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A new subspecies of *Tropidurus spinulosus* (Cope 1862) from the subtropical wet mesic Paraguayan region (Reptilia Squamata Tropiduridae)

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A new subspecies of the *Tropidurus spinulosus* group is recognized and described as *Tropidurus spinulosus guarani*. Its distribution area corresponds to the wet mesic region from central Paraguayan districts east of Asunción and Paraguay River. Morphological characters and peculiar features of the new taxon are analysed and discussed in comparison with COPE's nominal form. Populations of *Tropidurus spinulosus spinulosus* from the xerophytic Chacoan region of Argentina were used. Morphological differences between the uniform arboreal populations from northern and central Chacoan flats and the southernmost saxicolous populations from the Córdoba embossments are also reported and discussed.

KEY WORDS: Reptilia, Squamata, Tropiduridae, *Tropidurus*, speciation, evolution, Chacoan region, Paraguay, Argentina.

INTRODUCTION

Tropidurus spinulosus was described as *Microlophus spinulosus* by COPE (1862), having been collected by Capt. Page during the Paraguay-Paraná-Bermejo Exploration. COPE's original description includes data on lepidosis, metric measurements and body colouration, as well as the presence of palatine teeth. By the courtesy of Dr G. Zug from the US National Museum, Washington, new measurements and careful photographic records of the type of *M. spinulosus* have been available.

That species has since been reported from Paraguay as well as from Argentina by several authors, mainly BOETTGER (1885), BOULENGER (1885, 1894, 1902), KOSLOWSKY (1898), PERACCA (1904), BURT & BURT (1930, 1931), BERTONI (1939), LIEBERMANN (1939), HELLMICH (1960), GALLARDO (1969, 1979), GALLARDO et al. (1985, 1987), CEI (1986) and ALVAREZ et al. (1988). Some of these contributions (BOULENGER 1885, HELLMICH 1960, CEI 1986) gave more morphological details, concerning several meristic characters and nuchal, antehumeral or gular folds, etc.

A careful study of several specimens lately collected by the senior author in two localities from the Departamento Paraguarí, east of Asunción, Paraguay, showed a clear cut disagreement between the type characters and the observed characters of this new sample, for lepidosis, colouration and ecological trends. Likewise significant differences for some characters emerged when a direct comparison was made of these Paraguayan specimens with other samples of lizards collected by the senior author in the provinces of Chaco, Formosa and Santiago del Estero (Argentina), all belonging to the phytogeographic Chacoan district and its xerophilous environments (Fig. 1). It appears that the populations from the wet mesic eastern Paraguayan zone (such as the Departamento Paraguarí) do not fit the specific characterization of the nominate form *T. spinulosus*, whose taxonomic status is otherwise supported by the Argentine Chacoan populations. We suggest now a subspecific category for these Paraguayan populations in spite of their remarkable distinctive characters, keeping in mind their apparent allopatric condition, and the present lack of information on their genetic compatibility, and/or intergradation with the nominate form.

MATERIAL AND METHODS

Thirty-two specimens (20 ♂♂, 12 ♀♀) of Chacoan populations from the provinces of Chaco and Formosa, Argentina, together with 25 specimens (13♂♂, 12 ♀♀) from Piríbebuy and Paraguarí (Departamento Paraguarí), Paraguay, were examined and compared. In addition to these samples 11 specimens (8 ♂♂, 3 ♀♀) from Tanti, the central mountains of Córdoba, Argentina, were also examined. They come from the southernmost borders of Chacoan distribution of the *Tropidurus spinulosus* group.

Preliminary statistical analyses were performed using 13 meristic variables, 21 metric variables (in mm) and 8 indexes (Tables 1 and 2). Only 24 selected variables (8 meristic, 13 metric variables and 3 indexes) showed significant differences between Paraguayan and Chacoan populations. Abbreviations for the preliminary 42 variables used are defined in Table 1; in Table 2 these variables and their range, means and standard deviations (SD) are reported. Given the moderate size of the available samples and the very scarce sexual dimorphism observed for most of the metric and meristic variables, their sex discrimination was generally assumed as unnecessary.

To support a critical appraisal of the reciprocal relationships between population groups involved in this research, such as the Chacoan, Paraguayan and Córdoba populations, a discriminant

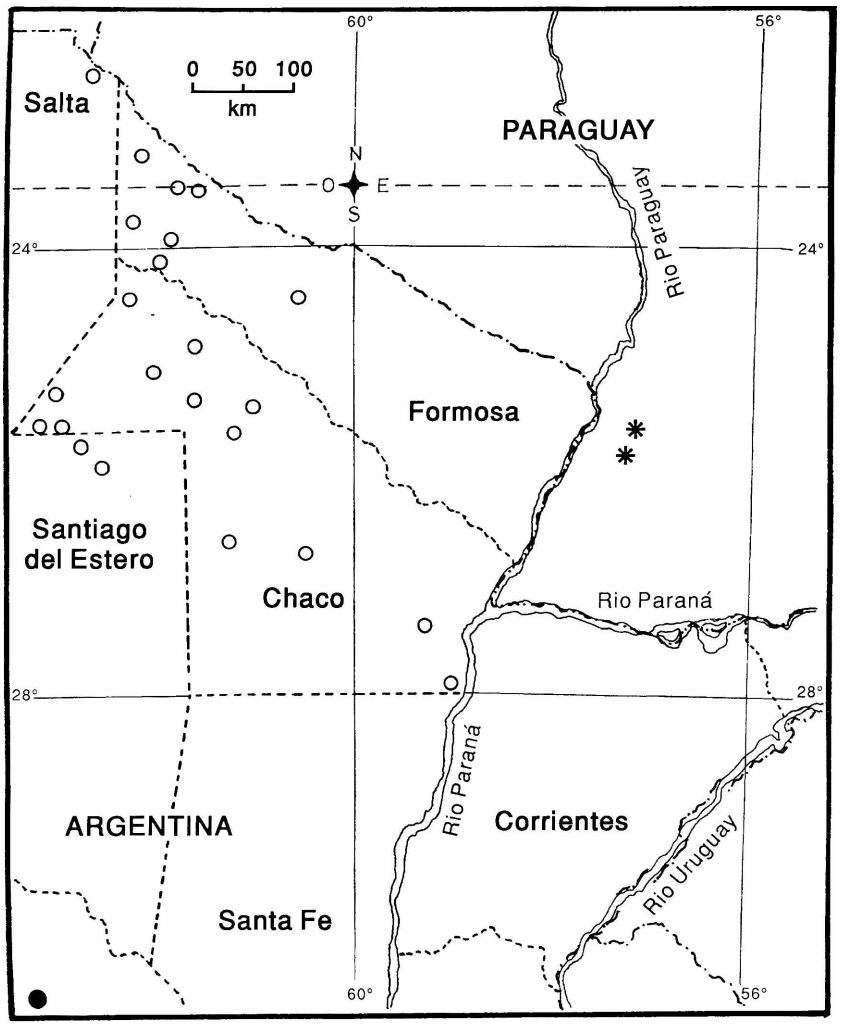


Fig. 1. — Distribution of the examined Chacoan and Paraguayan populations of the *Tropidurus spinulosus* complex. White circles: populations of *T. spinulosus spinulosus* from Argentine Chaco; asterisks: populations of *T. spinulosus guarani* from Paraguarí and Piríbebuy, near Asunción, Paraguay; black circle: northernmost point of distribution of the *T. spinulosus* populations from Córdoba embossments.

analysis of somatic characteristic variables was made by one of us (J.A. Scolaro). To this end, after progressive selection of nine significant variables ($r > 0.07$), all data have been treated by means of the discriminant analysis according to FOUCART's method (1982). Variables showing significant differences between groups were analysed for normalcy by means of the Snedecor's test. If normal Gaussian distributions were observed, a comparison between means by the Student t-test was made; in non-Gaussian distributions, the Mann-Whitney U-test or Z-test was used. The selected metric variables, and meristic variables, from the discriminant analysis (Table 1), were also measured for the holotype of *Microlophus spinulosus* (USNM.5956); a further discriminant analysis to assess its reciprocal position in relation to the Chacoan and Paraguayan populations was carried out, using the same method.

