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José Miguel CEI\* - José Alejandro SCOLARO\*\* - Fernando VIDELA\*\*\*

## An updated biosystematic approach to the leiosaurid genus *Pristidactylus*

### ABSTRACT

A general discussion of the intra- and intergeneric biological relationships of the leiosaurid genus *Pristidactylus* has been carried out. Its cis-trans cordilleran species groups are reported and compared, also in agreement with results of the very recent molecular and morphological research by Frost *et al.* (2001). The new family Leiosauridae, including *Enyalius*, *Diplolaemus*, *Leiosaurus* and *Pristidactylus*, is taken into account, and ancient evolutionary relationships of the last named genus are considered. Present specific characters of Chilean, but mainly of Argentinian *Pristidactylus* taxa, are analyzed and compared. They are likely adaptive features from ancestral times of their common preglacial origin. Critical comments on the now postulated primitive position of the terrestrial forms instead of the formerly accepted arboreal forms as plesiomorphic evolutionary stage are presented as well.

Key words: Iguanian taxonomy, *Pristidactylus*, Miocenic lizards, cis-trans Andean fauna, Dimorphism.

### INTRODUCTION

A general taxonomic assessment of the genus *Pristidactylus* and other "polychrotid" genera has been presented very recently by Frost *et al.* (2001), in an ambitious attempt to reformulate the whole phyletic-systematic relationships of the Iguania. As pointed out by these authors in their introduction, the initial objectives of such a major work were to test the still disputed monophyly of Polychrotidae, a remarkably diversified Neotropical taxon. Polychrotid generic taxa known up to date, scattered in the current literature besides *Anolis* and *Polychrus*, were the

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\* Honorary Professor, Facultad Ciencias Agrarias, Universidad Nacional de Cuyo, Mendoza, Argentina.

\*\* Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina.

\*\*\* Unidad de Ecología Animal, IADIZA, Mendoza, Argentina.

para-anoles *Anisolepis* and *Urostrophus*, plus an austral “leiosaur” group including *Enyalius*, *Diplolaemus*, *Leiosaurus* and *Pristidactylus*. The purpose of our present work is to provide more actualized biomorphological information about *Pristidactylus*, a peculiar genus of the above mentioned leiosaur polychrotids, well summarized in the former notes of Etheridge and Williams (1985), now extended and even preliminarily discussed in a recent paper of Cei *et al.* (2001). With the present contribution we add morpho-ecological and behavioral data on its species in order to facilitate the evolutive comprehension and the phylogenetic relationships of this iguanian group.

### THE *PRISTIDACTYLUS* SPECIES

Following the new provisional classification just emphasized in our Introduction, Polychrotidae is now restricted to *Anolis* and *Polychrus*: Both the new tribes Enyaliinae (*Enyalius*, *Anisolepis* and *Urostrophus*) and Leiosaurinae (*Leiosaurus*, *Diplolaemus* and *Pristidactylus*) belong now to Leiosauridae. This latter group of “Polychroids” is suggestive of a significant austral distribution in the Neotropical continent, with most of its terrestrial forms in dry, stony environments. In the popular Argentine expression, they are all named “matuastos”, being also characterized by a peculiar aggressive behavior as well as a very secretive nature.

As Frost *et al.* (2001) have pointed out, the establishment of the tribe, or subfamily, Leiosaurinae is a welcome confirmation of a very natural, intergeneric evolutionary group. Their changes in phyletic assessment of the morphological and biogeographical cis-transcordilleran grouping of the several taxa of *Pristidactylus* are an unusual, surprising statement, a reversion of a long-accepted conceptual situation. Two groups of *Pristidactylus* species have been commonly recognized, also and mainly by the authors of the present changes: a Chilean group, considered plesiomorphic and primitively arboreal, and an Argentinian group, apomorphic, mainly including terrestrial forms. These conditions have been now inverted on the bases of well supported analytical data. Then a further review synthesizing their paleogeographic and paleoclimatic history, as well as the morpho-ecological features of this genus, could contribute to a better approach to its evolutionary status or taxonomic assessment.

The Chilean group, now considered as derived, is composed by four species, listed here in order to their increasing arboreality. They are: 1- *Pristidactylus volcanensis* Lamborot and Diaz, 1987; 2- *P. alvaroi* (Donoso Barros, 1974); 3- *P. valeriae* (Donoso Barros, 1966); 4- *P. torquatus* (Philippi, 1861). A better identification of these taxa, and their geographical distribution shall be provided in Plates 1-3 and Fig. 1.

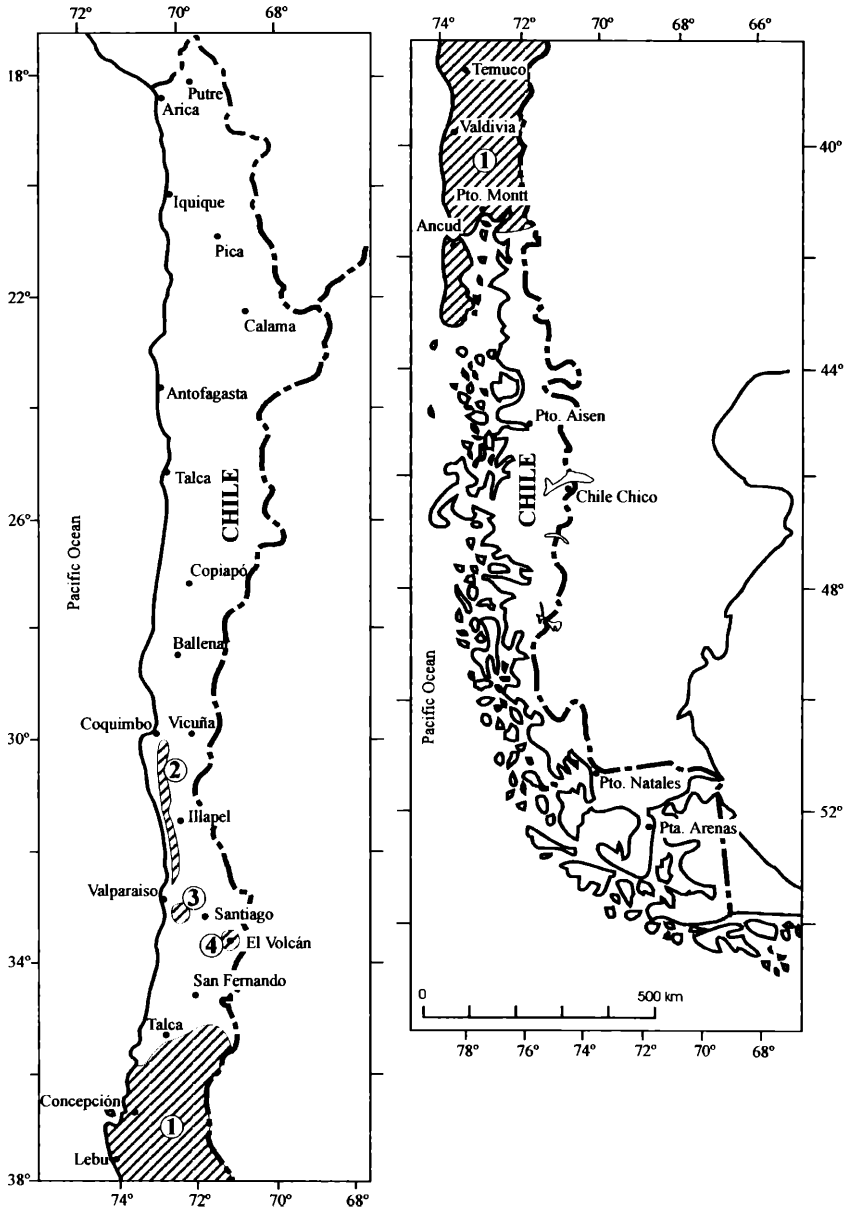


Fig. 1 - Present distribution of the genus *Pristidactylus* in Chile.  
 1- *P. torquatus*; in the *Nothofagus* temperate forest; 2- *P. valeriae*; 3- *P. alvaroi*; 4- *P. volcansensis* (all in relics of the austral humid temperate forest).

The Argentinian species of *Pristidactylus* are found from about 29° to 45° S lat., with disjunct distribution areas, whose localization often is difficult due to the secretive behavior and the ecological trends of these lizards. From North to South, along the limiting Cordilleran barrier, we find the following taxa: *P. scapulatus* (Burmeister, 1861), *P. achalensis* (Gallardo, 1964), *P. casuhatiensis* (Gallardo, 1968), *P. fasciatus* (D'Orbigny and Bibron, 1837), *P. araucanus* (Gallardo, 1964), *P. nigroiugulus* Cei, Sclaro and Videla 2001. An iconographic illustration of these leiosaurids and their geographical distribution are provided in Plates 4-10 and Fig. 2.

