



A new microendemic species of *Tropidurus* (Squamata: Tropiduridae) from southern Brazil and revalidation of *Tropidurus catalanensis* Gudynas & Skuk, 1983

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Abstract

The South American and cis-andean lizard genus *Tropidurus* has a complex taxonomic history. Most species were recently described and previous revisions included few specimens from the southern part of the continent. *Tropidurus torquatus* has the broadest geographic distribution in the genus and several morphological and ecological differences were described within its distribution. We analyzed the geographic variation in external morphological characters of *Tropidurus torquatus*, including large number of samples from southern Brazil. *Tropidurus catalanensis* is revalidated and *Tropidurus imbituba* sp. nov., with a restrict distribution in the southern coast of Brazil, is described. The new species is distinguished from *Tropidurus catalanensis* by the number of dorsal scales. It can be distinguished from *T. catalanensis* and *T. torquatus* by a distinct orange ventral coloration in adults, which can reach the lateral portion of the body in adult males. Our analysis also suggests that at least two other undescribed species could be recognized under the name *Tropidurus torquatus* in southeastern and central Brazil.

Key words: *Tropidurus torquatus*, Brazilian coast, La Plata Basin, Pampa, *Tropidurus imbituba* sp. nov.

Introduction

Among the lizard genus *Tropidurus* Wied-Neuwied, 1825, the *torquatus* group is characterized by lacking an enlarged middorsal scale row, imbricate and keeled dorsal scales and in not being extremely flattened. Lizards in this group are heliothermic, abundant, and broadly distributed along most of the open formations of South America east of the Andes, from Venezuela to northern Argentina and Uruguay (Rodrigues 1987; Frost *et al.* 2001).

Tropidurus torquatus (Wied-Neuwied, 1820) has a complex taxonomic history summarized in Rodrigues (1987) and Frost (1992). Its original description doesn't mention type specimens or locality, but according to Wied's itinerary it can be stated that his descriptions were based on specimens from eastern Brazil (see Rodrigues 1987). Burt and Burt (1930, 1931) synonymized *T. hispidus* (Spix, 1825) and *T. hygomi* (Reinhardt & Lütken, 1861) with *T. torquatus*. This taxonomy remained until Vanzolini and Gomes (1979) recognized *T. hygomi* as a valid species, although Etheridge (1970) had also considered both *T. hygomi* and *T. hispidus* as valid species without justification.

Tropidurus etheridgei Cei, 1982 was described from the arid Chacoan of western Argentina. In the original description, the author stated that "prior to the work of Burt and Burt (1930) it had long been believed that there were two widespread species – *Tropidurus hispidus* (Spix, 1825) with large body scales (54–94 around midbody) in northern and northeastern South America, and a small-scaled species (90–140 around midbody), *T. torquatus* (Wied, 1820) in eastern and southern Brasil" (Cei 1982, page 6). He argued that by having intermediate scale counts between *T. hispidus* and *T. torquatus*, specimens of his new species had lead Burt and Burt (1930) to recognize these taxa as subspecies. Cei also stated that "the small-scaled populations in northeastern Argentina, Paraguay and southern and eastern Brazil, formerly all included under the name *torquatus*, now appear to involve more than one taxon – *torquatus*, restricted to the eastern coast of Brazil north of Rio de Janeiro, and an unnamed taxon in the

Paraná Basin and inland to Paraguay, eastern Bolivia, and Misiones in northern Argentina” (Ceí 1982, pages 7–8). Subsequently, the populations of the Paraná Basin were described as *Tropidurus catalanensis* Gudynas & Skuk, 1983 based on specimens from northwestern Uruguay and northeastern Argentina. The main diagnosis presented for this species in relation to the remaining *T. torquatus* was the higher scale counts around midbody (89–121), yellow coloration on chest and throat and a small black antehumeral bar that does not reach the shoulder. In the original description, the type series was only compared with specimens of *T. torquatus* from central Brazil (states of Mato Grosso, Mato Grosso do Sul and Minas Gerais).

Rodrigues (1987) revised the lizards of the *torquatus* group south of the Amazon, establishing the form and position of the mite pockets as the main diagnostic character for this group. Studying the sympatric occurrence of lizards with distinct patterns of mite pockets, Rodrigues described seven new species for the group and considered *T. catalanensis* as a synonym of *T. torquatus*. Although recognizing several signs of geographical and ecological differences between coastal and inland populations of *T. torquatus*, he could not find geographic congruence on character variation justifying the maintenance of these populations as separated species. The coastal populations referred by Rodrigues are those from the city of Rio de Janeiro northward to the south of the state of Bahia, Brazil. These lizards live mainly on the sandy soils of the *restingas* and attain a smaller body length in relation to the remaining inland populations.

Ceí (1993) compared the Argentinean populations of *T. catalanensis* with *T. torquatus* from Cabo Frio, state of Rio de Janeiro, agreeing with the synonymization proposed by Rodrigues (1987) based on the similarity of the mite pockets and overlapping of meristic characters. However, he argued in favor of a subspecific status for *catalanensis*, “*en espera de futuros y más completos aportes sobre las poblaciones de la especie de Wied en los estados meridionales de Brasil: Paraná, Santa Catarina y Rio Grande*” (do Sul), emphasizing the lack of information about the intermediary populations between São Paulo and Argentina-Uruguay. In fact, despite the more than 6,000 specimens analyzed, Rodrigues (1987) had access to few specimens from southern Brazil, which included only two localities in the state of Paraná and one specimen (MZUSP 118) from Corupá, northeastern Santa Catarina, which needs confirmation. This locality lies on the slopes of the Serra do Mar mountains, covered by dense Atlantic forest without large natural enclaves of open formations, although there are isolated rocky outcrops. However, these lizards are usually very abundant where they occur. Since MZUSP 118 is an old specimen and until now there is no other record for the species in that region, a labeling mistake may have occurred.

Since Rodrigues (1987), only two new species were described in the *torquatus* group: *T. chromatops* Harvey & Gutberlet, 1998, a saxicolous form from Bolívia and *T. psammonastes* Rodrigues, Kasahara & Yonenaga-Yassuda, 1988, a psammophilous form with relictual distribution in the state of Bahia. Currently the group comprises 13 valid species (*T. chromatops*, *T. cocorobensis* Rodrigues, 1987, *T. erythrocephalus* Rodrigues, 1987, *T. etheridgei*, *T. hispidus*, *T. hygomi*, *T. insulanus* Rodrigues, 1987, *T. itambere* Rodrigues, 1987, *T. montanus* Rodrigues, 1987, *T. mucujensis* Rodrigues, 1987, *T. oreadicus* Rodrigues, 1987, *T. psammonastes* and *T. torquatus*).

Tropidurus torquatus has the broadest geographic distribution of the genus and there are evidences of a species complex under this name (Rodrigues 1987; Kasahara *et al.* 1996). Still, there are doubts on the application of the name *Tropidurus catalanensis*. Ceí (1993) considered it a subspecies of *torquatus* and later considered it a full species without justification (Ceí 2003).

In December 2008 we found a population of lizards isolated in a rocky seashore in the southern coast of the state of Santa Catarina, Brazil, related to the *torquatus* complex. This new coastal population is about 800 km away from the closest coastal populations in Rio de Janeiro. Besides, there are evident differences in coloration in relation to the geographically closest populations (about 200 km west), in the river valleys of the Uruguay Basin (400–600 m asl), in the border of the states of Santa Catarina and Rio Grande do Sul (Arruda *et al.* 2008). The finding of this new population and the great amount of specimens collected in southern Brazil in the last two decades motivated a review of the taxonomic status of these southernmost populations related to *Tropidurus torquatus*.

Material and methods

Material examined. We examined 366 specimens of *Tropidurus torquatus* (*sensu* Rodrigues 1987) deposited in the following collections: Brazil: Departamento de Zoologia da Universidade Federal do Rio Grande do Sul

(UFRGS), Porto Alegre; Departamento de Ecologia e Zoologia da Universidade Federal de Santa Catarina (CHUFSC), Florianópolis; Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN), Porto Alegre; Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre; Museu de História Natural “Capão da Imbuia” (MHNCD), Curitiba; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo. Uruguay: Museo Nacional de Historia Natural (MNHN), Montevideo. We examined the type of *Tropidurus catalanensis* and one paratype. We could not examine the neotype of *Tropidurus torquatus*; however we examined specimens from Macaé, Rio de Janeiro, distant only 30 km from Lagoa do Paulista, Restinga de Jurubatiba National Park, the type locality designated by Rodrigues (1987) for *T. torquatus*. All specimens examined had mite pockets of the type “A” (Rodrigues 1987), the diagnostic character for *T. torquatus*. Specimens and localities are listed in appendix I.

