. Cei (1986) proposed a *bibronii* group including *L. bibronii*, *L. sanjuanensis* and *L. exploratorum* and a *gracilis* only group for this species. Later, Cei (1993) included *L. gracilis* in the *bibronii* group. ** The monophyly of the *elongatus* group is recovered in one of the three most parsimonious trees founded.

Ortiz (1981)	Cei (1986, 1993)*	This study
1. <i>elongatus-kriegi</i> group: <i>austromendocinus</i> , <i>buergeri</i> , <i>ceii</i> , <i>elongatus elongatus</i> , <i>elongatus petrophilus</i> , <i>kriegi</i> .	<i>elongatus</i> group: <i>austromendocinus</i> , <i>capillitas</i> , <i>elongatus elongatus</i> , <i>elongatus petrophilus</i> . <i>kriegi</i> group: <i>buergeri</i> , <i>ceii</i> , <i>kriegi</i> .	** <i>elongatus</i> group: <i>austromendocinus</i> , <i>capillitas</i> , <i>cristiani</i> , <i>elongatus</i> , c.f. <i>elongatus</i> . <i>kriegi</i> group: <i>buergeri</i> , <i>kriegi</i> .
2. <i>alticolor-walkeri</i> group: <i>alticolor</i> , <i>walkeri</i> , <i>tacnae</i> .	<i>alticolor</i> group: <i>alticolor alticolor</i> , <i>alticolor walkeri</i> .	<i>alticolor</i> group: <i>alticolor</i> , <i>walkeri</i> , sp. nov.
3. <i>constanzae-paulinae</i> group: <i>constanzae</i> , <i>paulinae</i> .		
4. <i>leopardinus</i> group: <i>leopardinus</i> , <i>leopardinus leopardinus</i> , <i>leopardinus ramonensis</i> , <i>leopardinus valdesianus</i>		<i>leopardinus</i> group: <i>leopardinus</i> , <i>ramonensis</i> , <i>valdesianus</i> .
5. <i>altissimus-fitzgeraldi</i> group: <i>altissimus altissimus</i> , <i>altissimus araucanensis</i> , <i>altissimus moradensis</i> , <i>altissimus neuquensis</i> , <i>fitzgeraldi</i> .	<i>altissimus</i> group: <i>altissimus [altissimus]</i> , <i>fitzgeraldi</i> .	<i>altissimus</i> group: <i>altissimus</i> , <i>araucanensis</i> , <i>moradoensis</i> , <i>fitzgeraldi</i> .
6. <i>nigroviridis-lorenzmulleri</i> group: <i>nigroviridis nigroviridis</i> , <i>nigroviridis nigroroseus</i> , <i>lorenzmulleri</i> .	<i>nigroviridis</i> group: <i>nigroviridis</i> , <i>constanzae</i> .	<i>nigroviridis</i> group: <i>campanae</i> , <i>lorenzmulleri</i> , <i>maldonadae</i> , <i>nigroviridis</i> .
8. <i>pictus</i> group: <i>pictus argentinus</i> , <i>pictus chiloensis</i> , <i>pictus pictus</i> , <i>pictus major</i> , <i>pictus talcanensis</i> .	<i>pictu</i> group: <i>pictus pictus</i> , <i>pictus argentinus</i> .	<i>pictus</i> group: <i>argentinus</i> , <i>chiloensis</i> , <i>pictus</i> , <i>talcanensis</i> .
9. <i>tenuis</i> group: <i>tenuis tenuis</i> , <i>tenuis punctatissimus</i> .	<i>tenuis</i> group: <i>tenuis</i> , <i>coeruleus</i> .	<i>tenuis</i> group: <i>coeruleus</i> , <i>neuquensis</i> , <i>punctatissimus</i> , <i>tenuis</i> .
10. <i>gravenhorstii-schroederi</i> group: <i>gravenhorstii</i> , <i>schroederi</i> .	<i>gravenhorstii</i> group: <i>gravenhorstii</i> , <i>cyanogaster</i> .	<i>gravenhorstii</i> group: <i>chiliensis</i> , <i>gravenhorstii</i> , <i>nitidus</i> , <i>robermertensi</i> , <i>schroederi</i> .
11. <i>chiliensis-nitidus</i> group: <i>chiliensis</i> , <i>nitidus</i> .	<i>chiliensis</i> group: <i>chiliensis</i> , <i>robermertensi</i> .	
12. <i>monticola</i> group: <i>monticola monticola</i> , <i>monticola chillanensis</i> , <i>monticola villaricensis</i> , <i>curicensis</i> .		<i>monticola</i> group: <i>monticola</i> , <i>chillanensis</i> , <i>villaricensis</i> .
13. <i>fuscus-lemniscatus</i> : group: <i>fuscus</i> , <i>lemniscatus</i> .	<i>lemniscatus</i> group: <i>lemniscatus</i> .	
14. <i>hellmichi</i> group: <i>hellmichi</i> .		<i>hellmichi</i> group: <i>hellmichi</i> , <i>velosoi</i> .
15. <i>donosoi</i> group: <i>donosoi</i> .		see below <i>copiapensis</i> group.
16. <i>nigromaculatus</i> group: <i>bisignatus</i> , <i>copiapensis</i> , <i>kuhlmanni</i> , <i>nigromaculatus</i> , <i>platei</i> , <i>zapallarensis zapallarensis</i> , <i>zapallarensis ater</i> , <i>zapallarensis sieversi</i> , n. sp.1, n. sp.2.		<i>nigromaculatus</i> group: <i>ater</i> , <i>kuhlmanni</i> , <i>nigromaculatus</i> , <i>platei</i> , <i>sieversi</i> , <i>silvai</i> , <i>zapallarensis</i> . <i>copiapensis</i> group: <i>atacamensis</i> , <i>bisignatus</i> , <i>copiapensis</i> , <i>donosoi</i> , <i>nigroroseus</i> .
17. <i>modestus</i> group: <i>modestus</i> .		
18.	<i>bibronii</i> group: <i>bibronii</i> , <i>bitaeniatus</i> , <i>exploratorum</i> , <i>gracilis</i> , <i>sanjuanensis</i> , <i>saxatilis</i> .	