**Materials and methods.** All specimens directly observed were carefully examined, measured with precision calipers (0.1 mm accuracy) under a dissecting microscope, and compared with the phenetically closest species of the genus. The measurements were taken on adult individuals whose maturity was established by the presence of ripe gonads and the functional development of secondary sex characters.

Scale terminology follows Smith (1946) and Peters (1964). Head length was measured from a line between the inferior apex of each external auditory meatus to anterior surface of rostral; head width was measured across widest part of temporal region. Body length was considered as snout-vent length and compared with tail length. Two ratios were considered: head width/head length and snout-nostril distance/eye-nostril distance. A Fisher analysis of variance was applied to measurements of specimens, previously log-transformed, to detect differences among the species. Morphometric ratios were transformed by arc-sin of square root, and analyzed by a Kruskal-Wallis analysis of variance. Both analyses were completed with multiple comparisons by a Tukey test. In order to detect sexual dimorphism in the studied species, the measurements were analyzed by t-test of Student, and the ratios by Z-adjusted test of Mann-Whitney ( $p < 0.01$ ) (Zar, 1984).

The Argentinian specimens now analyzed were: *P. scapulatus* (N= 13), *P. nigroiugulus* (N = 12), *P. araucanus* (N = 24), *P. achalensis* (N= 29), *P. fasciatus* (N= 11), *P. casuhatiensis* (N= 11). Given the forced lack of suitable serial set of specimens of the Chilean taxa, we must emphasize that our present information was necessarily supported by the current bibliography and above all by the generous personal cooperation of colleagues from some trans-Andean and North-American centers, whose very valuable aid shall be later detailed in our acknowledgements.

Specimens listed in the final Appendix belong to the following institutions and personal diagnostic collections, whose abbreviations were widely following Leviton *et al.* (1985): MACN: Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina); MHNG: Museum d'Histoire Naturelle de Gêneve (Switzerland); IBA-UNC: Instituto de Biología Animal, Universidad Nacional de Cuyo

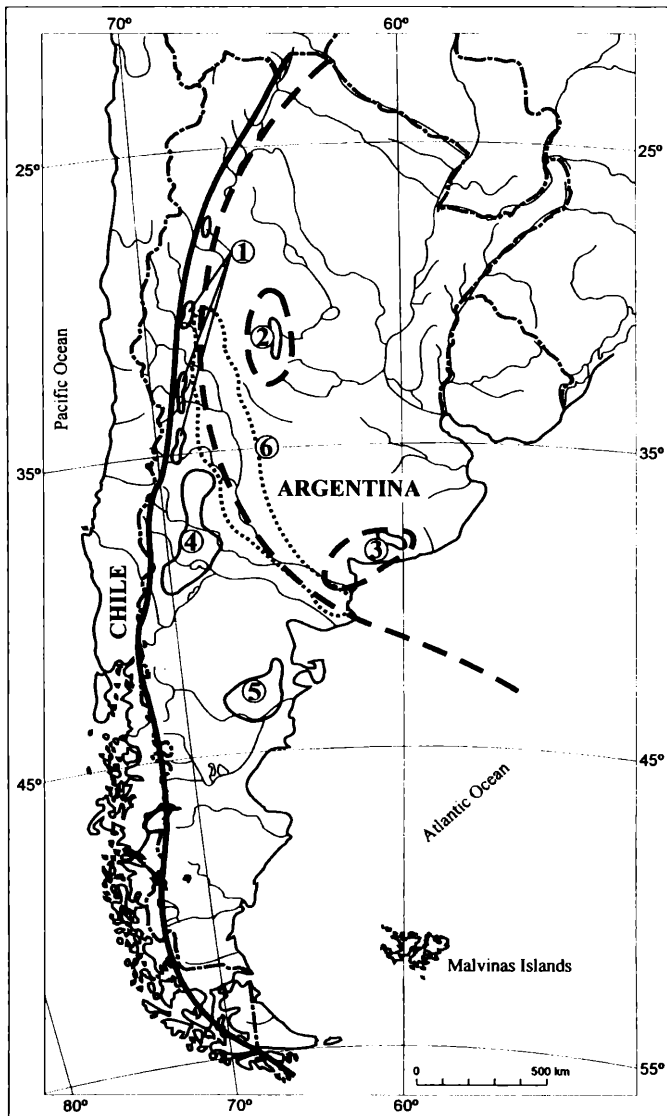


Fig. 2 - The Glaciation event and the present distribution of the genus *Pristidactylus* in Argentina.

— limits of Pleistocene Permafrost (permanent iced soil).

— actual limits of Permafrost.

Tentative distribution areas: 1- *P. scapulatus*; 2- *P. achalensis*; 3- *P. casuhatiensis*; 4- *P. araucanus*; 5- *P. nigroiugulus*; 6- *P. fasciatus* (Map redrafted according to Corte, Geociologia, 1997).

(Mendoza, Argentina); MCZ: Museum of Comparative Zoology of Harvard University (Cambridge, USA); CH-IADIZA: Colección Herpetológica del Instituto Argentino de Investigaciones en Zonas Áridas (Mendoza, Argentina); MMHNSR: Museo Municipal de Historia Natural de San Rafael (Mendoza, Argentina); JAS-DC: J.A. Scolaro Diagnostic Collection, CENPAT-CONICET (Puerto Madryn, Argentina); JMC-DC José M. Cei Diagnostic Collection (Mendoza, Argentina).

## RESULTS

### THE *PRISTIDACYLUS* CHILEAN GROUP

*Pristidactylus volcanensis* - This species, carefully studied by Lamborot and Diaz (1987), is a robust lizard (84-97mm snout-vent), with irregularly black-spotted head and granular dorsum crossed by six transverse darker bands extending onto the tail, 1.4 times body length. Sex dichromatism or ontogenetic change in color has been unreported. The hemigular and ante-humeral black collar, characterizing the genus, is not too evident. Remarkable is the reddish coloration on the venter of the body, limbs and cloacal region. The species was described for the sub-Andean sclerophyllous shrublands at the latitude of Santiago, having been interpreted as a form of ancient arboreal lineage, restricted to new marginal biotopes of xeric sub-Andean formations by adaptive processes referable to the eco-geographic vanishing refuge model of speciation proposed in the past by Vanzolini and Williams (1981).

*Pristidactylus valeriae* and *Pristidactylus alvaroi* - The mesophilous temperate forest reached central Chile at the beginning of the Miocene. Changes and climatic-vegetational sequence of Cenozoic and recent forested ranges in Chile have been detailed recently by Hinojosa and Villagran (1997) and Villagran and Hinojosa (1997). Several well-adapted species developed their ecological trends in such a wide-spread biota: *Pristidactylus valeriae* and *P. alvaroi* from coastal mountain ranges have been considered representative elements of a secondary adaptation to deteriorating biotopes, from mesic to xeric environmental conditions. They are medium-sized lizards (70-90mm, snout-vent), with elongate heads, densely scattered with enlarged dark marks and with granular dorsal scales that are broader and more prominent along the vertebral line of *P. alvaroi*. Tail is 1.5 times body length in both sexes of *P. valeriae*, compressed and 1.3 times body length in males of *P. alvaroi*, 1.5 times in females. Ground color is grayish with 5-6 rounded dark vertebral spots, paired in *alvaroi*, and a faint transverse series of four square marks is recognizable. The ante-humeral black collar is present

in both species, interrupted below: apparently, it is more prominent with age. The most brilliant colors are ventral: yellow abdomen, reddish on flanks and anterior limbs in *valeriae*, yellow belly in *alvaroi*.

*Pristidactylus valeriae* extends from Coquimbo (30° S lat.) to Valparaiso (33° S lat.); *P. alvaroi* is known from Cerro El Roble, at the latitude of Santiago. Both forms, formerly confused by their general aspect (Pl. 1, 3), were associated to relictual *Nothofagus* formations, but, according to Donoso Barros (1966), their habits are not exclusively arboreal.

*Pristidactylus torquatus* - It is the most arboreal species of the Chilean taxa and, of course, of the whole genus (Pl. 2, 1-3). Extending from Curicó (Los Queñes: 35° S lat.) to Puerto Montt (41° 30' S lat.), this robust leiosaurine reaches 95mm in length (snout-vent) in its stout females. It is considered a significant element of the *Nothofagus* forest, also when that overtook its major expansion. However, in spite of their habitual arboreal life and of their morphological climbing features, specimens of *Pristidactylus torquatus* were found under rocks in bunch-grass meadows near the forest, or foraging in the heath (Webb and Greer, 1969). Hard beetles are included in their diet and are crushed by their strong maxillas. The prehensile tail is 1.4 times body length: the tails of other arboreal forms, as *Polychrus*, can reach 2.0-2.2 times body length.

