

Insular morphological divergence in the lizard *Liolaemus pictus* (Liolaemidae)

Marcela A. Vidal^{1,4}, Alberto Veloso¹, Marco A. Méndez^{1,2,3}

Abstract. *Liolaemus pictus* is a widely distributed arboreal lizard species in southern Chile. Within this species, mainland and island subspecies have been described mainly based on external morphological characters, however, their diagnostic characters have not been accurately demarcated. We used both traditional and geometric morphometrics to study the morphological divergence in *L. pictus* subspecies. Since geographic isolation can be related to environmental variation (e.g., variation in abundance and richness of insects or fruits), we predict that the *L. pictus* morphology could vary in head shape between mainland and island localities.

Our results show morphological divergence in all variables analyzed among the island and mainland localities. The traditional morphometric approach reveals differences between populations from the mainland and island localities, where the mainland populations show a larger head size. Geometric morphometric data indicate that the eye orbits of the island specimens are more extended than in the mainland specimens in the dorsal view; this is probably related to a different capacity of substrate used. Also, in the lateral view, the eye orbits are extended and the head shape is less dorso-ventrally compressed in the island locality than in mainland populations and the terminal mouth position is more posterior in island specimens. We suggest that the morphological variation between mainland and island localities could be related to the fact that these populations were isolated during the last maximum glacial period in southern Chile, a period in which geomorphologic and bioclimatic features of this area were modified forming the present archipelago.

Introduction

The size of organisms has long been recognized to display important biogeographical variations between and within populations (Malhotra and Thorpe, 1991; Renaud and Michaux, 2003). Island vertebrate species, when compared to equivalent mainland species, are often characterized by peculiar morphological traits, a classical example being the evolution of body size toward gigantism or dwarfism (Renaud and Millien, 2001; Anderson and Handley, 2002; Clegg and Owens, 2002). According to the literature, the presence of few predators and competitors on islands, climatic differences and the role of colonization events of island populations

have been invoked to explain divergence in morphology, diet and genetic variability between island and mainland populations (Irschick et al., 1997; Clegg and Owens, 2002; Calsbeek and Smith, 2003). In this context, it has been suggested that the dietary divergence is the main promoter of the island – mainland morphological change (Clegg and Owens, 2002). Concerning lizard populations, Olesen and Valido (2003) suggested, based on density compensation, diet expansion and low predation levels, that island lizards tend to eat fruits and that these dietary changes could produce divergence given that morphological characters and diet are correlated (Ruber and Adams, 2001). For example, morphological changes have been described in two sympatric salamander species due to biomechanical differences in jaw closure associated with the differences in prey consumption (Adams and Rohlf, 2000).

Liolaemus lizards are widely distributed in South America (Donoso-Barros, 1966; Frost and Etheridge, 1989) and more than 160 living species have been described (Etheridge and Espinoza, 2000; Schulte et al., 2000). Given the

1 - Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

2 - Laboratorio de Bioinformática y Expresión Génica; Laboratorio de Bioestadística, INTA, Universidad de Chile, Casilla 138-11, Santiago, Chile

3 - Center for Advanced Studies in Ecology and Biodiversity; Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile

4 - Corresponding author; e-mail: marvidma@icaro.dic.uchile.cl, marcela.vidal@gmail.com

variety of habitats throughout Chile (di Castri, 1968), it is possible that different selective forces can promote morphological variation among populations (Vidal et al., 2004; for *Liolaemus tenuis*). Although some Chilean species of *Liolaemus* have been characterized in terms of their population variation (Lamborot, 1993, 1998; Torres-Perez et al., 2003), the literature concerning morphological variation is relatively scarce (Labra, 1997; Schulte et al., 2004).

Liolaemus pictus is one of most southerly distributed lizard species in Chile (37°S-43°S). Five subspecies have been described for this species according to morphological traits: *Liolaemus pictus pictus* (Duméril and Bibron, 1837) inhabiting the mainland from Concepción to Puerto Montt [37°-41°S] (Donoso-Barros, 1966, 1970; Veloso and Navarro, 1988), *L. p. argentinus* Müller and Hellmich, 1939 from Río Negro Province in Argentina (Donoso-Barros, 1966; Cei, 1986), *L. p. chiloensis* Müller and Hellmich, 1939 from Chiloé Island (Müller and Hellmich, 1939), *L. p. talcanensis* Urbina and Zúñiga, 1977 in Talcan Island (Urbina and Zúñiga, 1977) and *L. p. major* Boulanger, 1885 from islands in the vicinity of Chiloé Island (Donoso-Barros, 1966).

