

A TAXONOMIC REVISION OF RECOGNIZED ARGENTINE SPECIES OF THE LEIOSAURID GENUS *DIPLOLAEMUS* (REPTILIA, SQUAMATA, LEIOSAURIDAE)

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RESUMEN: Se ha realizado un cuidadoso análisis acerca de la inadecuada taxonomía actual de las escasas especies del género leiosaurino *Diplolaemus*. Las problemáticas poblaciones que se registran entre las provincias de Chubut y de Mendoza, provisoriamente identificadas como formas "alto-patagónicas" o "mendocinas", fueron reconocidas como la nueva especie *Diplolaemus sexcinctus*, cuya denominación se refiere a su característico patrón de coloración dorsal. Fueron analizadas y discutidas las diferencias morfológicas entre el nuevo taxón y *Diplolaemus bibronii*, así como con *Diplolaemus darwinii*. Las todavía inciertas relaciones entre *D. sexcinctus* y la forma chilena *Diplolaemus leopardinus* fueron también consideradas, y se plantea la conveniencia de un estudio binacional del problema, recurriendo eventualmente al análisis comparativo a través de la biología molecular.

ABSTRACT: A careful analysis of the up to date inadequate taxonomy of the few species of the leiosaurine genus *Diplolaemus* was attempted. The problematic "alto-patagonicus" or "mendocine" populations from Chubut province to Mendoza province were recognized as a new species named *Diplolaemus sexcinctus* by their characteristic dorsal color pattern. Morphological differences between the new northernmost *Diplolaemus* species and *Diplolaemus bibronii*, as well as *Diplolaemus darwinii*, were analyzed and discussed. The unsolved relationships between *D. sexcinctus* and the Chilean taxon *Diplolaemus leopardinus* were considered, and a necessary further research, supported by binational cooperation, was pointed out, taking into account the use of bio-molecular methods of comparative analysis.

Key words: *Diplolaemus*, Especiación, leiosaurine line, color patterns, glacial- postglacial periods, high-Patagonian and Mendocine populations.

Palabras claves: *Diplolaemus*, Especiación, leiosaurinos, patrones de coloración, períodos glacial-postglacial, poblaciones altopatagónicas y mendocinas.

INTRODUCTION

The austral South American iguanian genus *Diplolaemus* is known from Bell's reports (1843) on collections carried out by Charles Darwin during the classic Voyage of the HMS Beagle. Its generic status was confirmed by Frost and Etheridge (1989), and the family *Leiosauridae* to which it

belongs was recently discussed and established by Frost *et al.* (2001).

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Two sympatric species were formerly recognized by Bell (1843) for the Southern Patagonian Puerto Deseado region: *Diplolaemus bibronii* and *Diplolaemus darwinii*. A third taxon, *Diplolaemus leopardinus*, was later added by Werner (1898) for the Chilean region of Lonquimay, Mari-Menú and Pino Hachado, located on western Andean slopes (Donoso Barros, 1966).

In spite of the unquestionable specific rank of Bell's described taxa (Cei, 1986; Lavilla *et al.*, 2000), a morphological differentiation of their populations along a very extensive continental area appears unavoidable. That is less evident for *D. darwinii*, mainly distributed in Santa Cruz province and neighboring areas of Chubut and Río Negro provinces. A more impressive variation, however, has been observed and reported for *D. bibronii*, with often polymorphic populations located in Chubut, Río Negro, Neuquén and Mendoza provinces of Argentina. These populations have been alternatively cited, through about a century, as "intermediate forms between *D. bibronii* and *D. darwinii*", as well as "alto-patagonicus form", "mendocine form", or very poorly defined "northern *darwinii* populations" (Cei, 1986; Etheridge and Christie, 2003; Schulte II *et al.*, 2003).

Given such a persistent taxonomic uncertainty and its troubling effects on several systematic and/or biogeographic aspects of any regional research, we considered useful task a new critical morphological study of a significant number of *Diplolaemus* samples through their known distribution area. Results and conclusions of such an attempt to a better assessment of this still scarcely known iguanian genus are thus reported in the present paper.

MATERIAL AND METHODS

Samples of lizards from Santa Cruz, Chubut, Río Negro, Neuquén and Mendoza have been assembled: 154 specimens, mainly adults, have been examined (29% juveniles). All their localities were carefully controlled, but for several specimens (15) from Museo de La Plata, of particular morphological and historical interest, localities only indicating the province were accepted.

Measurements of specimens examined were made using dial calipers (0.1-mm accuracy) under a dissecting microscope. Scale terminology follows Smith (1946) and Peters (1964). Specific coloration patterns were registered in living or preserved specimens. Photographs included in this paper were taken with a camera Contax-Zeiss Ikon, objective Biotar 2/58 (Plate 1 and 2), and a digital camera Nikon Coolpix 4500 (Plate 3 and 4).

A parametric analysis of variance by the F-statistic of Fisher, with multiple comparisons by the Tukey test (Zar, 1984), was used to determine differences in snout-vent length among the four groups analyzed within the *Diplolaemus* genus and between sexes within each group. A difference between both groups distinguished within *D. bibronii*, with five and six bands respectively, was analyzed by the t-test of Student.