Table 1.
Abbreviations for the preliminary 42 variables used.

* MBS	Scales around midbody
* VS	Vertebral scales
* PVS	Paravertebral scales
* NES	Nostril-eye scales
ETS	Eye-tympan scales
AS	Scales between axillas
GT	Gular scales between tympani
* VSR	Ventral scale rows
SLS	Supralabial scales
ILS	Infralabial scales
FFL	Fourth finger lamellae
FTL	Fourth toe lamellae
* SV	Snout-vent distance
* AG	Axilla-groin distance
HL	Head length
HW	Head width
HH	Head height
FL	Forelimb length
HLL	Hindlimb length
DSL	Dorsal scale length
DSW	Dorsal scale width
VSL	Ventral scale length
VSW	Ventral scale width
SAR	Synphysial-antegular ridge distance
1FL-5FL	1st to 5th finger length
1TL-5TL	1st to 5th toe length
SV/HL	Index snout-vent/head length
HW/HH	Index head width/head height
HW/HL	Index head width/head length
AG/FL	Index axilla-groin/forelimb
AG/HLL	Index axilla-groin/hindlimb
* DSL/DSW	Index dorsal scale length/dorsal scale width
* VSL/VSW	Index ventral scale length/ventral scale width
SV/HLL	Index snout-vent/hindlimb length

Marked by asterisks the selected nine variables used in the discriminant analysis.

The specimens used in this work are deposited in several museums, identified by abbreviations as follows: FML (Fundación M. Lillo, Tucumán, Argentina); MRSN (Museo Regionale di Scienze Naturali, Torino, Italy); USNM (United States National Museum, Washington, USA); UNNE-CHC (Universidad Nacional del Nordeste, Colección Herpetológica, Corrientes, Argentina).

DESCRIPTION OF THE SUBSPECIES

Tropidurus spinulosus guarani n. subsp.

Material examined. Holotype: an adult male (FML.02752), Cerro Hu, Departamento Paraguarí, Paraguay (25°30'S, 57°00'W), collected 3 March 1989 by B.B. Alvarez and M. Culzoni. *Paratypes*: 1 ♂, 2 ♀♀ (MRSN.R.120, 1-2-3), Cerro Hu, Paraguarí, Paraguay, collected 16 October 1989 by B.B. Alvarez and M. Culzoni; 1 ♂ (USNM.319758), Cerro Hu, Paraguarí, Paraguay, collected 3 March 1989, same collectors; 1 ♀ (USNM.319759), Chololó, Paraguarí, Paraguay, 3 March 1989, same collectors; 5 ♂♂, 4 ♀♀ (UNNE-CHC.320-321, 357, 370, 395, 322, 324-326), Chololó,

Table 2.
Metric and meristic measurements and indexes in populations of *Tropidurus spinulosus* from Paraguay and northern and central Argentina.

Variable	Paraguay n = 25				Chaco n = 32				Córdoba n = 11			
	x̄	SD	Min	Max	x̄	SD	Min	Max	x̄	SD	Min	Max
MBS	102.20	2.50	97.00	106.00	85.59	2.58	81.00	92.00	92.54	2.65	89.00	98.00
VS	80.96	18.18	59.00	107.00	65.19	13.20	50.00	96.00	66.00	8.14	60.00	85.00
PVS	127.92	7.52	117.00	154.00	117.62	5.64	109.00	130.00	123.00	4.08	119.00	126.00
NES	2.10	0.53	2.00	3.00	2.84	0.36	2.00	3.00	2.90	0.30	2.00	3.00
ETS	12.72	1.33	11.00	15.00	11.56	0.98	10.00	14.00	11.80	0.75	11.00	13.00
AS	31.24	3.71	27.00	46.00	28.19	2.58	23.00	32.00	31.08	1.94	29.00	36.00
GT	57.80	6.40	48.00	74.00	46.88	3.88	39.00	55.00	51.72	2.61	48.00	56.00
VSR	132.50	6.43	120.00	143.00	105.90	7.68	87.00	119.00	109.00	3.64	105.00	117.00
SLS	4.73	0.54	4.00	6.00	5.40	0.51	4.00	6.00	5.72	0.46	5.00	6.00
ILS	5.03	0.45	4.00	6.00	5.40	0.46	5.00	6.00	5.72	0.46	5.00	6.00
FFL	22.75	1.46	20.00	26.00	21.10	1.33	20.00	24.00	21.30	1.02	19.00	23.00
FTL	28.15	1.34	25.00	30.00	27.20	1.38	24.00	30.00	26.20	1.48	23.00	29.00
SV	89.91	11.62	70.00	112.00	99.34	13.90	78.10	135.00	112.70	12.75	83.00	125.00
AG	38.33	4.95	31.00	50.00	38.33	6.99	33.80	65.00	49.36	5.85	37.00	55.00
HL	23.95	3.14	18.00	29.00	25.95	4.12	18.40	33.50	27.90	2.87	21.00	31.00
HW	18.47	2.11	15.00	23.00	21.29	3.61	14.50	27.00	22.54	3.01	16.00	27.00
HH	12.45	2.57	9.00	17.80	13.92	2.09	10.90	17.20	14.00	1.61	11.00	16.00
FL	39.16	5.52	30.00	48.80	44.70	6.81	36.00	56.70	43.20	4.26	35.00	49.00
HLL	56.42	8.79	35.00	71.00	61.92	9.61	43.20	79.00	66.90	7.28	53.00	77.00
DSL	1.06	0.21	0.70	1.40	1.47	0.36	0.90	2.10	1.46	0.28	0.90	2.00
DSW	1.14	0.17	0.90	1.50	1.40	0.23	1.00	1.95	1.36	0.19	0.90	1.50
VSL	1.04	0.20	0.70	1.50	1.36	0.19	1.00	1.75	1.30	0.18	1.00	1.60
VSW	1.06	0.22	0.70	1.40	1.48	0.17	1.20	1.80	1.38	0.18	1.00	1.60
SAR	51.16	4.48	41.00	59.00	44.81	3.15	36.00	52.00	49.72	1.27	47.00	50.00
1FL	5.46	0.91	4.00	7.00	5.91	0.87	4.40	7.50	5.94	0.66	5.00	7.30
2FL	8.17	1.12	6.00	10.00	8.80	0.96	7.40	11.00	9.31	0.93	8.00	11.40
3FL	10.34	1.33	8.00	13.40	11.16	1.14	9.30	13.00	11.25	1.13	10.00	13.80
4FL	11.56	1.33	9.00	14.20	12.47	1.98	8.00	17.00	12.74	1.42	10.80	15.30
5FL	8.63	1.33	6.00	10.40	9.41	1.04	7.90	11.85	9.74	0.93	8.30	11.30
1TL	5.10	0.70	4.00	6.70	5.32	0.78	4.30	7.20	6.15	0.80	5.20	7.30
2TL	8.15	0.93	6.80	10.20	8.94	0.95	7.50	11.00	9.48	0.87	8.00	11.30
3TL	12.46	1.52	10.00	15.50	13.37	1.51	11.00	16.00	13.88	1.04	12.20	15.80
4TL	15.24	2.27	10.00	18.50	16.79	9.68	14.30	24.00	17.54	1.43	14.60	19.40
5TL	12.07	1.72	9.50	15.00	13.30	1.76	10.50	17.00	13.23	2.01	12.20	15.90
SV/HL	3.73	0.19	3.49	4.00	3.88	0.16	3.57	4.15	4.03	0.18	3.84	4.31
HW/HH	1.51	0.20	1.22	1.88	1.45	0.22	0.94	1.77	1.61	0.11	1.45	1.83
HW/HL	0.77	0.05	0.68	0.94	0.77	0.08	0.51	0.92	0.79	0.04	0.72	0.87.
AG/FL	0.97	0.09	0.74	1.18	1.06	0.10	0.78	1.21	1.13	0.09	0.93	1.25
AG/HLL	0.67	0.07	0.51	0.79	0.73	0.06	0.61	0.89	0.71	0.03	0.64	0.76
DSL/DSW	1.00	0.17	0.77	1.25	1.06	0.16	0.83	1.58	1.06	0.15	0.90	1.33
VSL/VSW	1.07	0.20	0.85	1.57	0.91	0.12	0.73	1.23	0.99	0.12	0.75	1.25
SV/HLL	1.60	0.11	1.46	2.00	1.63	0.11	1.38	1.85	1.65	0.10	1.52	1.92