Because subspecies of *L. pictus* live in different types of habitats, it is possible that morphological variation observed could be influenced by local ecological factors. While Ortiz (1974) indicated that *L. p. pictus* from the mainland feed on dipters, homopters, arachnids, hymenopters and coleopters, Willson et al. (1995) and Willson et al. (1996) indicated that *L. p. chiloensis* from Chiloé Island is frugivorous, eating *Nertera granadensis* and *Relbunium hypocarpium*, suggesting that this subspecies is a seed disperser agent. If these ecological factors are present both in mainland and island populations of *L. pictus*, differences between the two regions may lead to morphological divergence, particularly in head shape when dietary differences are involved.

Traditional morphometric analyses are frequently used to test the hypotheses related to

morphological polymorphism in a microevolutionary context (Endler, 1977; Scolaro and Cei, 1987; Quatrini et al., 2001). However, due to scale problems with linear measurements, when used in morphometric analyses they do not take into account the morphological complexity of biological structures. (Humphries et al., 1981; Rohlf and Bookstein, 1987; Mousseau, 1991; Warheit, 1992). On the other hand, the geometric morphometric approach is a tool which allows the analysis of differences in shape without the influence of size variables (Rohlf and Slice, 1990; Rohlf et al., 1996; Bookstein et al., 1999; Rohlf, 1999; Rohlf and Corti, 2000). This second approach offers a geometric vision of a given structure (Rohlf and Slice, 1990; Adams and Rohlf, 2000), registering information regarding shape that allows a more complete biological interpretation of morphological variation (Rohlf and Marcus, 1993).

The aim of this study is to evaluate the morphological variation of *L. pictus* in different localities, comparing mainland and island populations applying both traditional and geometric methods. Given that dietary variation for *L. pictus* between mainland and island populations has been described, we predicted that head morphology could show variation according to this pattern.

Materials and Methods

All materials used in this study belong to the collection of the Museum of Zoology of the Universidad de Concepción (MZUC). Traditional morphometric analyses were performed on 88 adult *Liolaemus pictus* specimens from four localities (fig. 1): *L. p. pictus* from Antillanca [40°46'S, 72°12'W (8 males, 11 females)], Nahuelbuta [37°20'S, 73°30'W (10 males, 14 females)], Púesco [39°25'S, 71°40'W (10 males, 11 females)] and *L. p. chiloensis* from Ancud, Chiloé Island [41°56'S, 73°53'W (11 males, 13 females)].

Twelve morphological characters were studied: (SVL) snout-vent length, (ISD) interparietal scale-snout distance, (IS) interparietal scale size, (MHW) maximum head width, (ID) interocular distance, (HL) head length measured from the tympanic cavity to the snout, (ML) mouth length, (EL) eye length, (END) anterior eye-nose distance, (NSD) nose-snout distance, (ESD) anterior eye-snout distance, and (PERD) post-eye-rostral distance. All measurements were