Acronyms of the Argentinean herpetological collections where are deposited the specimens analyzed are: MLP-S, Museo de La Plata, Buenos Aires, province; IBA-UNC, Instituto de Biología Animal, Universidad Nacional de Cuyo, Mendoza; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; CH-IADIZA, Colección Herpetológica del Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza; MMHN-SR, Museo Municipal de Historia Natural de San Rafael, Mendoza; JMC-DC, José M. Cei- Diagnostic Collection, Mendoza; CH-JAS, Colección Herpetológica de José A. Scolaro, Chubut.

MORPHOLOGICAL AND TAXONOMIC RESULTS

A comparative diagnostic description was given first for the Bell's species *D. darwini* and *D. bibronii*, taking into account the populations from their Terra Typica, Deseado River region of Santa Cruz province (Fig. 1). Between the following summarized characters, those supporting significant interspecific differences were reported in italic (Plate 1, A, B; Plate 3, A, B; Fig. 2).

Diplolaemus darwinii: Body stout, median to large. Tail shorter than body. Thick head, slightly larger than wide. Snout moderately sharp-pointed. Adpressed hind limb reaches the shoulder: adpressed forelimb cross the middle of the axilla-groin distance. Nasal scales separated from rostral by 1-2 scales. Mental laterally bordered by contacting first infralabial and first postmental. Suboculars and supralabials separated by 2-3 scale rows. Nostrils separated by 4-5 scale rows. Temporal scales small, decreasing posteriorly next ear opening. Two distinct gular folds.

Dorsal color patterns, from sacral regions to shoulder, characterized by 5 transverse bands, bilaterally composed by a wide butterfly-like dark blotch on a light creamish or whitish background, scattered with diminute dark points or marks. Ringed dark bands on upper limbs and tail.

Belly whitish or creamish, immaculate. Mental and throat region whitish, regularly speckled with small, distinct, longitudinal black marks: a character clearly evident in adults, but also in juveniles.

Diplolaemus bibronii: Body stout, median too large. Tail shorter than body, some time equal or larger. Thick head, slightly larger than wide. Snout significantly sharper than in *darwinii*. Adpressed hind limb reaches the axilla: adpressed forelimb largely cross the middle of the axilla-groin distance. Nasal scales separated from rostral by 3 or more scales. Mental laterally bordered by no contacting first infralabial and first postmental. Suboculars and supralabials separated by 3-5 or more scale rows. Nostrils separated by 6-9 scale rows. Temporal scales uniformly small. A distinct gular fold.

Dorsal color patterns, from sacral region to shoulder, showing 5 transverse bands bilaterally composed by a symmetrical, wide, almost trapezoidal blotch, formed by dense dark marks and spot, on a reddish or grayish ground. These bilateral blotches present a posterior, central semicircular yellowish or whitish spot, or a brilliant semicircular light border. Dark ringed upper limbs and tail. Mental and throat region whitish immaculate, or with only confused, pale grayish spots.

As was commented in the Introduction, the above enumerated specific characters of *D. darwinii* did not still reveal in our research any significant population differences through its whole distribution area, from Magellanian districts of Chile and Argentina to north-

western Chubut and Río Negro provinces (Fig. 1). A quite different and often intriguing situation may be pointed out, however, for the many examined populations of *D. bibronii* (sensu lato), scattered from the limits between Santa Cruz and Chubut provinces to the South-western Mendoza province northwards (Fig. 1).

The unmistakable dorsal pattern, with five bilateral, transverse dark blotches, centrally exhibiting a showy semicircular yellowish spot, was a typical *D. bibronii* feature in any of the 26 checked specimens from Santa Cruz (Plate 1,C). However, such a specific trend can be observed only in 12 of the 45 checked specimens from Chubut, being completely absent in 63 specimens observed from Río Negro, Neuquén and Mendoza populations, where another kind of dorsal color pattern is shown, as well as in 33 of the 45 mentioned individuals from Chubut.

On the other hand, taking into consideration the diagnostic morphological characters distinguishing *D. bibronii* from *D. darwinii*, we could also stress that a significant number of the above reported characteristics of the *D. bibronii* scutellation is usually shown by the whole populations from Chubut northwards. Such a set of "bibronii characters" are enumerated below, for a total number of 96 examined specimens (Plate 3, A):

- 1) 3-4 scales between nasal and rostral;
- 2) mental laterally bordered by no contacting first infralabial and first postmental;
- 3) 3-6 scale rows between suboculars and supralabials;
- 4) 6-9 interposed scale rows between nostrils;
- 5) 9-16 dorsal scale rows (in 5mm) according to age and size in adults, from Santa Cruz to Mendoza (but 16-20 in *D. darwinii*); 5-9 ventral scale rows (in 5mm) in adults, from Santa Cruz to Mendoza (but 9-12 in *D. darwinii*).

Several scutellation characters, usually utilized in diagnostic measurements of lizards, are of scarce value in *Diplolaemus* taxonomy. The scale number at midbody, for example, does not represent a steady character in these leiosaurids, given their too much numerous and irregular dorsal scale rows. Thus, at last, only the clear-cut diverging color pattern provides the most useful tool to identify the many populations related to *D. bibronii*, from Chubut to Mendoza.