DISCUSSION

TAXONOMIC STATUS OF TERMINAL TAXA

In the *chiliensis* group, there are several taxa that have proved to be taxonomically contentious. Many of these controversies are discussed in Núñez & Jaksic (1992). These researchers proposed specific status for the three subspecies of *leopardinus* and they disagree with splitting the subspecies *nigroviridis* and *tenuis*. They also suggested conspecificity of *pictus talcanensis* and *pictus major*. Following the observations of Veloso *et al.* (1982), they also considered the possible conspecificity of *constanzae* and *donosoi*. Núñez & Jaksic (1992) included in their “*nomina dubia*” section *L. hernani* which they considered a possible synonym of *L. curicensis*.

According to the results obtained in these analysis, many taxa considered subspecies are independent lineages that should be considered full species: *moradoensis* (*altissimus moradoensis*), *campanae* (*nigroviridis campanae*), *ater* (*zapallarensis ater*), *sieversii* (*zapallarensis sieversii*), *nigroroseus* (*nigroviridis nigroroseus*), *chillanensis* (*monticola chillanensis*), *argentinus* (*pictus argentinus*), *chiloensis* (*pictus chiloensis*), *neuquensis* (*altissimus neuquensis*), *valdesianus* (*leopardinus valdesianus*).

SYSTEMATIC CONCLUSIONS

In the literature, there exist only a few proposals for grouping the species now included in the *chiliensis* group (*sensu* Etheridge, 1995). Two authors presented systematic arrangements in this sense: Ortiz (1981) and Cei (1986, 1993). In both cases the definition of groups were based on character combination instead of synapomorphies. Ortiz (1981) divided *Liolaemus* into 25 groups, 17 of them now should be included in the *chiliensis* group. Cei (1986, 1993) divided species in the *chiliensis* group into 12 more inclusive subgroups. Although the objective of this study was not to propose a new systematic rearrangement of the *chiliensis* group, it is useful to analyse the previous proposals and compare them to the cladistic approach presented here. Table 1 summarizes the systematic arrangements made by these two authors; there is a general overlap among the two arrangements. The composition of the different groups (previously recognized in the literature) that were monophyletic in PAUP analysis are included in the third column of Table 1.

The interesting finding of this study is the inclusion of *lineomaculatus* in the *chiliensis* group. The character apomorphic for the *chiliensis* group which is the enclosure of Meckel's groove is reverted in this taxon; the other character described by Etheridge (*op. cit.*) – lower number of precloacal pores – exhibits great variation: even more precloacal pores are lost in *cristiani*, *thermarum*, *neuquensis* and *coeruleus* than in the *lineomaculatus* group. The results of this analysis can be taken as preliminary, and more studies are needed to confirm or reject the hypothesis of the inclusion of *lineomaculatus* in the *chiliensis* clade.

SPECIES GROUPS

Species belonging to the *Liolaemus monticola* group form a monophyletic group. There is no evidence of a relationship between these three species and *curicensis* as proposed by Ortiz (1981; see Table 1).

Navarro & Núñez (1993) describe *isabelae*, which they include in the *nigroviridis* group based on the fact that these species plus *maldonadae* share some similar karyological features. In this analysis, these species were placed in different groups. PAUP analysis showed (*maldonadae* (*campanae* (*lorenzmulleri nigroviridis*))) as the *nigroviridis* group. It is interesting to note that Ortiz (*op. cit.*) included *lorenzmulleri* in this group; Cei (1993) did the same with *constanzae* (which is rejected in this analysis) and Navarro & Núñez (1993) with *maldonadae*.

The *Liolaemus altissimus* group (Ortiz, 1981; Cei, 1986) is monophyletic, including *moradoensis* as a sister taxon of the pair *altissimus* – *araucanensis*. The form named *neuquensis* was excluded from this group, being related to the *tenuis* group. *Liolaemus fitzgeraldi* is the sister taxon of the clade formed by *moradoensis*, *altissimus* and *araucanensis*. The relationship of *fitzgeraldi* with the *altissimus* group was postulated previously by Ortiz (*op. cit.*) and Cei (*op. cit.*).

The cladogram of Ortiz (*op. cit.*, Fig. 28) for the *nigromaculatus* group differs mainly from those obtained here in that the pair of sister taxa *copiapensis* – *bisignatus* is nested within a group that also contains *zapallarensis*, *kuhlmanni* and *silvai*. These last species, plus *sieversii*, *ater* and *nigromaculatus* form a monophyletic group and *copiapensis* and *bisignatus* form an independent lineage, as can be seen in Fig. 1. In fact, in his original description of *silvai*, Ortiz (1989)*b* notes the proximity of this taxon to *kuhlmanni* and *zapallarensis*, and provides a rigorous comparisons between them.