A dark cross-banded dorsal pattern is very distinct in young individuals, but it is still recognizable in adult females, on whose head and neck a coarse, horseshoe shaped, dark mark may be observed (Pl. 3, 1, 2). In adult males the transverse juvenile pattern is reduced (Pl. 2, 1), dissembling in their brilliant bluish, greenish or yellow-brown dorsal coloration. A distinct ante-humeral black collar, laterally notorious in males (Pl. 2, 1), faint in females, is present in that species.

A more thorough review, supported by intensive field work, could lead to modify a former impression about the postulated primitive arboreality of Chilean *Pristidactylus* species. Published data and observations of Webb and Greer (1969) in Malleco province, or Montecinos, Espinoza and Formas (1979) in Ñuble, Talca and Curicó provinces, for example, are very suggestive for a better understanding of the evolutionary history of the genus, as further we shall comment.

### THE *PRISTIDACTYLUS* ARGENTINE GROUP

**Morphological remarks.** The general morphological features of *P. scapulatus*, *P. achalensis*, *P. araucanus*, *P. nigroiugulus* and also *P. fasciatus*, mainly in male specimens, explain some past misidentifications in the taxonomic literature. Only very reduced darker remains of a cross-banded juvenile pattern are recognizable in the almost uniform brownish dorsal coloration shown by adult males of the first four species, and it changes to a brilliant green when exposed to the sun (Pl. 4, 1; 5, 1; 6, 1; 7, 1). However, some still-evident transverse marks and spots of a juvenile pattern can be observed in several males of *P. fasciatus* (Pl. 8, 1). Characteristic pattern of a juvenile specimen of this lizard (38mm, snout-vent) was clearly shown by the figure of the type of D'Orbigny (1847) from Carmen de Patagones, further commented by Barrio (1969).

In adult females of *achalensis*, *araucanus*, *nigroiugulus*, and *fasciatus* a more-or-less bright cross-banded pattern is present (Pl. 5, 2; 6, 2; 7, 2; 8, 2), very similar to that exhibited by their juveniles, as we pointed out previously for *P. torquatus* from Chile (Pl. 3, 1; 2, 3). However, a reduced residual cross-banded pattern, sometimes only represented by scattered small round spots (Burmeister's multipunctatus form, 1861), characterizes adult females of *P. scapulatus*, as formerly pointed out by Etheridge and Williams (1985). According to unpublished observations of Christie (1995-99: pers. comm.), young male specimens of *P. araucanus* from the vicinity of Zapala, Neuquén, still retain a clear-cut juvenile pattern until a size of 52-54mm snout-vent (Pl. 9, 3). Their diminute testicles (1.5x0.8 - 1.5x1mm) suggest that the loss of such a pattern, evident in females, is likely related to a later stage of sexual maturity with hormonal androgenic effect on coloration. That was not yet observed in young male individuals of the same size in *P. scapulatus*, whose evident juvenile cross-banded pattern was recently confirmed in its population from Paramillos, Uspallata, Mendoza province (Fig. 3, top).

Different enough from coloration of other Argentinian *Pristidactylus* is the specific pattern of *P. casuhatiensis* from Sierra de la Ventana (Buenos Aires province), whose adult males are dorsally green, scattered with black reticulations from head to tail and limbs: a reddish-orange shade extends from the checks to the humeral region, flanks and base of tail (Pl. 9, 1). According to Gallardo (1968), the dorsal ground color of females is light brownish, cross-banded by darker broad stripes not evident in preserved specimens: the whitish belly is scattered with grayish spots or marks. In *P. casuhatiensis* as well as in every *Pristidactylus*, the black ante-humeral collar is present. Such a black collar is peculiarly extended as a wide blade spot on the gular region of *P. nigroiugulus*. This unusual character, growing with the age (Pl. 10, 1), is unique in the genus and for any leiosaurid.





Fig. 3 - *Pristidactylus scapulatus*. Typical cross-banded juvenile pattern in a young specimen from Paramillos de Uspallata. 3000 m a.s.l., Mendoza, Argentina. February 2002. Photo: J. M. Cei (Top).

*Diplolaemus darwini*. Young specimen showing the typical juvenile pattern. Bajada del Buey. 950 m a.s.l. 60 km E of Gastre. Chubut, Argentina. March 2000. Photo: J. M. Cei (Bottom).

Inter-specific divergence between Argentinian taxa can be evidenced for a number of measurements and ratios of their anatomical parameters, as reported in Tables 1 and 2.

Data listed in Table 1 support sex dimorphism in “size” (SVL) for *Pristidactylus nigroiugulus* ( $t= 3.65$   $p= 0.004$ ) and *P. achalensis* ( $t= 3.99$   $p= 0.001$ ), but no dimorphism for the other species.

Species	Sex	N	SVL				N	SVL / TL			
			Mean	SD	Min	Max		Mean	SD	Min	Max
<i>P. scapulatus</i>	Males	8	101.1	4.4	95.0	110.0	6	0.86	0.06	0.77	0.94
	Females	5	90.8	10.6	75.0	100.0	2	0.94	0.00	0.94	0.94
<i>P. araucanus</i>	Males	13	95.8	5.3	85.0	103.0	6	0.89	0.06	0.82	0.98
	Females	11	91.4	9.9	74.0	103.0	7	0.89	0.03	0.86	0.94
<i>P. nigroiugulus</i>	Males	8	96.3	4.0	91.5	102.0	5	0.80	0.04	0.74	0.84
	Females	4	87.0	4.5	81.0	91.0	4	0.88	0.05	0.85	0.96
<i>P. achalensis</i>	Males	15	104.4	4.2	94.5	110.0	7	0.89	0.04	0.84	0.95
	Females	14	98.3	3.9	90.0	104.0	5	0.88	0.06	0.80	0.94
<i>P. fasciatus</i>	Males	8	87.6	6.1	80.0	99.0	4	1.27	0.04	1.22	1.31
	Females	3	95.0	6.1	91.0	102.0	3	1.42	0.19	1.21	1.56
<i>P. casuhatiensis</i>	Males	7	107.7	3.3	103.0	112.4	6	0.70	0.03	0.68	0.76
	Females	4	101.5	11.1	87.9	111.0	4	0.71	0.04	0.67	0.76

Tab. 1 - Sex dimorphism and inter-specific character differences in Argentine taxa of *Pristidactylus*. Mean values for the snout-vent length (SVL, in mm) and the body length/tail length ratio (SVL / TL) in males and females of the six species analysed.

Inter-specific differences in size (SVL) are detected in males ( $F= 20.48$   $p= 0.001$ ), being *P. fasciatus* shorter than the other species, and *P. casuatiensis* larger than *P. araucanus* and *P. nigroiugulus*; inter-specific differences are insignificant or faint in females ( $F= 2.50$   $p= 0.049$ ). In accordance to Table 1 the SVL / TL ratio is lower than 1, being the tail larger than body in most registered species, but notoriously shorter in *P. fasciatus*: an opposite diagnostic character, former emphasized by Etheridge and Williams (1985). A tail (TL) significantly larger in males than in females is shown by *P. scapulatus* ( $t= 4.06$   $p= 0.007$ ) and *P. nigroiugulus* ( $t= 4.36$   $p= 0.003$ ). The high frequency of autotomy in these leiosaurines explains the troubling scarcity of data for intact tail lengths in every sample. A very low frequency of autotomy is only remarkable in *P. casuhatiensis*.

Other remarkable somatic characters belong to the head shape and the snout morphology of *Pristidactylus*. Several of their measurements and ratios in Argentinian species have been analyzed in the Table 2. The lack of sex dimorphism for the head shape (HW / HL) is the rule in most

Species	Sex	N	HW / HL				SND / END				
			Mean	SD	Min	Max	N	Mean	SD	Min	Max
<i>P. scapulatus</i>	Males	8	0.85	0.03	0.82	0.90	8	0.47	0.02	0.43	0.49
	Females	5	0.85	0.02	0.83	0.88	5	0.45	0.04	0.40	0.48
<i>P. araucanus</i>	Males	13	0.77	0.02	0.71	0.79	13	0.60	0.05	0.50	0.67
	Females	11	0.75	0.03	0.69	0.78	11	0.61	0.05	0.50	0.67
<i>P. nigroiugulus</i>	Males	8	0.83	0.02	0.80	0.87	8	0.46	0.03	0.43	0.49
	Females	4	0.87	0.07	0.80	0.94	4	0.46	0.04	0.42	0.50
<i>P. achalensis</i>	Males	15	0.83	0.03	0.78	0.89	15	0.90	0.05	0.82	0.96
	Females	14	0.78	0.03	0.73	0.84	14	0.83	0.06	0.73	0.94
<i>P. fasciatus</i>	Males	8	0.89	0.04	0.83	0.94	8	0.81	0.02	0.80	0.84
	Females	3	0.84	0.03	0.81	0.88	3	0.78	0.01	0.77	0.79
<i>P. casuhatiensis</i>	Males	7	0.69	0.03	0.66	0.74	7	0.63	0.04	0.56	0.68
	Females	4	0.71	0.02	0.69	0.72	4	0.59	0.04	0.54	0.63

Tab. 2 - Sex dimorphism and inter-specific character differences in Argentine taxa of *Pristidactylus*. Mean values for the head width/head length ratio (HW / HL) and snout-nostril distance/eye-nostril distance (SND / END) in males and females of the six species analysed.

of these species, except in *P. achalensis* ( $Z= 3.49$   $p= 0.001$ ). Interspecific dissimilarity can be pointed out in both sexes ( $H= 45.68$   $p= 0.001$  in males and  $H= 28.72$   $p= 0.001$  in females), being the HW / HL ratio lower in *P. araucanus* and *P. casuhatiensis*, and higher in *P. fasciatus*, than in the other species. Snout measurements and shape (SND / END) presented significant interspecific differences ( $H= 53.60$   $p= 0.001$  in males, and  $H= 35.34$   $p= 0.001$  in females), being in *P. scapulatus* and *P. nigroiugulus* lower than in the other species. Both species show a noticeable similarity, opposing to *P. araucanus*, whose ratios are further more very distinctive from the ratios of *P. achalensis*, the isolated inhabitant of the Sierras de Córdoba. The general peculiarity of *P. fasciatus* must be recalled for the here considered somatic features.

