

THE GENUS *STENOCERCUS* (SQUAMATA: TROPIDURIDAE) IN EXTRA-AMAZONIAN BRAZIL, WITH THE DESCRIPTION OF TWO NEW SPECIES

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ABSTRACT: The genus *Stenocercus* includes over 50 species, distributed mainly in elevated areas in the Andes and adjacent lowlands, with only a few taxa known to occur in Brazil. The easternmost populations of the genus are poorly studied and represented in collections. Herein we describe *Stenocercus quinarius* sp. n. from northwestern Minas Gerais and western Bahia states, and *Stenocercus squarrosus* sp. n. from the southern portion of the state of Piauí, two previously poorly sampled areas in central and northeastern Brazil. The two new species seem closely related to *Stenocercus dumerilii* and *Stenocercus tricristatus*, but are easily diagnosed from all *Stenocercus* and from each other based on morphometric and meristic characters. The distribution patterns and possible phylogenetic affinities of the easternmost, pyramidal headed *Stenocercus* group are discussed, along with an overview of distribution patterns of the genus in extra-amazonian open domains.

KEYWORDS: Squamata; Tropiduridae; *Stenocercus*; *Ophryoessoides*; Cerrado; Caatinga.

INTRODUCTION

The iguanid genus *Stenocercus* Duméril and Bibron, 1859 is a fairly heterogeneous assemblage composed of over 50 species, including lizards formerly allocated in *Proctotretus* Duméril and Bibron, 1867, *Ophryoessoides* Duméril, 1851 and *Leiocephalus* Gray, 1827 (Etheridge, 1966; Fritts, 1974; Cadle, 1991; Frost, 1992; Torres-Carvajal et al., 2006). Most species in the genus are restricted to elevated areas in the Andes and adjacent lower areas (Fritts, 1974; Cadle, 1991; Torres-Carvajal, 2005), except for *Stenocercus fimbriatus* Ávila-Pires, 1995 and *S. roseiventris* Duméril, 1837, from western Amazonia (Ávila-Pires, 1995). *Stenocercus caducus* (Cope, 1862) and *Stenocercus sinesaccus* Torres-Carvajal, 2005 are from the Chaco and Cerrado regions. Finally, *Stenocercus azureus* (Müller, 1862), *Stenocercus dumerilii* (Steindachner, 1867) and *Stenocercus tricristatus* (Duméril, 1851) are distributed sparsely on the eastern portion of the continent, from east of Belém to southern Brazil.

Stenocercus dumerilii and *Stenocercus tricristatus*, described in the genus *Ophryoessoides*, share combined morphological features (three or five dorsal crests, enlarged post-supraciliary scale, head blunt, pyramidal, bordered by supraciliary crests) unseen in the remainder of the genus (see Duméril, 1851 and

discussions in Ávila-Pires, 1995). *Ophryoessoides tricristatus* Duméril, 1851, the type species of the genus *Ophryoessoides*, is still known from a single specimen collected in an uncertain locality in Minas Gerais state, southeastern Brazil (Ávila-Pires, 1995). A closely related species, *Ophryoessoides dumerilii* Steindachner 1867, was later described based on a single specimen from Pará, Brazil (Cunha, 1981; Ávila-Pires, 1995). Boulenger (1885) included *O. tricristatus* in *Leiocephalus* Gray, 1827, an arrangement that persisted until Etheridge (1966), studying the species at the time allocated in *Leiocephalus*, revalidated *Ophryoessoides* for 17 South American species. He admitted a close relationship between *Ophryoessoides* and *Stenocercus*, emphasizing that some species referred to *Stenocercus* could be transferred to *Ophryoessoides*. He subsequently listed *O. dumerilii* as a junior synonym of *O. tricristatus* (Etheridge, in Peters & Orejas-Miranda, 1970), without further comments. Fritts (1974) maintained the genus *Ophryoessoides* for *tricristatus* and five other species (*aculeatus*, *caducus*, *erythrogaster*, *iridescens*, and *scapularis*) with enlarged head scales, keeled ventral scales, and the condition of inscriptional ribs. Later, due to the lack of decisive sinapomorphies for both *Ophryoessoides* and *Proctotretus*, Frost (1992) included these two genera in *Stenocercus*, the oldest available generic name.

This conservative approach is still accepted until more extensive data are available on variation and systematic relationships within the group, including its poorly sampled, easternmost extra-andean forms (Cadle, 1991; Ávila-Pires, 1995).

Recently, Torres-Carvajal et al. (2006), based on a large taxon sampling (32 of the 54 presently admitted species) performed a phylogenetic analysis of *Stenocercus* using mtDNA sequence data. Their results indicate that *Proctotretus* and *Ophryoessoides* (sensu Fritts) are deeply nested in *Stenocercus*. They also recognize several clades in *Stenocercus*, although the eastern forms *Ophryoessoides tricristatus*, the type species of the genus, and *S. dumerillii*, two of the most morphologically distinct species of *Stenocercus*, were not included in the analysis.

The best available account on variation, geographic distribution and natural history of eastern *Stenocercus* was provided by Cunha (1981). He obtained and studied a large series of *Stenocercus dumerillii*, at the time considered under *Ophryoessoides tricristatus*, its senior synonym. Unaware of the distinctiveness between *Ophryoessoides tricristatus* and *O. dumerillii* he restricted the type locality of *O. tricristatus* to the surroundings of Belém, Pará. It was only recently, after the examination of the type specimen of *S. tricristatus*, that Ávila-Pires (1995) resurrected *Stenocercus (Ophryoessoides) dumerillii* from the synonymy of *S. tricristatus*, and restricted the type locality of *S. tricristatus* to an unprecise locality in the state of Minas Gerais, South-central Brazil.

Up to now, *Stenocercus dumerillii* and *S. tricristatus* were the only *Stenocercus* characterized by a pyramidal head with a distinctive and straight canthal ridge continuous with the superciliary series and ending posteriorly in a prominent and enlarged post-supraciliary. Herein we describe two new species of *Stenocercus* that share these features with *S. dumerillii* and *S. tricristatus*. We describe these two new taxa, collected recently in previously unsampled Cerrado and Caatinga areas of central and northeastern Brazil, as an attempt to improve the available knowledge on the poorly known extra-andean populations of *Stenocercini* (sensu Frost, 1992). We compare the new taxa to other components of *Stenocercus*, providing the first account on diversity and distribution in the genus in eastern South America and along the diagonal belt of open formations (sensu Vanzolini, 1988).

MATERIALS AND METHODS

For standardization purposes, species characterization was adapted from Cadle (1991), including number of internasals (counted immediately posterior to postrostrals), number of gular scales (between ventral edges of ear-openings) and number of supraoculars (in a transverse line across the greatest width of the left orbit). Description and other meristic characters follows Ávila-Pires (1995), except for the number of longitudinal caudal rows which is added here. All measurements were taken with an electronic caliper to the level of 0.1 mm, except snout-vent length (SVL) and tail length (TL), taken with a ruler to the nearest millimeter. Head length was measured from the snout tip to the anterior border of the ear-opening; head width at the widest point of the head; head height at highest mid-dorsal point; and limb length from axil/groin to tip of claw of longest digit. Infradigital lamellae were counted on the left side. Museum acronyms are according to Leviton et al. (1985), with CHUNB referring to Coleção Herpetológica da Universidade de Brasília.

Due to their shared characteristics (see Ávila-Pires, 1995), we compared the two new species to *S. tricristatus* and *S. dumerillii*, the two known species described in *Ophryoessoides*. We obtained data for *S. tricristatus* in Boulenger (1851) and Ávila-Pires (1995) and for *S. dumerillii* in Cunha (1981) and Ávila-Pires (1995). To provide an overview of distribution of the genus in Brazil we also analysed specimens of *Stenocercus caducus*, *Stenocercus sinesaccus* and *Stenocercus azureus*, other members of the genus occurring in extra-amazonian open domains, according to the Brazilian vegetation map (IBGE, 1993) and the map of Neotropical terrestrial ecoregions (Olson et al., 2001).