Paraguarí, Paraguay, 3 March 1989, same collectors; 1 ♀ (UNNE-CHC.600), Chololó, Paraguarí, Paraguay, 9 March 1989, same collectors; 2 ♂♂ (UNNE-CHC.596, 598), Cerro Hu, Paraguarí, Paraguay, 3 March 1989, same collectors; 2 ♂♂, 2 ♀♀ (UNNE-CHC.358, 599, 601-602), Cerro Hu, Paraguarí, Paraguay, 21 May and 16-23 March 1989, same collectors; 1 ♂, 2♀♀ (UNNE-CHC.606, 603-604), Piríbebuy, Departamento Cordillera, Paraguay, 3 March 1989, same collectors.

Diagnosis. This subspecies may be distinguished from the nominate form by: smaller size in both sexes; dorsal crest less high, and somewhat reduced in females; moderate spiny tufts on the preauricular, temporal, nuchal and lateral cephalic regions; dorsal scales moderately keeled and mucronate; a significant higher scale number around midbody, as well as a higher number of ventral, vertebral, paravertebral and intertympanic gular scales joined to pronounced differences in cephalic lepidosis (Figs 2-4); less spinous tail; a different colour pattern, with dark, bluish-green or whitish-yellow shades, sometimes with dorsal light spots, and dorsal scales entirely white. Yellow preanal scales in males, as well as on the ventral femoral surface; ventrally whitish or pale pinkish. Laterally striped, medially convergent gular

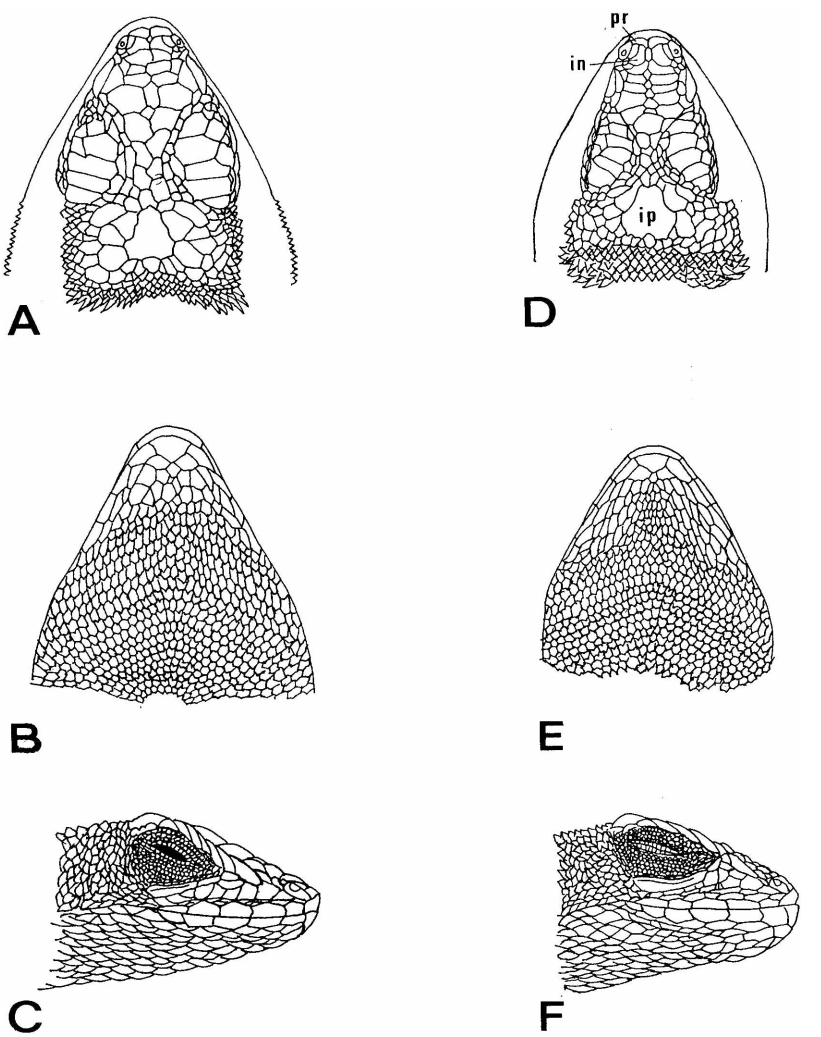


Fig. 2. — Cephalic lepidosis (dorsal, ventral, lateral) of: A-C, *Tropidurus spinulosus spinulosus* from Taco Pozo, Departamento A. Brown, province of Chaco, Argentina; D-F, *T. spinulosus guarani*, holotype, from Paraguarí, near Asunción, Paraguay. (Different magnifications; *pr*, postrostral; *in*, internasal; *ip*, interparietal).

pattern, not spotted as in the nominate form. *Tropidurus spinulosus guarani* is recognizable at first sight from other *Tropidurus* species of Argentina such as *T. etheridgei* Cei 1982, *T. catalanensis* Gudynas & Skuk 1983, *T. melanopleurus pictus* Müller 1923, by its peculiar morphological characters of spiny tufts and dorsal crest, as well as several striking differences in colour pattern.

Description of the holotype. A stout, moderately large lizard, with subtriangular head and somewhat blunt snout, the head being more than 1/4 of the body length. Autotomic tail, 1 1/2 longer than snout-vent. Slender forelimbs and hindlimbs: if extended along the body, the forelimbs do not reach the groin, the hindlimbs cross the axilla with the tip of 4th toe. Antehumeral fold deep; a broad dark band crossing the shoulder and connecting with the opposite band from the other side. A deep oblique neckfold, extended as a complete antegular fold, being also joined to a deep "mite pocket", greyish and finely granular; second antegular present; gular fold not complete, laterally confluent within the antehumeral fold; rictal fold barely reaching the tympanic opening, elliptical, with enlarged spiny scales on its frontal border.

Rostral twice as broad as high, often contacting nasals; nares more distant from the anterior corner of the eye than from the snout, large and opening laterodorsally. In the nasal and frontal zones large cephalic scales (Fig. 2D), subimbricate, bulky or convex, mostly irregular; two postrostrals and four internasals; canthal scale large with canthus rounded; only one scale between canthal and nasal. Interparietal large, bulky and smooth, subtriangular in shape, surrounded by minor parietal scales, irregular and convex; occipitals heterogeneous, much smaller than parietals, conical or convex; temporals smaller than parietals, irregular, often conical or mucronate. Lepidosis of nuchal region or neck showing mucronate scales, with the outstanding presence of the above mentioned spinous tufts. Orbital semicircles almost complete, irregularly scaled, separated by two bulky scale rows; six supraocular enlarged and convex, separated by very small scales from semicircles and supraciliaries. Supraciliaries enlarged, strongly imbricate, sharpened, forming a projecting arc above the orbits; eyelids granular; subocular enlarged and smooth, broken, with a sharpened ridge in its upper border. Two enlarged scale rows between suboculars or loreals and the 4-5 supralabials, smooth and convex (Fig. 2F). Mental smooth, small and triangular (Fig. 2E), narrower than rostral; five infralabials; a row of enlarged sublabials; three postmentals enlarged but decreasing in size.