Outstanding specific characters may be moreover provided for peculiar cephalic lepidosis pattern of these reptiles, as well as for some of their anatomical structures, such as the shape of posterior marginal teeth, the smooth or multicarinate lamellae of ventral digital surface, and the hemipenis morphology.

The supraocular scutellation is an unmistakable one in every Argentinian species of *Pristidactylus* (Cei 2003: in press). Its taxonomic interest was not yet taken into account for its diagnostic value. As shown in Fig. 4 a-f, size and distribution of scales between ciliaries and supraorbital semicircles are significantly different in the six observed taxa, their individual and geographical variation or sex dimorphism

being negligible. The still available information about Chilean species can also suggest the presence of this morphological condition in the trans-Andean species of the genus (Fig. 4 g).

Specific differences in posterior marginal teeth are likely suggestive of functional dietary adaptations (Fig. 5 a-c). Crowns flared, strongly compressed, with larger anterior and posterior cusps, are shown by the omnivorous *Pristidactylus achalensis*; crowns tapered, slightly compressed, with reduced anterior and posterior cusps, are present in *P. scapulatus*, *P. araucanus*, *P. nigroiugulus*, *P. fasciatus* and the miocene *Pristidactylus* sp. fossil from Chubut, whose affinities with *P. scapulatus* or *P. nigroiugulus* have been recently pointed out (Albino and Etheridge, 2000). Crowns somewhat swollen, with cusps absent or very faint, belong to the peculiar poorly known *P. casuhatiensis*, mainly feeding on terrestrial snails (*Plagiodontes patagonicus*).

Ventral digital lamellae, more over, are smooth in the most species of Argentinian *Pristidactylus* (Fig. 5 f), but carinate in *P. casuhatiensis* and multicarinate in *P. fasciatus*, a well differentiated form of the group (Fig. 5 d-e). Such a distinctive condition, is in agreement with several other metric or meristic characters opposing *P. fasciatus* to any other member of the cis-Andean group. As shown in Fig. 5 g-h), morphological features of the hemipenis must be further investigated in these polychrotids, as peculiar organs of systematic interest.

**Ecology and specialization.** In their Argentinian habitats *Pristidactylus* species show specific adaptive trends as result of so many ancestral evolutionary events. In Andean localities where populations of *Pristidactylus scapulatus* have been occasionally found and described, they are separated by considerable topographic gaps, often interposed with true orographic barriers. Besides an unspecified locality in the cordilleras of Catamarca province (Koslowky, 1895), these lizards were collected in San Juan and Mendoza provinces, above altitudes of 2000 m a.s.l. as, in San Juan, the still uncontaminated San Guillermo plateau (3500 m) and Tocota (2500 m), Iglesias Dept., or in Mendoza Paramillos de Uspallata, Las Heras Dept. (3000 m) and Cuesta del Choique, Malargüe Dept. (2300 m). Habits of *Pristidactylus scapulatus* and its secretiveness are relatively uniform in so large an area of latitudinal distribution. They find shelter under stones and isolated ravines in bushy slopes of its cordilleran habitat (Pl. 4, 3), standing out, owing to the showy green coloration when basking on top of small rocks and shrubs. In San Guillermo high tableland we observed their fossorial ability, quickly reaching deep refuges in the radical system of major plants in their environment, as *Lycium chañar*, probably searching for a better water equilibrium in relative humidity. Low temperatures in winter, or on summer nights, are tolerated by these xerophile lizards, likely of ancient periglacial adaptation and irregularly following in post-glacial stages the

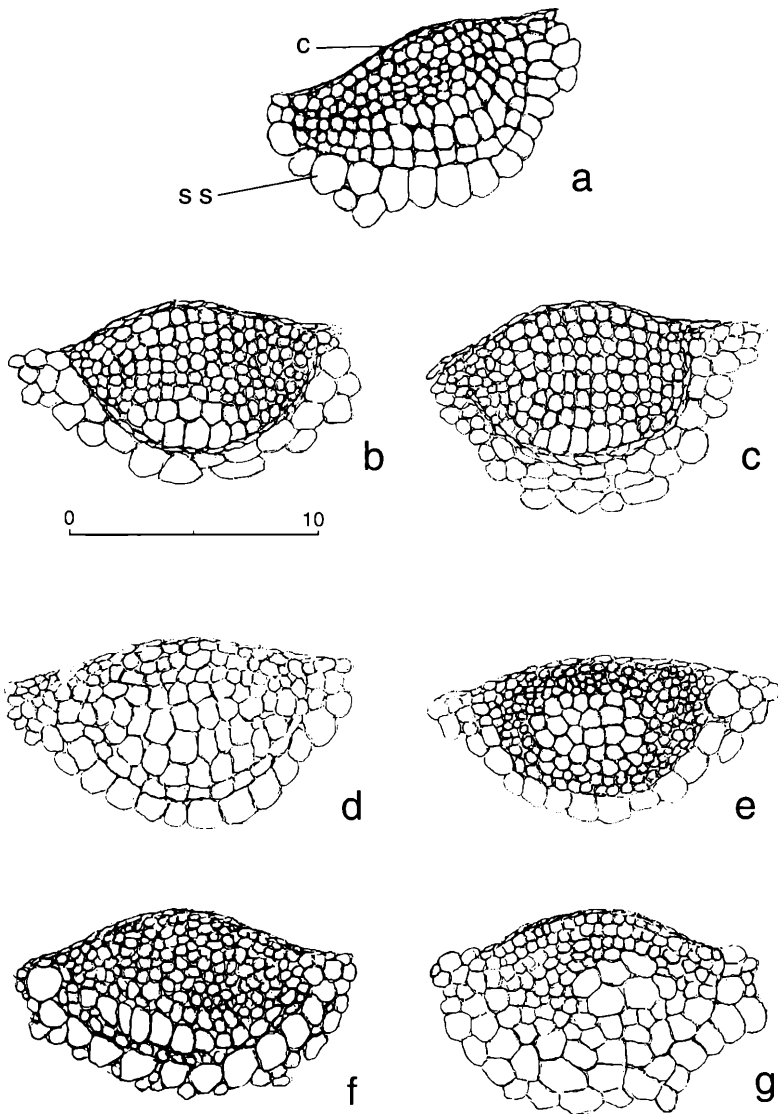


Fig. 4 - Specific patterns of the supraocular lepidosis in the genus *Pristidactylus*. a- *P. scapulatus*, Uspallata, Mendoza; b- *P. araucanus*, Zapala, Neuquén; c- *P. achalensis*, Pampa de Achala, Córdoba; d- *P. nigroiugulus*, Telsen, Chubut; e- *P. fasciatus*, El Nevado, Mendoza; f- *P. casuhatiensis*, Sierra Ventana, Buenos Aires; g- *P. alvaroi*, El Roble, Santiago, Chile. (The Fig. 4, g from Donoso Barros, 1974; the line indicates the major length of the supraocular region, in mm; SS- supraorbital semicircles; C- ciliares).