According to the results of this phylogenetic analysis, the *nigromaculatus* group should be considered as consisting of the following species: *nigromaculatus*, *zapallarensis*, *ater*, *sieversii*, *silvai*, *kuhlmanni* and *platei*. The other species previously considered belonging to this group are not related and form an independent clade (Fig. 1, node 125): (*donosoi* (*nigroroseus atacamensis* (*copiapensis bisignatus*))), with the exception of *velosoi* which is the sister taxon of *hellmichi* (Fig. 1, node 87).

Species belonging to the *elongatus-kriegi* group (Ortiz, 1981) do not form a monophyletic group. Only as separate groups (Cei, 1986, 1993) is the *elongatus* group monophyletic in one of three trees, and the *kriegi* group monophyletic in all trees. Videla & Cei (1996) described a new species of the *chiliensis* group called *thermarum* and they suggested that it is related to *neuquensis*, *coeruleus* and *cristiani* because all these lizards lack precloacal pores. In this analysis, characters related to precloacal pores were included (numbers 47-48), scoring the state “precloacal pores absent” for these species (with the exception of *thermarum* for

which we could not examine specimens for this study). In Fig 1 these species are included in different and independent lineages. It is, therefore, preferable not to consider this grouping as valid until we have more evidence supporting the hypothesis of monophyly.

Species belonging to Cei's *bibronii* group (Table 1) in this analysis do not form a monophyletic group and are split into three independent lineages (nodes 101, 112 and 116).

Separate groupings of the *chiliensis* group and the *gravenhorsti* group as were proposed (see Table 1) are not recovered. There is only the *chiliensis* group (*sensu* Ortiz, 1981) plus *robertmertensi*. A broader, more inclusive group is proposed here including species of both groups previously proposed in the literature, containing: *chiliensis*, *nitidus*, *robertmertensi*, *gravenhorstii* and *schroederi*. (Table 1).

DISTRIBUTION

The species of the *chiliensis* group are distributed over a wide latitudinal–elevational range. For example, *bisignatus* lives in low-elevational coastal areas, whereas *walkeri* lives at elevations as high as 4800 m in the Peruvian Andes (Veloso & Navarro, 1988). They occupy almost every type of habitat, from grasslands of the Puna and other high elevation regions, to low elevation habitats such as deserts and *Nothofagus* forests. They can live in deserts (Atacama), going through the central valleys of Chile to the southern *Nothofagus* forests, etc. Thus, almost every group of *Liolaemus* has representatives in these quite different areas. It is also valid to say that each region has generated sufficient conditions for the origin and development of groups of species (as we will see below).

The major clades discovered in this analysis have a high geographic homogeneity. Species belonging to the *kriegi*, *leopardinus*, *monticola* and *altissimus* groups all inhabit the Andina region. The majority of species of the *nigroviridis* group are distributed in the Andina area as well. The *pictus* group is distributed mainly in Selva Valdiviana and Maulina areas (80% of the species). The stem of the *nigromaculatus* group, comprising 71.4% of the species (5 spp.), is distributed in Coquimbo area (two other species live in the Valle Central area 28.6%). Species belonging to the *alticolor* group are all distributed in Puna. Species included in the *gravenhorstii* group are distributed mainly (80% of the species) in Valle Central and Maulina and another lives in the Monte area (*robertmertensi*).

Hellmich (1951, 1952) compared the distribution of *Liolaemus nigromaculatus* and its races, the species living in central Chile, the Andes and the austral forests with his own biogeographic regions (Atacama, Espinal, de los Bosques, Andina). He compared his observations with those for mammals and he divided the Puna and the southern Argentine-Chilean Andes into different areas. Later, Donoso-Barros (1966; lam. IXXV) indicated six ecological areas for Chile (Desiertos, Matorral, Centrochilena, Selva, Patagonia and

Cordillera). Veloso & Navarro (1988; Fig. 1), based on Di Castri (1968), described seven ecological areas of distribution for the Chilean herpetofauna, adding one area to the six described by Donoso-Barros (1966): Desertica, Tropical, Mediterránea Arida, Mediterránea, Mediterránea Húmeda, Oceánica and Andina. Veloso & Navarro (1988) divided the Cordillera of Donoso-Barros (1966) into Tropical and Andina, Selva into Mediterránea Húmeda and Oceánica, but they did not recognize Patagonia.

For assigning areas to terminal taxa in the cladograms of Fig. 1, I followed Hellmich (1952): Atacama; Roig Juñent (1994): Coquimbo, Valle Central, Maulina, Selva Valdiviana; Cabrera and Willink (1980): Chaco, Monte, Patagonia; Veloso and Navarro (1988): Andina; Morrone (1996): Puna. I prefer the divisions proposed by Roig Juñent (1994) and Morrone (1996) because they applied a cladistic methodology for determining areas of endemism.

Among the basic requirements needed today for cladistic biogeographic studies are: (1) the delimitation of areas of endemism, and (2) the phylogenetic analysis of different groups of organisms (plants or/and animals). In this manner, Roig Juñent (1994) identified 12 areas of endemism for southern South America, based on overlaying the distribution of different groups of Arthropoda and plants. In that paper, the historical relationships between these areas, and New Zealand, New Caledonia, Australia and South Africa were analysed cladistically. *Liolaemus* has representatives in every area. However those areas specially rich in species of this genus are located in the western half of southern South America, including his Coquimbo, Valle Central, Maulina, Selva Valdiviana, Monte and Bosques Orientales areas and his three subdivisions of Patagonia. The major groups identified in the *chiliensis* group seem to represent endemic areas of speciation in almost every one of the areas discovered by Roig Juñent (op. cit.). There are 11 monophyletic groups, eight of which exclusively inhabit the Puna area (one species group), Coquimbo area (one species group), Valle Central and Maulina (one species group), Selva Valdiviana (one species group) or the Andean area (four species groups). These main *Liolaemus* areas were previously drawn by Hellmich (1951; Fig 1).