Dorsals rhomboidal, keeled, mucronate, in medially convergent rows; dorsal crest poorly developed, outstanding on the neck; 70 vertebral scales; 130 paravertebral scales; 100 scales around midbody; lateral scales quite similar to the dorsals. Gulars polygonal, smooth and imbricate, smaller in size in the region of antegular and gular folds; 52 gulars between tympani. Ventrals and precloacals rhomboidal, keeled, imbricate, slightly smaller than dorsals; 126 ventrals. In forelimbs and hindlimbs: dorsally rhomboidal scales, keeled and mucronate, imbricate, larger than body scales; ventrally smaller than dorsals, smooth, imbricate, slightly smaller on the axilla and groin. Caudal scales larger and broader than dorsals, but similarly arranged; ventrally smooth, much larger than ventrals, triangular, very acuminate but gently keeled in the distal region. On the femoral ventral surface, as well as in the preanal region, of this male specimen, a band of opaque yellow scales is seen (Fig. 5D). Subdigital lamellae tricarinate, imbricate in fingers and toes: 23 and 16 in the 4th and 5th finger, 29 and 21 in the 4th and 5th toe.

Measurements of the holotype (in mm). Snout-vent 100; head length 27; head width (near ear opening) 20.5; forelimb 20.5; hindlimb 60; axilla-groin 41.

Colouration. Dorsally brownish grey, with yellowish and/or greenish or bluish shades, speckled with whitish and black marks, being irregularly reticulated broken lines recognizable, but with distinct dark transverse stripes on the cephalic surface, mainly in nuchal and suprascapular, paler in dorsal regions. Some irregular polygonal marks along the vertebral line are present. Caudal pattern similar to dorsal pattern. Gular surface light, yellowish white, with lateral blackish bars medially confluent in a vertical dark bar reaching the antegular fold (Fig. 5B). Lower gular and pectoral regions pigmented: ventrally whitish, except the posterior yellow scale bands. Tail whitish-grey.

Variation in paratypes. A moderate sex dimorphism is shown in *Tropidurus spinulosus guarani* by the larger size, the major axilla-groin distance and the larger forelimb and hindlimb in males (P = 0.01-0.001). However, the females show a higher number of vertebral scales (P = 0.001), intertympanic gulars and ventral scale rows. No sex differences were observed in the number of scales around midbody (82-92, $\bar{x} = 85.80 \pm 2.72$ in ♂♂, 80-89, $\bar{x} = 85.08 \pm 2.23$ in ♀♀). Dorsal crests are lower, often reduced in females: their colouration is darker, with irregular blackish marks on the head, never showing greenish or bluish yellow shades, or the distinct opaque yellow scale bands in lower femoral surfaces of the males. Chromatic differences in colour patterns between *T. spinulosus guarani* and the nominate form are easily appreciated in the photographs of living specimens of Fig. 6. Variation in paratypes may be also observed for the cephalic lepidosis, such as in postrostral and internasal scales (cf. Fig. 2D: *pr*, *in*): in the size of the enlarged tropidurine interparietal (cf. Fig. 2D: *ip*); in the number of supra-infralabiales (4-6 and 4-6, respectively); in the different growth of spinous scales in the neck; in the rictal and antegular folds; in the number of intertympanic gular scales (48-84); in the number of vertebral and paravertebral scales, or ventral scale rows; at last in the subdigital lamellae of 4th finger (20-26) and 4th toe (25-30).

Etymology. The subspecific name *guarani* refers to the ancient native culture and language "guaraní" spread on the wet mesic Paraguayan region where the new taxon was discovered.

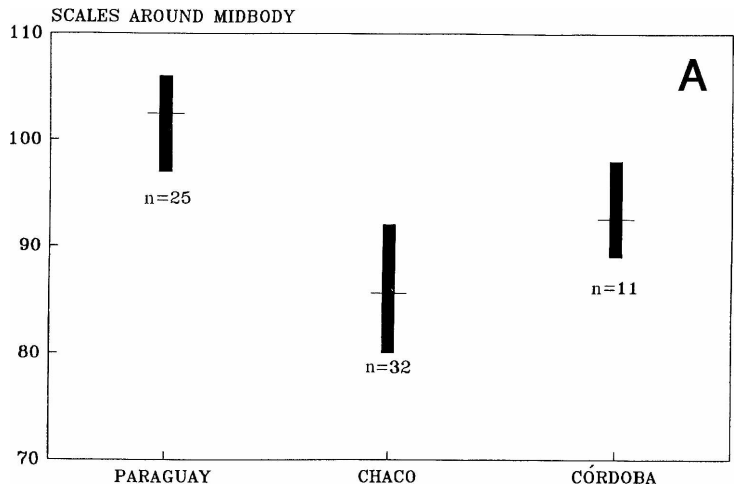
Distribution. In the wooded districts of the Republic of Paraguay, east of Paraguay River, such as the Departamentos of Paraguarí and Cordillera. Probably other populations of this form extend eastward in the Departamentos of Caapazá, Guairá, Caaguazú and Itapúa. The nominate form is found with a remarkable population density in the arid western Chacoan districts of Argentina, Bolivia and Paraguay, west of the Paraguay River. The exact locality of the COPE's type is still unknown (terra typica "Paraguay"): the presence of the nominate form was originally unreported east of the Paraguay River but it could be now reasonably restricted to the western side of the Paraguay River, between 21° and 24° South latitude, in accordance with Capt. Page's itinerary (Paraguay-Paraná-Bermejo Exploration). Both *T. spinulosus guarani* and *T. spinulosus spinulosus* are also apparently unknown for the Province of Corrientes, Argentina.

Ecological remarks. T. spinulosus guarani is a nimble opportunistic lizard, often climbing on the highest branches of larger trees of the mesic Paraná subtropical forest, scattered by arboreal ferns and surrounded by open savannas, covering the declivous rocky ground of central low embossments of Paraguay. It is fundamentally a saxicolous form, sheltering in broken stones or crevices of the rocky substratum of the wood, among which its colour pattern may exhibit some degree of mimicry. Oviparous and insectivorous, its annual cycle, reproduction and egg-laying are not known.

DISTRIBUTIONAL AND MORPHOLOGICAL TRENDS IN *TROPIDURUS SPINULOSUS* SUBSPECIES AND POPULATIONS

South of the wide xerophilous Chacoan flats, the central longitudinal embossments of the Sierras de Córdoba arise. In their different, isolated mountain environments, populations of *Tropidurus spinulosus* live, from Capilla del Monte northward to La Punilla on eastern slopes of the Sierras southward, reaching altitudes of about 1200 m (Durazno, Cosquin, Tanti, etc.). The variables of a sample of this southernmost saxicolous population were reported in the Table 2, together with the variables of *T. spinulosus spinulosus* from Chaco and *T. spinulosus guarani* from Paraguay. Significant differences for some metric and meristic characters appear. In fact, the Chacoan populations show significant differences in the number of scales around midbody with the Paraguayan populations ($P<0.001$), but also with the Córdoba population ($P<0.01$): likewise a significant difference ($P=0.001$) may be observed between *T. spinulosus guarani* and the Córdoba population (Fig. 3A). For the metric character of snout-vent distance, a significant difference ($P<0.01$) between *T. spinulosus guarani* and the Chacoan populations is shown (Fig. 3B), but it is also present between the Córdoba specimens and the specimens from the Chacoan area ($P=0.01$), increasing between the Córdoba specimens and the specimens of *T. spinulosus guarani* ($P<0.001$). Meristic differences are obviously significant for ventral scale rows ($P<0.001$) between *T. spinulosus guarani* and both the Chacoan and Córdoba samples (Fig. 4A). For the vertebral scales, lastly, meristic differences do not exist between the Chacoan and Córdoba populations (Fig. 4B), but they are present between *T. spinulosus guarani* and both the Chacoan ($P=0.001$) and the Córdoba population ($P<0.02$). Morphologically it is in agreement with the stronger dorsal crest of the Chacoan-Córdoba populations and its broad and larger scales.