A general description of such a northernmost dorsal color pattern must be drawn up now, before to get in shape any taxonomic conclusion or discussion. From sacral region to the shoulder, six transverse dark bands are

recognizable (Plate 2), often irregular or broken as isolated rounded spots filled with black points or marks (Plate 2,C). These six bands are often longitudinally interrupted by a light vertebral line, as well as being strangled by a lighter continuous or discontinuous longitudinal dorso-lateral stripe, thicker in some population behind the pigmentary bands (Plate 2, A,B). In spite of its minor individual or population variation, this distinctive pattern is covering a remarkable latitudinal distribution, without any recognizable cline from the limits Santa Cruz-Chubut northwards.

The presence of a noticeable number of similar morphological characters and the general trends of its geographic distribution, could suggest a likely subspecific status for the northernmost six-banded populations, having as nominal form *D. bibronii* from Santa Cruz and neighboring Chubut borders. In spite of the general similarity and remarkable uniformity of some metric and meristic characters, the several cases of registered sympatry in Chubut (Fig. 1), apparently without intergradation, as well as some preliminary observations on the hemipenis shape and structure of both the five-banded and six-banded populations (Plate 4, A, B), may suggest a possible genic amixy or specific status of the northern six-banded form.

In accordance with the widely known criteria of Frost and Hillis (1990) and Frost *et al.* (1992), the subspecific status is presently submitted to a careful discussion or limited acceptance: however the nomenclatural use of the subspecies is still admitted by the last Code (2000) of the ICZN (Art. 5.2, Art. 45-49). At any rate, in our case, other ponderable reserves may play their role. The third species of the genus, *Diplolaemus leopardinus* Werner, is a Chilean lizard, scarcely and poorly cited for its still uncertain areas in Neuquén. Recently, preliminary commentaries point out its possible relationships with the Argentinean six-banded populations, evidently sympatric in such a bordering zone (Nenda and Scanferia, 2002). Thus, we are dealing with not yet solved taxonomic and nomenclatural problems, wanting Chilean cooperation, but impossible to be developed in our present research on Argentinean taxa.

With the support of the mentioned evolutionary considerations, but mainly pointing out a controlled marginal sympatry without intergradation, and the generic similarity but also the specific features of clearly

documented hemipenis structures (Plate 4, A, B), we estimate as the best nomenclatural decision, at the present, to propose a specific rank for the several six-banded populations of *D. bibronii* group from Chubut northwards. It would end, lastly, the decennial disorder of provisional, subjective denominations, or pseudo-geographical forms, hitherto circulating, also in outstanding scientific literature.

By its peculiar banded color pattern we propose to name the new species *Diplolaemus sexcinctus*, whose description follows.

Diplolaemus sexcinctus sp. nov.

Holotype - IBA-UNC-605-1, an adult male from Meseta Pedregosa, 1100 m.a.s.l., 10 km south of Las Bayas, Río Negro province, Argentina (41°30'S, 70°38'W). Collected by J.M. Ceí, L. M. Ceí and R. Ferreira, 24 January 1970. (Plate 2, C).

Paratypes - IBA-UNC-605-2, some data as holotype; IBA-UNC-1412-1, 2, adults, male and female, from between Puesto Alvarado and Cruz de Piedra, road to Diamante lake, Mendoza province, 2750 m.a.s.l., collected by L.P. Castro, G. Macola and J. García, 22 March 1982; IBA-UNC-926, an adult female, from Portillo Argentino, 2500 m.a.s.l., Tunuyán department, Mendoza province, collected by A. Mataloni, 12 February 1973; MMHN.SR-H-1113, an adult male, from P. Coihueco, southern border of Payún, Malargüe department, Mendoza province, collected by MMHN, no data; IBA-UNC-461, an adult female, from Raimunda lagoon, Somuncurá plateau, 1400 m.a.s.l., Valcheta department, Río Negro province, Argentina, collected by J.M.Ceí, 20 February 1967; IBA-UNC-418, an adult female from Laguna Blanca, 1275 m.a.s.l., 35 km SW Zapala, Neuquén province, collected J. M. Ceí, 2 December 1965; IBA-UNC-513, an adult female, from Cerro Merlo, 1200 m.a.s.l., Somuncurá plateau, Valcheta department, Río Negro province, Argentina, collected by J. M. Ceí and L. P. Castro, 18 November 1968; IBA-UNC-1177-1,2, two adults males from a plateau 80 km south Nihuil, 15 km W Nevado embossment, 1800 m.a.s.l., San Rafael department, Mendoza province, Argentina, collected by J. M. Ceí, P. Tuzi and F. Videla, 23 December 1975; IBA-UNC-611-1,2, juveniles males, from Arroyo Las Bayas basaltic slopes, 850-1100 m.a.s.l., Río Negro province, collected by J. M. Ceí, L.M. Ceí, 9 January 1975; CH-IADIZA-242, an adult female, from El

Nihuil, San Rafael department, Mendoza province, Argentina, collected by F. Videla and S. Puig, 22 February 1987; MLP-1652, 1656, 1658, adult males from byway Rincón-Raimunda lagoon, 1200-1400 m.a.s.l., Somuncurá plateau, Valcheta department, Río Negro province, collected by J. D. Williams, 25 November 1995; MLP-1653, 1657, adult female, the same anterior data.