The species selected for rooting the analysis (*kingii*) and those most basal for the genus (*archeforus*, *lineomaculatus*) are distributed mainly in Central Patagonia. The *pictus* group (four subspecies) is found in the Selva Valdiviana. This area shows the climatic and ecological characteristics of the Zona Mediterránea húmeda and Zona Oceánica described by Veloso & Navarro (1988). *Liolaemus brattstroemi* is another endemic of that area. The *Liolaemus gravenhorstii* group (five spp.) is present in Valle Central and Maulina (Chile, between 32 and 38° of latitude) and in western Argentina (*L. robertmertensi*). Other species are distributed in Valle Central and/or Maulina (*L. fuscus*, *L. lemniscatus*, *L. hernani*, etc.). Another monophyletic

group, the *nigromaculatus* group (seven spp.) extends its distribution mainly through the Coquimbo area, an area between 32 and 27° of latitude. The Andean areas: Puna and southern Chilean Andes of moderate to high elevations, exhibit their own endemisms. The Puna region has the *alticolor* group (three spp.) and the Andes of southern Chile and Argentina have the *altissimus* group (four spp.), *kriegi* group (two spp.), *leopardinus* group (three spp.), *monticola* group (three spp) and *nigroviridis* group (three out of four spp.).

The Puna province extends across north-western Argentina, north-eastern Chile, western Bolivia and south-western Perú (Morrone, 1996). The equivalent zones of Veloso & Navarro (op. cit.) are Zona Andina and Tropical (Puna). The individual areas of distribution and the ecological regions of the species of the *chiliensis* group can be traced from Donoso-Barros (1966), Donoso-Barros (1973a) and Veloso & Navarro (1988), but only for Chilean species. Data on the Argentine species can be found in Ceï (1986, 1993).

The results presented here represent the first cladistical approach to the analysis of the *chiliensis* group of *Liolaemus*. New observations and characters are being studied at this time that hopefully will bring new evidence for a better understanding of the phylogenetic relationships within this large clade of *Liolaemus*.

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APPENDIX 1

LIST OF CHARACTERS

Squamation. A total of 24 characters were scored:

1. Nasal-rostral contact (Fig. 3): (0) absent; (1) present. **FREQ. BINS.**
2. Width of the nasal at the mid-point of the external nares / width of the scale in contact with the rostral (Fig. 3): ranging from a mean of 18.2 to 1.6. **GAP WEIGHTING METHOD.**
3. Number of scales between canthal and nasal (Fig. 4): (0) two scales; (1) one scale. **FREQ. BINS.**
4. Dorsal head scales (rostral to occiput): ranging from a mean 16.0 to 10.5. **GAP WEIGHTING METHOD.**
5. Neck scales (along the longitudinal fold where present, or mid-distance between auditory meatus and shoulder): (0) granular, hemispherical; (1) laminar (flattened). **FREQ. BINS.**
6. Neck scales II: (0) smooth; (2) keeled. **FREQ. BINS.**
7. Dorsal head surface: (0) smooth; (1) rugose. **FREQ. BINS.**
8. Temporal surface: (0) smooth; (1) keeled. **FREQ. BINS.**
9. No. of temporals in a vertical count (counted at the mid-distance between subocular and auditory meatus from the oral commissure upwardly to the level of supraciliars): means ranging from 12.0 to 5.5. **GAP WEIGHTING METHOD.**
10. Number of scales in contact with the interparietal: (0) 8 scales; (1) 7 scales; (2) 6 scales; (3) 5 scales. **MAJORITY RULE.**
11. Number of enlarged supraoculars: (0) 6 scales; (1) 5 scales; (2) 4 scales; (3) 3 scales. **MAJORITY RULE.**
12. Posterior circumorbital scales: (0) forming a complete row of scales; (1) forming an interrupted row of scales. **FREQ. BINS.**
13. Contact between 4th supralabial and subocular (Fig. 5): (0) no contact; (1) contact. **FREQ. BINS.**
14. Number of lorilabials: means ranging from 9 to 5. **GAP WEIGHTING METHOD.**
15. Height of supralabials: (0) wide and short with the fourth scale not differentiated; (1) slender with the fourth usually showing its posterior tip incurved upwardly. This character is the synapomorphy of Etheridge's (1995) *nitidus* group. **BINARY NOT POLYMORPHIC.**
16. Auricular scale (Fig. 6): (0) not differentiated; (1) differentiated. **FREQ. BINS.**
17. Scales along the anterior border of the auditory meatus (Fig. 6): (0) no enlarged scales at the anterior margin of the auditory meatus. (1) one or two small laminar to granular scales differentiated slightly projecting on the anterior margin; (2) one enlarged laminar scale; (3) two to four enlarged laminar scales; (4) two to four enlarged lobulate scales. **MULTISTATE NOT POLYMORPHIC. UNORDERED.**