Moreover, the lepidosis and colouration of the Córdoba mountain populations are very similar to the lepidosis and colouration of the nominate form *T. spinulosus spinulosus* (Figs 5 and 6): the size of vertebral scales and the development of the dorsal crest; the prominent bristled tufts on the neck; the oblique antehumeral, antegular and gular folds; and the dorsal and ventral colour patterns. The characteristic greenish or bluish shades are present in the males; rounded dark spots are also scattered in the whitish gular region; the ventral ground shows a quite immaculate, pinky-whitish colouration, without the yellow femoral and precloacal bands, such as in *T. spinulosus guarani*. Of course, a better knowledge of the saxicolous populations from the Córdoba mountains is needed, and their relationships with Chacoan populations must be again carefully analysed (cf. the following discriminant analysis). The simplest interpretation would seem to be a case of geographic variation, resulting from local conditions of topographic and environmental isolation probably extended through a



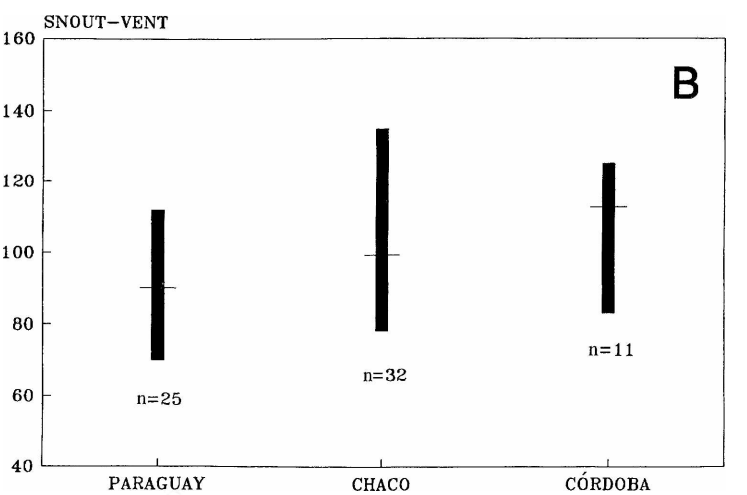
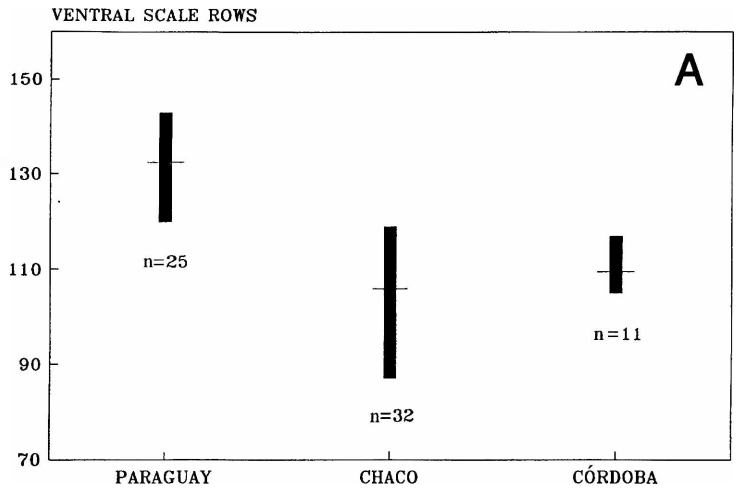


Fig. 3. — Differences (means and range) in number of scales around midbody and size, in populations of *Tropidurus spinulosus guarani* from Paraguay (n = 25), and in populations of *T. spinulosus spinulosus* from Chaco (n = 32), and Córdoba (n = 11). A, number of scales around midbody; B, size (snout-vent, in mm).

remarkable length of time. It would be advisable to take into consideration, at this point, the available names of some Argentine forms currently placed in synonymy with *Tropidurus spinulosus*, such as *Leiocephalus (Craniopeltis) variegatus* O'Shaughnessy 1879 from Cosquín, Córdoba, as well as *Plica stejnegeri* Burt & Burt 1930, from Argentina, the types of which have been compared.



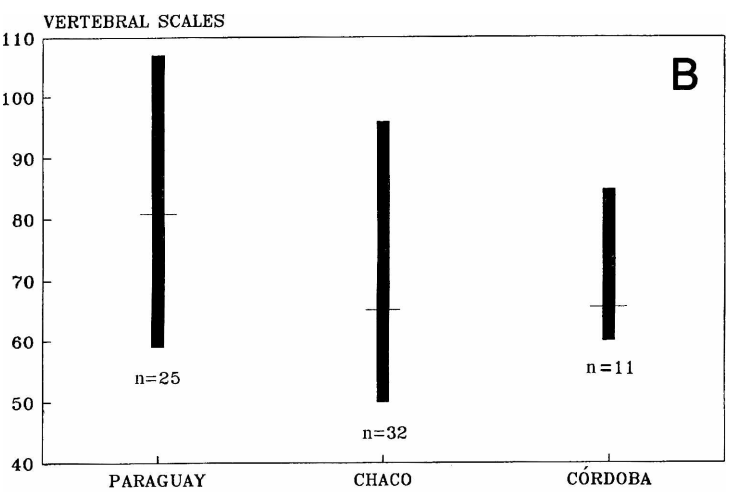


Fig. 4. — Differences (means and range) in ventral scale rows and in vertebral scale number, in populations of *Tropidurus spinulosus guarani* from Paraguay (n = 25), and in populations of *T. spinulosus spinulosus* from Chaco (n = 32) and Córdoba (n = 11). A, ventral scale rows; B, vertebral scales (number).

In the hypothetical case that the study of southernmost saxicolous populations would prove to be taxonomically distinct, *Plica stejnegeri*, well studied by ETHERIDGE (1970), is an unreliable name because of its ill-defined locality (Argentina) and the fact that its morphological patterns fit with the general character combinations of the northernmost *Tropidurus spinulosus* populations. *Tropidurus variegatus* (O'SHAUGH-

NESSY 1879) on the contrary, both by its morphology and montane locality, could be quite distinct coming from Cosquín, its *terra typica*, at a lineal distance of only 14 km from Tanti which is the locality of all the specimens used in the present work.

After the summarized data of our Diagnosis, a critical discussion of the significant distinctive characters of the nominate form and *T. spinulosus guarani* is necessary. The larger size and the stouter body of *T. spinulosus spinulosus* have been emphasized, as well as its higher crest and the lower number of scales in the ventral line. A tendency to a shorter hindlimb is also recognizable in *T. spinulosus spinulosus*, but it does not reach a statistical significance; however, such a tendency is significant in the montane population from Córdoba ($P = 0.01$-0.001) and a clinal adaptive trend could be taken into account. The number of scales around midbody is lower in *T. spinulosus spinulosus* as well as the lower number of vertebral scale, both of which resemble the isolated montane population from Córdoba. Significant differences characterize the number of ventral scales between the axillas and the number of gular scales between tympani, both higher in *Tropidurus spinulosus guarani*. Among the distinctive morphological conditions of *T. spinulosus spinulosus* are the stronger spinous temporal scales; more mucronate dorsal scales; larger caudal scales; deeper lateral and antehumeral folds on the neck; and the spiny tufts that are more prominent than in *T. spinulosus guarani*.