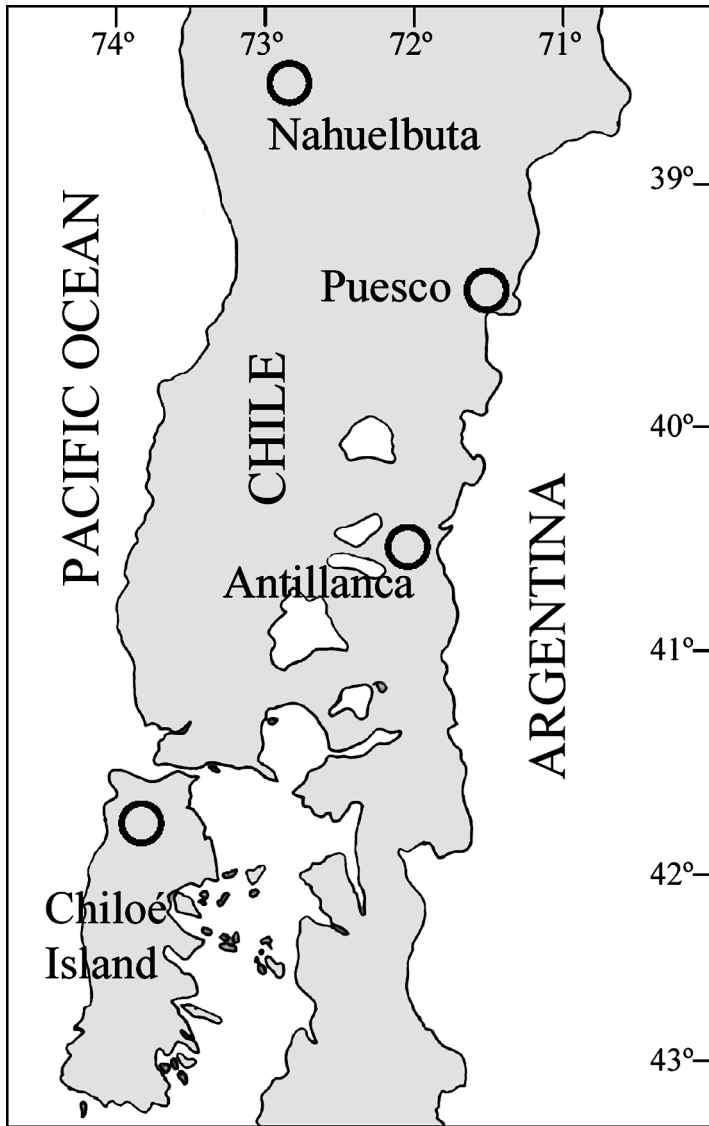


Figure 1. Geographic locations of the populations studied.

taken with a digital micrometer Mitutoyo (± 0.01 mm). These morphological variables were analyzed with a one-way multivariate covariance analysis (MANCOVA); geographic locations were included as a factor and SVL as a covariate. An *a posteriori* Tukey test (Sokal and Rohlf, 1995) was used to determine differences between pairs of localities. A cluster analysis using the unweighted pair group average method (UPGMA) was performed on the Euclidean distances in order to show hierarchically the morphometric differences among populations. Samples had a normal distribution for all analyses performed. The SYSTAT 10.0 software for Windows (SPSS, 2000) was used in all analysis.

A geometric morphometric analysis (Bookstein, 1991) was used to assess the variation attributed exclusively to

shape. Dorsal and lateral views of heads of 88 adult specimens were registered with a Sony-Mavica digital camera. Ten homologous landmarks, coincident with the intersections of the cranial scales and soft tissues were digitalized in the dorsal view and ten homologous landmarks in the lateral view (fig. 2) were analyzed following procedures of Rohlf and Slice (1990) and Rohlf et al. (1996). The x, y coordinates of biologically homologous landmarks were aligned and superimposed using the least squares method based on the generalized procrustes analysis (GPA), allowing for the removal of variations not due to shape (e.g. rotation, movement). Digitalization was performed with Tpsdig version 1.22 and further superimposition was performed with TpsSuper version 1.06 (Rohlf, 2003a, 2003b).

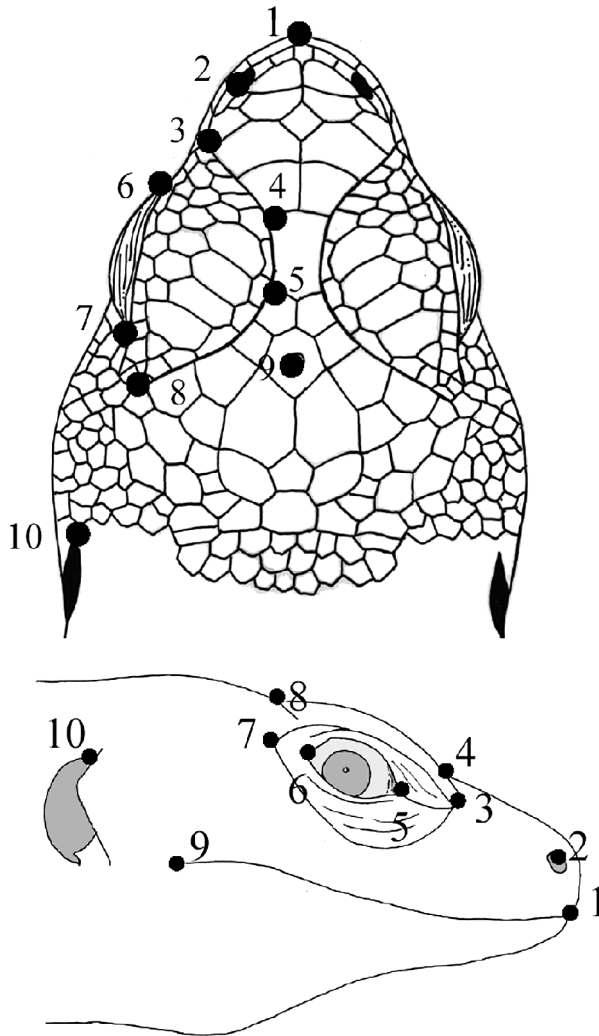


Figure 2. Location of landmarks used in this study in the dorsal and lateral views of the head.