We analysed 11 meristic characters (midbody scales, transversal dorsals, laterals, transversal and longitudinal ventrals, number of vertebrae, gulars, toe and finger lamellae, longitudinal caudal rows, number of postrostrals and internasals) in a detailed comparison with *S. dumerillii*. We used these characters in a stepwise discriminant analysis, ($\mu = 0,05$; missing values replaced by means) in SPSS (SPSS, 2003), in order to detect the most powerful meristic variables for diagnosing the three taxa. In order to investigate meristic differences, these variables were used to produce canonical discriminant functions. These functions were tested as

predictors of specific identity with error-rate estimates based on crossvalidation. We used in these comparisons 15 specimens of *S. dumerilii* from MPEG and MZUSP (Appendix I), and all available individuals of the two new species.

RESULTS

The genus *Stenocercus* is represented in Brazil by at least eight species. *Stenocercus roseiventris* and *Stenocercus fimbriatus* occur in western Amazonia (Avila-Pires, 1995; Torres-Carbajal, 2005), and were studied in detail in Avila-Pires (1995). During the compilation of data from specimens obtained in recent field collections and analysis of museum specimens for Cerrado Squamate Reptiles (see partial results in Nogueira, 2006), we obtained the first documented records of *Stenocercus caducus* for Brazil, as well as new records for *Stenocercus dumerilii* and *Stenocercus sinesaccus* in central Brazilian savannas. We also examined specimens and mapped the available records of *Stenocercus azureus* from south-southeastern Brazil, and detected two new species from central and northeastern Brazil, in previously unsampled Cerrado and Cerrado/Caatinga contact areas.

According to a combination of shared morphological characters, the two new taxa seem closely allied to *S. tricristatus* and *S. dumerilii* (see discussions in Ávila-Pires, 1995). However, the two new species differ from each other and from these two closely relat-

ed taxa in morphometric and qualitative morphological characters (Table 1).

Moreover, meristic characters clearly distinguish the two new species from each other and from *S. dumerilii* (Fig. 1). A stepwise discriminant analysis selected six meristic characters as the most powerful discriminators of the three taxa (Table 2), and these were used in a canonical discriminant function analysis. The first two canonical discriminant functions explained 100% of the meristic variation (Table 3). According to posterior error rates in cross-validation, the two canonical variables correctly classified 100% of the specimens (Table 3).

The first canonical function promoted a clear separation of the three taxa (Fig. 1), and represents primarily a contrast between longitudinal caudal rows (positive coefficient) and internasals (negative coefficient). *Stenocercus squarrosus* sp. nov., with lowest, negative means on the first canonical variable, presents lowest numbers of caudal rows and highest numbers of internasals; in the other extreme is *S. dumerilii*, with the highest numbers of caudal rows and lowest number of internasals and transversal dorsal rows. *Stenocercus quinarius* sp. nov. shows intermediate values. The second canonical function primarily represents a contrast between number of longitudinal ventrals (positive coefficient) and fourth toe lamellae (negative coefficient), and separated *Stenocercus quinarius* sp. nov., with lowest numbers of fourth toe lamellae and highest numbers longitudinal ventrals, from the remaining two taxa.

Table 1. Comparison of morphometric and qualitative characters in species of *Stenocercus* sharing enlarged post-supraciliary scales and pyramidal head.

	<i>Stenocercus quinarius</i> sp. nov.	<i>Stenocercus squarrosus</i> sp. nov.	<i>Stenocercus dumerilii</i>	<i>Stenocercus tricristatus</i>
SVL in adult males	65-75 mm	76-88 mm	84-104 mm	60 mm
Tail shape	Depressed near base, rounded distally, tapering towards end	Depressed, blunt and thick towards end	Depressed near base, rounded distally, tapering towards end	Compressed near base, rounded distally, tapering towards end
Tail length / SVL	1.0-1.1	0.8-0.9	1.2 – 1.4	1.7
Body shape	Slightly depressed	Strongly depressed	Slightly depressed	Slightly compressed
Post-supraciliaries	pointed	pointed	pointed	blunt
Scales on chin	Smaller than gulars	Smaller than gulars	Smaller than gulars	Rather similar to gulars
Vertebral crest	Low	Prominent, serrated	Low	Prominent, serrated
Paravertebral crests	Low	Prominent, serrated	Low	Prominent, serrated
Lateral crests	Low	Prominent, serrated	Low, sometimes inconspicuous	Absent/ inconspicuous
Color pattern	Uniform or dark dorsal bands	Dark dorsal bands or uniform	Dark dorsal bands or uniform	Dorsolateral dark bands with light borders

Species Accounts

Stenocercus quinarius sp. nov.

(Figs. 2 and 3)

Holotype - MZUSP 94069, field number CN 593, adult male, collected on 31 October 2001 by C. Nogueira and F. França in a pitfall trap located in 15°15'13"S; 45°53'20"W, Parque Nacional Grande Sertão Veredas, municipality of Formoso, state of Minas Gerais (Figure 4).

Paratypes - MZUSP 94068, adult male, collected on 22 October 2001 by C. Nogueira and F. França in a pitfall trap located in 15°20'38"S; 45°57'01"W, Parque Nacional Grande Sertão Veredas, municipality of Formoso, state of Minas Gerais. CHUNB 33967, female, collected by P. H. Valdujo and G. Costa on 5 November 2003, Lagoa do Triste, Parque Estadual de Serra das Araras (15°30'38"S; 45°23'01"W), Serra das Araras, Minas Gerais. CHUNB 37266-268, females, collected by P. H. Valdujo, M. G. Zatz and M. B. Lion, on 14-20 May 2004 in RPPN Arara Vermelha (15°27'20"S; 45°48'35"W), Arinos, Minas Gerais. CHUNB 11208-211, one female, 3 juv. collected by F. H. G. Rodrigues in October 1992. CHUNB 24154, 24156, 2 males, collected by A. F. B. Araújo in October 1993, all from Fazenda Jatobá (13°56'15"S; 45°56'15"W), Correntina, Bahia.

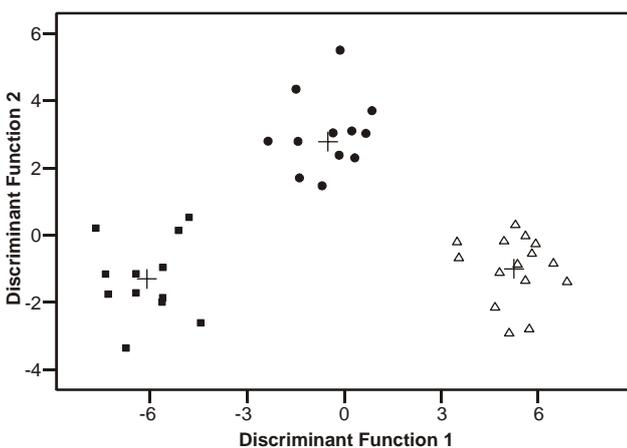


Figure 1. Canonical Discriminant Analysis according to six meristic characters selected as the most powerful discriminators of the three taxa (see Table 2). Squares: *Stenocercus squarrosus* sp. nov.; circles: *Stenocercus quinarius* sp. nov.; triangles: *Stenocercus dumerilii*; crosses: centroids for each species. According to posterior error rates in cross-validation, the two canonical variables correctly classified 100% of the specimens.

Characterization - *Stenocercus quinarius* sp. nov. is characterized by the following combination of features (adapted from Cadle, 1991): (1) Dorsal head scales keeled. (2) Interparietal distinct, moderately enlarged, followed by a pair and a triad of moderately enlarged scales that reach the occipital region. (3) Internasals 3-6, mostly five. (4) No distinctly enlarged supraoculars. (5) An enlarged canthal at each side, continuous with supraciliary series and in anterior contact with two elongate smaller scales, forming a double canthal ridge. (6) An enlarged, prominent, pointed scale immediately posterior to supraciliaries; no projecting, blade-like, angulate temporal scales. (7) Gulars and ventrals distinctly keeled. (8) Parietal eye distinct. (9) Neck folds absent. (10) Dorsals phylloid, keeled, imbricate, generally with a small mucron; lateral scales similar to dorsals. (11) A low vertebral crest, and at each side a pair of low but distinct dorsolateral and a pair of lateral crests. (12) Mite pockets absent. (13) Scales on posterior surface of thighs imbricate, keeled. (14) Tail moderately short, depressed near the base, rounded and tapering from mid section to the end. (15) Dorsal coloration uniform, less frequently with narrow dark brown dorsal bands on back (common in juveniles), with a distinctive dark blotch above forelimbs, no sexual dimorphism in color pattern. (16) Scales around midbody 47-56, (17) Maximum SVL 90 mm. (18) preauricular fringe present. (19) vertebrales 23-29. (20) paravertebrals 36-46. (21) scales around midbody 47-56. (22). Lamellae on finger IV 14-16. (23) Lamellae on toe IV 16-19. Variation in type series summarized in Table 4.