18. Separation of second chinshields (Fig. 7): (0) second chinshields always separated one from the other by one or two scales; (1) second chinshields in contact. In *copiapensis* and *bisignatus* more than 90% of individuals have these scales in contact. In other species it is less common (*silvai*, *platei*, *nigromaculatus*, *hellmichi*, *zapallarensis*, *sieversi*). All the remaining species of the *chiliensis* group exhibit the first condition. **FREQ. BINS.**

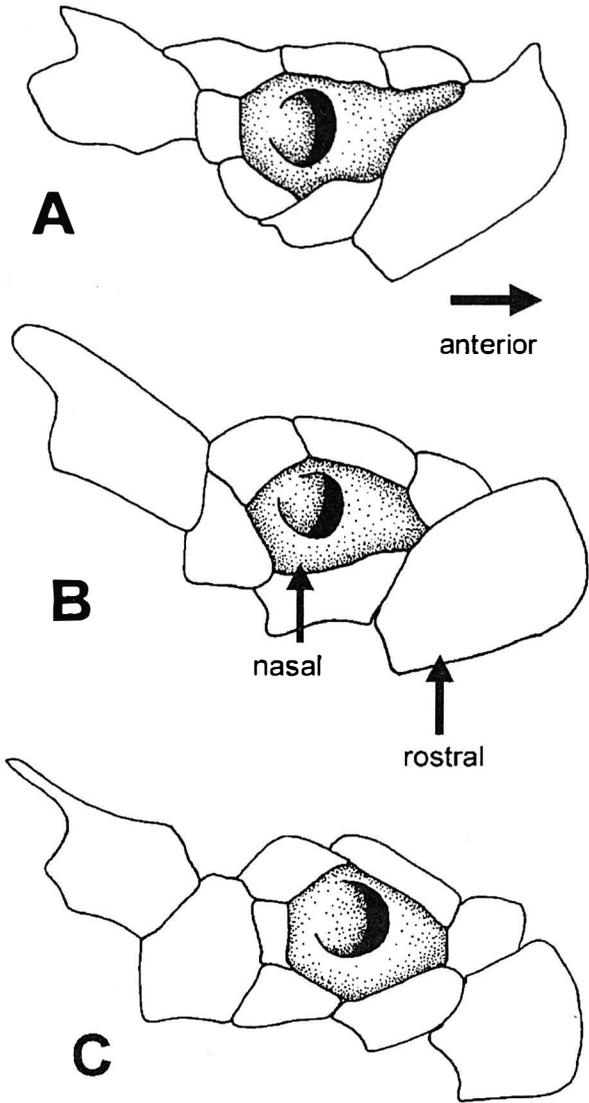


FIG. 3. A, *Liolaemus pagaburoi* (FML 2248). Character 1, state 1 (nasal-rostral contact present); character 2 (broad contact between nasal and rostral scales). B, *Liolaemus ramirezae* (FML 2940). Character 1, state 1 (nasal-rostral contact present); character 2 (slight contact between these scales). C, *Liolaemus capillitas* (FML 1229). Character 1, state 0 (nasal-rostral contact absent). Drawings made at different scales.

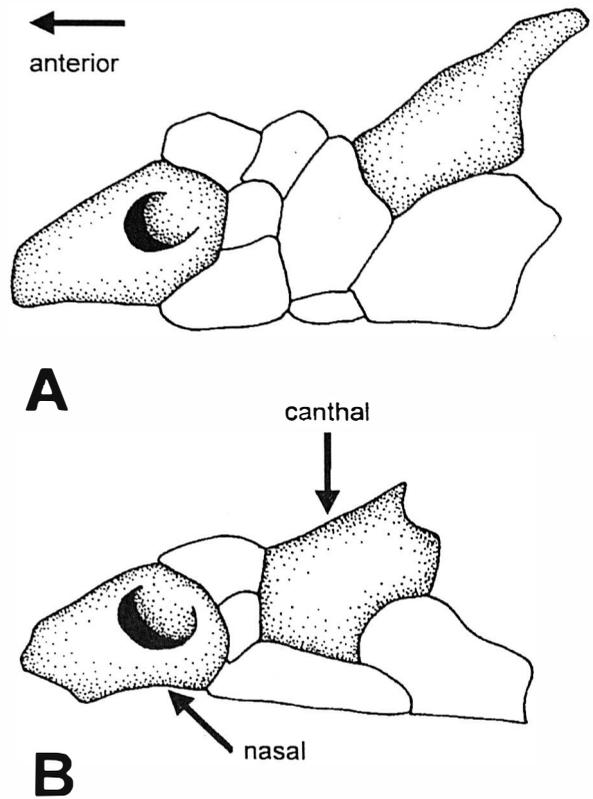


FIG. 4. A, *Liolaemus capillitas* (FML 1229). Character 3, state 0: canthal separated from nasal by two scales. B, *Liolaemus bitaeniatus* (FML 2918). Character 3, state 1: canthal separated from nasal by one scale. Drawings made at different scales.