We made several field expeditions to the states of Santa Catarina and Rio Grande do Sul and one to the state of Rio de Janeiro, so that most of the information presented on ecology, behavior and color patterns of live specimens was obtained directly in the field.

Meristic and morphometric characters. Nomenclature of scales follows Smith (1946). The method of counting ventrals, dorsals, gulars, number of scales on the dorsum of the tibia and scales rows around midbody (SAB) follows Rodrigues (1987). Other scale counts and character follows Ávila-Pires (1995) and Harvey and Gutberlet (1998). Measurements were taken with a caliper to the nearest 0.1 mm except for the tail length, taken with a ruler to the nearest 1.0 mm. The measurements follow Ávila-Pires (1995) except for head length taken obliquely from the tip of the rostral to the first dorsal scale. Specimens under 60 mm of snout–vent length (SVL) were not included, to prevent ontogenetic allometric bias. Tail length was not considered on analysis due to the large number of specimens with incomplete tail. Sex was determined through a “L” shaped incision on the posterior region of the venter, laterally positioned so that it does not impair future ventral scale counts.

Geographic coverage of the samples. Initially, considering the great number of localities and differences in the amount of specimens from each locality, we grouped samples with apparent geographic continuity and without evident morphological differences. Lizards were grouped by this criterion into nine groups: (1) Imbituba; (2) lowlands of the La Plata Basin, including specimens from southwestern Rio Grande do Sul (Brazil), Corrientes (Argentina) and Ñeembucú (Paraguay); (3) upper Uruguay River Basin (one of the main tributaries of the La Plata River) in the Brazilian states of Santa Catarina and Rio Grande do Sul; (4) Iguazú River Basin (a large tributary of the Paraná River) in the Brazilian state of Paraná; (5) middle Paraná River, including specimens from northwestern Paraná, southeastern extreme of state of Mato Grosso do Sul and the southwestern extreme of state of São Paulo; (6) north and northwestern state of São Paulo, including specimens from a set of populations apparently associated with the Rio Grande and Tietê Basins (both tributaries of the Paraná River); (7) Central Brazil, including specimens from the Cerrado domains in the Brazilian states of Minas Gerais, Mato Grosso, Goiás and Tocantins; (8) mountain ranges of the state of Rio de Janeiro, in the border with the state of Minas Gerais; (9) eastern Brazilian coast, including specimens from Rio de Janeiro, Espírito Santo and Bahia.

Statistical analysis. To investigate sexual dimorphism we performed parametric (Student *t*) and non-parametric (Mann-Whitney) univariate statistical tests, depending on the normality and homogeneity of the variables. Exploratory statistical analyses were performed in STATISTICA 7.1 (StatSoft 2005). Data for five meristic characters (dorsals, ventrals, gulars, tibia and SAB) were square-rooted and a canonical variate analysis (CVA) was performed in PAST (Hammer *et al.* 2001) to verify morphological variation between the nine groups defined *a priori*. The results of the CVA allowed the redefinitions of the subpopulations and a second CVA was performed with the redefined groups. Missing data were substituted by means. Specimens with missing data for more than two characters were excluded from the analysis.

Results and discussion

Although most of the meristic characters analyzed overlapped, dorsals, gulars and SAB show different tendencies between groups (Table 1). Group 1 (Imbituba) presents the lowest mean of dorsals (males 104.9 ± 4.6 ; females 110.6 ± 3.7) while group 3 (upper Uruguay Basin), geographically closer, presents the highest mean in males (119.8 ± 4.3) and the second highest mean among females (130.4 ± 5.5). Group 5 (northwestern state of Paraná and extreme southwest of São Paulo, along the Paraná Basin) presents high dorsal mean while groups 6 and 7 (north of state of São Paulo and Central Brazil) present low means. Males of group 9 (all from the coast of Rio de Janeiro

State) show intermediary counts (102–121, mean 113.6 ± 5.5). Females of this group are the only ones with a lower mean in relation to males (110 ± 5.6). However, only four specimens of these populations were analyzed (three from the coast of Rio de Janeiro and one insular specimen from the coast of Espírito Santo). Group 8 (mountain ranges of Rio de Janeiro) presents high means (males 115 ± 5.7 ; females 132.3 ± 5.1), close to those of samples 2–5.

TABLE 1. Variation in dorsals, scales around midbody (SAB) and gulars of nine groups of the *Tropidurus torquatus* complex. Values are mean \pm SD, observed limits, and group size (*n*). Groups are: (1) Imbituba; (2) lowlands of the La Plata Basin; (3) upper Uruguay River Basin; (4) Iguaçu River Basin; (5) middle Paraná River, south of São Paulo; (6) north and northwestern São Paulo; (7) Central Brazil; (8) mountain ranges of Rio de Janeiro; (9) eastern Brazilian coast.

	dorsal		SAB		gulars
	male	female	male	female	male + female
Group 1	104.9 \pm 4.6 99–113 <i>n</i> = 11	110.6 \pm 3.7 102–116 <i>n</i> = 14	99.3 \pm 5.6 87–109 <i>n</i> = 11	106.3 \pm 4.2 98–112 <i>n</i> = 14	50.8 \pm 3.0 43–55 <i>n</i> = 25
Group 2	113.2 \pm 4.6 104–121 <i>n</i> = 18	122.4 \pm 4.7 114–132 <i>n</i> = 21	99.5 \pm 3.2 93–106 <i>n</i> = 19	110.5 \pm 3.7 105–119 <i>n</i> = 21	56.2 \pm 3.5 46–63 <i>n</i> = 43
Group 3	119.8 \pm 4.3 106–130 <i>n</i> = 38	130.4 \pm 5.5 116–140 <i>n</i> = 60	106.5 \pm 4.5 96–115 <i>n</i> = 35	119.4 \pm 5.6 106–131 <i>n</i> = 57	58.6 \pm 2.7 52–64 <i>n</i> = 100
Group 4	115.3 \pm 4.0 110–122 <i>n</i> = 27	121.3 \pm 5.7 110–133 <i>n</i> = 19	101.3 \pm 5.3 91–116 <i>n</i> = 25	115.3 \pm 5.1 110–131 <i>n</i> = 18	53.8 \pm 3.7 47–65 <i>n</i> = 45
Group 5	117.5 \pm 2.3 112–124 <i>n</i> = 18	123.9 \pm 6.9 113–135 <i>n</i> = 10	104.3 \pm 5.3 97–115 <i>n</i> = 18	108.1 \pm 4.4 103–116 <i>n</i> = 9	54.6 \pm 3.6 48–63 <i>n</i> = 28
Group 6	109.4 \pm 4.5 100–120 <i>n</i> = 21	116.6 \pm 5.8 108–124 <i>n</i> = 11	94.7 \pm 3.7 88–103 <i>n</i> = 20	104.9 \pm 6.6 93–113 <i>n</i> = 10	52.1 \pm 2.5 47–57 <i>n</i> = 33
Group 7	108.1 \pm 3.9 101–116 <i>n</i> = 15	115.6 \pm 8.2 102–136 <i>n</i> = 20	94.5 \pm 6.1 86–105 <i>n</i> = 16	101.8 \pm 5.8 91–114 <i>n</i> = 22	50.3 \pm 3.7 42–58 <i>n</i> = 37
Group 8	115 \pm 5.7 107–128 <i>n</i> = 10	132.3 \pm 5.1 124–140 <i>n</i> = 7	108.4 \pm 6.2 100–119 <i>n</i> = 10	126.6 \pm 2.2 123–130 <i>n</i> = 7	57.6 \pm 4.6 49–63 <i>n</i> = 16
Group 9	113.6 \pm 5.5 102–121 <i>n</i> = 26	110 \pm 5.6 102–115 <i>n</i> = 4	105 \pm 6.0 92–117 <i>n</i> = 26	109.3 \pm 6.6 102–117 <i>n</i> = 4	49.4 \pm 3.9 41–61 <i>n</i> = 32

Mean values for SAB show a great difference between group 8, with very high mean, and groups 6–7, with the lowest means. There is no overlap between females and, among males, there is only a small overlap. Also, there is no overlap between females of groups 8–9, although both samples are small. For the males of these populations, there is broad overlapping. For the southern samples (1–5), this counting follows the same patterns of the dorsals, with lower values for group 1 and higher values in groups 2–5. Again, group 3 (geographically closer to sample 1) presents the highest mean.