Diagnosis - *Stenocercus quinarius* sp. nov. is distinguished from all other *Stenocercus*, except *S. tricoloratus* and *S. dumerilii*, by the presence of the following characters (adapted from Ávila-Pires, 1995): head pyramidal, enlarged prominent post-supraciliary scales

Table 2. Significant meristic variables in stepwise discriminant analysis of the two new species and *Stenocercus dumerilii*.

Step	Meristic character	Exact F	Wilks' Lambda	P
1	Longitudinal caudal scales	211.889	0.076	<0.001
2	Fourth toe lamellae	62.609	0.046	<0.001
3	Internasals	60.720	0.024	<0.001
4	Longitudinal ventrals	59.005	0.014	<0.001
5	Transverse laterals	53.043	0.011	<0.001
6	Transverse dorsals	48.441	0.009	<0.001

Table 3. Results of Canonical Discriminant Analysis of meristic characters in three species of *Stenocercus*.

Canonical function	Eigenvalue	% of Variance	Cumulative %	r ²
1	24.741	87.8	87.8	0.980
2	3.438	12.2	100.0	0.880

Meristic character	Standardized canonical coefficients	
	Canonical Function 1	Canonical Function 2
Internasals	-0.692	0.728
Longitudinal ventrals	-0.191	0.792
Longitudinal caudals	0.967	0.557
Toe lamellae	0.360	-1.244
Dorsals	-0.493	-0.100
Laterals	0.551	0.365

Species	Means of raw canonical coefficients	
	Canonical Function 1	Canonical Function 2
<i>Stenocercus dumerilii</i>	5.267	-1.000
<i>Stenocercus quinarius</i> sp. nov.	-0.527	2.781
<i>Stenocercus squarrosus</i> sp. nov.	-6.101	-1.299

continuous to a distinct crest formed by supraciliaries and canthals. Supraoculars not enlarged. One elongate subocular. Interparietal small, parietal eye distinct. Gular or neck folds absent, sides of neck with large, imbricate scales. Vertebral and dorsolateral crests present.

Dorsals, laterals and ventrals relatively large, imbricate, keeled, sometimes mucronate. Mite pockets absent.

From *S. tricristatus* (characters in parentheses) it is distinguished by having a shorter tail, 1.0-1.1 times



Figure 2. Holotype (MZUSP 94069) of *Stenocercus quinarius* sp. nov. in life. Grande Sertão Veredas National Park, central Brazil.

Table 4. Morphometric and meristic variation in the type series of *Stenocercus quinarius* sp. nov. and *S. squarrosus* sp. nov.. DB = Dorsal Bands (presence/absence); SVL = Snout-vent length; TL = Tail length, HW = Head width; HL = Head length; HH = Head height; AL = Arm length; LL = Leg length; MB = Scales around midbody; TV = Transverse ventral rows; TrD = Transverse dorsal rows; TrL = transverse lateral rows; VeC = scales in vertebral crest; LoV = scales in longitudinal ventrals; TLa = 4th toe lamellae; Fla = 4th finger lamellae; Lca = longitudinal caudal rows; Int = internasals. All measurements in mm. * Holotypes.

Voucher#	species	Sex	DB	SVL	TL	HW	HL	HH	AL	LL	MB	TV	TrD	TrL	VeC	LoV	TLa	Fla	Lca	Int
CHUNB 11208	<i>S. quinarius</i>	j	p	34	34	8,2	9,8	12,0	15,0	21,0	51	26	13	12	26	33	18	15	56	4
CHUNB 11209	<i>S. quinarius</i>	j	p	34	33	8,9	10,4	6,1	12,0	19,0	55	29	14	12	24	30	17	14	59	4
CHUNB 11210	<i>S. quinarius</i>	j	p	40	40	9,3	11,4	6,4	18,0	24,0	54	29	15	10	25	31	18	15	59	5
CHUNB 11211	<i>S. quinarius</i>	f	a	74	75	16,5	19,7	12,7	32,0	40,0	55	30	14	11	27	31	17	14	59	5
CHUNB 24154	<i>S. quinarius</i>	m	a	75	79	17,1	19,6	12,3	32,0	41,0	48	27	13	8	25	32	18	15	62	4
CHUNB 24156	<i>S. quinarius</i>	m	a	69	75	15,0	18,2	11,9	29,0	41,0	51	27	13	11	26	31	19	15	56	5
CHUNB 33967	<i>S. quinarius</i>	f	a	90	95	19,1	23,3	15,5	39,0	47,0	55	30	13	12	30	30	18	14	61	5
CHUNB 37266	<i>S. quinarius</i>	f	a	83	88	18,2	20,4	13,9	35,0	42,0	54	30	13	11	27	35	18	14	58	3
CHUNB 37267	<i>S. quinarius</i>	f	a	75	81	18,6	20,0	13,0	34,0	43,0	48	25	13	10	24	30	19	16	59	5
CHUNB 37268	<i>S. quinarius</i>	f	p	77	cm	18,3	20,1	12,2	33,0	43,0	56	30	13	13	27	34	18	14	cm	5
MZUSP 94068	<i>S. quinarius</i>	m	a	65	72	14,5	17,7	10,2	29,0	35,0	47	25	13	9	25	30	16	15	60	3
MZUSP 94069*	<i>S. quinarius</i>	m	a	70	76	15,7	18,5	11,7	28,0	36,0	50	27	13	10	24	33	19	16	58	5
MZUSP 94066	<i>S. squarrosus</i>	f	a	88	69	17,7	21,2	11,5	35,0	43,0	48	27	13	8	25	32	18	13	43	4
MZUSP 94067	<i>S. squarrosus</i>	f	p	79	69	17,0	21,3	12,1	35,0	40,0	47	25	13	9	23	29	19	14	47	5
MZUSP 94056*	<i>S. squarrosus</i>	m	a	88	75	18,4	21,5	13,1	34,0	44,0	53	31	15	10	27	31	20	14	49	4
MZUSP 94057	<i>S. squarrosus</i>	f	p	82	66	17,0	20,9	11,8	34,0	41,0	49	26	14	9	24	33	20	14	47	5
MZUSP 94058	<i>S. squarrosus</i>	jm	p	62	52	14,0	17,0	10,2	28,0	32,0	46	25	13	8	22	28	17	14	47	4
MZUSP 94059	<i>S. squarrosus</i>	f	p	86	75	17,0	20,4	17,2	35,0	41,0	49	28	13	8	25	33	20	14	49	5
MZUSP 94060	<i>S. squarrosus</i>	jm	p	53	49	11,4	14,9	9,3	22,0	30,0	50	27	13	10	23	30	18	14	42	5
MZUSP 94061	<i>S. squarrosus</i>	m	p	76	68	16,5	20,5	17,5	32,0	39,0	47	26	13	8	24	30	20	14	45	5
MZUSP 94062	<i>S. squarrosus</i>	jm	p	61	56	14,3	16,5	10,0	26,0	32,0	50	27	13	10	24	30	18	15	48	5
MZUSP 94063	<i>S. squarrosus</i>	jm	p	51	48	11,7	14,3	7,8	25,0	31,0	53	28	15	10	24	34	19	14	45	5
MZUSP 94064	<i>S. squarrosus</i>	f	a	82	67	16,9	21,5	12,8	34,0	41,0	49	26	14	9	26	30	18	15	52	5
MZUSP 94065	<i>S. squarrosus</i>	jf	m	55	45	11,8	15,6	9,1	24,0	31,0	53	29	15	9	25	29	16	13	45	3

SVL (1.7 times SVL), 47-56 midbody scales (33), 11-14 scales from one dorsolateral crest to the other (8), five low dorsolateral crests: one vertebral, two dorsolateral and two lateral (only three conspicuous crests, lateral crests undistinguishable), body depressed (body laterally compressed), tail depressed near the base (compressed near the base), and uniform color pattern (banded color pattern).