To obtain shape variables, optimally aligned individuals were compared using TpsRelw version 1.21 (Rohlf, 2003c), which performed a thin-plate spline interpolation function to project the data onto a Euclidean plane. Thus, shape variables with both uniform and non-uniform components (total of $2 + 2k - 4$ variables, where k is the number of landmarks used) were obtained. These variables were then used in multivariate statistical analyses (Rohlf et al., 1996; Adams and Rohlf, 2000). TpsRelw version 1.21 (Rohlf, 2003c) was used to perform a principal component analysis (Relative warp analysis). A one-way multivariate analysis of variance (MANOVA) (comparing by locality) and a cluster analysis was performed using Euclidean distances in order to hierarchically depict the shape differences among populations.

In order to determine if the shape incorporated an allometric effect, regression analysis was performed between the first axis of the principle components analysis (shape variables) and the centroid size (CS), which is defined as the

sum of squared Euclidean distances from each landmark to the centroid of the shape (Bookstein, 1991). The centroid size (Log [CS]) of all specimens was compared using one-way analysis of variance (ANOVA), with locality as a factor.

Results

The morphometric measurements by locality are show in table 1. Because not sexual dimorphism were found (Wilks' Lambda = 0.884; $P > 0.1$), male and female data were pooled. MANOVA analysis, which included geographic location as a factor for all the analyzed variables, indicates significant differences among

Table 1. Morphometric variables of *Liolaemus pictus* that showed significant differences among localities by traditional morphometric method. Data are shown as mean and standard error in parenthesis. See Materials and Methods for meaning of the variables.

Locality	SVL	ISD	IS	MHW	ID	HL	ML	EL	END	NSD	ESD	PERD
Antillanca	60.57 (5.13)	10.58 (0.62)	1.61 (0.20)	11.15 (0.84)	7.85 (0.40)	13.81 (1.04)	9.01 (0.67)	3.26 (0.20)	2.60 (0.32)	1.97 (0.25)	4.67 (0.54)	9.66 (0.69)
Chiloé	56.37 (5.85)	9.67 (0.85)	1.56 (0.23)	10.14 (0.83)	7.19 (0.56)	12.24 (1.07)	8.44 (0.66)	2.96 (0.45)	2.38 (0.28)	1.79 (0.26)	4.24 (0.45)	8.64 (0.64)
Nahuelbuta	57.34 (3.66)	10.36 (0.60)	1.88 (0.24)	10.97 (0.72)	7.84 (0.53)	12.88 (0.78)	8.95 (0.70)	3.77 (0.36)	2.89 (0.30)	1.82 (0.19)	4.59 (0.42)	9.14 (0.52)
Puesco	61.20 (4.46)	10.99 (0.52)	1.53 (0.23)	11.90 (0.76)	8.58 (0.51)	14.14 (0.62)	9.41 (0.74)	3.45 (0.31)	3.11 (0.45)	1.95 (0.21)	5.05 (0.36)	10.15 (0.66)

Table 2. One-way analysis of variance for variables that showed significant differences using locality as a factor and SVL as a covariate for *Liolaemus pictus*. (IS) interparietal scale size, (MHW) maximum head width, (ID) interocular distance, (HL) head length measured from the tympanic cavity to the snout, (ML) mouth length, (EL) eye length, (END) anterior eye-nose distance, (ESD) anterior eye-snout distance, and (PERD) post-eye-rostral distance.

Source variation	Degrees of freedom	Variable	F-value	P-value
Locality	3, 79	IS	12.47	0.001
		MHW	8.75	0.001
		ID	24.32	0.001
		HL	5.83	0.001
		ML	3.54	0.018
		EL	27.8	0.001
		END	14.93	0.001
		ESD	4.50	0.005
		PERD	6.81	0.001

Table 3. Variables of traditional morphometric analysis performed in *Liolaemus pictus* showing significant differences ($P < 0.01$) in the *post-hoc* test (HSD-tukey). See Materials and Methods for meaning of the variables.