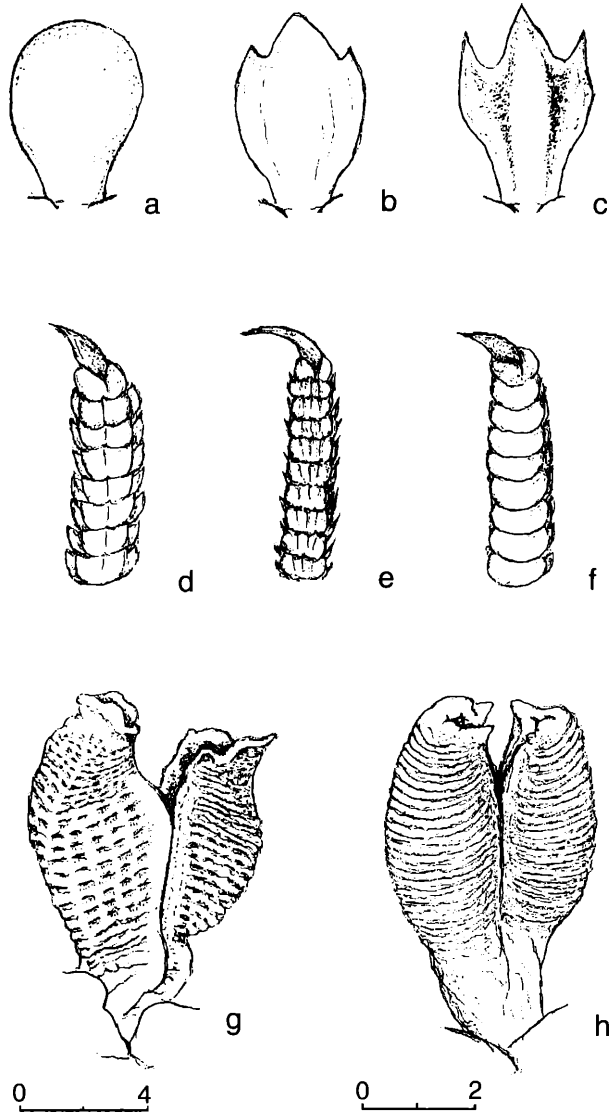


Fig. 5 - Different specific characters in *Pristidactylus*.

Posterior marginal teeth of: a- *Pristidactylus casuhatiensis*; b- *P. fasciatus*; c- *P. achalensis*.

Subdigital lamellae: carinate in d- *P. casuhatiensis*; smooth in f- *P. achalensis*; tricarinate in e- *P. fasciatus*.

Hemipenis, sulcate side, in: g- *P. scapulatus*; h- *P. fasciatus*.

(Fig. 5, g, redrawn from Böhme, 1988; Fig. 5, h, original: all strongly augmented; the lines indicate the general size of the hemipenis, in mm).

altimetrical variation of their mountain or sub-mountain limits of settlement.

The distributions of *Pristidactylus achalensis* and *P. araucanus* do not overlap the high mountain distribution of *P. scapulatus*. Their remarkable distinctive character is the above mentioned persistence of juvenile patterns in adult females. Granitic tops of Pampa de Achala, Champaquí and Comechingones Sierras, Córdoba province, at about 1800-2500 m a.s.l. (Pl. 5, 3), are the exclusive range of the endemic *P. achalensis*, a saxicolous leiosaurine abundant in a less xerophilous stony habitat, scattered with frequent pools and marshes, and covered by a peculiar vegetation, sometimes reminiscent of far Southern formations, as *Maitenus*, *Baccharis*, *Berberis*, from the Patagonian biota. Biologically it is the most studied taxon of *Pristidactylus*, (Di Tada *et al.* 1977; Di Tada *et al.* 1980; Di Tada *et al.* 1982). Likely adaptive trends of this omnivorous member of segregated biotopes could be associated to its above reported dentition, with strongly compressed crowns whose lateral larger cusps contrast with the tapered crowns and the small cusps of *P. scapulatus* and *P. araucanus*.

Ecologically *Pristidactylus araucanus* can be characterized by its unusual apparent fitness to the specialized basaltic environments of the sandy or rocky volcanic landscapes of the Central and North-Patagonian Argentina. Historical and nomenclatural vicissitudes of such a discussed taxon have been summarized by Etheridge and Williams (1985) and Cei *et al.* (2001). Habits and behavior of this still more secretive lizard are very poorly known. Samples of specimens were reported from Neuquén (Laguna Blanca, Zapala, 1200 m a.s.l.: type and paratypes) and Payún volcanic highlands (southern Mendoza Province, 1800 m.a.s.l.). Biocenotic communities of their habitats show a floristic Patagonian shrub physiognomy, with *Nardophyllum deserticola*, *Anarthrophyllum macrophyllum*, *Stillingia patagonica*, *Grindelia chiloensis*, *Junellia spathulata*, *Stipa speciosa var. media* and *Stipa speciosa var. manlequensis* as dominant elements.

Similar remarks can be made for the other mountainous endemic *Pristidactylus casuhatiensis* from restricted tops of the Sierra de la Ventana, Buenos Aires province, at an altitude of about 1000 m a.s.l. (38° 08' S lat.), in a landscape of flat no volcanic rocks, with low and scarce vegetation and sinkholes filled by rainwater (Pl. 9, 2). Floral endemisms are abundant, such as *Festuca ventanicola*, *Briza* spp., *Aira* sp., *Grindellia ventanicola*, *Poa iridifolia*, *Plantago bismarcki*, *Polystichum* sp. and saxicolous lichens (Kristensen and Frangi, 1995; Perez and Grassini, 1997). Even this species is ecologically very poorly known. It feeds on small arthropods but preferably on the very abundant terrestrial snails as *Plagiodontes patagonicus*. These dietary habits can be related to its peculiar dentition, with crowns swollen and vestigial lateral cusps, able to crush hard, calcareous shells.

More recently, Cei *et al.* (2001) described a new species named *Pristidactylus nigroiugulus* (Pl. 7, 1) living in the basaltic Telsen tableland, at about 850-1000 m. a.s.l., some 230 km West of Pt. Madryn (Chubut province). Such a monotonous biotope shows a typical Patagonian environment with low spinous bushes between the major stones (Pl. 7, 3). According to our comparative earlier notes, the attenuated traces of juvenile pattern are recognizable in the males, and the juvenile coloration remains neat and regular in the females (Pl. 7, 2). Moreover, on the male's throat, upon the mark of the evident black collar, the enlarged black spot is a color character unique in the genus (Pl. 10, 1-3). Also the biological and ecological knowledge of the new lizard is, of course, still poor: the apparently gregarious behavior, at the moment of annual breeding, is noticeable, and its saurophagy was recently checked, preying on juvenile *Liolaemus fitzingeri* and *L. boulengeri* (Scolaro: pers. obs.). The biotope of the Telsen tableland is physiognomically marked by predominant stony tracks and impoverished ecotonal community, with enlarged extension of uncovered soil (Ruiz Leal, 1972). In the rocky conglomerates also live woody plants, whose canopies and root systems are utilized as shelter by this *Pristidactylus*, analogously to *P. scapulatus*.

*Pristidactylus fasciatus* may be considered lastly as an arenicolous lizard in the whole area of its wide central distribution, from Baldecitos (La Rioja) and Ischigualasto (San Juan) deserts (30° 10' S lat.) to Southern La Pampa province and its type locality on Atlantic coast (41° S lat.). This medium-sized Iguanian lives at altitudes between 1000 and 1700 m a.s.l. or less, as in the case of its type locality. It is a burrowing form, often sheltering in mounds of sand that accumulate around the trunks of *Prosopis alpataco*, but in the volcanic region of Payunia, Southern Mendoza province, it can contact *Pristidactylus araucanus* in habitats of loose sand alternating with rocky areas (Pl. 8, 3).

**Discussion.** In the Quaternary period, the Andean high mountains established a complete orographic isolation between "*scapulatus*" populations and the trans-Andean forms of the genus. Any eventual evolutionary cis-trans-relationships must therefore be placed in a very distant pre-glacial time, under distinct paleo-environmental and paleoclimatic factors.

A tentative reconstruction of the phyletic roots of *P. achalensis*, as well as of its limited distribution, is of course a very puzzling one. Likely, it is related to *P. araucanus* and *P. scapulatus*, being probably primitive with regard to the latter for its conservative juvenile coloration in females, which occurs also in *P. araucanus*. The extant populations of *P. achalensis* on isolated summits of the Sierras de Córdoba may be the result of a former major periglacial expansion, then restricted and reduced by a general worsening of former conditions in intervening areas.



Similarly to the *achalensis* distribution, merely tentative hypotheses can be suggested to explain the ancestral vicissitudes of *P. casuhatiensis* and its present trends of unusual endemism.

In spite of their reluctance for a nomenclatural definition, Etheridge and Williams gave in the tentative key of their revision (1985) a strikingly careful diagnosis of *Pristidactylus* populations from Payún, Laguna Blanca in Neuquén, and Canquel (Chubut). So far reported as belonging to *P. scapulatus*, as well as to *P. fasciatus* in other misled paper (Barrio, 1969), two clear-cut diagnostic characters are enough for a suitable separation of *Pristidactylus araucanus* (Gallardo, 1964) from *P. scapulatus*, or *P. achalensis*: besides metric characters and ratios given in Tables 1 and 2, or the lepidosis, teeth, digital lamellae differences documented in Fig. 4 and 5. Indeed, cordilleran *scapulatus* are unmistakable by their lack of cross-banded juvenile pattern in females, as well as the distinct morphology of crowns of posterior marginal teeth and their cusps can represent a significant specific character to separate *araucanus* from *achalensis*, or *casuhatiensis*. No populations of *araucanus* are present in Canquel plateau (Chubut). *Pristidactylus nigroiugulus* is the taxon found in that region: former confusions have been really provoked by ancient recollections of only females in Chubut province, being this sex practically unrecognizable at first sight both in *araucanus* or *nigroiugulus*. Presence of *P. nigroiugulus* from Paso de Indios (Chubut, at 44° S lat. and 69° W) is documented since 1985 by two adult male specimens from the collection of the Genève Museum, Switzerland (MHNG 2146-39, 2146-40).