- 19. Number of chinshields (Fig. 7): means ranging from 5.6 to 3.0. **GAP WEIGHTING METHOD.**
- 20. Shape of dorsal body scales: (0) with the posterior margin rounded; (1) rhomboidal; (2) lanceolate. **MAJORITY RULE**
- 21. Keels of dorsal body scales: (0) not forming a projecting spine at the median posterior margin (mucrone); (1) forming a mucrone. **BINARY NOT POLYMORPHIC.**
- 22. Number of midbody scales (mean value): from 99.5 to 32. **GAP WEIGHTING METHOD.**
- 23. Infradigital scales of fourth finger (counted over the entire finger): means ranging from 24.4 to 15.4. **GAP WEIGHTING METHOD.**

Body patterns. A total of 18 characters were scored:

- 24. Subocular distinct from the general coloration of the head: (0) subocular not distinct; (1) subocular white distinct. **FREQ. BINS.**
- 25. Ventral melanism (belly plus abdomen): (0) immaculate white. (1) spotted. (2) black. **MULTISTATE NOT POLYMORPHIC.**
- 26. Prescapular spot: (0) absent; (1) present. **BINARY NOT POLYMORPHIC.**

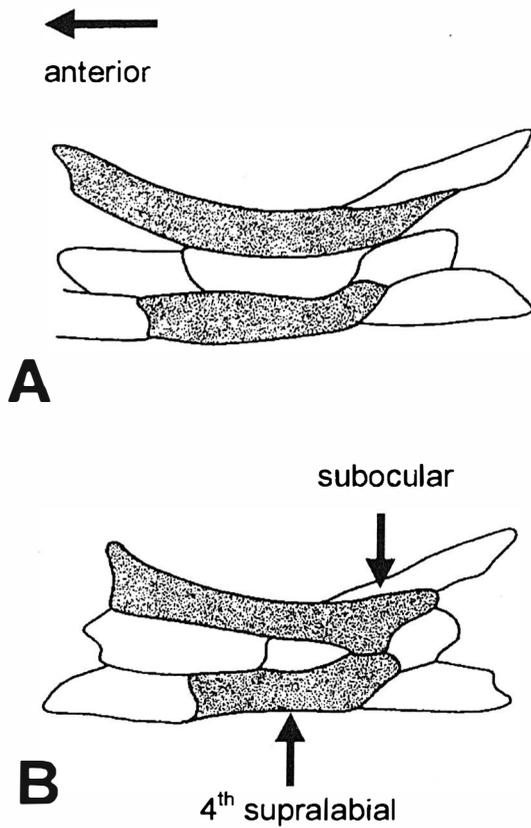


FIG. 5. A, *Liolaemus pagaburoi* (FML 2248). Character 13, state 0: fourth supralabial and subocular scales separated one from the other. B, *Liolaemus* n.sp. (FML 1761). Character 13, state 1: fourth supralabial and subocular scales in contact. Drawings made at different scales.

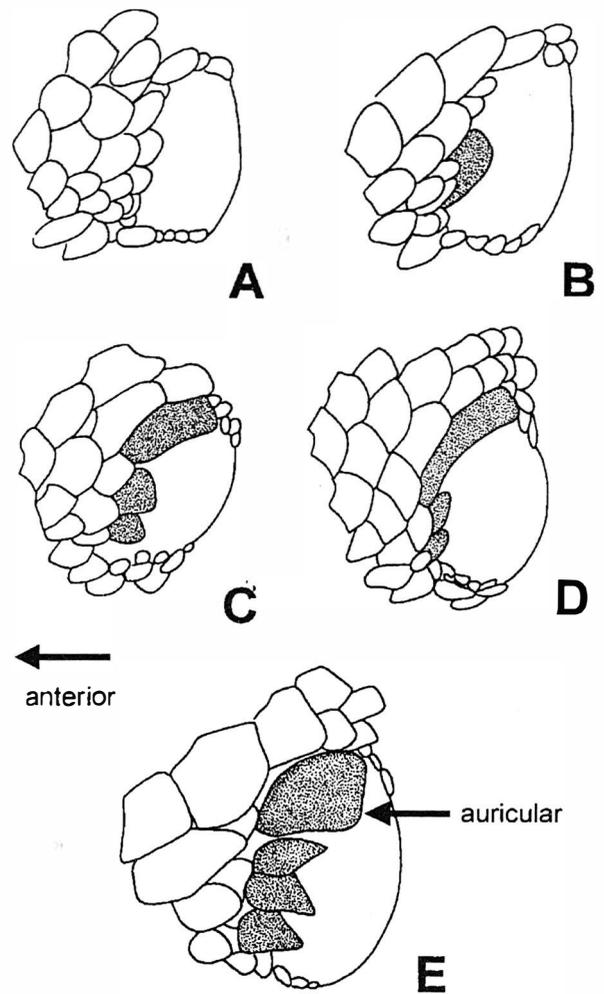


FIG. 6. A, *Liolaemus alticolor* (AMNH 16904). Character 16, state 0: auricular scale not differentiated; character 17, state 0: auditory meatus without enlarged scales on anterior bordering. B, *Liolaemus gravenhorsti* (AMNH 80054). Character 16, state 0: auricular scale not differentiated; character 17, state 3: auditory meatus with one enlarged laminar scale. C, *Liolaemus fuscus* (AMNH 131833) and D, *Liolaemus lemniscatus* (AMNH 21145). Character 16, state 1: auricular scale differentiated plus two other enlarged scales (character 17, state 2). Notice the elongated auricular scale of *lemniscatus* reaching at least half the length of the auditory meatus height. E, *Liolaemus zapallarensis* (AMNH 37574). Character 16, state 1: auricular present plus three enlarged lobed scales (character 17, state 4) which in this case, sometimes almost completely enclose the meatus. Drawings made at different scales.