Gulars and tibia show no significant differences between sexes and were grouped together. For gulars, despite less variation and broad overlap between groups, mean values show similar patterns as to the dorsals and SAB, with higher means in groups 2–5 and 8, and lower in groups 1, 6–7 and 9. Tibia shows little variation between groups, except for group 9 (Figure 1). In this group, tibia ranged 20–33 (24–33 if only Rio de Janeiro populations are considered). Together, all other groups range 17–26. However, most of the variation is within 19–24. Only one specimen presents 17 scales (MHNCI 7125), four present 18 (MCP 4622, MCP 11759, MHNCI 8219 and MZUSP 10179), one 25 (CHUFSC 595) and one 26 (UFRGS 5225). These last two are statistical outliers. Thus, there is very few overlapping considering only the coastal populations from the state of Rio de Janeiro in relation to all

other groups. Group 9 (eastern Brazilian coast) includes only one insular female specimen from Espírito Santo (MCP 6643) and one from south of Bahia (MHNCI 3648; sex not determined). These specimens have, respectively, 22 and 20 scales on the tibia, corroborating Rodrigues (1987), who found a clinal pattern in tibia scales among coastal populations from southern Bahia to Rio de Janeiro, diminishing from south to north.

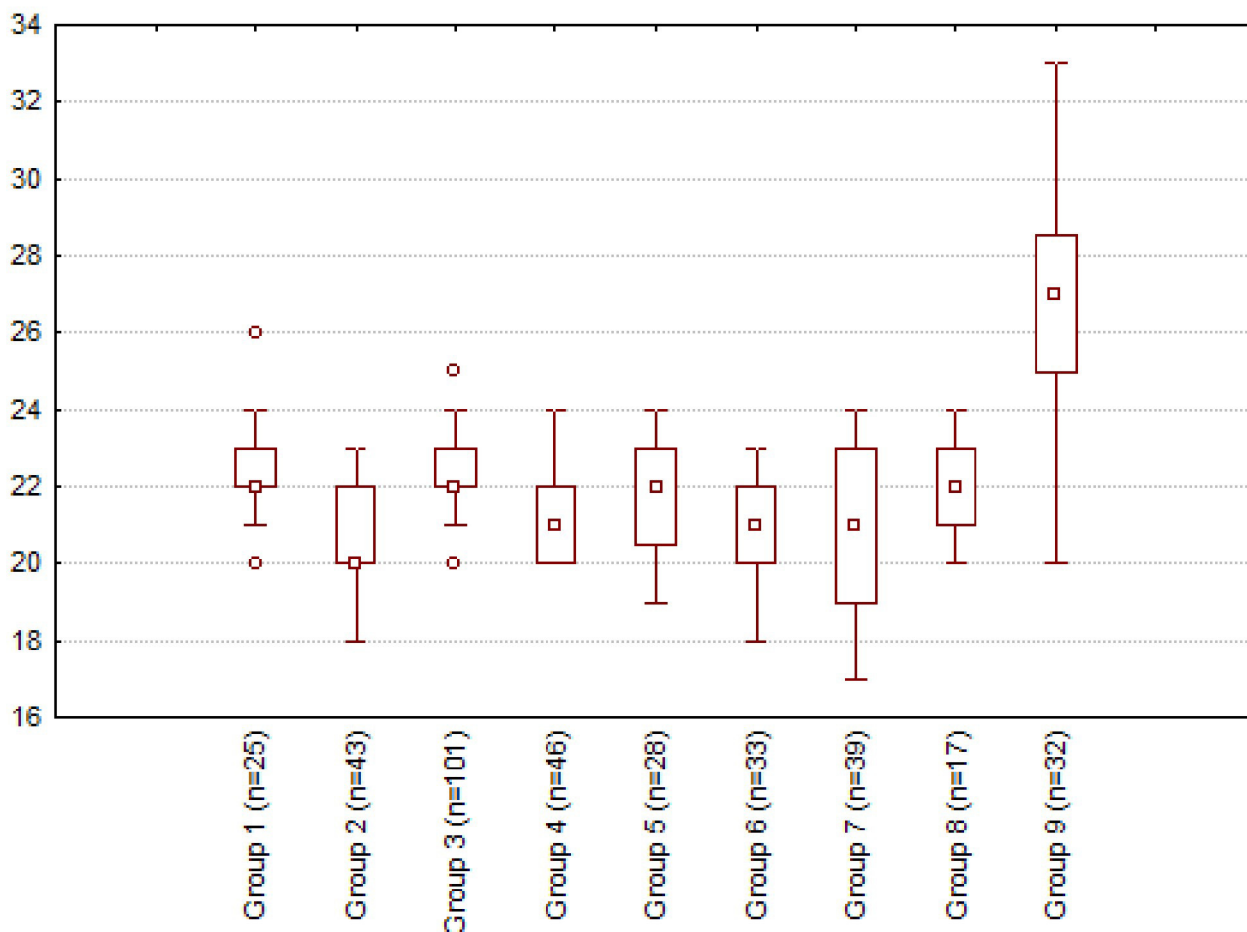


FIGURE 1. Variation in the number of scales on the dorsum of tibia in groups of the *Tropidurus torquatus* complex (males and females grouped). (1) Imbituba; (2) lowlands of the La Plata Basin; (3) upper Uruguay River Basin; (4) Iguaçu River Basin; (5) middle Paraná River, south of São Paulo; (6) north and northwestern São Paulo; (7) Central Brazil; (8) mountain ranges of Rio de Janeiro; (9) eastern Brazilian coast. Boxes: 25-75% of the variation; squares: median; circles: outliers.

Other distinctive character for the coastal populations in eastern Brazil is the smaller body size attained in relation to all other populations. The larger specimen analyzed presents 107 mm SVL (male; MZUSP 36432), while males of all other populations exceed 120 mm in SVL. Rodrigues (1987) compared and reported the existence of ecological differences between these coastal populations which live mainly on the *restingas* and the “inland” populations, with more generalized habits. In fact, in central Brazil these lizards can be seen occupying a great variety of microhabitats, including rocks, tree trunks, termite mounds, walls and other urban or man-made environments. However, our observations on southern Brazilian populations and literature information on the Argentinean and Uruguayan populations (Gudynas & Skuk 1983; Cei 1993; Álvarez *et al.* 2002) revealed that both populations of the Uruguay-Paraná Basin (La Plata Basin; groups 2–5) and of Imbituba (group 1) are primarily saxicolous, only occasionally using vegetation and anthropic environments as substrate, although this may be locally common, as seen in the Iguaçu National Park, where lizards often use the walls and walkways built for the visitors of the Iguaçu Falls.

One of the diagnostic characters used by Gudynas and Skuk (1983) in the description of *Tropidurus catalanensis* was the intense yellow coloration on the chest and throat. This coloration is lost on fixed specimens and was not mentioned by Rodrigues (1987). We examined this character in several live specimens (or

photographs) from all regions included in the analyzed groups (Figure 2). All adult males of populations belonging to groups 2–5 present the characteristic yellow coloration in the chest and throat (mainly on the mental region and including the infralabials). This characteristic is less evident or lacking in females and juveniles. These populations (groups 2–5) along with the one from Imbituba represent the southernmost populations of *Tropidurus torquatus* and, except for the last, are strongly associated with the Paraná and Uruguay Basins (the two main tributaries of the La Plata River). This color pattern was not observed in any other population. Large males from Imbituba exhibit an orange or bronze coloration on the throat and chin (never reaching the infralabials) as well as on the venter. All other populations examined exhibit a white or cream ventral coloration, including chest and chin.

Based on morphological similarities, groups were reassembled, and all populations distributed along the Paraná-Uruguay Basin were grouped together (the “*catalanensis*” group), except the one from north and northwestern São Paulo (group 6) distributed mainly along the Rio Grande and Tietê Basins (both tributaries of the Paraná River). These populations are morphologically similar and contiguous northward to that from Central Brazil (group 7) with which they were grouped (the *Cerrado* group). Groups 1, 8 and 9, Imbituba, Mountain Ranges of Rio de Janeiro and eastern Brazilian coast, respectively, were kept independent (Figure 3). This reassembling of the *a priori* defined groups was supported by CVA.

A second CVA was performed with the redefined groups. This analysis shows little overlap between the geographically closer groups (Figures 4–5). Most of the variation of canonical discriminant axis 1 is explained by tibia, both for males and females, while most of the variation of axis 2 is explained by dorsals for males and SAB for females (Tables 2–3). There is little overlapping between Imbituba and *catalanensis* and the greatest difference is between the geographically closest populations, from the eastern coast of Brazil (most of the group from Rio de Janeiro) and the mountain range of Rio de Janeiro, near the border with Minas Gerais. These coastal populations show little overlap only with populations from Imbituba. This, in its turn, shows more similarity with *Cerrado* (geographically distant), with which shares low values on meristic characters. Similarly, the populations from the mountain ranges of Rio de Janeiro share high meristic values with the geographically distant *catalanensis*. All these populations differ in coloration.

TABLE 2. Results of discriminant analysis of five meristic variables in males of five morphological groups of the *Tropidurus torquatus* complex.