Somewhat surprising is the association between *Pristidactylus araucanus* and the basaltic volcanic districts in Southern Mendoza (Payunia) and Zapala tablelands in Neuquén, scattered with permanent or seasonal shallow lacustrine basins; such as Laguna Blanca and neighboring lagoons. Several other reptilian groups, in similar landscapes, show analogous preferences in their habitats, such the iguanian phyletic stem *Phymaturus*, for example, and a number of species groups of *Liolaemus*. No alimentary preferential trends can be invoked for so selective a distribution in the case of *Pristidactylus araucanus*, given its common diet of ants and beetles in Laguna Blanca biotopes. Likewise, the unusual shelter in crevices of basaltic rocks, utilized by the herbivorous *Phymaturus*, cannot be taken into account, given the different behavior of the leosaurines. The advantages of a constant temperature at its yearly average, going down in the basaltic crevice until reaching a depth of about a meter, are useless for *Pristidactylus araucanus*, living and foraging in open stony flats.

*Pristidactylus fasciatus*, the Argentinian species phyletically more related to the Chilean group, according to the morphological analysis of Frost et al. (2001), may be opposed to any other cis-Andean taxon in

having multicarinate, instead of smooth or very faintly keeled, digital scales. It is unique in its genus in having the tail shorter than body; A major affinity of *Pristidactylus fasciatus* with Chilean *Pristidactylus*, in order to our reported comparative data, could only find some clear support by common adaptive morphological trends as well as by paleogeographic events. Scutellation characters of *P. fasciatus* are all referable to the character combination of Argentinian species in the key of Etheridge and Williams (1985). No arenicolous tendencies are shown by any of extant species of the Chilean group. Ecological adaptability of *P. fasciatus* to arid and sandy habitats is likely a derived condition prevailing in post-glacial climatic stages, not corresponding to similar contemporaneous trans-Andean periods. Perhaps very ancient phyletic relationships could have played a role in preglacial times, with a paleogeographic continental morphology differing from the present-day orographic structure.

**General remarks and conclusions.** The southernmost areas of the Neotropical continent appear to show an early presence of leisaurine lizards referable to *Pristidactylus*. Fossil remains of the genus, in fact, were found in lower Miocene sediments of Gaiman, near Trelew (Chubut): undetermined remains of several *Liolaemus* species have been discovered in the same deposits (Albino and Etheridge 2000). The chronological interval between the present time and such a distant Cenozoic period is a very large one: probable specific genetical changes and sequential DNA modifications, since then, likely can be assumed.

Our available phenotypic information about genome arrangement in the genus is synthesized by its specific karyotypic expressions. The remarkably conservative diploid chromosome formula of *Pristidactylus* is  $2n = 36$  (12M + 24m). It was found for the Chilean *Pristidactylus volcanensis* (Lambrot and Diaz, 1987), *P. torquatus*, *P. valeriae* (Navarro and Veloso, pers. comm.), and for the Argentinian *P. aчалensis* (Pinna Senn *et al.*, 1987), *P. scapulatus* and *P. nigroiugulus* (unpubl. obs.: Pereyra, pers. comm.). For Argentinian taxa, a stable morphological ordering has been presumed, with a metacentric first macro-chromosome pair, a submetacentric second macro-chromosome pair, and four following pairs metacentric, gradually decreasing. The first pair of micro-chromosomes may be heteromorphic in all of the studied species: a condition assumed as derived by Gorman *et al.* (1967). However, in Chilean species no largest pair of micro-chromosomes is apparently heteromorphic in males, a trend that fits in the conservative pattern believed to be a primitive one in the iguanids (Paull *et al.* 1976). Unfortunately, we need available karyological data for *Pristidactylus fasciatus*, whose phyletic relationships with the Chilean taxa were pointed out in the most parsimonious trees based on morphological analysis (Frost *et al.*, 2001). On the other hand, the fundamental morphological affinities of *P. fasciatus* with the other members of the Argentinian group sound undeniable, as shown by the former key of Etheridge and Williams (1985).

The evidence that ancestral *Pristidactylus* were likely widespread, in different preglacial habitats prior to the segregative Andean uplift, could suggest a primitive cis-trans-Cordilleran dispersal of ecologically versatile populations, such as the little specialized terrestrial or saxicolous lizards. Peculiar relic of this primitive stage may be the formerly cited phyletic relationships between the distinct species of the Chilean biota, and *P. fasciatus*, now adapted to an arenicolous life. Another recent finding may be emphasized with the observation that in Miocenic *Pristidactylus* from Chubut the crowns of the posterior marginal teeth are slightly tapered and have small anterior and posterior cusps, similar to those of *P. fasciatus* and *P. scapulatus*. The last species is not present in Chubut where it is replaced by its similar co-generic taxon *P. nigroiugulus* (Cei *et al.*, 2001). The ancestral roots of these leiosaurine lizards and their early preglacial relationships can be again pointed out by the position of the ancient genus *Diplolaemus* in the different parsimonious trees by Frost *et al.* (2001), cited earlier. Ontogenetically, significant morphological relationships in coloration are shown between juveniles of *Diplolaemus* and *Pristidactylus*. The juvenile patterns, maintained by *Diplolaemus* in both sexes, is only retained by females of *Pristidactylus* with the only exception of *P. scapulatus* probably as a secondary adaptive condition (Plate 3, 1,3; Plate 9, 3; Fig. 3, top and bottom).

In our previous systematic analysis several ecological objections arose to the so-far argued plesiomorphic condition of Chilean taxa, given their tendency toward arboreality, considered as the primitive habit of that leiosaurine group. But ecological behavior of semi-terrestrial reptiles was reported, though as secondary adaptation, for *Pristidactylus volcanensis*, *P. valeriae*, *P. alvaroi*; exceptionally for *P. torquatus* from the Southern temperate forest, whose morphological adaptive trends toward a close arboreality are comparatively limited. The cited former observations of Webb and Greer (1969) and Montecinos Espinosa and Formas (1979) must be opportunely taken into account.

No essential reservations can be made about the probability that a primitive terrestrial stem of trans-Andean *Pristidactylus*, isolated on Pacific slopes by the insurmountable cordilleran barrier and facing a widely expanded humid forest, could have initiated and further completed an adaptive process toward an arboreal life, such as today that of *Pristidactylus torquatus*. Arboreal and terrestrial biotopes are not biologically incompatible for reptiles. In the genus *Tropidurus*, i.e., several Argentinian species, as *T. etheridgei*, *T. torquatus catalanensis* or *T. spinulosus*, can profitably live in rocky as well as in wooded environments. *Tropidurus spinulosus* nimbly climbs on large trees of the Chacoan belt (*Aspidosperma*, *Schinopsis*), *T. torquatus catalanensis* is a common arboreal species in Corrientes, *T. etheridgei* also climbs on tall trees in La Rioja flats, in Chacoan *Prosopis* woods, or in the Paraná shores. However, in leiosaurids, only the transcordilleran *Pristidactylus*, besides the Enyaliinae, showed a definite tendency to a true arboreality. Likely also

the large, scanty autotomic tail of the specialized cis-Andean *P. casuhatiensis* could be suggestive of a derived trend to less terrestrial habits.

**Conclusion.** No biological or paleogeographical arguments will clearly contrast with the new assumption that pristidactylines were primitively terrestrial and secondarily arboreal, an assumption supported by analytical data and by Bremer values, in strict consensus of the most parsimonious trees (crf. Frost *et al.* 2001: pp. 8-10). The scattered distribution of Argentinian species, prevailing in dry mountains or basaltic habitats, is congruent with an ancient evolutionary history culminating with discriminate or selective biogeographic effects of the last glaciation. The extant morphological and karyological differences between Chilean and Argentinian groups are thus easily referable to the postulated ancestral partition of an originally indistinct, common and perhaps terrestrial base during pre-glacial times. Genetic determinism of reciprocal isolation, not at random but in natural equilibrium with environmental and historical local factors, may give the reasons of at first sight unintelligible primitive or derived characters in both populational stocks on the eastern and western sides of the millennial Andean barrier.