Localities	Antillanca	Chiloé	Nahuelbuta	Puesco
Antillanca	***	MHW, ID, HL, PERD	IS, ID, EL, END	MHW, ID, HL, END, ESD, PERD
Chiloé		***	IS, MHW, ID, HL, ML, EL, END, PERD	MHW, ID, HL, ML, EL, END, ESD, PERD
Nahuelbuta			***	IS, ID, HL, EL, ESD, PERD
Puesco				***

the geographic locations (Wilks' Lambda = 0.135; $P < 0.0001$). Differences were found among localities for nine variables – IS, MHW, ID, HL, ML, EL, END, ESD, and PERD (table 2) – and lower average values were registered for Chiloé Island (table 1). Differences were found between mainland and island populations (Wilks' Lambda = 0.631; $P < 0.0003$); Chiloé Island showed great morphological differentiation when compared with Nahuelbuta

and Puesco (table 3). Cluster analysis showed two groups: Antillanca, Nahuelbuta and Puesco forming one, and the Chiloé Islands forming another (fig. 3A).

Multivariate analysis of shape variables showed differences among localities when dorsal and lateral head shapes were compared (Wilks Lambda = 7.03; $P < 0.001$, Wilks, Lambda = 5.92; $P < 0.001$, respectively). The dorsal view landmarks 3, 4, 5, 6, 7 and 8, and

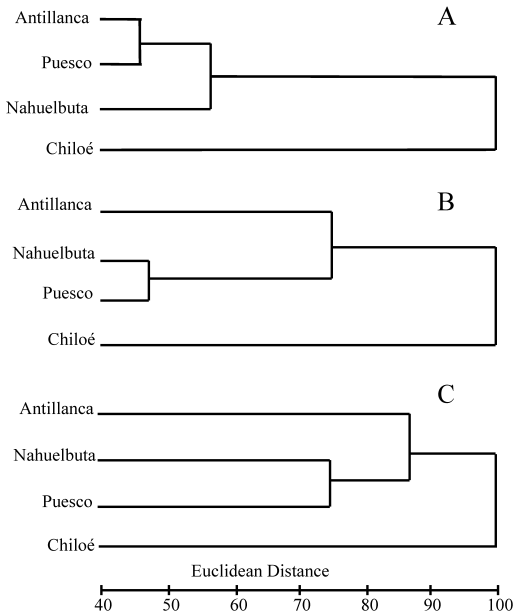


Figure 3. UPGMA phenogram constructed from Euclidean Distances computed on (A) traditional morphometric variables and geometric morphometric variables in (B) dorsal view and (C) lateral view.

in the lateral view landmarks 3, 5, 6, and 7, showed a higher contribution in differentiating localities. All these landmarks were related to eye shape, and in the dorsal view eye orbits were more extended in lizards from Antillanca and Chiloé than in those from Nahuelbuta and Puesco, the most northern localities. These differences were also observed in comparisons between lizards from Antillanca – Chiloé and Puesco – Nahuelbuta, respectively (Tukey Test-HSD, $P < 0.001$). However, the cluster analysis showed that studied populations were assigned to different groups according to their respective origin. Localities within the mainland (Antillanca, Nahuelbuta and Puesco) were grouped together in the phenogram, while Chiloé Island was allocated in a separate cluster (fig. 3B).

In the lateral view, the head shape is less dorso-ventrally compressed in populations from Chiloé than in those from the mainland. Although the relative contribution of landmark 9 was low, in populations from Chiloé is-

land its position is more posterior than in those from other localities. Also, cluster analysis showed two very distinct clusters according to their respective area. Localities within the mainland (Antillanca, Nahuelbuta and Puesco) were grouped together in the phenogram, while Chiloé Island was separated (fig. 3C). Furthermore, when data were pooled, we found differences in head shape between mainland and island populations in the lateral view (Wilks' Lambda = 0.472; $P < 0.001$), but not in the dorsal view (Wilks' Lambda = 0.848; $P = 0.358$).

An allometric effect was not found for the shape variables since no significant relationship ($r = 0.002$; $P = 0.98$) was found between centroid size and the first component in the principal components analysis (31% explained variance) in the dorsal view. Single classification ANOVA, however, indicates a significant difference in centroid size ($F_{3,87} = 12.42$, $P = 0.0001$) among the localities; a *post-hoc* test showed that specimens from Puesco differed from those from the other localities (Tukey Test-HSD, $P < 0.001$). In the lateral view there was no allometric effect ($r = 0.17$; $P = 0.10$) between centroid size and the first component of the principal components analysis (44% explained variance). ANOVA suggested a significant difference in centroid size ($F_{3,87} = 10.14$, $P = 0.0001$) among the localities and a *post-hoc* test showed that Puesco is different from Chiloé Island and Nahuelbuta. This test also showed that population from Antillanca was different from this in Chiloé Island (Tukey Test-HSD, $P < 0.001$). When data were pooled in mainland and island populations, differences in the centroid size were found in both dorsal (ANOVA, $F_{1,86} = 13.51$; $P = 0.0004$) and lateral views (ANOVA, $F_{1,86} = 6.12$; $P = 0.015$). Island populations showed lower centroid size in both views (centroid size in dorsal view: island = 255.6 ± 5.6 , mainland = 277.7 ± 2.89 ; centroid size in lateral view: island = 279.4 ± 9.9 , mainland = 299.9 ± 4.6).