27. Postcapular spot: (0) absent; (1) present. BINARY NOT POLYMORPHIC.
28. Paravertebral markings: (0) present; (1) absent. Paravertebral markings are those symmetrically positioned markings in the dorsal field of many members of the *chiliensis* group (see also Lobo and Espinoza, in review). Although these markings exhibit variation in shape and number, at this point, I only considered their presence. Paravertebral markings can be shaped subquadrated (for example *lemniscatus*, *walkeri*, etc.), slender transversal stripes (as in *altissimus*), subtriangular (*pictus* group), etc. FREQ. BINS.
29. Throat in males: (0) spotted; (1) immaculate. BINARY NOT POLYMORPHIC.
30. Throat II (females): (0) spotted; (1) immaculate. BINARY NOT POLYMORPHIC.
31. Vertebral stripe: (0) present (in some individuals fragmented); (1) absent. "Vertebrallinie" of Hellmich (1934). FREQ. BINS.
32. Dorsolateral stripes: (0) absent; (1) present; (2) present only in females. These stripes were termed "parietalband" by Hellmich (1934; Abb. 2). Donoso-Barros (1966) referred to them as "bandas supraoculares" because they initiate from this area of

the head. Cei (1993) used the name "bandas dorsolaterales." Lobo & Espinoza (1999) provide a figure and detailed descriptions of dorsal patterns and their variation among species of the *alticolor* group. BINARY NOT POLYMORPHIC.

33. Dorsolateral stripes II: (0) uniformly slender exhibiting the same width all along their extension. (1) Slender over the neck and shoulders and becoming wider posteriorly. BINARY NOT POLYMORPHIC.
34. Subtriangular paravertebral markings in zigzag pattern: (0) absent; (1) present. This pattern is distinct

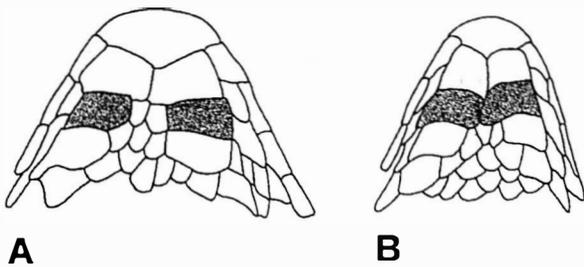


FIG. 7. A, *Liolaemus donosoi* (FML 1340). Character 18, state 0: second chinshields separated one from the other by two scales; character 19 (number of chinshields). B, *Liolaemus hellmichi* (FML 1339). Character 18, state 1: second chinshields in contact; character 19 (number of chinshields). Drawings made at different scales.

in members of the *pictus* group, having subtriangular markings at each side of the vertebral band or field (vertebral line is absent in these taxa), alternately positioned on either side. *Liolaemus fitzgeraldi* has similar pattern, but almost no vertebral band, and these markings (left and right sides) are in contact with the vertebral line; this was not considered homologous in this analysis. BINARY NOT POLYMORPHIC.

- 35. Paravertebral markings transversely elongated: (0) absent; (1) present. This pattern, very often, is more evident in females than males.
- 36. Occellations over the dorsum: (0) absent; (1) present. These markings are big and black and resemble the skin pattern of a leopard. This pattern is present in the three forms of the *leopardinus* group with varying degrees of distinctness. BINARY NOT POLYMORPHIC.
- 37. Irregularly fine "spotted" pattern on dorsum in males: (0) absent; (1) present. BINARY NOT POLYMORPHIC.
- 38. Same pattern in females: (0) absent; (1) present. BINARY NOT POLYMORPHIC.
- 39. Dorsal pattern formed by scattered longitudinal dark markings, like very short segments irregularly located: (0) absent; (1) present. Originally this character was drawn by Cei (1986, Fig. 50) for *exploratorum*, *bibroni*, *sanjuanensis*.

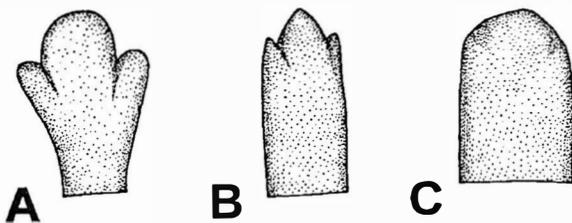


FIG. 8. A, *Liolaemus kriegi* (REE 2412). Character 53, state 0: maxillary teeth crowns expanded, tricuspid. B, *Liolaemus bibroni* (REE 2305). Character 53, state 1: maxillary teeth crowns slender, untapering, cusps reduced. C, *Liolaemus copiapensis* (REE 2560). Character 53, state 2: maxillary teeth with crowns broad and untapering, almost round, cusps slightly differentiated or absent. Drawings made at different scales.

- 40. Melanism on flanks: (0) absent; (1) present as a variegated pattern of large, fused spots; (2) uniformly black. State 1 is typical (with some variation) in *monticola* subspecies. State 2 is exhibited by *cristiani* and *maldonadae*. MULTISTATE NOT POLYMORPHIC.
- 41. Metallic or iridescent scales on the belly or flanks: (0) absent; (1) present. Distinct in *chiliensis*, and present, but less evident in *fitzgeraldi*, *gravenhorsti* and *robertmertensi*. BINARY NOT POLYMORPHIC.

Colours. Two characters were scored:

- 42. Pregnancy colour restricted to cloacal and adjacent areas: (0) absent; (1) present. This colour is bright red, strongly marked on the cloacal region, proximal part of ventral surfaces of thighs and posterior extreme of the abdomen. BINARY NOT POLYMORPHIC.
- 43. Sexual dichromatism showing a dense pattern of light blue to green or turquoise scales scattered on flanks and dorsum of males: (0) absent; (1) present. BINARY NOT POLYMORPHIC.