Etymology: The specific name is easily referable to the six pigmentary bands (latin sex: six, cinctus: girdle) dorsally and laterally shown by these lizards, from shoulder to sacral region.

Diagnosis: *Diplolaemus sexcinctus* differs from *D. darwinii*, in having a major size; more than 2 scales between nostril and rostral; mental bordered by no contacting first infralabial and first postmental; temporals uniformly small; supraoculars and supralabials separated by 3-5 or more scale rows; only a distinct gular fold; a very different dorsal color pattern, with the regular black marks on immaculate throat absent. It differs from its nearly relative taxon *D. bibronii* in having a peculiar six-banded color pattern, always recognizable in all sympatric populations, as well as a bilobate hemipenis differing in shape and ornaments from the larger and apically dilated hemipenis of *D. bibronii*. Apparently, it differs from the poorly known *D. leopardinus* in having more scale rows between suboculars and supralabials (2-3 scale rows in *D. leopardinus*, fide Donoso Barros, 1966); no contacting first infralabial and first postmental bordering mental, a dorsal color pattern contrasting with *D. leopardinus* pattern, whose large rounded dorsal spots are composed by few dark heavy marks more irregularly distributed in six transverse bands, giving thus the coarse appearance of a leopard skin.

Description: Head large, stout, a third of the body length, very distinct from neck, widest across temporal region, but slightly longer than wide (length being measured from inferior apex of auditory meatus to rostral extremity; width being measured across widest part of temporal region). Masseteric region strongly developed. Snout moderately large (as measured from anterior corner of orbit to tip of snout: 0.39 times head length), no projecting beyond lower jaws. Orbit large; about a third of head length. Nasal region moderately swollen: fronto-nasal region slightly convex in profile. Width of rostral 4.5 mm, height 2 mm; 4 postrostrals, being rostral separated from nasal scale by 3 scale rows. Nostrils projecting

oriented latero-posteriorly; nasal scale separated from anterior supralabials by 3-4 scale rows. Dorsal head scales large, very irregularly convex and differentiated in size, several of them with central depression; supraorbital semicircles evident, three of their largest medianscales contacting between orbits, anteriorly separated by 2-3 irregular scale rows, posteriorly separated by 1-5 smaller scale rows, belonging to the very irregular, enlarged parietals; interparietal almost indistinct, with a very reduced eye, without larger posterior parietals. Supraoculars small, irregular, except three short enlarged scale rows contacting on the middle the supraorbital semicircles; in a horizontal line across widest part of supraocular region, 11 scale rows between superciliarues and supraorbital semicircles. Superciliaries smooth, 2-3 times longer than wide, decreasing behind, preceded anteriorly by two large canthals. Palpebrals very small, rectangular as inner ciliaries; outer ciliaries of the upper and lower lid 23-24, very small, subtriangular, slightly projecting; very diminute lower palpebral granular scales until enlarged flat suboculars. Scales of the preocular-subocular-postocular arc 9, longer than high or subequal, with a superior blunt keel; the third, fourth and fifth suboculars fused; eight scale rows of lorilabials separating suboculars from supralabials; superior and lower lorilabials rows largest than others. Supralabials 13-14, decreasing in size posteriorly. Temporals small, granular, about 22-24 between postocular and anterior margin of the deep external auditory opening, large, triangular, bordered by diminute granules. Mental larger than rostral, but equal in width, bordered by separated first infralabial and first postmental: 11-11 infralabials. Gulars small, subimbricate, decreasing from anterior latero-mental region; two large post-mentals, followed by 10-12 smaller scales.

Dorsal granular scales very small on neck, slightly larger on body, aligned in very irregular transverse rows, making a normal count at midbody impossible, becoming smaller on the sides, grading gradually into the rows of smooth, flat, subimbricate ventral scales. Ventrals squared or rhomboidal, 6 in a row of 5 mm, being the dorsal granular scales 14 at random in a row of 5 mm. Scales of precloacal and cloacal region slightly smaller than the abdominals; a deep gular fold, laterally short irregular folds entering gular region.

Limbs moderately slender: extended forelimb cross midbody, extended hind limb cross the axilla. Brachial and antebrachial scales similar to dorsal scales, but smaller in their ventral surface; femorals and tibials similar to dorsal body scales but somewhat smaller; postfemorals and posttibials minutely granular, infra-femorals and infratibials similar to ventrals but smaller and subimbricate on tibia. Supracarpals smooth, imbricate, extending posteriorly as wide, imbricate, laterally granular; subdigital lamellae of fourth finger 18-19, of fourth toe 28-29. Claws short and sharp-pointed, yellowish; fourth toe claw about as long as 5 distal supradigitals.

Tail no autotomic, shorter than body, slender and sharp-pointed, proximally wider than high, almost rounded distally. Dorsal and lateral caudal scales similar to those of dorsal body, becoming subimbricate on middle third of tail, until the tip.