From *S. dumerilii* (characters in parentheses, from Ávila-Pires, 1995 and 15 examined specimens) it differs by having 47-56 midbody scales (41-50); shorter tail, 1.0-1.1 times SVL (1.2-1.4); 3-6, mostly five, in-

ternasals (2-3); rostral roughly twice as wide as high (approximately four times as wide as high); smaller adult size; dorsal scales keeled throughout the length of the scale (keel restricted to or more prominent on the distal part of dorsals); dorsals generally with a small mucron (most non-mucronate); 56-62 caudal scale rows (64-74); anterior canthal shorter than posterior (longer than posterior), adjacent to a strongly keeled first internasal, both scales forming a double canthal ridge (anterior part of canthal ridge restricted to anterior canthal, single canthal ridge); 16-19 lamellae under fourth toe (18-24).

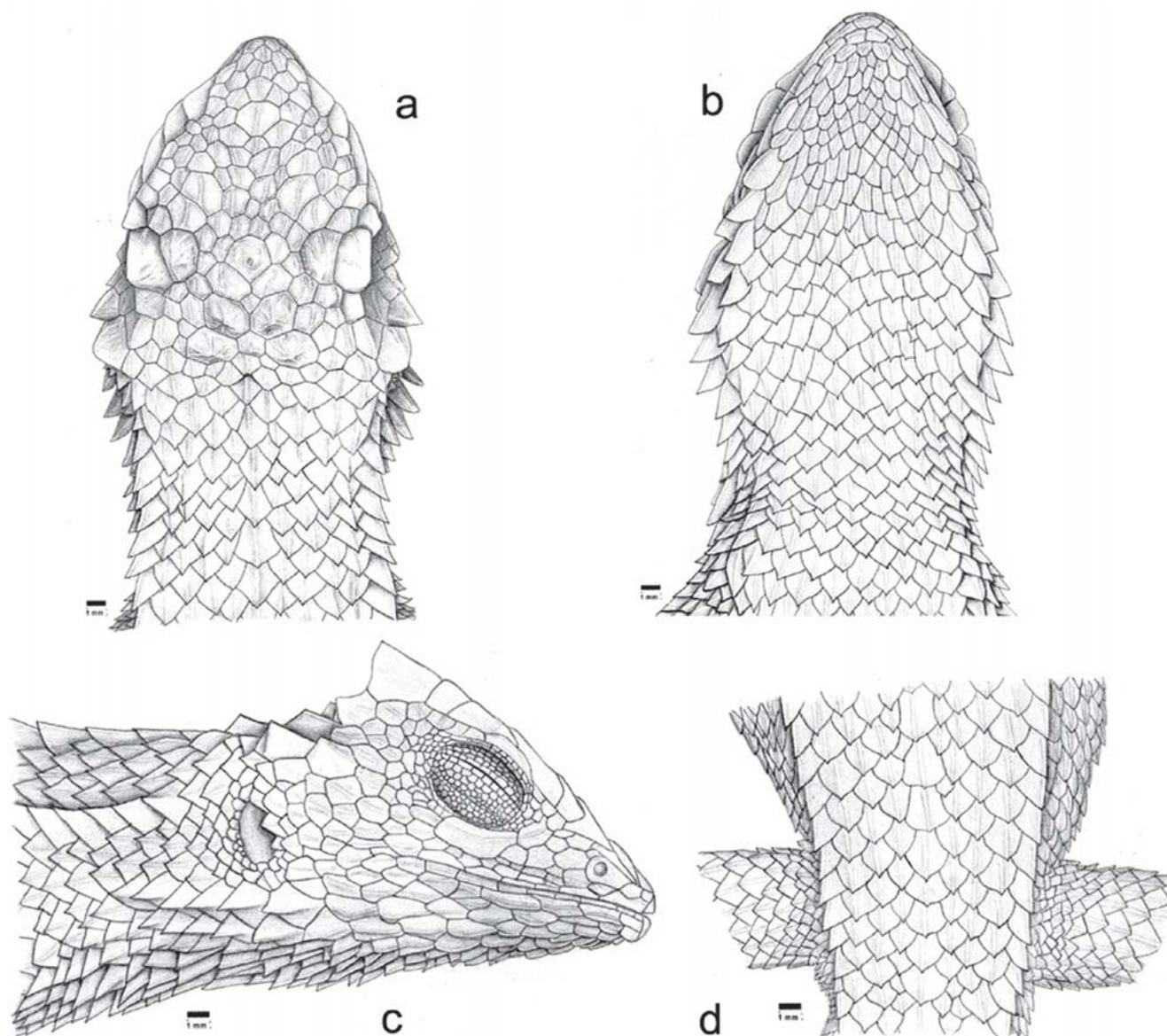


Figure 3. Holotype (MZUSP 94069) of *Stenocercus quinarius* sp. nov. A, Dorsal view of head; B, Ventral view of head; C, Lateral view of head; D, Dorsal view of posterior part of the body.

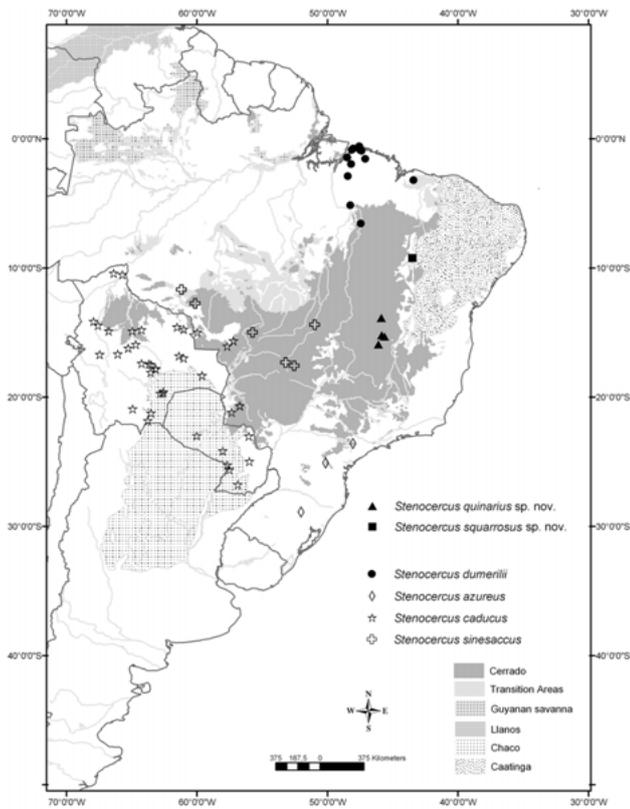


Figure 4. Distribution map of *Stenocercus* in extra-andean Neotropical open domains (cf. IBGE, 1993 and Olson *et al.* 2001).

Description of holotype - Adult male, 70 mm SVL. Head 0.3 times SVL, 1.2 times as long as wide, 1.3 times as wide as high. Snout bluntly pointed in dorsal view, pointed in profile. Canthus rostralis well defined, continuous with supraciliaries, which are followed posteriorly by a prominent, trihedral scale, giving the head the shape of a four-sided pyramid. In profile, the head shows an ascending line until the top of the prominent post-supraciliary scale, then a descending line toward neck. Neck slightly narrower than head and body. Body slightly depressed. Limbs developed, slender, forelimbs 0.4 times SVL, hind limbs 0.5 times. Tibia 0.2 times SVL, and 0.4 times length of hindlimb. Tail depressed at its base, round in cross-section from midpoint to tip, 1.1 times SVL.

Tongue wide, villose, with rounded, nicked tip. Teeth small, anterior conical, posterior slightly compressed with three small cusps.

Rostral semicircular, largest width about two times median height, barely visible from above. Four postrostrals. Snout, supraocular and interorbital regions forming a continuous, rather flat surface, covered with irregularly polygonal, and variable in size, subimbricate

to juxtaposed flat scales, with a distinct low keel. Five scales across snout between posterior canthals. Supraorbital semicircle and supraocular scales inconspicuous, scarcely differentiated from surrounding scales. Two canthals, anterior one not reaching the postrostrals, bordered dorsally by an elongate, keeled internasal, forming a double canthal ridge which imbricates with posterior canthal. Posterior canthal longer, continuous and imbricating with supraciliary series. Supraciliaries four, first two overlapping posteriorly, first shorter than second, which is the longest. Third shorter than first, overlapped anteriorly and posteriorly. Fourth shortest. In lateral view an additional median, elongate and internal superciliary scale is present. Canthals and supraciliaries form a distinct crest which ends in a very prominent pyramidal scale immediately posterior to supraciliaries. This crest delimits a sharp angle between dorsal and lateral surfaces of head. Interparietal moderately enlarged, in the shape of an asymmetric pentagon, parietal eye distinct. Two pairs of slightly enlarged, irregular in size, obliquely keeled scales following interparietal, and in broad contact at midline except for presence a small keeled scale indenting and partially separating them. The first smaller and contacting interparietal, the second much larger and with a sharper keel. These scales are followed by three transversely disposed enlarged scales on the posterior border of the head, of which the median is the smallest. Laterally to these post-interparietal enlarged scales, the scales are similar to those on snout, though slightly smaller.