	Canonical axis 1	Canonical axis 2
Dorsals	-0.093053	0.69921
Ventrals	-0.21409	-0.00081675
Scales at midbody	0.16176	0.61472
Gulars	-0.38707	0.34684
Tibia	0.87722	0.11366

TABLE 3. Results of discriminant analysis of five meristic variables in females of five morphological groups of the *Tropidurus torquatus* complex.

	Canonical axis 1	Canonical axis 2
Dorsals	0.57576	0.087635
Ventrals	0.21192	-0.36723
Scales at midbody	0.41739	0.70505
Gulars	0.43549	0.082868
Tibia	-0.50963	0.59456

The geographic pattern of the variation found on meristic characters and coloration allows the recognition of a group of morphologically similar populations, with a distinct throat and chest coloration pattern in males and high values for dorsals, SAB and gulars. These populations are associated to the La Plata Basin. Considering that the meristic mean values for these populations are significantly higher than those of the geographically closest populations (Imbituba and *Cerrado*) and the presence of a diagnostic character, the yellow coloration in males, we

consider *Tropidurus catalanensis* a full species, parapatric in relation to all other populations attributable to *T. torquatus*, except for the population from Imbituba, from which it is largely disjunct.

Although there is broad overlap on meristic values between Imbituba and *Cerrado*, there is also a large disjunction between these groups. Lizards from Imbituba also present a distinct color pattern, an orange coloration on the belly that can reach the lateral portion of the trunk on adult males, contrasting with the grayish coloration of dorsum, cryptic in relation to the rocks where they live. Moreover, these populations are easily distinguished from *T. catalanensis* on the basis of meristic and coloration patterns. Considering its restrict and disjunct distribution in relation to all other *Tropidurus* populations, we considered it an independent lineage that we describe here as a new species.

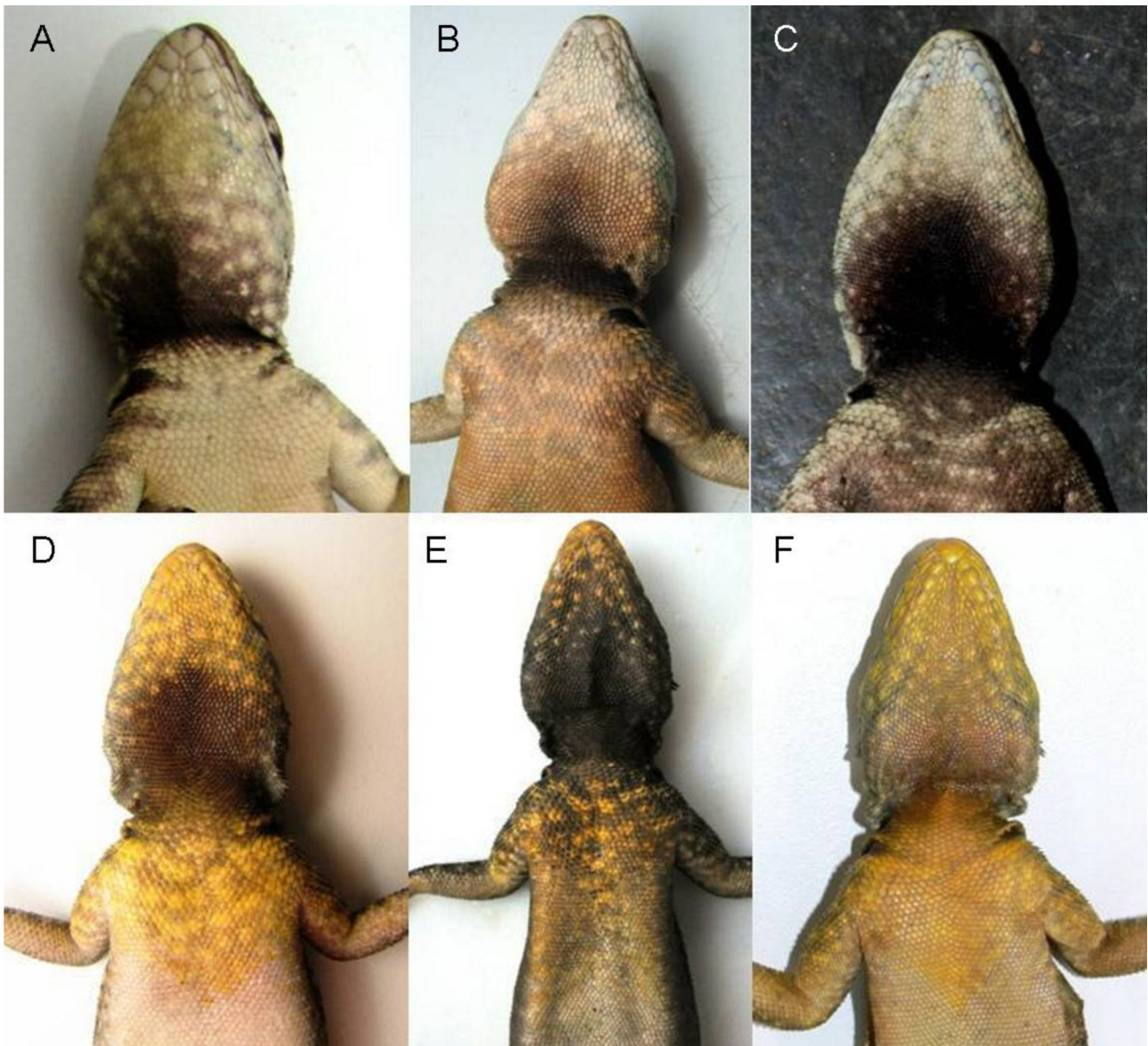


FIGURE 2. Chest and chin coloration in adult male specimens of the *Tropidurus torquatus* complex: A) Arraial do Cabo, North coast of Rio de Janeiro State (UFRGS 5756; SVL 70 mm); B) Imbituba, south coast of Santa Catarina (UFRGS 5302; SVL 116.6 mm); C) Comendador Levy Gasparian, mountain ranges of Rio de Janeiro (UFRGS 5832; SVL 121.4 mm); D) São Francisco de Assis, southwestern Rio Grande do Sul (UFRGS 5324; SVL 95 mm); E) Aratiba, northern Rio Grande do Sul (UFRGS 5579; SVL 107.9 mm); F) Ipuaçú, western Santa Catarina (UFRGS 5452; SVL 98.6 mm).