The new subspecies may be recognized, at first sight, by its colour pattern. The dorsal ground of *T. spinulosus spinulosus* is yellowish gray with obvious greenish or bluish shades, exhibiting darker, confused spots, crossed by irregular blackish lines, bordered by white, and oblique to the lateral body sides, but forked at their beginning on the vertebral line (Fig. 6B-D). On the contrary, *T. spinulosus guarani* is dorsally darker, or brownish, with faded spots or marks, somewhat similar to the *T. spinulosus spinulosus* pattern, but appearing at a very subdued, profusely scattered with minute white spots, generally on only a single scale, sometimes spread on several scales (Fig. 6A). The gular pattern is very distinct in both forms (Figs 5, 7). A whitish or yellowish ground scattered with regular rounded dark spots in *T. spinulosus spinulosus*: in *T. spinulosus guarani* showing short, sharp black stripes, converging from the jaw borders towards a dark median line (Fig. 5A, C). Ventrally a whitish-pink or yellowish immaculate ground in both forms, but enlarged opaque plates with brilliant yellow scales on the femoral and precloacal region in *T. spinulosus guarani* (Fig. 5B, D). Such yellow scales are completely absent in all the specimens of both sexes of *T. spinulosus spinulosus* examined, juveniles and adult.

DISCRIMINANT ANALYSIS OF MORPHOLOGICAL CHARACTERS IN POPULATIONS OF THE *TROPIDURUS SPINULOSUS* COMPLEX FROM THE CHACO-PARAGUAY REGION: RESULTS AND CONCLUSIONS

The groups submitted to discriminant analysis were samples of *Tropidurus spinulosus* populations from Paraguay, Chaco and Córdoba localities. Two canonic axes were obtained absorbing 66.3% and 33% of the total variance. Discriminant components of variables and squared cosine of the group's centroids associated to the axes are shown in Table 3. The axis I allows separation of Paraguay and Chaco from the remaining Córdoba group. Such an axis allows also separation between the former groups by a major expression in Paraguay for the variables "midbody scales"

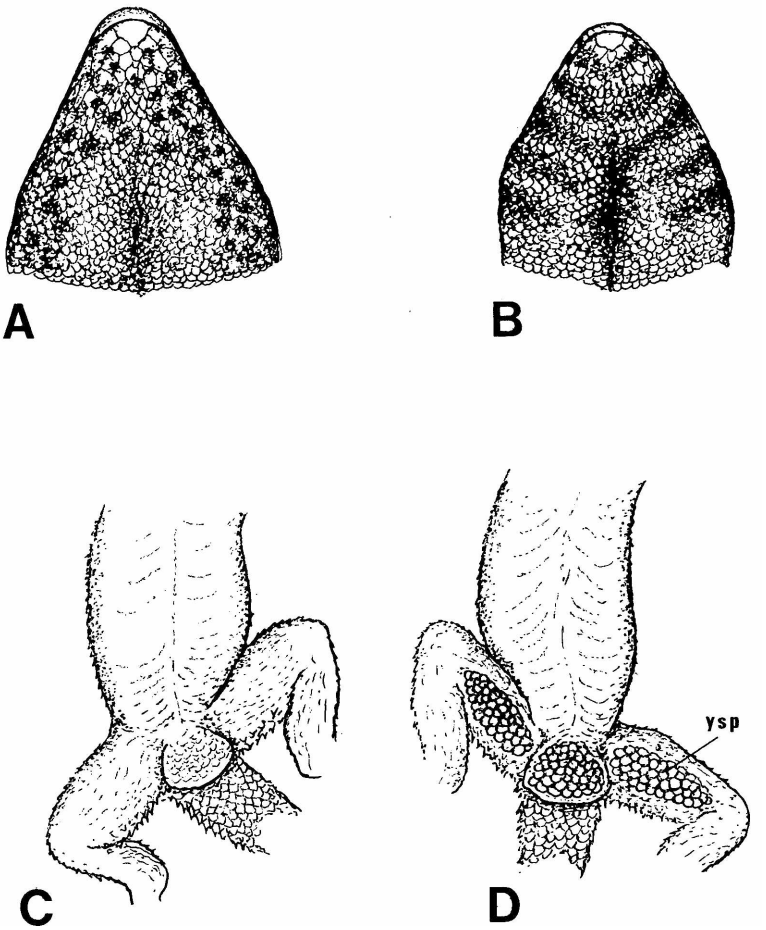


Fig. 5. — Comparison for gular colour pattern and femoral-precloacal lepidotic and colour pattern between *Tropidurus spinulosus spinulosus* from Chacoan flats (A, C) and *T. spinulosus guarani* from Paraguarí, Paraguay (B, D). In D, yellow scale plates in femoral-precloacal region (*ysp*). (Different magnifications).

($P<0.001$), "vertebral scales" ($P<0.001$), "paravertebral scales" ($P<0.001$), "gular scales between tympani" ($P<0.001$), "scales between axillas" ($P<0.01$) and "ventral scale rows" ($P<0.001$). The negative sector of the axis I associates the Chaco group with a major expression for the variables "nostril-eye scales" ($P<0.001$) and "axilla-groin length" ($P<0.001$) and by a minor expression for the above mentioned variables. The canonic axis II associates the Córdoba group with a major expression of the variable "snout-vent length" ($P<0.001$) and strengthens the differences with the former groups. Córdoba group also shows a major expression for the variable "axilla-groin length" ($P<0.001$ and $P<0.05$). If the means of the remaining variables are compared, Córdoba versus Paraguay shows a minor expression of "midbody scales" ($P<0.001$), "vertebral scales" ($P<0.001$), "gular scales between tympani" ($P<0.001$)

Table 3.
Discriminant components of variables and squared cosine of the group's centroids associated to the axes.

Variables	Discriminant component axis	
	I	II
Midbody scales (MBS)	0.99	0.12
Vertebral scales (VS)	0.95	−0.32
Paravertebral scales (PVS)	0.99	0.07
Gular scales between timpani (GT)	0.99	−0.01
Scales between axillas (AS)	0.86	0.51
Ventral scale rows (VSR)	0.98	−0.21
Snout-vent length (SV)	−0.54	0.84
Axilla-groin length (AG)	−0.73	0.69
Nostril-eye scales (NES)	−0.92	0.40
	Squared cosine of centroids	
Paraguay group	0.94	−0.06
Chaco group	−0.91	−0.09
Córdoba group	0.01	0.99

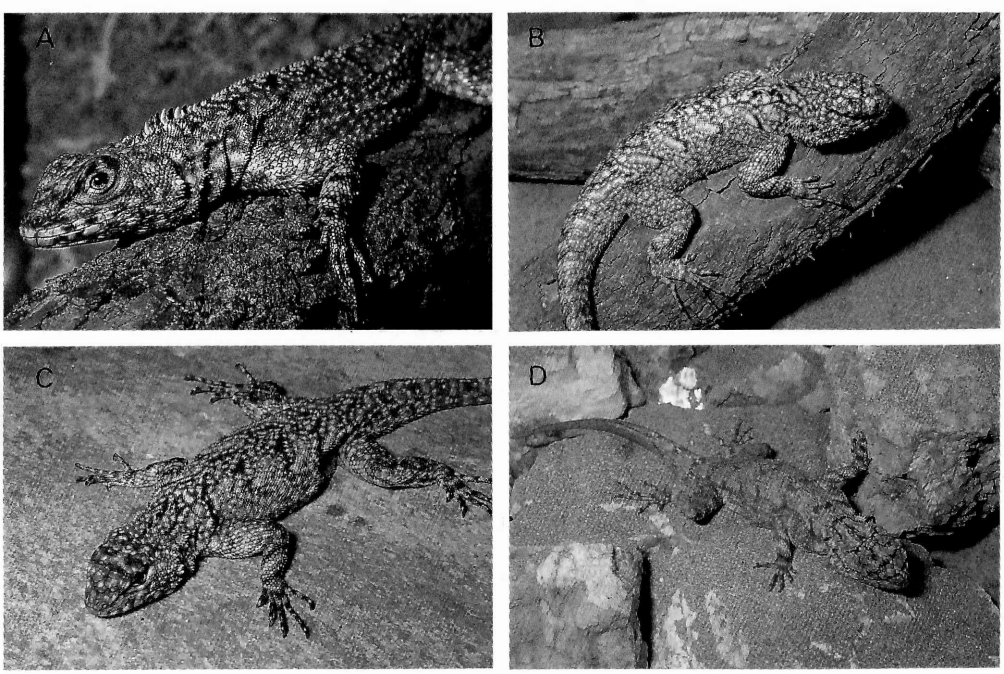


Fig. 6. — Living specimens of the *Tropidurus spinulosus* complex, from natural environment: A, *T. spinulosus guarani*, male, from Paraguarí, Paraguay, paratype, 3 March 1989; B, *T. spinulosus spinulosus*, male, from Palmar Largo, province of Formosa, central Chaco, Argentina, 24 February 1991; C, *T. spinulosus spinulosus*, male, from Tanti, Sierras de Córdoba, 1000 m, Argentina, 15 January 1979; D, *T. spinulosus spinulosus*, female, from Taco Pozo, province of Chaco, austral Chaco, Argentina, 23 February 1989.