Nasal below anterior canthal, lateral in position, large, undivided; nostril in posterior part of nasal, directed laterally. Loreal region with two rows of slightly keeled lorilabials, anteriorly and posteriorly single, medially double; between lorilabials and posterior canthal a few large irregularly polygonal, flat and keeled scales. Five scales in transverse row between posterior canthal and supralabials. One subocular, about three times as long as high, with a longitudinal keel close to its upper margin; followed by smaller, keeled scales to ear opening. Subocular separated from supralabials by lorilabials. Supralabials eight, narrow, anterior one smallest, seventh largest, below center of eye and followed to commissure of mouth by one small, keeled scale. Temporal region with irregularly polygonal, strongly keeled scales; five scales in an oblique row from lower posterior border of orbit to above ear opening, the two posterior ones distinctively enlarged,

trihedral. A supratemporal row of scales formed by the enlarged post-supraciliary scale, the enlarged scale above ear opening and two scales in between. Ear opening relatively large, vertically oval, anteriormost part covered by three slightly enlarged scales. Tympanum slightly recessed.

Mental small, not distinctively larger than adjacent infralabials; bordered posteriorly by two bulky, keeled scales and by two (one each side) elongate and keeled sublabials. Infralabials seven, elongate, strongly keeled; first smallest, posterior one largest, below posterior half of eye, followed by two scales to commissure of mouth. Three rows of elongated sublabials, with a right median keel, two of the rows continue until below ear opening, becoming progressively prominent, with distinctive keel and mucron. The lower rows continue past ear opening, ending as mucronate, projecting phylloid scales on the prehumeral region. Scales on chin anteriorly relatively small, elongate, subimbricate, posteriorly grading into gulars. Gulars larger than scales on chin and adjacent ventrals, strongly keeled and mucronate, in irregular longitudinal rows; no gular or lateral folds.

Scales on nape similar to dorsals, anteriormost ones smaller, followed by scales with a more prominent keel and mucron than midbody dorsals. A vertebral crest of enlarged, slightly prominent and sharply keeled scales extends from nape to first rows of caudal scales. Vertebral crest more prominent on anterior part of dorsum. A dorsolateral crest of scales, more prominent on its anterior third, extends from above ear opening to anteriormost part of tail. Scales on sides of neck similar to but smaller than dorsals, in two irregular longitudinal rows, limited ventrally by a row of larger prominent scales that follows the sublabial rows of scales. Dorsals phylloid, imbricate, more sharply keeled on anterior half of dorsum, where most scales bear a distinctive mucron. Twelve transverse rows of dorsal scales at midbody, between dorsolateral crests (included). Twenty six vertebral scales from occiput to base of tail. Flanks with similar but distinctively smaller scales, and with another median crest extending from just behind the insertion of forelimbs to near groin. Ventrals subequal, smaller than dorsals, identical to flank scales situated below crest. Ventral scales with irregular edges due to minute spiny projections, two or three on each side of the median keel. Thirty irregularly longitudinal and oblique rows of ventral scales between anterior level of forelimbs and anterior level of hind limbs. Forty five scales around midbody. Scales on

preanal plate in irregular transverse rows, mite pockets absent.

Scales on dorsal part of tail similar to dorsals, phylloid, flat, keeled, anteriormost ones bearing a short mucron, distal ones smaller. On ventral surface similar but with more prominent keels, forming longitudinal ridges. No distinct verticils.

Limbs with phylloid, imbricate, strongly keeled and mucronate scales, smaller than dorsals. The keels form distinct ridges on dorsal, anterior and posterior aspect of limbs. Subdigital lamellae single, tricarinate, 16 under fourth finger and 19 under fourth toe.

Color in life – Dorsal ground color uniform light brown, dorsal part of head same color as dorsum. Gular and ventral region slightly lighter, uniform light cream. Tail region with slightly darker flecks of light tan, alternating with shaded greyish areas, lighter ventrally. A distinct horizontally elongated black spot just above and anterior to insertion of forelimbs (see Figure 2).

Color in preservative – Dorsal ground colour slightly faded, uniform light cream with an horizontally elongated black spot just above and anterior to insertion of forelimbs. Ventral surfaces straw cream, immaculate. Dorsal pattern on tail slightly less conspicuous, greyish areas faded to light brown.

Distribution and ecology – Known from a relatively restricted area (Fig. 4), located in the core area of the Cerrado morphoclimatic domain (Ab'Saber, 1977). All records are from northwestern Minas Gerais and southwestern Bahia states (Fig. 4), in elevated (800–1200 m), gently-rolling plateaus of the “Serra Geral de Goiás” or “Chapadão Ocidental da Bahia” (RADAM-BRASIL, 1982).

Most specimens collected in a dense form of Cerrado with some Caatinga floristic elements, locally known as *carrasco*, with a well-developed arboreal stratum forming a nearly closed canopy of 5–6 m, a poorly developed scrub layer and an absent ground stratum, replaced by a sparse layer of leaf-litter, covering quartzitic, sandy soils. A few specimens were also collected in typical Cerrado savannas (cerrado *sensu stricto*, cf. Eiten, 1972). In Grande Sertão Veredas National Park region, the new species is not abundant, being sympatric with at least 25 other lizard species, including the dominant species *Tropidurus oreadicus*, *Vanzosaura rubricauda* and *Cnemidophorus ocel-*

lifer, from more open, Cerrado grasslands and savannas.

Etymology - *quinarius*, from the Latin “pertaining to five”, in allusion to the five well-marked crests along the body.

Stenocercus squarrosus sp. nov.
(Figs. 5 and 6)

Holotype - MZUSP 94056, field number MRT 08106, adult male collected by H. Zaher and F. Curcio in January 2002 in “Chapada dos Gerais”, a sandstone plateau in Parque Nacional Serra das Confusões, (9°13’S; 43°29’W), Piauí state. (Fig. 4).

Paratypes - MZUSP 94057-067, two males, five females, four juveniles, same data as holotype.

Characterization - *Stenocercus squarrosus* sp. nov. is characterized by the following combination of features (adapted from Cadle, 1991): (1) Dorsal head

scales keeled. (2) Interparietal distinct, moderately enlarged, followed by a pair and a triad of moderately enlarged scales that reach the occipital region. (3) Internasals 3-5, mostly five. (4) No distinctly enlarged supraoculars. (5) Two canthals, anterior one reaching the post rostrals. Posterior canthal longer than anterior, continuous with supraciliaries, forming a single canthal ridge (6) An enlarged, prominent, pointed scale immediately posterior to supraciliaries; no projecting, blade-like, angulate temporal scales. (7) Gulars and ventrals distinctly keeled. (8) Parietal eye distinct. (9) Neck folds absent. (10) Dorsals phylloid, keeled, imbricate, generally with a small mucron; lateral scales similar to dorsals. (11) A low vertebral crest, and at each side a pair of very distinguished dorsolateral and a pair of well distinguished lateral crests. (12) Mite pockets absent. (13) Scales on posterior surface of thighs imbricate, keeled. (14) Tail short, depressed and tapering from mid section to the end. (15) Dorsal coloration generally with narrow, transverse, dark brown dorsal bands, a distinctive dark blotch above insertion of forelimbs and a faint vertical dark band across the



Figure 5. Holotype (MZUSP xx) of *Stenocercus squarrosus* sp. nov. in life. Serra das Confusões National Park, central Brazil.

eyes, no sexual dimorphism in color pattern. (16) Scales around midbody 46-53. (17) Maximum SVL 88 mm. (18) preauricular fringe present. (19) vertebrals 22-27. (20) paravertebrals 35-45. (21) scales around midbody 46-53. (22). Lamellae on finger IV 13-15. (23) Lamellae on toe IV 16-20. Variation in the type series summarized in Table 4.