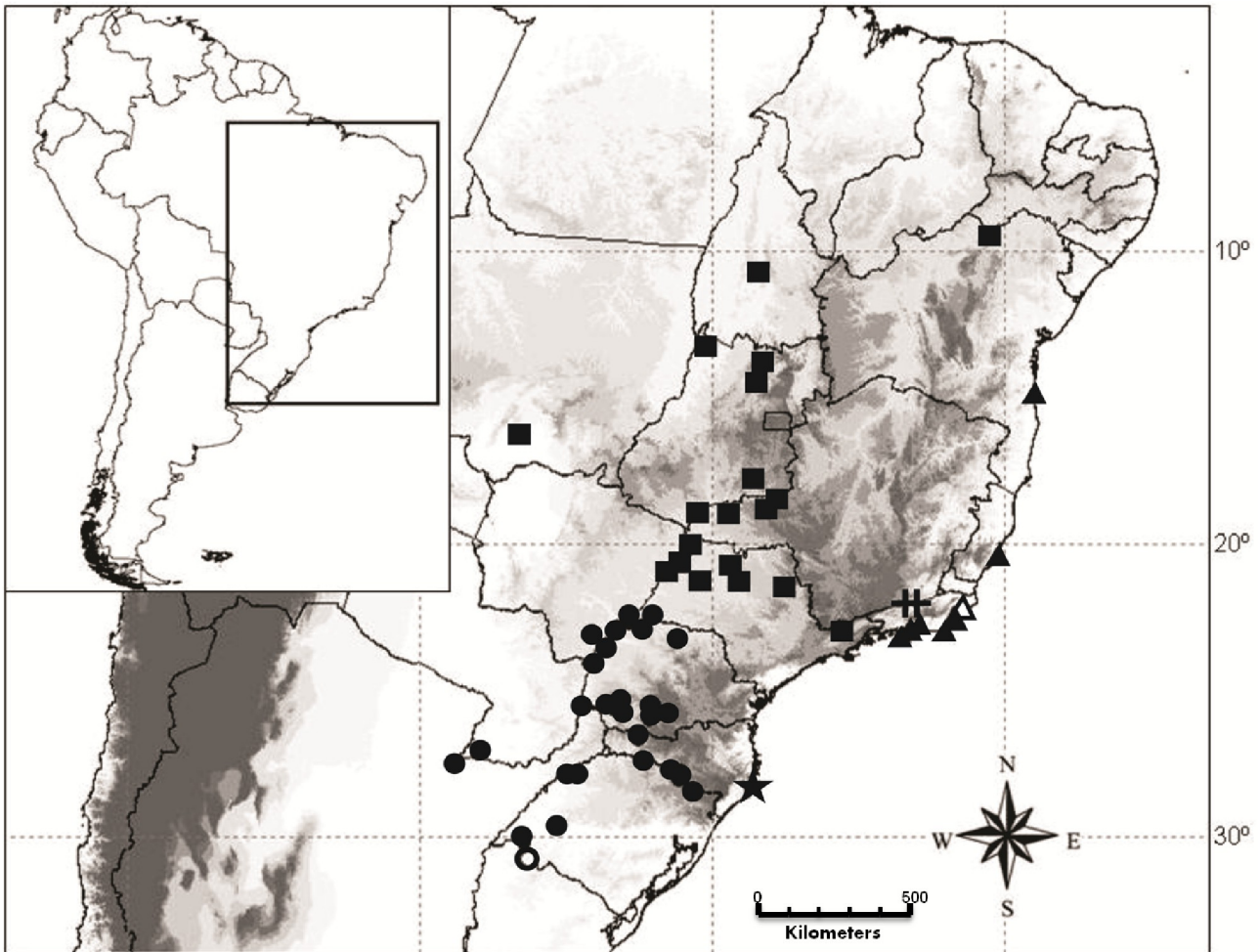


FIGURE 3. Geographic distribution of five distinct morphological groups of the *Tropidurus torquatus* complex: star: Imbituba (group 1); black circles: the *catalanensis* group (groups 2–5); squares: the *Cerrado* group (groups 6–7); crosses: mountain ranges of Rio de Janeiro (group 8); black triangles: eastern Brazilian coast (group 9); white triangle: type locality of *Tropidurus torquatus* (Lagoa do Paulista, Restinga de Jurubatiba National Park, Rio de Janeiro State, Brazil); white circle: type locality of *Tropidurus catalanensis* (Arroyo Catalán Grande, Artigas, Uruguay).

Although the geographic patterns of the variations found on the northern populations (groups 6–9) indicate the existence of at least three taxa, we judge these groups coverage insufficient to delimit geographically the variation found, therefore we maintain all these populations under the name *Tropidurus torquatus*. We could not analyze larger groups from the coast of Bahia and Espírito Santo. These populations differ in tibia counts in relation to that from the coast of Rio de Janeiro. The number of analyzed specimens from the mountain range in the border of the states of Rio de Janeiro and Minas Gerais was also small. Rodrigues (1987) stated that in Petrópolis (half way between the coast of Rio de Janeiro and the border with Minas Gerais) both forms (coastal and “inland”) occur. The lack of intermediary forms would be an evidence of two full species but we could not analyze specimens from this locality. Despite the broad geographic amplitude, the *Cerrado* group is relatively homogenous. Nevertheless, more than one form could be involved. The only two specimens analyzed from Poconé, state of Mato Grosso (MHNCI 987, 989; both females), more than 700 km distant from the nearest groups (São Simão and São Miguel do Araguaia, state of Goiás) present the highest values for dorsal scales within this group. Given the geographic amplitude of this region, we think that a large number of localities should be analyzed to elucidate geographic variation in morphological characters of these northern populations.

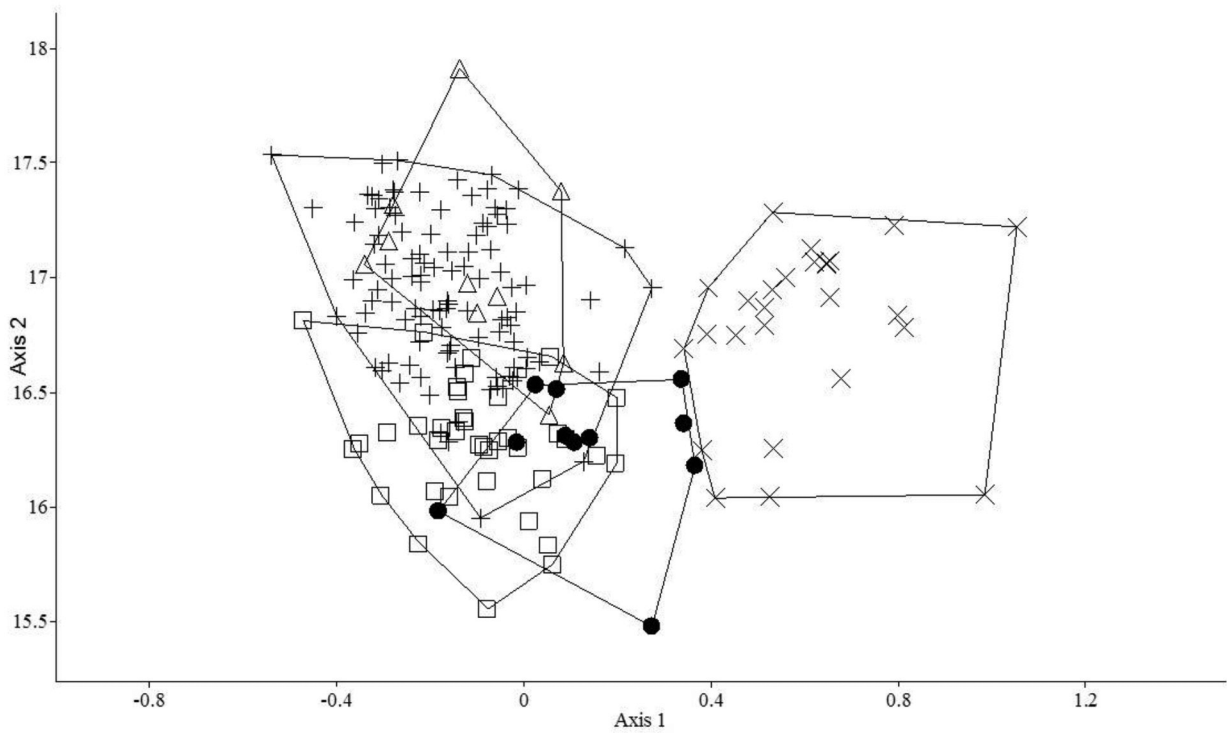


FIGURE 4. Discriminant analysis among meristic variables of males of five morphological groups of the *Tropidurus torquatus* complex. ● = Imbituba; + = “catalanensis”; □ = *Cerrado*; Δ = mountain ranges of Rio de Janeiro; x = eastern brazilian coast.

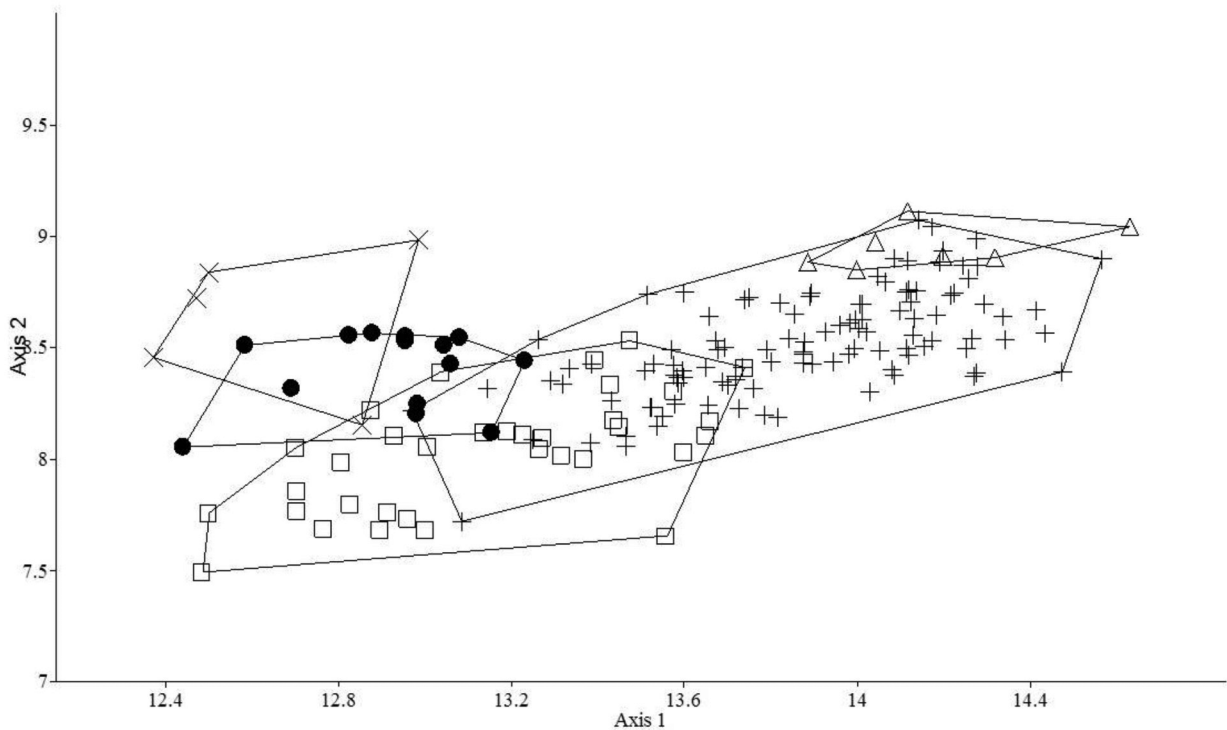


FIGURE 5. Discriminant analysis among meristic variables of females of five morphological groups of the *Tropidurus torquatus* complex. ● = Imbituba; + = “catalanensis”; □ = Central Brazil; Δ = mountain ranges of Rio de Janeiro; x = eastern brazilian coast.