At last we will recall the thorough work of Frost *et al.* (2001), not only for its valuable attempt to make clear several yet controversial problems of Iguania systematic, but for its fair, objective conclusions made on the basis of some impressive modern techniques, chiefly those dealing with molecular biology. Nobody can disregard or impair the great importance of careful comparative research on specific DNA sequence as fundamental support for settling or overcoming problems of phyletic relationships, which in previous times were based on phenotypical observations or subjective understanding. However, to avoid undue dependence upon any single technique, a very attentive reading of the paper of Frost *et al.* (2001) is sincerely advisable.

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### RIASSUNTO

Si presenta una discussione generale delle relazioni intra e intergeneriche del genere leiosauride *Pristidactylus*. Si riportano e si confrontano comparativamente i suoi due gruppi di specie, cistranscordiglienerani, tenendo conto dei risultati delle ultime ricerche molecolari e morfologiche di Frost *et al.* (2001). Si considera la nuova famiglia Leiosauridae, che comprende *Enyalius*, *Diplolaemus*, *Leiosaurus* e *Pristidactylus*, con riferimento alle antiche relazioni evolutive di questo ultimo genere. Si analizzano e si comparano inoltre le caratteristiche specifiche referibili ad adattamenti evolutivi dei vari taxa cileni e argentini di *Pristidactylus*, esibiti probabilmente fin dai primi tempi della loro comune origine preglaciale. Vengono infine presentati commenti critici sulla posizione di forme primitive dei *Pristidactylus* terricoli, mentre non viene più accettata la plesiomorfia per le forme arboree, rappresentate dalle specie cilene.

Josè M. CEI  
Hilario Cuadros 81, Godoy Cruz  
5501 Mendoza (Argentina)

Fernando VIDELA  
Unidad de Ecología Animal  
IADIZA C.C. 507  
5500 Mendoza (Argentina)  
E-mail: fvidela@lab.cricyt.edu.ar

José Alejandro SCOLARO  
Centro Nacional Patagónico, C.C. 69  
9120 puerto Madryn, Chubut (Argentina)  
E-mail: scolaro@cenpat.edu.ar

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## APPENDIX I

### SPECIMENS EXAMINED

*Pristidactylus scapulatus*.- IBA-UNC,R: 578-1, -2, 465-1, -2, Uspallata, Mendoza: 1013-1, -2, -3, Cuesta del Choique, Mendoza; IADIZA-CH: 122, 291, 292, 293, Uspallata, Mendoza; JMC-DC: 004, 1135, Uspallata, Mendoza.

*Pristidactylus achalensis*.- IBA-UNC,R: 494-1, -4, -5, -6 -7,-9, -11, -12, -13, 575-1, -2, -3, -4, -6, -9, -10, -11, -12, -17, 1014-1, -2, -3, -4, -5, -6, -7, -8, -10, -11, Pampa de Acha, Córdoba.

*Pristidactylus araucanus*.- MACN: 17702, 17703, 17704, 17705, 17706, Laguna Blanca, Zapala, Neuquén; IBA-UNC,R: 775-1, -2, -3, -4, 727-1, -2, -3, -4, 781-5, 782-1, -2, -3, -4, 790, 1012-1, -2, -4, -5, -6, -10, -11, La Payunia, Mendoza.

*Pristidactylus casuhatiensis*.- MACN: 24849, 24850, 24851, 24852, 24853, 24854, 24856, 36163, 19742, 19743, Sierra de la Ventana, Buenos Aires.

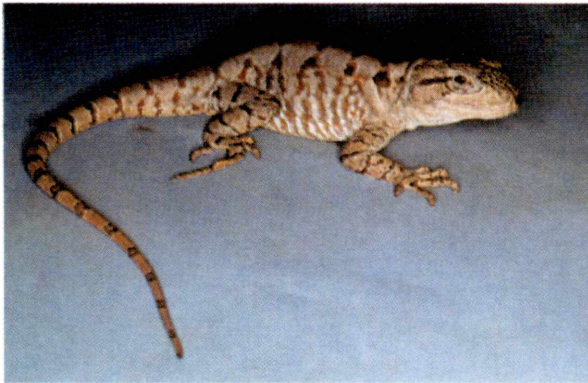
*Pristidactylus nigroiugulus*.- IBA-UNC,R: 784, 934, Meseta Canquel, Chubut, 1477, Telsen, Chubut; IADIZA-CH: 288, 289, 290, Telsen, Chubut; MCZ. Harvard Un: 182.882, 182.883, Telsen, Chubut; MACN: 37092, 37093, Telsen, Chubut; JMC-DC: 1196, 1197, Telsen, Chubut; JAS-DC: 594, Telsen, Chubut.

*Pristidactylus fasciatus*.- IBA-UNC,R: 1026, 1174, 1181, Carrizal, Nihuil, Mendoza; IADIZA-CH: 163, 152, 192, La Payunia, Mendoza; MMHNSR: H-290, H-362, H-401, H-800, H-888, Nihuiel, La Payunia, Mendoza.



Plate 1

Pl. 1.1  
*Pristidactylus volcanensis*. Male. El Volcán, Maipo. Chile. 1400 m a.s.l.. December 1989. No remarkable sex-dichromatism has been reported. Photo. A. Labra.



Pl. 1.2  
*Pristidactylus alvaroi*. Cerro El Roble, Valparaiso. Chile. 1100 m a.s.l.. No remarkable sex-dichromatism has been reported. Photo. H. Nuñez.



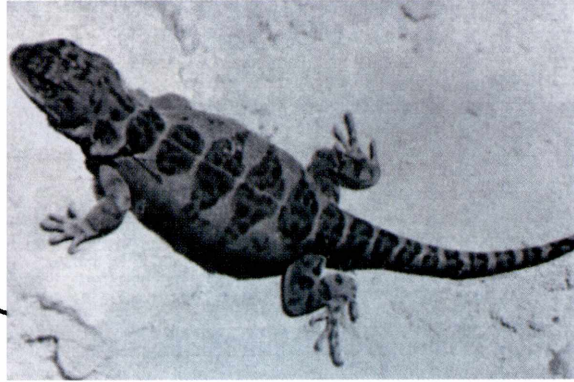
Pl. 1.3  
*Pristidactylus valeriae*. Cerro Cantillana, central region of Chile (33° 58' S, 70° 58' W), near of Type Locality. 2050 m a.s.l. January 2002. Photo. Y. Hussein.



## Plate 2

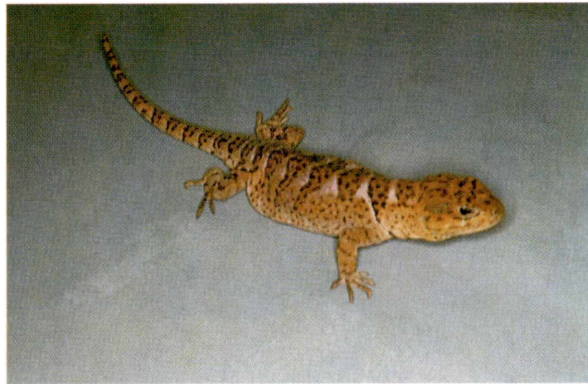
## Pl. 2.1

*Pristidactylus torquatus*.  
Adult specimen from  
Valdivia, Chile. September  
1986. Diminished remains  
of the juvenile color  
pattern. Inhabitant of  
temperate *Nothofagus*  
forest climax. Photo. W.  
Hellmich.



## Pl. 2.2

*Pristidactylus torquatus*.  
Female specimen from  
the northern relicts of  
the *Nothofagus* forest at  
Ñuble and Concepción  
provinces, Chile. Summer  
1988. Remains of the ju-  
venile color pattern are  
very evident. Photo. A  
Veloso - J. Navarro.



## Pl. 2.3

Temperate *Nothofagus* and  
*Araucaria* forest in  
Nahuelbuta Cordillera  
slopes, in Arauco and  
Malleco provinces.  
Populations of *Pristidactylus*  
*torquatus* are still living  
in these marginal forest areas.  
October 1965. Photo. J. M.  
Cei.

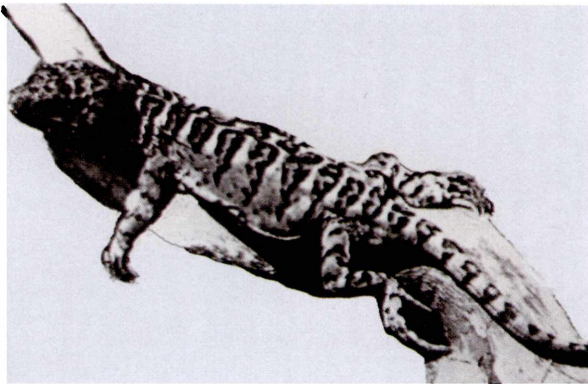




## Plate 3

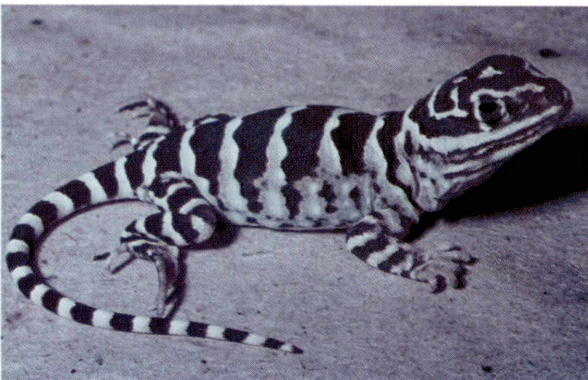
## Pl. 3.1

Characteristic cross-banded juvenile pattern in young specimens of *Pristidactylus torquatus*: 36-39 mm in length. Laguna Malleco, 976 m a.s.l., Chile. Summer 1966. Photo. R. G. Webb - J. K. Greer.