and "ventral scale rows" ($P<0.001$). Comparing Córdoba versus Chaco a major expression for "midbody scales" ($P<0.001$), "paravertebral scales" ($P<0.01$), "gular scales between tympani" ($P<0.001$) and "scales between axillas" ($P<0.01$) is apparent for the former group.

Discriminant analysis of individual specimens resulted in a very high percentage of correct classification (95.6%). Ellipses of equiprobability for all specimens ($P<0.01$: SOKAL & ROHLF 1979) revealed no overlap between the groups considered (Fig. 8). The distance between ellipse centroids appears to be equidistant between all the forms. The large size of the Córdoba ellipse is due to the small sample considered here.

The correct classification of the holotype of *Microlophus spinulosus* and its relationship with the Chaco, Paraguay and Córdoba groups, were the purpose of additional numerical research, using the same classification equations leading to the above mentioned high percentage of correct classification (95.6%). The result shows that the COPE's type does not belong to the wet mesic Paraguayan localities of our subspecies *T. spinulosus guarani*. It is probably a specimen from some population of Paraguayan Chaco which does not reach the normal species mean for most of its morphometric parameters. It could be a somewhat atypical individual lying outside the equiprobability ellipses set at the $P<0.001$ level: if so, its classification could fall

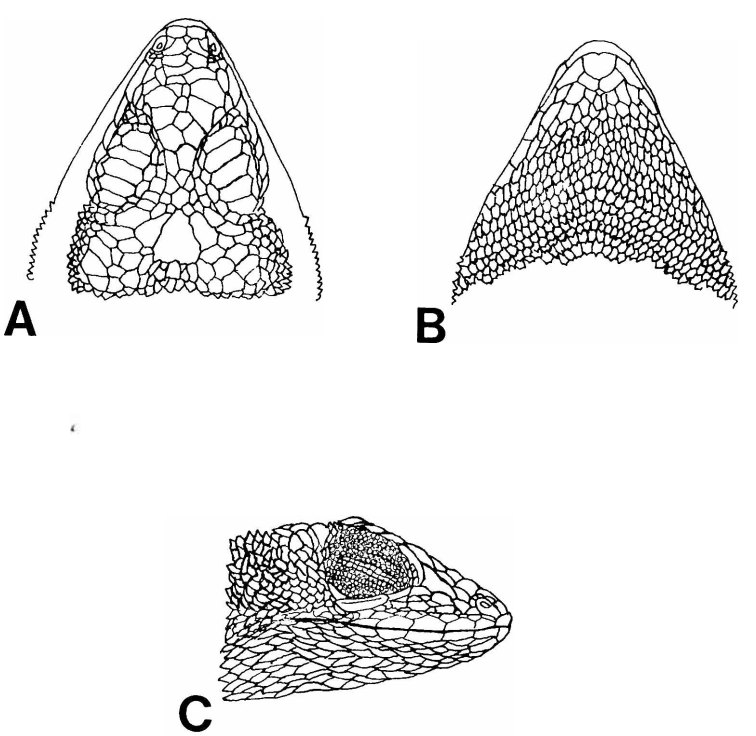


Fig. 2. — Cephalic lepidosis (dorsal, ventral, lateral) of: A-C, *Tropidurus spinulosus spinulosus* from Taco Pozo, Departamento A. Brown, province of Chaco, Argentina; D-F, *T. spinulosus guarani*, holotype, from Paraguarí, near Asunción, Paraguay. (Different magnifications; *pr*, postrostral; *in*, internasal; *ip*, interparietal).

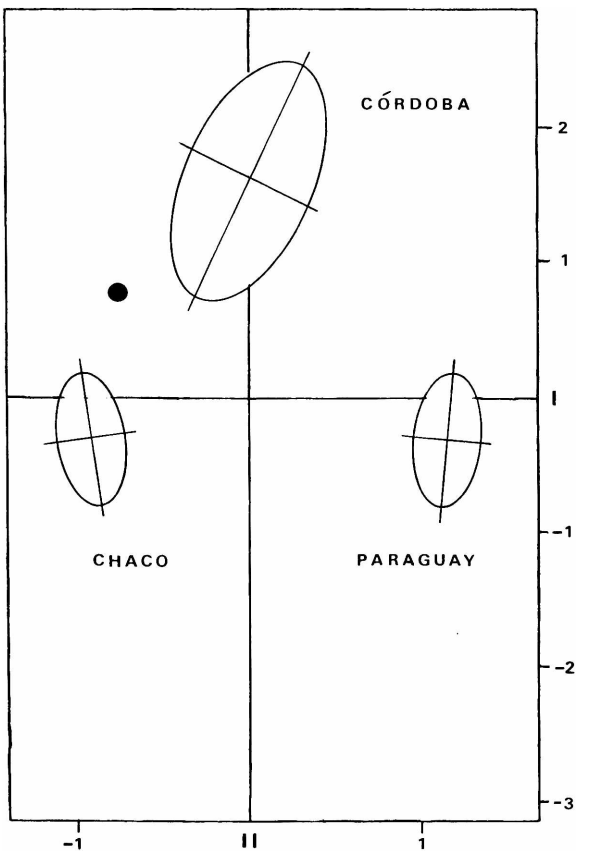


Fig. 8. — Ellipses of equiprobability for all the cases ($P<0.01$). Black dot indicates the intermediate position shown by the holotype of *Microlophus spinulosus* between the ellipses of equiprobability for the Chaco and Córdoba populations.

within an error range of 1%. However, its intermediate position between the Córdoba and Chaco population ellipses of equiprobability (Fig. 8) could be interpreted as the effect of the small sized sample of the Córdoba group. Also the age and prolonged conservation of the type must be taken into account. The need for a more intensive research on relationships between the Córdoba and Chacoan populations must again be emphasized.

Conclusions from che discriminant analysis:

(1) the Paraguay group (or *T. spinulosus guarani*) is characterized by its minor body size and major expression in scale number;

(2) the Chaco group (or the nominate form) shows minor expression in all variables of scale number;

(3) the Córdoba group (or a local population of the nominate form) is a form of great body size but of intermediate expression in scale number;

(4) the holotype of *M. spinulosus* does not belong to the Paraguay group, lying at a somewhat intermediate position between the larger Chaco and Córdoba groups.

GENERAL CONCLUSIONS

Our former critical discussion of a new subspecies of *Tropidurus spinulosus*, named *guarani*, and its morphological relationships with the nominate form, is in agreement with the general results of the discriminant analysis of some of their variables, primarily identified by a previous Analysis of Principal Components (BMDP 4M-Factor Analysis), and corresponding to variables for phenotypic characters used in our above mentioned discussion.