Color pattern (Plate 2,C). Little difference between living and preserved animals. Evident six dorsal dark bands from shoulder to sacral region, on a yellowish or greenish background; every band composed by four vertebral and dorso lateral almost oval spots, given by a confluence of dark, black or brown, marks: laterally by two confuse, irregular spots of similar dark marks or dots. Symmetrical dark marks or spots scattered on head and neck. Limbs banded by 5-6 transverse dark spot belts; tail ringed by 11 similar dark belts, paler on ventral surface. Gular region, belly and lower surface of limbs whitish.

Measurements - snout-vent length (SVL): 112 mm, tail: 86 mm, head length (HL): 31.2 mm, head width (HW): 31 mm, snout length: 11 mm, forelimb: 35 mm, hindlimb: 51 mm, orbital diameter: 9 mm, snout-nostril distance (SND): 5 mm, anterior corner of eye-nostril distance (END): 6 mm, SND/END 0.83.

Variation - The polymorphism of this species is remarkable and individual variation for dorsal color pattern supported several past misleading taxonomic identifications north of Chubut River. In the Plate 2, A-C examples of striking diversity in different geographic and biocenotic environments are shown. The prevailing features of paratypes are referable to the holotype pattern, being variously pigmented or dilated the irregularly enlarged spots composing transverse bands. Notwithstanding, in samples of many specimens from localities of Chubut (Telsen plateau) or Río Negro (Somuncurá plateau) a

noticeable somatic uniformness was observed. A similar range of variation can be reported also for some registered metric or meristic characters of compared populations of *D. sexcinctus* from different areas into its geographic distribution.

Range of ratios head width/head length for the Holotype and 18 Paratypes was 0.87 - 1.00.

Means and ranges of SVL measurements, HW/HL and SND/END ratios for *D. sexcinctus* and the other taxa of the genus have been given in Table 1.

Table 1: Comparison of means (\bar{x}), standard deviations (SD) and ranges (in parenthesis) of SVL (millimeters), HW/HL and SND/END ratios for the four analysed cases of adult *Diplolaemus*: *D. darwini*, *D. bibronii*, and two morphs of *D. sexcinctus*

Variable	<i>D. darwini</i> (n = 13)	<i>D. bibronii</i> (n = 26)	<i>D. sexcinctus</i> (Northern morph) (n = 17)	<i>D. sexcinctus</i> (Southern morph) (n = 36)
SVL	\bar{x} = 76.72 SD = 8.39 (65.5 - 97.0)	\bar{x} = 88.44 SD = 9.19 (75.0 - 105.0)	\bar{x} = 101.50 SD = 11.28 (85.0 - 120.0)	\bar{x} = 96.24 SD = 8.52 (85.0-112.0)
HW/HL	\bar{x} = 0.90 SD = 0.02 (0.87 - 0.91)	\bar{x} = 0.92 SD = 0.03 (0.88 - 0.98)	\bar{x} = 0.91 SD = 0.04 (0.86 - 0.96)	\bar{x} = 0.94 SD = 0.04 (0.86 - 1.03)
SND/END	\bar{x} = 0.68 SD = 0.04 (0.62 - 0.74)	\bar{x} = 0.85 SD = 0.04 (0.80 - 0.91)	\bar{x} = 0.83 SD = 0.03 (0.77 - 0.89)	\bar{x} = 0.84 SD = 0.02 (0.81 - 0.88)

Analysis of variance showed that the snout-vent distance in *D. darwini* was significantly lower than in *D. bibronii* (from Santa Cruz and Southern Chubut), and in both significantly lower than in the Northern morph (from Mendoza) and the Southern morph (from Chubut, Río Negro, Neuquén) of *D. sexcinctus* ($F = 31.73$ $p = 0.0000$). Differences in snout vent distance between sexes were not significant for all cases ($F = 0.02$ $p = 0.8899$ for *D. bibronii*, $F = 1.75$ $p = 0.1956$ for Southern *D. sexcinctus* morph, $F = 1.95$ $p = 0.1827$ for Northern *D. sexcinctus* morph, $F = 0.39$ $p = 0.5449$ for *D. darwini*). The SVL between *D. bibronii* and *D. sexcinctus* (both morphs grouped) significantly differed from each other ($t = -4.09$ $p = 0.0001$).

About the considered meristic characters, it is evident that the head width and head length ratio do not present any significant difference between all the reported cases. On the contrary the observed ratios between snout-nostril distance and eye-nostril distance show a notorious, obvious dissimilarity between *D. darwini* and the other cases here analyzed (Table 1).

Natural History - Ecological trends and behavior of *Diploalemus sexcinctus* are the same of the other species of the genus, and more or less of all the predatory and aggressive leiosaurid lizards, mainly feeding on arthropods, other invertebrates or small reptiles. They live easily in captivity, nourishing with mealworms, maintaining their ferocious temper. Heavy stones or crevices are their habitual shelter, moving quickly to foraging or overtaking their basking position on summit of rocks and stones, after 8 AM to late afternoon in summer. Resistance of *Diplolaemus* species to cold temperatures is exceptional: in Canquel plateau (Chubut) and other embossments, their normal activity and aggressive behavior at environmental temperatures of about 5°C have been observed.