Neck-folds. Two characters were scored:

- 44. Lateral neck-folding (rictal, postauricular and longitudinal): (0) absent; (1) poorly developed (foldings slightly projecting over the lateral wall of the neck); (2) well developed (foldings strongly projected over the lateral wall of the neck). The folds identified in this case are equivalent to those described by Frost (1992). Rictal, postauricular and longitudinal folds appears always to exhibit the same degree of development. The antegular fold appears to change independently of the others. MULTISTATE NOT POLYMORPHIC.
- 45. Antegular fold: (0) present as a deep pocket; (1) not forming a pocket (evident because of differences in the size of the scales); (2) absent (no pocket and all scales between ear and shoulder identical). MULTISTATE NOT POLYMORPHIC.

Fat pouches. Only one character scored:

- 46. Fat pouches prominent on the sides of the neck: (0) present; (1) absent. BINARY NOT POLYMORPHIC.

Precloacal pores. Two characters were scored:

- 47. Number of precloacal pores in males: means ranging from 8.0 to 0.0. GAP WEIGHTING METHOD.
- 48. Precloacal pores in females: means ranging from 4.0 to 0.0. GAP WEIGHTING METHOD.

Hemipenis. Only one character scored:

- 49. Hemipenis ornamentation: (0) with calices restricted to the base of apical lobes, up to the level of the sulcus spermaticus bifurcation; (1) calices extended below that level.

Size and ratios. Three characters were scored:

50. Snout-vent length (taken from adult specimens only): means from 92.0 to 41.5 mm. GAP WEIGHTING METHOD.
51. Tail length / Snout-vent length ratio (tail length measured on apparently non-regenerated tails): ranging from means of 1.0 to 2.1. GAP WEIGHTING METHOD.
52. Subocular length / eye diameter (eye diameter taken between both angles formed by upper and lower ciliar scales): ranging from means of 1.1 to 1.7. GAP WEIGHTING METHOD.

Teeth and lower jaw. Three characters were scored:

53. Maxillary teeth crowns (Fig. 8): (0) expanded and tricuspid; (1) slender, untapering, anterior and posterior cusps reduced; (2) broad and untapering, crown almost round, cusps slightly differentiated or absent. Only mid-maxillary teeth were considered in this analysis. MULTISTATE NOT POLYMORPHIC. UNORDERED.
54. Heterodonty (cusped posterior maxillary teeth becoming uncusped anteriorly): (0) absent (all maxillary teeth have the same cusp morphology); (1) present (anterior maxillary teeth become uncusped and subconically shaped). BINARY NOT POLYMORPHIC.
55. Meckel's groove: (0) open; (1) enclosed. The second condition is the synapomorphy uniting the *chiliensis* group (Etheridge, 1995). BINARY NOT POLYMORPHIC.

Karyotype. Only one character was scored:

56. Number of macrochromosomes: (0) 12 macrochromosomes; (1) 14 macrochromosomes; (2) 15 macrochromosomes; (3) 16 macrochromosomes; (4) 18 macrochromosomes; (5) 20 macrochromosomes; (6) 22 macrochromosomes; (7) 24 macrochromosomes. *Liolaemus monticola* was scored polymorphic (14/15/16 at its type locality) data tak-

en from Lamborot, Alvarez, Campos & Espinoza (1981). Data for karyotypes were taken from Valencia, Veloso & Sallaberry (1975); Espinoza & Formas (1976); Lamborot, Espinoza & Alvarez (1979); Navarro, Veloso, Valencia & Sallaberry (1979); Lamborot et al. (1981), Navarro, Sallaberry, Veloso & Valencia (1981); Sallaberry, Núñez & Yáñez (1982); Veloso, Sallaberry, Navarro, Iturra, Valencia, Penna & Díaz (1982); Lamborot & Alvarez-Sarret (1989); Lamborot (1991); Navarro & Núñez (1992, 1993); Navarro (1992); Iturra, Veloso, Espejo & Navarro (1994); Quatrini, Bunge & Albino (1997); Aiassa, Gorla, Avila & Martori (1998). MULTISTATE NOT POLYMORPHIC.

Biology and ecology. A total of five characters were scored:

57. Maximum number of yolked-follicles: (0) 4; (1) 5; (2) 6; (3) 7; (4) 8; (5) 9; (6) 10; (7) 11; (8) 12; (9) 13; (10) 14; (11) 15. Data were taken from Ortiz (1981), Leyton, Miranda & Bustos Obregón (1980), Leyton, Veloso & Bustos Obregón (1982) and Ramírez Pinilla (1991). No raw data available to analyzing using the Gap Weighting Method. MULTISTATE NOT POLYMORPHIC.
58. Reproductive mode: (0) viviparous; (1) oviparous. Robert Espinoza pers. obs. BINARY NOT POLYMORPHIC.
59. Life style I: (0) saxicolous; (1) terrestrial; (2) psamophilous. Robert Espinoza pers. obs. MULTISTATE NOT POLYMORPHIC. UNORDERED.
60. Life style II: (0) not arboreal; (1) terrestrial with arboreal tendencies; (2) arboreal. Those scored 1 were coded terrestrial (1) for character 52. MULTISTATE NOT POLYMORPHIC.
61. Diet: (0) insectivorous; (1) omnivorous; (2) herbivorous. Robert Espinoza pers. obs. MULTISTATE NOT POLYMORPHIC.

Data matrix and information on specimens studied is available at: <http://www.unsa.edu.ar/acunsa/index02.html>