Diagnosis - *Stenocercus squarrosus* sp. nov. is distinguished from all other *Stenocercus*, except *S. tri-*

cristatus, *S. dumerilii*, and *S. quinarius* by the presence of the following characters (adapted from Ávila-Pires, 1995): head pyramidal, enlarged prominent post-supraciliary scales continuous to a distinct crest formed by supraciliaries and canthals. Supraoculars not enlarged. One elongate subocular. Interparietal small, parietal eye distinct. Gular or neck folds absent, sides of neck with large, imbricate scales. Vertebral and dorsolateral crests present. Dorsals, laterals and ventrals relatively large, imbri-

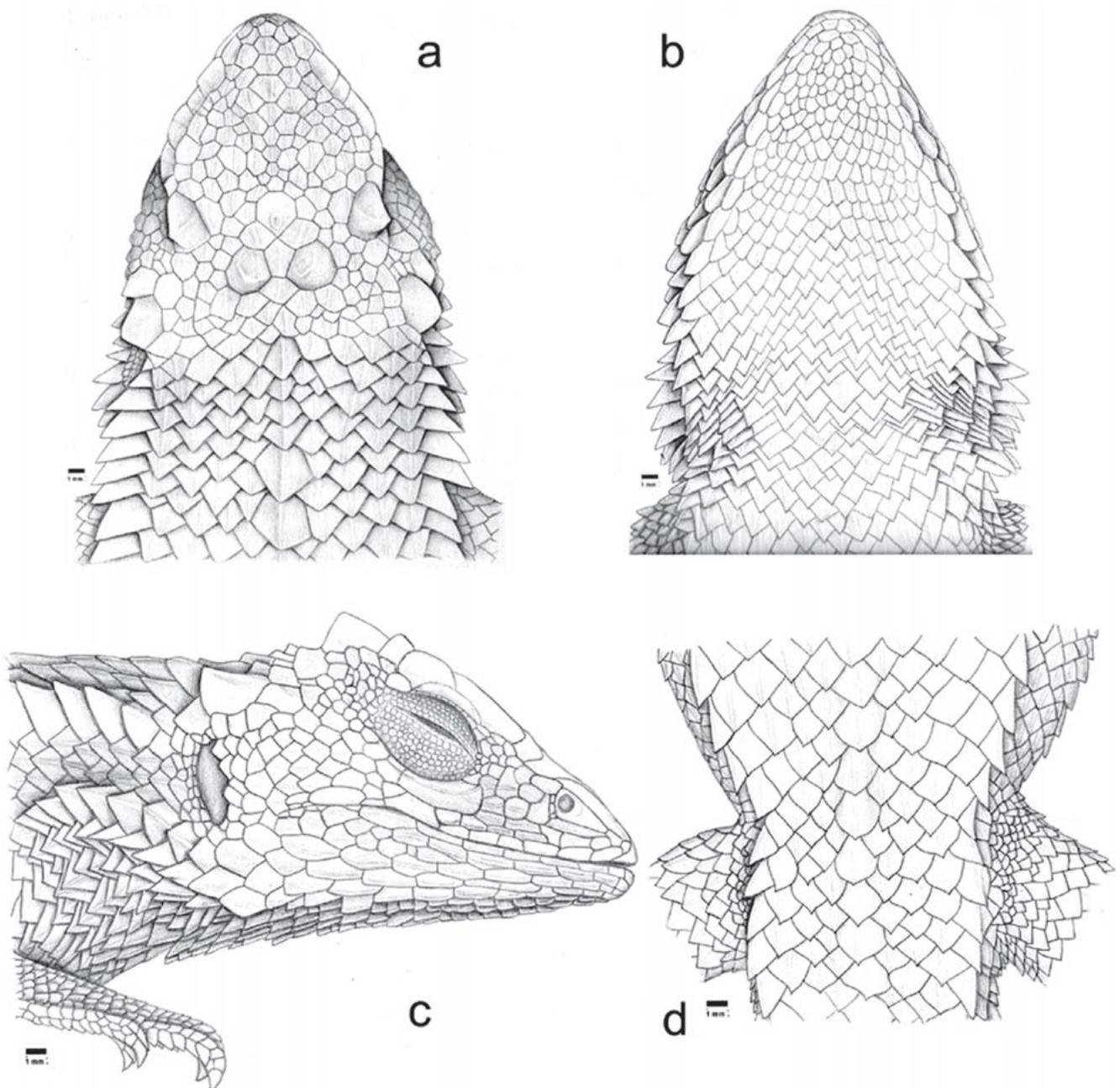


Figure 6. Holotype (MZUSP 94056) of *Stenocercus squarrosus* sp. nov. A, Dorsal view of head; B, Ventral view of head; C, Lateral view of head; D, Dorsal view of posterior part of the body.

cate, keeled, sometimes mucronate. Mite pockets absent.

From *S. tricristatus* (characters in parentheses) it is distinguished based on the shorter tail, 0.8-0.9 times SVL (1.7 times SVL), 46-53 midbody scales (33), 13-15 scales from one dorsolateral crest to the other (8), five prominent, dorsolateral crests: one vertebral, two dorsolateral and two lateral (lateral crests undistinguishable), body depressed (body laterally compressed), tail depressed near the base (compressed near the base) and uniform, light brown dorsal pattern, with transverse dark brown markings in juveniles and some adult specimens (banded dorsal pattern).

From *S. dumerilii* (characters in parentheses, from Ávila-Pires, 1995 and 15 examined specimens) it differs by showing 46-53 midbody scales (41-50); shorter tail, 0.8-0.9 times SVL (1.2-1.4); 3-5, mostly five, internasals (2-3); rostral roughly three times as wide as high (approximately four times as wide as high); smaller adult size; dorsal scales keeled throughout the length of the scale (keel restricted to or more prominent on the distal part of dorsals); dorsals generally with a small mucron (most non-mucronate); 42-52 caudal scale rows (64-74); all five dorsal crests prominent, serrated (dorsal crests low, lateral crests poorly distinguishable in some specimens), body depressed (body slightly depressed), tail elliptical in cross section (round in cross section).

From *S. quinarius* sp. nov. (characters in parentheses) it differs by having a shorter tail, 0.8-0.9 times SVL (1.0-1.1); rostral roughly three times as wide as high (approximately twice as wide as high); 42-52 caudal scale rows (56-62); all five dorsal crests prominent, serrated (dorsal crests low), body depressed (body slightly depressed), tail elliptical in cross section (round in cross section), anterior canthal ridge single (double canthal ridge), anterior canthal longer than posterior (shorter), contacting post-rostrals (not contacting post-rostrals).

Description of holotype - Adult male, 88 mm SVL. Head 0.2 times SVL, 1.2 times as long as wide, 1.4 times as wide as high. Snout bluntly pointed in dorsal view and in profile. Canthus rostralis straight, well defined, continuous with supraciliaries, which are followed posteriorly by a prominent trihedral scale, giving the head the shape of a four-sided pyramid. In profile, the head shows an ascending line until level of the prominent post-supraciliary scale, then a descending line to-

ward neck. Neck not distinctively narrower than head and body. Body depressed. Limbs short, stout, well developed; forelimbs 0.4 times SVL, hind limbs 0.5 times. Tibia 0.2 times SVL, and 0.4 times length of hindlimb. Tail short, depressed, elliptical in cross-section, 0.8 times SVL.

Tongue wide, villose, with rounded, nicked tip. Teeth small, anterior conical, posterior slightly compressed with three small cusps.

Rostral low subtriangular, its largest width about three times median height, barely visible from above. Five postrostrals. Snout, supraocular and interorbital regions form a continuous, rather flat, surface, covered with irregularly polygonal and variable in size, subimbricate to juxtaposed flat scales, with a distinct low keel. Five scales across snout between posterior canthal. Supraorbital semicircle inconspicuous, barely differentiated from supraocular and other scales of top of head. Two canthals, anterior one reaching the post rostrals. Posterior canthal longer than anterior, continuous with supraciliaries. Supraciliaries four, first two broadly overlapping posteriorly, first smaller than second, which is the longest. Third elongate, longer than first, fourth shortest. In lateral view an additional internal median, elongate scale is present above orbit. Canthals and supraciliaries form a distinct crest which ends in a very prominent pyramidal scale immediately posterior to supraciliaries. This crest delimits a sharp angle between dorsal and lateral surfaces of head. Interparietal moderately enlarged, roughly heptagonal, with parietal eye distinct in posterior part of scale. A pair of obliquely keeled scales, smaller than the interparietal, are in slight contact at midline, and borders the interparietal posteriorly. This pair of scales is followed by three scales with a central conical elevation, the medial one smaller. These scales are followed by an irregular row of five scales with a posterior conical elevation. Laterally to these post-interparietal enlarged scales, the scales are similar to those on snout, though slightly smaller.