Habitat of these leiosaurine iguanians is almost periglacial or mainly related to usually cold and dry ecosystems, such as those of the Patagonian and Andean regions. Then they cross 2000-2500 m.a.s.l. in the mountains, but *Diplolaemus bibronii* and *Diplolaemus darwinii* are also present until sea beaches in the arid Deseado basin of Santa Cruz province. Common vegetal associations of their biotopes are the spiny, creeping plants of the patagonian or Andean bushes, being also found in the marginal ecotonal formation of their austral distribution. Some *Diplolaemus sexcinctus* populations enter the bordering western remains of relict ancient wet forest in Río Negro and Neuquén provinces (Plate 2, B).

Distribution - A very extensive one, from central Mendoza province, to the limits between Chubut and Santa Cruz provinces, with a latitudinal range of about 1400 km (Fig. 1).

DISCUSSION AND CONCLUSIONS

Concluding this work, we can assume that postulated relationships between *Diplolaemus sexcinctus* and *Diplolaemus bibronii*, as well as between *D. sexcinctus* and *Diplolaemus darwinii*, could represent peculiar cases of relatively recent speciation, likely through glacial or post-glacial events. That in spite of a very ancient ancestry of the leiosaurine lineage, having in mind the just discovered fossil specimens, in the Miocene beds of Chubut province, strongly similar or identical to living

species of the leiosaurine *Pristidactylus* (Albino and Etheridge, 2000).

Adaptive features of current *Diplolaemus* taxa to hard environmental conditions, reminiscent of Pleistocenic biocenotic communities, are suggested by their geographical distribution, ecological trends and unusual physiological or behavioral tolerance to low temperatures. Evolutionary history of living species of this genus is certainly related to geophysical conditions of the southern continent during glacial periods, such as the growing of iced soils and the contemporary remarkable variation of its sea- shore line. A map by the late Dr. A. Corte, in his last important contribution to Cryogeology (1997), reported here in Fig. 3, may provide a general approach to the Pleistocenic extension of the so-called "permafrost" or permanent iced soil in austral Argentinean and Chilean territories, intervening in the present distribution of Argentinean *Diplolaemus* species shown in our map of Fig. 1.

It is evident that all the regions south of Colorado River approximately were included in the continental "permafrost", then all the above mentioned *Diplolaemus* species could to be able to occupy their present areas only after the gradual ice retrocession of post-glacial times.

It is still mere speculation any hypothetical attempt to get in shape a phyletic reconstruction of the speciation process leading to the now recognized taxa of *Diplolaemus*. Our mainly morphological analysis is certainly insufficient, but a bio-molecular essay by DNA sequencing technics would likely contribute to stablish real genetic distances in terms of phyletic relationships. Purpose of our paper was to get a positive rearrangement of the relative interspecific relationships and a taxonomic revision of a longtime intermixed genus, deteriorating or often making useless most of its literature of the past decades. We hope to have obtained some valuable results for that matter.

Lastly, but as simple complementary notice, we will report a no morphological comparative research on interspecific relationships carried out several years ago by now no longer in use immunological methods, in spite of their relative accuracy, such as the Libby's photronreflectometer technique (Cei, 1975). In these serological tests an anti-*Diplolaemus darwinii* serum from Mendoza (now an anti-*Diplolaemus sexcinctus* serum) was

reacting with its homologous antigens and with some heterologous antigens, giving the following results in percentages of measured precipitins: anti-*D. sexcinctus* (Portillo Argentino, Mendoza) serum x *D. sexcinctus* (same locality) antigens = 100%; anti-*D. sexcinctus* (same locality) serum x *D. darwinii* (Petrified Woods, Deseado River, Santa Cruz) antigens = 91.5%; anti-*D. sexcinctus* (same locality) serum x *D. bibronii* (Petrified Wood, Deseado River, Santa Cruz) antigens = 77.5%; anti-*D. sexcinctus* (same locality) serum x *D. bibronii* (Canquel plateau, Santa Cruz) antigens = 80.3%; anti-*D. sexcinctus* (same locality) serum x *Pristidactylus araucanus* (Payún volcanic plateau, Mendoza) antigens = 67.4%.

We do not comment these data, surprising for the nearby serological affinity between *Diplolaemus darwinii* and *Diplolaemus sexcinctus*. Of course, an actualized new research on this matter should be welcome, by more recent immunological methods as those used by Maxon and Maxon (1986), Mayer and Lutz (1989) and several others, or comparatively by the above invoked bio-molecular DNA technique.

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Appendix

Specimens examined

All specimens examined are reported as male, female and juvenile samples. Several general data on the specimens were given previously in Material and Methods. Also in Material and Methods, abbreviations for names of the utilized herpetological collections were reported with their usual acronyms.