***Tropidurus imbituba* sp. nov.**

(Figs. 6–10)

Holotype: Adult male, UFRGS 5932; collected on the 10th of January 2011 by T. S. Kunz and R. F. Bressan, in the rocky seashore of Praia da Vila (Morro do Farol; 28°14'20''S / 48°39'10''W), municipality of Imbituba, Santa Catarina, Brazil.

Paratypes: 10 males (MCP 18947-49; UFRGS 5044, 5092, 5203, 5225, 5302, 5354, 5358) and 14 females (MCP 18944-46; UFRGS 5043, 5045, 5093, 5164-65, 5205-07, 5357, 5545-46), all collected in the type locality by T. S. Kunz between December 2008 and January 2011.

Diagnosis. *Tropidurus imbituba* sp. nov. is distinguished from all other species of the *torquatus* group, except from *T. catalanensis* and *T. torquatus*, by having folds and pockets of the type “A” (*sensu* Rodrigues 1987). From *T. catalanensis* it differs in lower dorsal scales counts; from *T. catalanensis* and *T. torquatus*, by the distinctive bronze or orange coloration of the venter and sides of the trunk and neck in adult males (yellow in the chest and throat in *T. catalanensis* and white or cream in *T. torquatus*).

In relation to *T. torquatus*, the new species presents broad overlap in meristic characters with specimens from the Cerrados, differing in coloration (venter orange-bronze in *T. imbituba* sp. nov.; white or cream in *T. torquatus*). From specimens of the mountain ranges of Rio de Janeiro, it is well distinguished by meristic characters (dorsals, gulars, SAB); and from the coastal ones, it differs in attaining larger body size (SVL of the larger male of the new species is 125.8 mm, while the larger male of the coastal populations of eastern Brazil attained 107 mm.).



FIGURE 6. Holotype (UFRGS 5932) of *Tropidurus imbituba* sp. nov. in life (SVL 122.7 mm).

Description of holotype. Adult male, 122.7 mm SVL; intact tail, 206 mm; head length 28.2 mm; head width 25 mm; head height 17.1 mm; frontal scales of the head irregular and convex; nasals in contact with rostral and separated by a minimum of two scales; 3 canthals; anteriormost canthal separated from supralabials by one row of lorilabials; 9 infralabials; 5 enlarged supralabials to below center of eye, followed by 6 elongated scales to the commissure of mouth, of which the posterior five are very small; 5th supralabial in contact with the subocular; 7 spines in the preauricular fringe; 5 angulate, enlarged postmentals; first postmental in contact with first infralabial; first postmental not contacting one another; subocular separated from the preauricular fringe by a minimum of 10 scales; interparietal irregular, longer than wide; 10 scales in the medial line between interparietal and rostral; superciliary composed by two series, the anterior one with 5 scales and the posterior one with 2, separated by one

scale overlapped by scales of the two series; two rows of enlarged supraoculars, 9 in the first row and 6 in the second row (Figure 9).

Antehumeral fold present; two pockets under oblique neck fold; three axillary granular pockets; inguinal granular pocket present; scales of the sides of the neck much smaller than the adjacent dorsals; 100 keeled and mucronate dorsals; 94 scales around midbody; 81 ventrals; 53 gular scales; 20 scales on the dorsum of tibia; 25 subdigital lamellae under fourth finger; 31 subdigital lamellae under fourth toe; subdigital lamellae tricarinate; black, thick and strongly curved claws; femoral and preanal patches of black pigmented glandular scales present; without midventral patch of black pigmented glandular scales.



FIGURE 7. Dorsal (left) and ventral (right) views of the holotype (UFRGS 5932) of *Tropidurus imbituba* sp. nov.



FIGURE 8. Lateral view of head of the holotype (UFRGS 5932) of *Tropidurus imbituba* sp. nov. Freshly killed adult male (head length 28.2 mm).

Variation within type series: Head length 21–25% of SVL; tail length 60–64% of total length; largest male 125.8 mm SVL; largest female 86.7 mm SVL; smaller gravid female (with oviductal eggs) 74.9 mm SVL.

Frontal scales of head convex in adults; 2–4 scales between nasals; rostral contacting nasals in 44% of specimens; 10–13 scales between rostral and interparietal; 2–3 scale rows of enlarged supraoculars, generally three; 7–9 enlarged supraoculars in the first row; 5–6 supralabials to below centre of eye, generally 5, followed by 4–8 (generally 5) small elongated scales to the commissure of mouth; supralabials contacting subocular in 68% of specimens, generally with 5th and less frequently with 6th, 7th or both; 7–10 infralabials, generally 8–9; 6–8 spines in the preauricular fringe; 8–11 scales between the subocular and the preauricular fringe, generally 9–10; mental polygonal, followed by 3–5 enlarged postmentals; first postmentals contacting one another in only one specimens (UFRGS 5354); 2–4 canthals, generally 3; 43–55 gular scales (mean 50.8 ± 3.0 , $n=25$).

Two mite pockets under the oblique neck fold, the upper pocket is well developed and the lower one is poorly developed; antehumeral fold present; 2–3 axillary pockets, generally 3; inguinal granular pocket present; 27–33 subdigital lamellae under fourth toe (mean 30 ± 1.5 , $n=25$); 20–26 scales on the dorsum of tibia (mean 22.5 ± 1.4 , $n=25$). 99–113 dorsals in males (mean 104.9 ± 4.6 , $n=11$) and 102–116 in females (110.6 ± 3.7 , $n=14$); 87–109 SAB in males (mean 99.3 ± 5.6 , $n=11$) and 98–112 in females (mean 106.3 ± 4.2 , $n=14$); 70–89 ventrals (78.0 ± 5.3 , $n=25$).

Color in life. Dorsal color is light gray, cryptic in relation to the local rocks, with a pattern of black paravertebral patches and numerous cream colored spots along the trunk and limbs; in large males the spots in the sides of the trunk and neck may be bronze or orange; some females are almost uniform gray; black antehumeral band occupying 5–11 scale rows, separated (rarely not) from the opposite one by up to 17 scales (mean 10.9 ± 4.0); venter bronze in adults, cream in juveniles; adult males have femoral and preanal patches of black pigmented glandular scales; some large males present few black pigmented glandular scales on venter, but none presented a well developed midventral patch; adults have black gular patches; chin cream; dark gular reticulations enclosing cream blotches in juveniles but usually not evident in adults.

Etymology. The specific epithet is derived from the Tupí-guarani language, meaning “*imbé* in abundance” (*imbé* = a name used for some species of lianas and other plants, and *tuba* = abundance) and refers to the type locality, the municipality of Imbituba, the only place where the species is known to occur. The name is used as an indeclinable noun in apposition.