Nasal below anterior canthal, lateral in position, large, undivided; nostril in its posterior part, directed latero-posteriorly. Loreal region with two rows of lorilabials, anteriorly and posteriorly single, medially double; between lorilabials and canthals a few large irregularly polygonal scales, posterior ones keeled. Five transverse rows of scales in between posterior canthal and supralabials. One elongate, keeled subocular, contacting posterior lorilabial and seventh supralabial. Suprala-

bials nine, narrow, elongate, seventh longer and higher, followed to commissure of mouth by two small, keeled posterior supralabials. Temporal region with irregularly polygonal, keeled scales; seven scales in an oblique row from lower posterior border of orbit to above ear opening, the two posterior ones distinctively enlarged, conical. A supratemporal row of scales formed by the enlarged post-supraciliary scale, the enlarged scale above ear opening and two smaller, keeled scales in between. Ear opening relatively large, vertically oval, with smooth margins. Tympanum recessed.

Mental larger than adjacent infralabials, bordered posteriorly by four equally sized scales, including the anterior sublabials. Infralabials eight, elongate, narrow, flat, seventh below center of eye, followed a smaller keeled scale to commissure of mouth. Four irregular rows of elongated sublabials with a high median keel; lower two rows of sublabials continuous until below ear opening, smaller anteriorly but becoming progressively larger, keeled, more mucronate and more prominent posteriorly. Scales on chin relatively small anteriorly, elongate, subimbricate, posteriad grading into gulars. Gulars larger than scales on chin and adjacent ventrals, strongly keeled and mucronate, in longitudinal rows; no gular or lateral folds. Anterior scales on nape smaller, posterior ones with a more prominent keel and mucron than dorsals. A vertebral crest of large, prominent, sharply keeled and mucronate scales extends from nape (not reaching occipital region) to first rows of caudal scales. Vertebral crest more prominent on anterior part of dorsum. A dorsolateral row of scales, more prominent in its anterior third and much more conspicuous than the dorsal one, forms another high, serrate, prominent crest at each side of body. This crest extends from above ear opening to anteriormost part of tail.

Scales on sides of neck strongly imbricate, keeled and mucronate, varying in size and shape from scales similar to but smaller than dorsals, to much larger, highly imbricate and prominent forming two irregularly arranged series of spines. Dorsals phylloid, imbricate, more sharply keeled on anterior half of dorsum, where most scales bear a distinctive mucron. Vertebral crest low, with sharp keels, mucronate, with 28 vertebral scales from occiput to base of tail. Fifteen dorsal scales in transverse row at midbody, between and including dorsolateral rows. Flanks with similar but slightly smaller scales, with less pronounced keels and mucrons. A lateral crest extends from behind the insertion of fore-

limbs to the groin. Ventrals phylloid, smaller and narrower than dorsals, identical to flank scales situated below flank crest with minute spiny projections, two or three on each side of the median keel, more visible on posterior ventrals. Thirty six irregularly longitudinal and oblique rows of ventral scales along a midventral line between anterior level of forelimbs and anterior level of hind limbs. Fifty six scales around midbody. Scales on preanal plate in transverse rows, mite pockets absent.

Scales on dorsal part of tail rhomboid, flat, keeled and mucronate, distal ones smaller. On ventral surface smaller, with a pronounced mucron and keel, which forms longitudinal ridges. No distinct verticils.

Limbs with rhomboid, imbricate, strongly keeled and mucronate scales, smaller than dorsals. The keels form distinct ridges on all aspects of limbs, except on the ventral part of hind limbs. Subdigital lamellae single, tricarinate, 14 under fourth finger and 19 under fourth toe.

Color in life - Dorsal ground color uniform tan, dorsal part of head same color as dorsum. Gular and ventral region slightly lighter, uniform light brown. Tail region with slightly darker flecks of reddish brown, alternating with lighter areas. A dark brown ocular stripe is visible from the orbit to commissure of mouth. On the photographed specimen, four dark brown transversal chevrons are present on the dorsum, along the vertebral row of enlarged, erected scales, being absent on the holotype. A distinct horizontally elongated black spot just above and anterior to insertion of forelimbs (see Figure 5).

Color in preservative - Dorsal ground colour almost uniform, varying slightly from light brown to straw cream, except for the presence of an horizontally elongate dark brown region above insertion of forelimbs. Ventral surface lighter immaculate. Tail dorsally with slightly darker areas alternating with light tan areas, ventrally identical to venter. A narrow, faint, ocular stripe extends from below orbit to sublabial region.

Distribution and ecology - This species is known from the Southern portion of Serra das Confusões National Park, Piauí state, in a contact area between Caatinga and Cerrado (see Figure 4). Most specimens were collected on top of a sandstone plateau called "Serra Grande" or "Chapada dos Gerais" (elevation

~600 m), with only a few specimens obtained in adjacent depressions. The dominant vegetation on the tabletop is “carrasco”, a semi-open habitat combining Cerrado and Caatinga floristic elements growing on sandy soils. Bour and Zaher (2005) provided a detailed description of the type locality.

Etymology - “*squarrosus*”, Latin, rough, with stiff, erected scales. In allusion to the prominent, serrate dorsal crests.

DISCUSSION

Although the herpetofauna of Cerrado/Caatinga and Amazonia contact zones in central and northeastern Brazil remain poorly sampled, a specimen of *Stenocercus* with a distinctive pyramidal head, three dorsal crests, and a tail shorter than the body had already been figured in pre-Linnean times. It was clearly represented between 1634 and 1641 by Zacharias Wagner in Figure 91 of his “Thierbuch”, when northeastern Brazil was under Dutch possession (Wagner, 1964; Teixeira, 1997). During the early period of European colonization, the Dutch prince Maurice Nassau-Siegen received at Recife animals from several parts of northeastern Brazil, while his personnel traveled extensively across the region.

Although the picture has been attributed to *Tropidurus torquatus* (Wagner, 1964), the features referred above confirm its identity as a *Stenocercus* specimen. It is possible that the specimen was drawn based on one of the new species described herein or on a specimen of *Stenocercus dumerilii*. However, considering the rarity and relictual distribution of this species assemblage, the depicted specimen might represent another undescribed species that remains concealed in the complex and poorly studied interior landscapes of northeastern Brazil.

The knowledge of phylogenetic relationships among species of *Stenocercus* has been recently improved, and there is evidence supporting the recognition of two major clades within this radiation (Torres-Carvajal et al., 2006), although taxon sampling is still inadequate to depict a broad picture concerning phylogenetic affinities and evolution within the genus. For example, morphologically distinctive species with an enlarged post-supraciliary scale and a blunt, pyramidal head, bordered by conspicuous supraciliary crests were not included in recent studies and, although suggested by their

unique morphology, their monophyly has not been tested adequately. Additionally, their phylogenetic affinities within the *Stenocercus* radiation remains unknown.

Nevertheless, species of *Stenocercus* from eastern portions of South America show a disjunct, probably relictual, distribution pattern. Their rarity and restriction to semi-open woodlands (“carrascos”), dry forests (*Stenocercus caducus* and *sinesaccus* complex, see Torres-Carvajal, 2005) and even semi-closed forests (“capoeiras”, the typical habitat of *Stenocercus dumerilii* in Pará, see Cunha, 1981) is an indication that the presence of these species is no longer favoured by the climatic conditions nor by the vegetation physiognomies that dominate in the Cerrado, Amazonia and Caatinga core areas, as defined in the Brazilian vegetation map (IBGE, 1993, see discussions in Rodrigues, 2003, 2005).

Apparently, the *Stenocercus* species with pyramidal head and enlarged post-supraciliary are confined to eastern Brazil, east of the Araguaia basin, being allopatric with *Stenocercus caducus* and *S. sinesaccus*, that range west of the Araguaia basin. The occurrence of five of the eight Brazilian *Stenocercus* in the Cerrado region highlights the importance of central Brazilian savannas as a center of Neotropical lizard diversity, harboring rich but formerly poorly studied lizard assemblages (see discussions in Nogueira et al. 2005), not properly described in previous studies which favoured the view of a poorly diversified lizard fauna across the diagonal belt of open formations (Vanzolini, 1988; Vitt, 1991), a misconception probably due to the lack of proper samplings across central Brazil. New data on Caatinga and mainly Cerrado lizard assemblages (Colli et al., 2002; Nogueira, 2006) are slowly changing the prevalent idea that the South American open formations diagonal belt harbored a homogeneous and relatively poor herpetofauna due to extensive faunal mixing and unfavorable conditions for speciation (see new interpretations in Vanzolini, 2005).