Leiosauridae, Leiosaurinae:

Diplolaemus darwini: (Santa Cruz, Chubut and Río Negro provinces) - MLP-S: 867, 1797 (males), 852, 871, 880, 889 (females); MACN: 32203 (male); IBA-UNC: 613-1, 924-2 (males), 522-1, 536, 612, 626, 924-1 (females), 522-2-3, 613-2, 622 (juveniles); JMC-DC: 536 (female); JAS-HC: 626 (female).

Diplolaemus bibronii: (Santa Cruz province) - IBA-UNC: 437, 439, 621-1, 914-2 (males), 621-2, 923 (Females), 451, 914-1 (juveniles); CH-IADIZA: 217 (female); JMC-DC: 315, 316, 537, (males), 539, 540, 541 (females), 534, 535, 536, 538 (juveniles); CH-JAS: 40, 107, 358 (males), 359, 360 (females), 206, 234 (juveniles). (Southern Chubut province) - IBA-UNC: 801-1-2, 910-2 (males), 619, 838, 909, 910-1, 922 (females), 584, 801-3 (juveniles); JMC-DC: 1222 (female); CH-JAS: 717 (female).

Diplolaemus sexcinctus: (Chubut, Río Negro, Neuquén provinces) - MLP-S: 415, 865, 873, 877, 887, 901, 1652, 1656, 1658, 2039 (males), 878, 1653, 1657 (females), 857, 883, 884, 895, 897, 1830, 1831, 1961 (juveniles); IBA-UNC: 370, 605-1, 611-1 (males), 418, 438, 461, 511, 513, 811-1-2, 921, 1024, 1060 (females), 511-2-3, 605-2, 611-2, 811-3 (juveniles); CH-IADIZA: 174, 250 (females); CH-JAS: 34, 47, 150, 151, 161, 701, 703, 705, 708, 711 (males), 38, 702, 704, 706, 707, 709, 710, 716 (females), 36, 712, 713, 714, 715, (juveniles). (Mendoza province) - MLP-S 868 (male), 268, 866 (females); IBA-UNC: 776-1, 812-1-2, 1177-1-2, 1412-1 (males), 926, 417, 1412-2,

925-1-2 (females), 371-1-2-3, 372, 776-2, 911 (juveniles); MMSR: 1113 (male), 1114, 12887 (females), 848, 948, 1133, 1189 (juveniles); CH-IADIZA: 242-1 (female), 96-1-2, 242-2-3 (juveniles).



Fig. 1: Geographical distribution of the *Diplolaemus* species in Argentina.

Fig. 2: A) Infralabial and postmental scales (i,p) contacting along mental scale of *Diplolaemus darwini*. B),C) Infralabial and postmental scales (i,p) separated by interposed scales along mental scale in *Diplolaemus sexcinctus*. C) Different cloacal regions in adult males and females of *Diplolaemus sexcinctus* from Cruz de Piedra, San Carlos Dept., Mendoza, 2750 m.a.s.l. Left, in male showing ejected hemipenes; right in female. (A, B, C : 10X; D: slightly magnified).