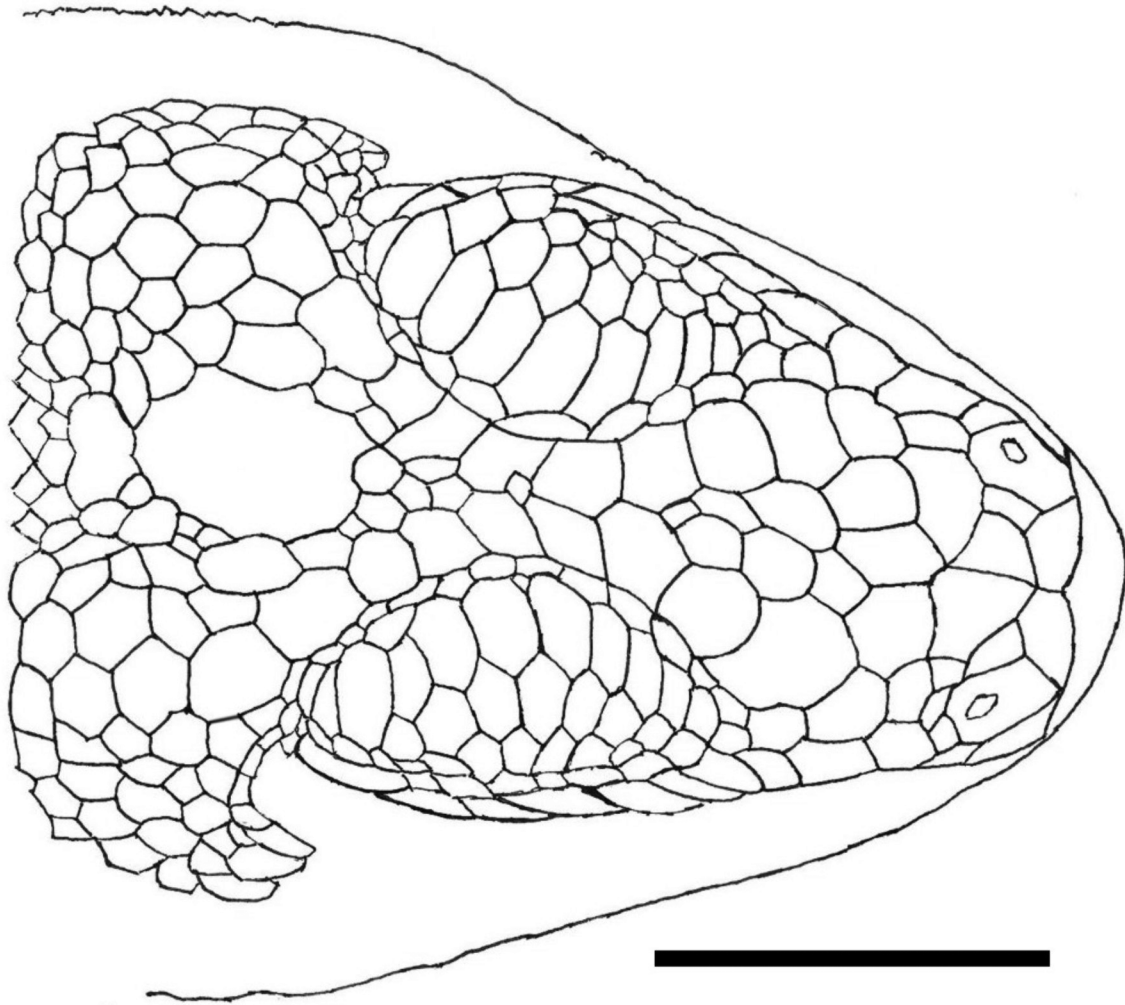


FIGURE 9. Dorsal view of head of the holotype of *Tropidurus imbituba* sp. nov. (UFRGS 5932; head length 28.2 mm). Scale bar = 10 mm.

Distribution. Restricted to a small and isolated granitic hill known as “Morro do Farol”, situated between Praia da Vila (Vila’s Beach) and the Port of Imbituba, in the municipality of Imbituba, southern coast of the state of Santa Catarina (28°14’S / 48°39’ W). The hill is about 1200 x 500 m large and reaches 100 m a.s.l. and is surrounded by a large sandy coastal plain. Most of the adjacent plain is currently occupied by the city of Imbituba. Vegetation of Morro do Farol is composed mostly by shrubs and low herbs, similar to that of the adjacent open *restingas*, with many rocky outcrops, and by portions of Atlantic Forest with low canopy (about 10 m tall) due to the strong ocean influence, mainly on the higher portions and on the western slope. The surrounding plain was originally covered by open *restingas* and sand dunes near the ocean, turning gradually westward to lowland Atlantic Forest. There are, also, many swamps in these plains (Figures 11–12).

Remarks. During the period of this study (2009–2011), we made several field expeditions to the coast of Santa Catarina searching for new *Tropidurus* populations. These expeditions included all rocky seashores near the Morro do Farol, Imbituba (e.g. Itapirubá, 28°20’24’’S, 48°42’11’’W; Pedra do Frade, 28°25’23’’S, 48°44’26’’W; Canto da Praia do Porto, 28°12’36’’S, 48°39’49’’W; Barra de Ibiraquera, 28°08’33’’S, 48°38’30’’W), including also a small island with an isthmus of only 80 m from Morro do Farol and distant places such as Farol de Santa Marta (28°36’13’’S, 48°48’47’’W) and Morro dos Conventos (28°56’03’’S, 49°21’47’’W). All these expeditions failed in localizing new populations.



FIGURE 10. *Tropidurus imbituba* sp. nov. at the rocky seashore (Morro do Farol) of Praia da Vila, Imbituba, Santa Catarina, Brazil. Adult male (not collected).

The distribution pattern of *T. imbituba* is uncommon among lizards from the Atlantic Coast of South America and we are unaware of other species of lizards with a similar distribution in that region. We believe that the sandy plains and dunes surrounding Morro do Farol represent barriers to the dispersal of these lizards.

Morro do Farol is a relatively well preserved area, neighboring a marine conservation unit, the “Área de Proteção Ambiental da Baleia Franca”. However, there is a great amount of tourists in summer and it is adjacent to the Port of Imbituba which is expected to expand in a few years. A portion of the western slope of Morro do Farol is already occupied by activities of the port. Considering the extremely restricted distribution and a expected decline of habitat quality and extension, *T. imbituba* can be categorized as Critically Endangered (CR), according to criteria B1a+b(iii) (known and estimated area of occurrence <100 km² and presence of relevant human impacts) of the IUCN Red List (IUCN 2001).



FIGURE 11. Morro do Farol, Imbituba, the type locality of *Tropidurus imbituba* sp. nov. Praia da Vila (Vila’s Beach) on the left and Port of Imbituba right behind the hill. The city of Imbituba is in the background. Photograph courtesy of the Port of Imbituba.



FIGURE 12. Rocky seashore at Praia da Vila, Imbituba, Brazil. Arrow indicates the exact place where most of the type series was collected, including the holotype.

***Tropidurus catalanensis* Gudynas & Skuk, 1983, revalidated**

(Figs. 13–17)

Tropidurus catalanensis Gudynas & Skuk 1983: 2. Type locality: “from a hill 1 km 300 ESE of route N° 30 and Catalán Grande stream (airline), Departamento de Artigas, Uruguay”. MNHN 3489.

Tropidurus torquatus—Rodrigues 1987: 190 (*Partim*).

Tropidurus torquatus catalanensis—Ceï 1993: 315.

Tropidurus catalanensis—Ceï 2003: 135.

Holotype. Museo Nacional de Historia Natural, Uruguay (MNHN) 3489; male, from a hill near route n° 30 and Arroyo Catalán Grande (airline), Departamento de Artigas, Uruguay; collected 30 March 1983 by L. Amato, E. Gudynas and G. Skuk; by designation on the original description (Figure 13).

Diagnosis. *Tropidurus catalanensis* is distinguished from all congeners, except those of the *torquatus* group, by lacking a middorsal scale row and by having imbricate and keeled dorsal scales. From those of the *torquatus* group, except from *T. torquatus* and *T. imbituba* **sp. nov.**, it can be distinguished by having folds and pockets of the type “A” (*sensu* Rodrigues 1987). From *T. imbituba* **sp. nov.** and *T. torquatus*, it differs in the yellow coloration of the chest and throat, more intense in adult males. From *T. imbituba* **sp. nov.** it also differs, with little overlap, in dorsal scale counts, ranging 104–130 (mean 116.9 ± 4.8) in males and 110–140 (mean 126.7 ± 6.8) in females, while in *T. imbituba* it ranges 99–113 (mean 104.9 ± 4.6) in males and 102–116 (mean 110.6 ± 3.7) in females.

Variation. Head length 21–25% of SVL; tail length 58–64% of total length; largest male presented 127.9 mm SVL; Smaller male with opaque and convoluted efferent ducts presented 79.1 mm SVL; largest female presented 98.8 mm SVL and the smaller female with oviductal eggs presented 72.7 mm SVL.



FIGURE 13. Dorsal (left) and ventral (right) views of the holotype (MNHN 3489; SVL 114.8 mm) of *Tropidurus catalanensis*.

Frontal scales of the head generally convex in adults; 2–4 scales between the nasals; rostral contacting nasals in 37.3% of specimens; 10–15 scales between rostral and interparietal; 2–4 scale rows of enlarged supraoculars, generally three; 6–9 enlarged supraoculars in the first row (examples of the supraocular scuttellation patterns are in Gudynas & Skuk 1983, p. 4, fig. 1; Cei 1993, p. 319, fig. 49A; and Cei 2003, p. 135, fig. 2F); 4–7 supralabials to below the center of eye generally 5, followed by 3–7 (generally 4–5) small elongated scales to the commissure of mouth; supralabials contacting subocular in 60% of specimens, generally with 5th or 6th (rarely with both), and less frequently with 4th or 7th; 6–10 infralabials, generally 8–9; preauricular fringe with 4–9 spines, generally 7; 9–15 scales between the subocular and the preauricular fringe, generally 11–12; mental triangular or polygonal, followed by 2–5 (generally 3–4) angulated postmentals; first postmentals contacting one another in 13.8% of specimens; 2–4 canthals, generally 3; 46–65 gular scales (mean 56.6 ± 3.8 , $n=216$) (47–64 in Gudynas & Skuk 1983).