## Pl. 3.2

Adult gravid female of *Pristidactylus torquatus* from Laguna Malleco temperate forest. Summer 1966. Remarkable remains of the juvenile dorsal cross-banded pattern. Sexual dichromatism is evident in this species. Photo. R. G. Webb - J. K. Greer.



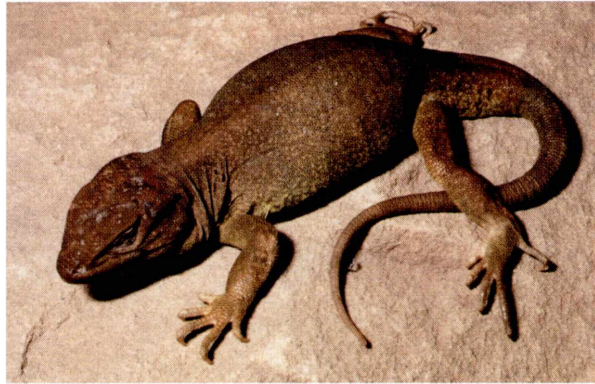
## Pl. 3.3

Cross-banded juvenile pattern very similar to the juvenile pattern of *Pristidactylus torquatus*, shown by a young specimen of *Pristidactylus nigroiugulus* from Argentina; Callejas, Canquel tableland, Chubut. 900 m a.s.l., January 1972. Photo. J. M. Cei.

## Plate 4

## Pl. 4.1

*Pristidactylus scapulatus*.  
Male. Paramillos de  
Uspallata, Las Heras,  
Mendoza. 3000 m a.s.l..  
February 2000. Photo. J.  
M. Cei.



## Pl. 4.2

*Pristidactylus scapulatus*.  
Female. Paramillos de  
Uspallata, Las Heras,  
Mendoza. 3000 m a.s.l..  
February 2000. Photo. J.  
M. Cei.



## Pl. 4.3

Paramillos de Uspallata,  
Las Heras, Mendoza.  
3000 m a.s.l.. January  
1999. Habitat of *P.*  
*scapulatus*. Photo. F.  
Videla.



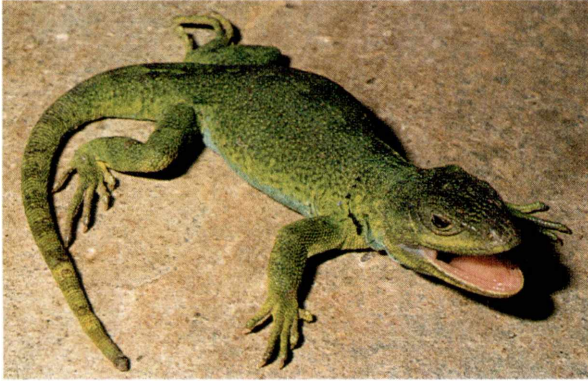
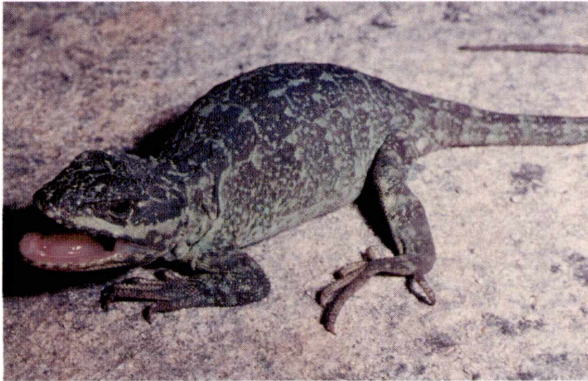


Plate 5

Pl. 5.1  
*Pristidactylus achalensis*.  
Male. Pampa de Achala,  
Córdoba. January 1980.  
Photo. J. M. Cei.



Pl. 5.2  
*Pristidactylus achalensis*.  
Female. Pampa de  
Achala, Córdoba.  
January 1980. Photo. J.  
M. Cei.



Pl. 5.3  
Sierras de Pampa de  
Achala, Córdoba. 1900  
m a.s.l.. *Habitat* of *P.*  
*achalensis*. March 1990.  
Photo. J. M. Cei.

## Plate 6

## Pl. 6.1

*Pristidactylus araucanus*.  
Male. Laguna Blanca,  
Zapala, Neuquén.  
Paratype. October 1964.  
Photo. J. M. Cei.



## Pl. 6.2

*Pristidactylus araucanus*.  
Female. Laguna Blanca,  
Zapala, Neuquén.  
Paratype. October 1964.  
Juvenile dorsal pattern  
present in adults. Photo.  
J. M. Cei.



## Pl. 6.3

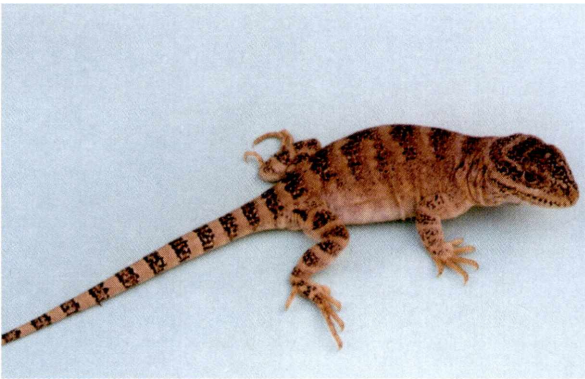
Landscape at Laguna  
del Burro, Zapala,  
Neuquén. 1200 m a.s.l..  
Habitat of *P. araucanus*.  
February 1983. Photo. J.  
M. Cei.





Plate 7

Pl. 7.1  
*Pristidactylus nigroiugulus*. Male. Sierra Negra, Telsen, Chubut. February 1999. Photo. J. A. Scolaro.



Pl. 7.2  
*Pristidactylus nigroiugulus*. Female. Sierra Negra, Telsen, Chubut. February 1999. Photo. J. A. Scolaro.



Pl. 7.3  
Patagonian shrubby steppe. Sierra Negra tableland, Telsen, Chubut, 850 m a.s.l.. March 2000. Habitat of *Pristidactylus nigroiugulus*. Photo. J. A. Scolaro.

## Plate 8

Pl. 8.1

*Pristidactylus fasciatus*.  
Male. Payunia Reserve,  
Mendoza. February  
1990. Photo. F. Videla.



Pl. 8.2

*Pristidactylus fasciatus*.  
Female. Carrizal del  
Medio, Mendoza.  
December 1975. Faint  
sex-dichromatism.  
Photo. J. M. Cei.



Pl. 8.3

Xeric shrubby landscape  
in the Payunia Reserve,  
Malargüe, Mendoza.  
1500 m a.s.l.. June 1999.  
Habitat of *Pristidactylus  
fasciatus*. Photo. S. Puig.





Plate 9

Pl. 9.1  
*Pristidactylus casuhatiensis*. Male. Sierra de la Ventana. 1100 m a.s.l.. Buenos Aires province. March 2001. Photo. S. Cairo.



Pl. 9.2  
Landscape of Cerro de la Ventana. Buenos Aires province. 1100 m a.s.l.. Habitat of *P. casuhatiensis*. March 2001. Photo. C. M. Grassini.



Pl. 9.3  
*Pristidactylus araucanus*. Young male, juvenile pattern still permanent at this stage. Near Zapala, Neuquén. 1100 m a.s.l.. February 1995. Photo. M. Christie.



## Plate 10

## Pl. 10.1

*Pristidactylus nigroiugulus*. Male. Ventral view. Black gular spot evident. Sierra Negra, Telsen, Chubut. 900 m a.s.l.. February 1999. Photo. J. M. Cei.



## Pl. 10.2

*Pristidactylus scapulatus*. Male. Ventral view. Black gular spot absent. Paramillos de Uspallata, Mendoza. 3000 m a.s.l.. January 2000. Photo. J. M. Cei.



## Pl. 10.3

*Pristidactylus araucanus*. Male. Ventral view. Black gular spot absent. Paratype. Laguna Blanca, Zapala, Neuquén. 1200 m a.s.l.. January 1964. Photo. J. M. Cei.