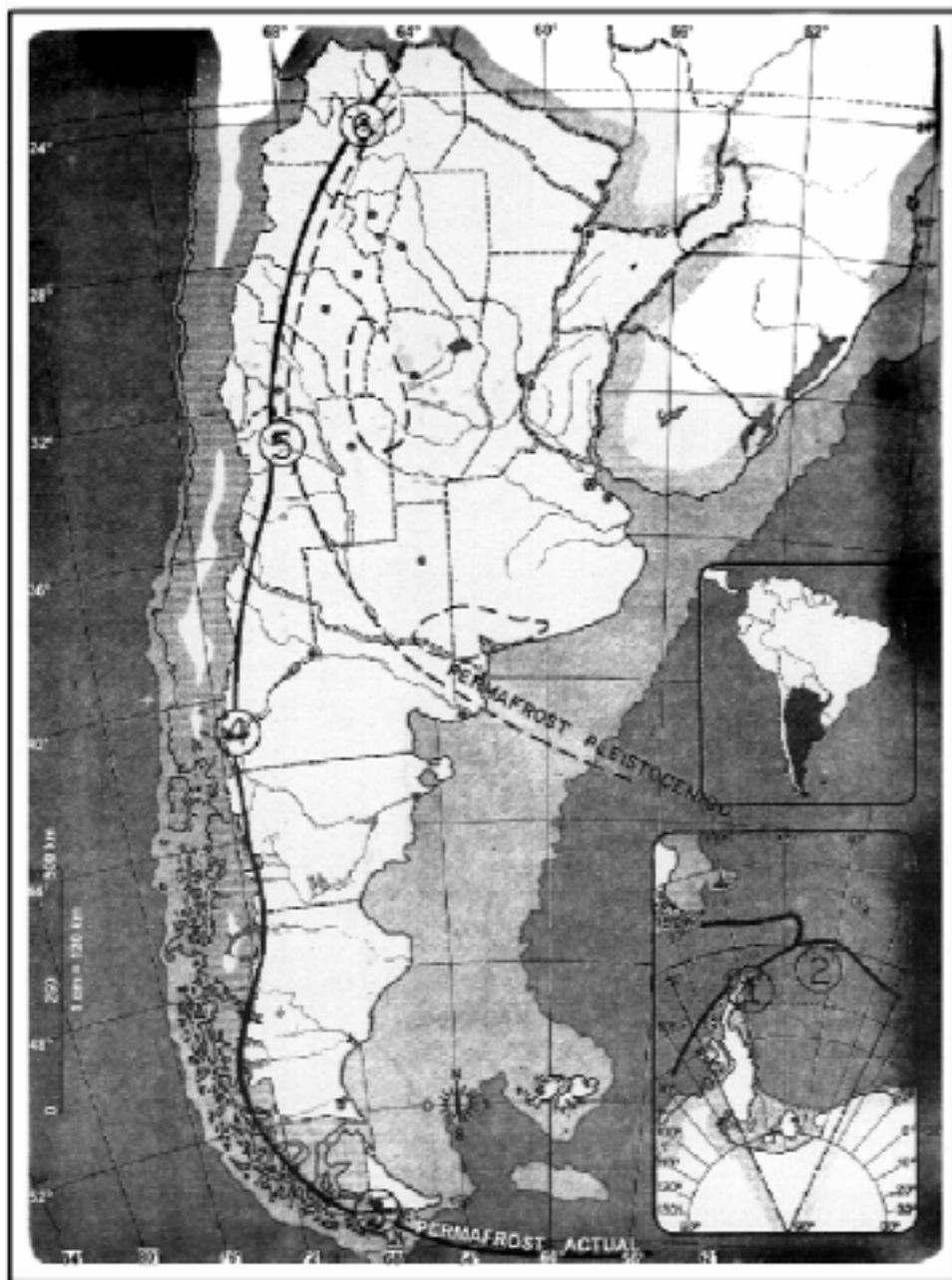


Fig. 3: Map of southern South American continent during the glacial period. Approximate boundaries of Pleistocenic permafrost, or perennial iced soil, compared with its actual limits. Numbers on the line of actual Permafrost limits in Argentina are referred to stations of glaciological and geological research. (Original map from Corte's book, 1997, by kind permission).

Plate 1

A) Sympatric *Diplolaemus* species from Puerto Deseado, Santa Cruz province, Argentina, their Terra Typica: top, *Diplolaemus darwini*; bottom, *Diplolaemus bibronii*, adult specimens. In the specific dorsal color patterns a different number of dark tail rings can be observed, ranging from 14 to 16 in *D. darwini*, from 10 to 12 in *D. bibronii*. Photograph at about natural size, as for the following lizards.

B) The same anterior specimens: ventral view. Left, *D. darwini*; right, *D. bibronii*: characteristic longitudinal black marks of *D. darwini* in its gular region can be pointed out.

C) Adult specimen of *D. bibronii* from basaltic ravines at about 40 km W Lago Argentino, along Santa Cruz river, Santa Cruz province, Argentina. The evident five-banded dorsal color pattern is shown.

(Photo J.M.Cei).

Plate 2

A) Characteristic adult specimen of *Diplolaemus sexcinctus* from basaltic Somuncurá plateau, Raimundo lagoon, 1400 m.a.s.l., Valcheta Dept., Río Negro province, Argentina. The remarkable color polymorphism of this species must be stressed for that individual and the following specimens reported on Plate 2.

B) Adult *Diplolaemus sexcinctus* from northern shores of Lakar lake, Neuquén province, Argentina. Its habitat belongs to woody environments of the Valdivian rain-forest.

C) Holotype of *Diplolaemus sexcinctus* (IBA-UNC- 605-1), from basaltic ravines, 1100 m.a.s.l., 10 km south Las Bayas creek, Río Negro province, Argentina.

(Photo J. M. Cei).

Plate 3

A) Head of a *Diplolaemus sexcinctus*, adult male, from 10 km W Primeros Pinos, 1700 m.a.s.l., Zapala Dept., Neuquén province, Argentina.

B) Head of *Diplolaemus darwini*, adult male, from Estancia Esperanza, 3 km south Coig river, 350 m.a.s.l., Santa Cruz province, Argentina. (Several specific characters of cephalic lepidosis are easily recognizable in the magnified phothographs: 5X).

(Photo J.A. Scolaro)

Plate 4

A) Hemipenis of *Diplolaemus sexcinctus*, adult male (SVL: 98,5 mm), from Somuncurá plateau, 1400 m.a.s.l., Valcheta Dept., Río Negro province, Argentina. Its goblet-like, slightly bilobate shape can be observed from the sulcal side. Differences in the very moderately sinked, lateral apical ornaments, in comparison with the hemipenis of the following species, can be pointed out. (15 X).

B) Hemipenis of *Diplolaemus bibronii*, adult male (SVL: 79 mm) from Puerto Deseado, Santa Cruz province, Argentina. In sulcal view, the remarkable bilobed, almost two-headed shape of the hemipenis, can be observed, as well as the deep, wide sulcus along the short, stout pedicel of the organ. The apical cuplike calyces, surrounded by circular, digged ornamentations, characterize both the hemipenis lobes, separated by a relatively open, flat sulcal depression. The lower peculiar region, from the apical calyces to the pedicel basis, shows several, very accentuated, lamellar structures. (20X).

(Photo J.A. Scolaro)