Discussion

In this study, we examined variation in both head measurements and head shape in *L. pictus* from mainland and island populations. Although there are also some differences in head measurements and shape among specimens from the mainland localities, however, major trends in morphological variation pointed out by traditional and geometric morphometric analysis show that *L. pictus* specimens from Chiloé Island are divergent from mainland localities (Antillanca, Nahuelbuta and Puesco). Populations from the mainland show a continuous distribution range, but the connection between island and mainland was interrupted with the last glacial maximum (18,000 Bp; Abarzúa et al., 2004). Pleistocene events, such as glaciations, could determine different island and mainland refuges that would explain the present distribution of many species (Moreno et al., 1994; Formas and Brieva, 2000). The connection between island and mainland, and their posterior separation, may be relevant to explain present morphological differences between disjunct Chiloé island and mainland populations.

Other species inhabiting this region also show changes in morphology but that seem to be more conservative than in *L. pictus*. Anuran amphibians, including *Eupsophus calcaratus*, *E. emiliopugini*, *Batrachyla leptopus* and *B. taeniata* show moderate population differentiation between both areas of insular divergence (Formas, 1989; Núñez et al., 1999; Formas and Brieva, 2000; Brieva and Formas, 2001). Populations on Chiloé Island could afford different ecological pressures than those from mainland concerning intraspecific competence, food availability and absence of predator (Clegg and Owens, 2002; Olesen and Valido, 2003), and could, therefore evolve towards a distinct morphological differentiation.

In the morphological context, various patterns of size variation have been recognized such as gigantism of insular mammal and bird populations (Lomolino, 1985; Clegg and Owens, 2002). Our results are unexpected be-

cause all variables from traditional morphometrics and centroid size (geometric morphometric) for island *L. pictus* show lower values. Donoso-Barros (1966) indicated that island *L. pictus* has a larger body size than other mainland populations, however, this may be due to sampling effects. An alternative explanation for our results could be the existence of a different pattern for island vertebrate evolution, as was pointed out by studies on island birds where it was shown that large birds evolve toward a smaller size while small birds evolve toward a larger size (Roth, 2001; Clegg and Owen, 2002).

Head size is related to the size of prey consumed (Schöener, 1967; Schöener et al., 1982). Morphometric results derived from *L. pictus* may support the hypothesis of insular divergence associated with dietary changes because individuals from mainland populations feed on insects while island population are frugivorous (Ortiz, 1974; Willson et al., 1996). However, since *L. pictus* is a semi-arboreal lizard (Donoso-Barros, 1966), the ocular extension in the island population could also be related to a better capacity to view food while perching. In fact, several studies indicate an association between morphological characteristics and type of habitat (Jaksic and Nuñez, 1979; Jaksic et al., 1980; Losos and Irschick, 1996). According to Schulte et al. (2004), a significant relationship was found between perch variables and escape in *Liolaemus* species, suggesting that this behaviour may also have a possible role in phenotypic evolution (Huey et al., 2003).

Both traditional and geometric morphometric approaches reveal a divergence pattern in *L. pictus*. Unlike traditional morphometrics, the second approach gives information regarding shape and allows for a more complete biological interpretation (Rohlf and Marcus, 1993). However, the use of both traditional and geometric methods allows for a better exploration of morphological variations (Rohlf and Marcus, 1993), in this case, changes in head size (traditional approach) and head shape (geometric approach). The existence of *L. pictus* populations on other

small islands from the Chiloé Archipelago offers the prospect to explore the processes of insular divergence in a wider scope.

Acknowledgement. We thank Juan Carlos Ortiz and Pedro Victoriano (Departamento de Zoología, Universidad de Concepción) for providing specimens from different localities used in this study; Jarmo Perälä made helpful comments on the manuscript. MAV thank CONICYT for the Doctoral Scholarship and AT-24050037 Project.

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