At least for *S. quinarius*, its association to relatively scattered “carrasco” and dense cerrado patches in the western Bahia plateau and Grande Sertão Veredas region (and the rarity or absence in dominant open Cerrado grasslands) corroborates local distribution patterns found in Cerrado lizard assemblages (Colli et al., 2002; Nogueira et al., 2005), where most species show patchy distributions according to the typical Cerrado habitat mosaics. The typical habitat of *S. squarrosus* is also semi-open “carrasco” patches, restricted to the elevat-

ed plateau of “Chapada dos Gerais”, being relatively rare in lower parts of Serra das Confusões National Park, which are dominated by dry forests at the contact zone between Cerrado and Caatinga (see habitat descriptions in Bour and Zaher 2005). The study of other isolated plateaus within northeastern Brazil, such as the Ibiapaba or the Araripe plateaus, covered by “carrasco” and mosaics of Caatinga and Cerrado (see Araújo et al, 1999), may reveal the presence of other undescribed species of *Stenocercus*. Unfortunately, the floristic affinities and origins of the “carrasco” vegetation, typical of sandstone tabletops on the contact zone between Cerrado and Caatinga (see Lombardi et al., 2005), are still poorly studied, and this type of vegetation is either considered as a degraded type of dense cerrado (“cerradão”), or as a relict of a distinct vegetation type (see Araujo et al., 1999).

Stenocercus dumerilii, a closely related species, is also reported from semi-open habitats in easternmost Amazonia and its transition to non-forested domains (see IBGE, 1993). The typical habitat of this species is described as “capoeiras”, considered by Cunha (1981) as degraded, second growth lowland forests. However, the occurrence of this species in eastern Amazonia is probably related to the presence of naturally occurring isolated patches of semi open woodlands, as those occupied by both species described herein. The confinement of other members of the genus, such as *Stenocercus sinesaccus* (see habitat use data in Gainsbury & Colli, 2003) and *Stenocercus caducus* to patches of semideciduous forests or “cerradão” woodlands, in the western portion of the Cerrado, corroborates the pattern of patchy distributions according to available habitat mosaics. The distribution pattern found in *Stenocercus*, with many allopatric species occurring in Brazil, favors interpretations pointing to historical changes in geomorphology and vegetation (see Pennington et al., 2004) as the main driving factor of speciation. Actually, it was this relictual and patchy distribution pattern that led to suggestions that these lizards may have been much more largely distributed in the past, before the expansion of the components belonging to the genus *Tropidurus* (Rodrigues, 2003, 2005), a closely related clade within Tropiduridae. If their restriction to relictual, semi-open habitats (see Cunha, 1981 for *Stenocercus dumerilii* in Pará) is corroborated, the distribution patterns found in *Stenocercus* would resemble those described for vascular plants that occur in the arc of dry semideciduous forests from northern

Brazil to the eastern versant of the Andes (see Prado & Gibbs, 1993; Pennington et al., 2004), a pattern also found for lizards within Cerrado dry forest enclaves (Werneck & Colli, in press).

As no populations of *Stenocercus* are known from the depressions and dry forests of the Paranã river valley in Central Brazil (see Werneck & Colli, 2006), the distribution of *Stenocercus* in the Cerrado and Caatinga contact areas may document the relictual distribution of poorly studied faunal assemblages associated to blocks of semideciduous woodlands, restricted to elevated sandstone plateaus in central and northeastern Brazil, and absent in their lower counterparts, the dry forests on limestone soils in the Paranã valley (see Pennington et al, 2004). The association to elevated areas is recurrent and probably an ancestral condition in the genus, as the andean slopes are the main center of diversity of *Stenocercus* (see Cadle 1991).

With the available data and the lack of reliable phylogenetic studies including the recently described species of *Stenocercus*, we refrain to interpret biogeographical affinities between Brazilian, andean and periandean forms of the genus. New samplings providing evidence on habitat use and distribution of poorly known species (such as *Stenocercus tricristatus* or even undescribed taxa) would be extremely relevant in attempts to link local distribution to biogeographical patterns in this lizard group. Molecular and morphological comparative studies could provide extremely valuable information on evolutionary ages of disjunct populations of *Stenocercus*, providing a test to the relictual distribution hypothesis.

Thus, further collections and studies of *Stenocercus* in extra-amazonian open domains, in some of the least studied South American herpetofaunas, are still crucial for understanding the history of Stenocercini. The inclusion of these eastern populations in future systematic studies is necessary to clarify if the components of *Stenocercus* with a pyramidal head and enlarged supraciliaries form a monophyletic group (see discussions in Ávila-Pires, 1995) and represent a relict of past herpetofaunal assemblages. Unfortunately, the time to document and conserve these biogeographical entities is running out, due to the extremely rapid pace of habitat destruction in the Cerrado savannas and transition to Caatinga, where over 2 million hectares of pristine habitats are destroyed each year (Klink & Machado, 2005) by the advance of the agricultural frontier, in one of the most threatened regions in the world.

RESUMO

O gênero *Stenocercus* abrange aproximadamente 50 espécies, distribuídas principalmente pelas regiões mais elevadas dos Andes e áreas de baixada adjacentes, com apenas algumas poucas espécies conhecidas para o território brasileiro. As populações mais orientais do gênero são pouco estudadas e representadas nas coleções. Neste trabalho descrevemos *Stenocercus quinarius* sp. nov., do noroeste do estado de Minas Gerais e oeste da Bahia, e *Stenocercus squarrosus* sp. nov. do sul do Piauí, duas regiões até então pouco amostradas no centro e nordeste do Brasil. As duas espécies novas são mais proximamente aparentadas a *Stenocercus dumerilii* and *Stenocercus tricristatus*, mas se distinguem claramente entre si e entre todas as espécies de *Stenocercus* por caracteres morfométricos e merísticos. O padrão de distribuição e as afinidades filogenéticas presumidas do grupo de espécies com cabeça piramidal da região oriental da distribuição do gênero são discutidos, juntamente com uma visão geral dos padrões de distribuição dos *Stenocercini* nas regiões extra-amazônicas.

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APPENDIX I

Specimens examined

Stenocercus azureus – BRAZIL: São Paulo: Itapeitinga: MZUSP 13881, Limeira: MZUSP 04249; Paraná: Ponta Grossa: MZUSP 04642, MZUSP 04051; Rio Grande do Sul: Itapuca: MZUSP 04641.

Stenocercus caducus – Mato Grosso: Cáceres: MZUSP 89548, Estação Ecológica Serra das Araras: MZUSP 74990, MZUSP 94249-51, MZUSP 94676-77. Vila Bela de Santíssima Trindade: MZUSP 82812-16. Mato Grosso do Sul: Bodoquena, Fazenda Califórnia: MZUSP 93413, MZUSP 94242-48, MZUSP 94588-97.

Stenocercus dumerilii – BRAZIL: Pará: Acará: MPEG 9484. Belém: MZUSP 07133. BR 010 km 93: MZUSP 08069. Curuçá: MPEG 7331, MPEG 7333, MPEG 7334, MPEG 7335. Maracanã: MPEG 6511, MPEG 6512, MPEG 6514. Ourém: MPEG 7164. Santarém Novo: MPEG 16324. São Caetano de Odivelas: MPEG 8020. São Roberto: MZUSP 56985. Vigia: MPEG 6495. Maranhão: Estreito: MZUSP 94470, MZUSP 94471. São Pedro da Água Branca: MPEG 21370. Urbano Santos: MPEG 21371.

Stenocercus sinesaccus – BRAZIL: Rondônia: Pimenta Bueno: CHUNB 18041-49. Vilhena: CHUNB 11473-74. Mato Grosso: UHE Manso: MZUSP 88209-21. MZUSP 92030, MZUSP 92049. Cocalinho: MZUSP 89549. Goiás: Mineiros: CHUNB 32754. Santa Rita do Araguaia: CHUNB 32755.