Significant differences for several characters (continuous and discontinuous variables) support a high degree of evolutionary divergence between the Chacoan populations from a very arid, xerophilous environment, and the southern Paraguayan populations, from a wet mesophilous area, alongside the Paraguay River. The apparent continuing condition of allopatry for both Chacoan and Paraguayan populations (Fig. 1) was pointed out, as well as the absence of available kinds of information concerning either a possible intergradation, or indications of ecological and/or physiographic isolation, making gene flow difficult between the recognized taxa. We prefer, therefore, for the moment, not to propose a specific status for the Paraguayan form, but to identify it at a subspecific level, having in mind the operative and pragmatic concept of the subspecies, sufficiently debated since MAYR's time (1963). In fact, the category and combination of characters supporting our new taxon, could justify postulation of a specific status for the southern Paraguayan populations; a further taxonomic step, which could be easily tenable, when other comparative morphological argumentations, mainly osteological, are available, joined to a wider information about ecophysiology, strategy of alimentation, behaviour, reproductive cycle and modes, etc.

We will recall the obvious difficulty associated with clarifying the reciprocal distribution of these taxa in such an extensive and poorly known regions as the northern and north-eastern Paraguayan Chacoan borders, as well as the wet riparian environments along the Paraguay River. However, in spite of this difficulty, general morpho-ecological trends of *T. spinulosus spinulosus* stress its full physiognomy of a specialized tropidurine lizard, adaptive to xerophilous ecosystems, a seasonally very differentiated climate and remarkable thermo-hygrometric variations. All these bioclimatic parameters fit the natural environment of its Chacoan home and its ecological habits: they are opposed to the more climatically equable habitat of *T. spinulosus guarani* through its southern Paraguayan distribution.

Thus, among the *Tropidurus* species groups, there can, as yet, be only a suggestive hypothesis about the evolutionary process leading to the present step of speciation in the *spinulosus* species group. As in other similar cases, in the same genus (RODRIGUES 1987), it should be remembered as a discriminant factor the quaternary, glacial-interglacial climatic fluctuations, acting as relative filter on the distribution of the most favoured genetic lines for open, arid or subarid environments. A general parallelism between the present distribution pattern of *T. spinulosus spinulosus* and that of *T. etheridgei*, or other xerophilous forms of the *torquatus* group (RODRIGUES 1981, 1984, 1987), seems to provide a convincing answer to this question. The model of probable mechanisms of eco-geographic speciation proposed by VANZOLINI & WILLIAMS (1981), may be of interest for the postulated origin of these taxa, peculiarly related to the arid continental biomass.

The mountain populations of Córdoba, to which further research will be devoted, are probably only a geographically isolated and a morphologically adaptive form of *T. spinulosus*. The present wide distribution of the nominate Chacoan form surrounds southwards and eastwards the Sierras de Córdoba. But, in not too distant geological times, great natural barriers, likely from the beginning of the Holocene, must have been an obstacle making gene flow difficult between the rock inhabitant tropidurine population of the sierras and the widespread and ecologically more opportunistic populations from the Chacoan flats. Such a barrier is still present, with the almost azoic Salinas Grandes or Ambargasta salt flats, westwards with the Salinas San Bernardo and other salt flats on La Rioja borders. Meristic differences in some characters of the mountain tropidurine dwellers in the Sierras de Córdoba, may be, therefore, a natural adaptive answer to a distinct ecological territory, such as ravines, rocks and their crevices, as well as the effect of the well known "genetic drift" in isolated populations, submitted to demic restrictions and to continued selection.

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We are specially grateful to Drs R. Heyer, G. Zug and R. Crombie, from the Smithsonian Institution, Washington, for their substantial assistance in providing an invaluable documentary information on type specimens of the National Museum of Natural History, in their care.

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ADDENDUM

By courtesy of Prof. Wolfgang Böhme, it was also possible to check the provenance of several specimens of *Tropidurus spinulosus* from Paraguay and Bolivia deposited in the collections of the A. Koenig Museum, Bonn, Germany. The northernmost locality for these specimens is Villa Montes, Bolivia, about 21°10'S latitude. The specimens from Paraguay were mostly collected from Filadelfia and Boqueron, in localities characteristic of the xerophilous Chacoan wood habitat, thus within the range of the nominate form of the species. On the contrary, the few specimens from San Bernardino (SE Asunción, near Paraguarí) should be compared with specimens of the new form described to establish their taxonomic identity.

ERRATA CORRIGE

Due to a typographical error the legend for Fig. 2 was erroneously inserted under Fig. 7 on page 175 of Vol. 7, No. 1, 1994.

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and "ventral scale rows" ($P<0.001$). Comparing Córdoba versus Chaco a major expression for "midbody scales" ($P<0.001$), "paravertebral scales" ($P<0.01$), "gular scales between tympani" ($P<0.001$) and "scales between axillas" ($P<0.01$) is apparent for the former group.

Discriminant analysis of individual specimens resulted in a very high percentage of correct classification (95.6%). Ellipses of equiprobability for all specimens ($P<0.01$: SOKAL & ROHLF 1979) revealed no overlap between the groups considered (Fig. 8). The distance between ellipse centroids appears to be equidistant between all the forms. The large size of the Córdoba ellipse is due to the small sample considered here.

The correct classification of the holotype of *Microlophus spinulosus* and its relationship with the Chaco, Paraguay and Córdoba groups, were the purpose of additional numerical research, using the same classification equations leading to the above mentioned high percentage of correct classification (95.6%). The result shows that the COPE's type does not belong to the wet mesic Paraguayan localities of our subspecies *T. spinulosus guarani*. It is probably a specimen from some population of Paraguayan Chaco which does not reach the normal species mean for most of its morphometric parameters. It could be a somewhat atypical individual lying outside the equiprobability ellipses set at the $P<0.001$ level: if so, its classification could fall

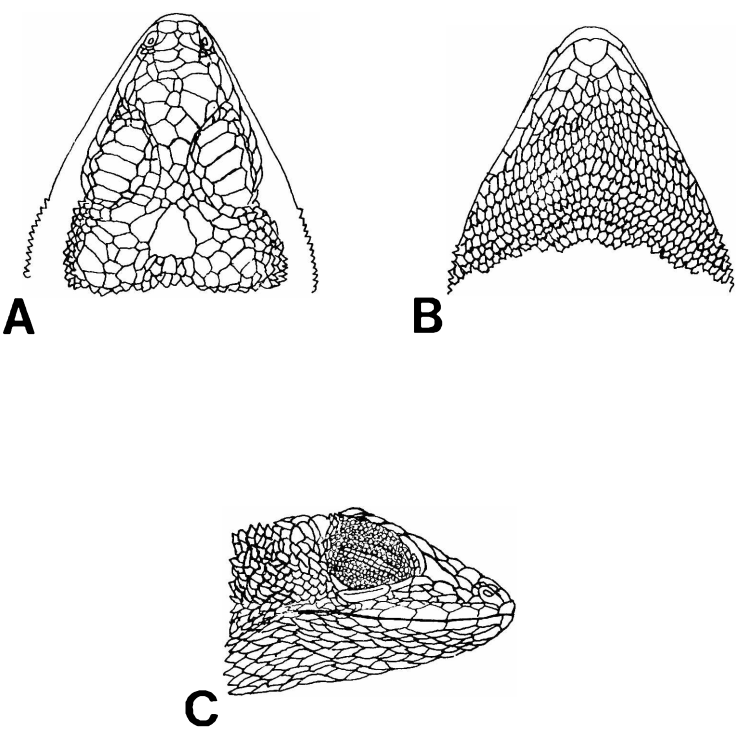

Fig. 7. — Cephalic lepidosis (dorsal, ventral and lateral) in a specimen of *Tropidurus spinulosus* from Tanti, Sierras de Córdoba, 1000 m, Argentina. A remarkable similarity with lepidosis of the Chacoan specimens is shown (cf. Fig. 2A-C). (Moderate magnification).