Two mite pockets under the oblique neck fold, the upper pocket is well developed and the lower one is poorly developed; antehumeral fold present; 2–3 axillary pockets, generally two; inguinal granular pocket present; 24–34 subdigital lamellae on the fourth toe (mean 29 ± 1.9 , $n=216$) (26–32 in Gudynas & Skuk 1983); 18–25 scales on the dorsum of tibia (mean 21.6 ± 1.3 , $n=217$), usually 21–23.

In the original description, Gudynas and Skuk (1983) stated that there were no significant sexual differences, thus, presenting all meristic and morphometric variables grouped for both sexes. Our data do not corroborate this statement in relation to dorsal scales and SAB. Males present 104–130 imbricate, mucronate and keeled dorsals (mean 116.9 ± 4.8 , $n=103$), while females present 110–140 (mean 126.7 ± 6.8 , $n=110$). Specimens from lowlands

of southwestern Rio Grande do Sul and the vicinities of the mouth of the Paraguay River (northern Argentina and southern Paraguay) present the lowest means (113.2 ± 4.6 in males; 122.4 ± 4.7 in females) while those of the valleys of the upper Uruguay Basin present the highest means (119.8 ± 4.3 in males; 130.4 ± 5.5 in females).

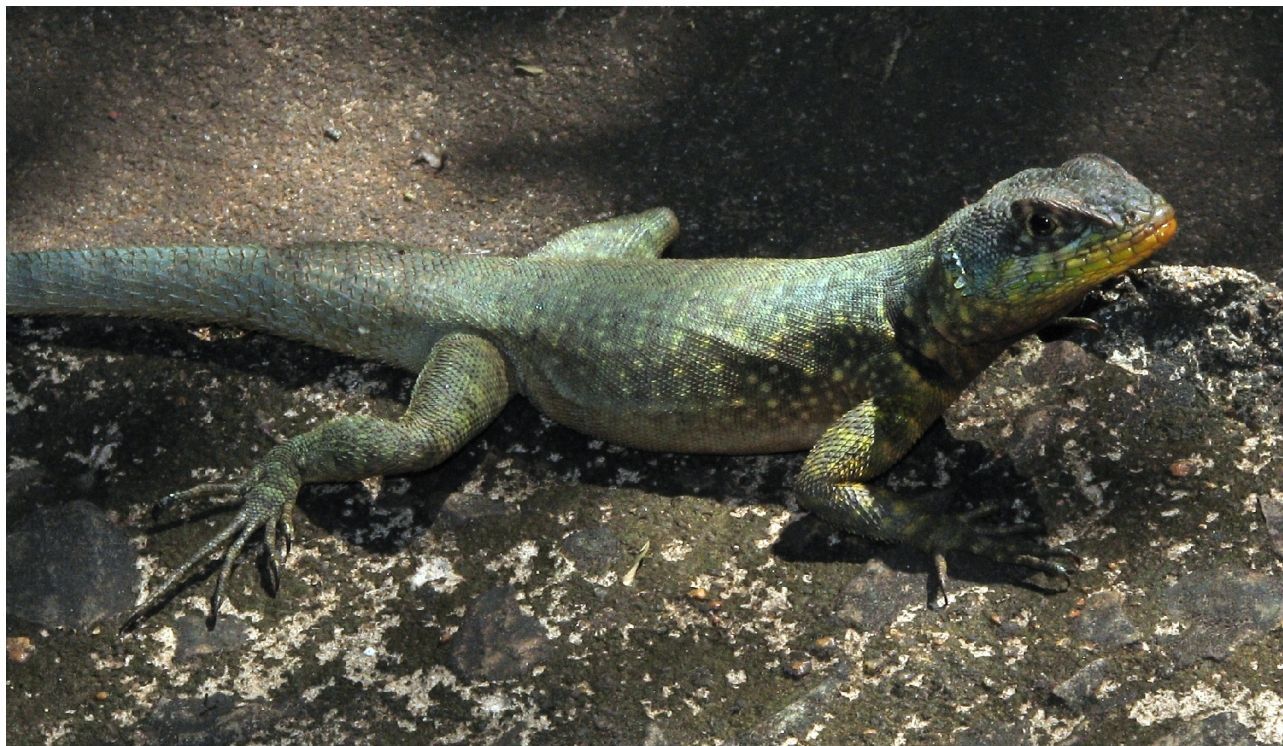


FIGURE 14. *Tropidurus catalanensis* from Iguaçu National Park, Foz do Iguaçu, Paraná, Brazil (not collected). Note the yellow coloration of chin, including infra and supralabials.

Gudynas and Skuk (1983) presented vertebral and paravertebral scale counts, which ranged, respectively, 107–131 and 110–142. Since lizards of the *torquatus* group lack a vertebral crest or enlarged vertebral scale rows, distinguishing vertebrals and paravertebrals is difficult, but these values are similar to what we found in our dorsal counts. SAB ranged 91–116 (mean 103.4 ± 5.4 , $n=97$) in males, and 103–131 (mean 115.9 ± 6.6 , $n=105$) in females (89–121 in the original description, for males and females grouped). As for dorsals, specimens from the lowlands of southwestern Rio Grande do Sul, northeastern Argentina and southern Paraguay present the lowest means (99.5 ± 3.2 in males, 110.5 ± 3.7 in females), and those of the upper Uruguay Basin, the highest means (106.5 ± 4.5 in males, 119.4 ± 5.6 in females). Ventrals 72–103 (mean 86.2 ± 6.1 , $n=214$; the original description didn't present variation of this character).

Color in life. Dorsal color is brown, gray or greenish, with an irregular pattern of black paravertebral patches and many yellow or cream spots in the dorsum of the trunk and limbs; yellow or cream spots are more numerous in males; black antehumeral band occupying 4–10 scale rows, separated from the opposite one by 3–35 scales (mean 15.7 ± 6.3); venter white or cream; adult males with femoral and preanal patches of black pigmented glandular scales; presence of midventral patches variable but rarely lacking in specimens larger than 100 mm SVL; temporal region usually bluish; adults with black gular patches; chin yellow with dark reticulations enclosing yellow blotches; yellow pigment reaches the chest and sometimes the infra and supralabials; yellow pigment lacking in juveniles and usually less evident, or lacking, in females.

Distribution. Northwestern Uruguay, northeastern Argentina, southern Paraguay and southern Brazil, reaching southwestern São Paulo and southeastern Mato Grosso do Sul extremes. In northwestern Uruguay and southwestern Rio Grande do Sul, the species is found on isolated rocky hills of low altitude regionally known as “cerros”. These hills are sparsely distributed along wide areas of *campos* (grassland) of the Pampa Biome. In the remaining areas, species distribution follows the course of the main tributaries of the Paraná and Uruguay Rivers (La Plata Basin). Along the valleys and canyons of these rivers, the species occurs mainly on isolated populations in rocky outcrops among areas originally covered by seasonal forests.



FIGURE 15. *Tropidurus catalanensis* from Campos Novos, Santa Catarina, near the Uruguay riverbank (not collected).



FIGURE 16. *Tropidurus catalanensis* from São Francisco de Assis, Rio Grande do Sul. Adult male (not collected).



FIGURE 17. Lateral view of head of *Tropidurus catalanensis* (UFRGS 5324) from São Francisco de Assis, Rio Grande do Sul, Brazil. Freshly killed subadult male (head length 21.4 mm).

Remarks. The distribution of *T. catalanensis* in southern Brazil shows an interesting pattern, in association with river valleys and very restricted and localized populations, sometimes a hundred kilometers apart from other populations. The lack of gene flow between these populations is evidenced by some differences in meristic characters. For example, specimens from upstream of the Iguaçu river present, with high frequency, contact of the first post-mental with the opposite one (and, in this case, there is no contact of the gular scales with the mental scale). The frequency of this condition decreases downstream toward its mouth, and is rare in all other analyzed populations. Other variable condition is the contact between the nasals and the rostral scale, which is very frequent in some populations from southwestern Rio Grande do Sul (e.g. from São Francisco de Assis) and in those from Foz do Iguaçu (state of Paraná), but not frequent in other populations.

Populations of the river valleys inhabit rocky outcrops with abundant crevices. This punctual distribution pattern, at least in the low meanders of the Southern Brazilian Plateau, seems to indicate that the current climatic condition is unfavorable for the species (see Behling *et al.* 2009 for evidences of the climate dynamics of southern Brazil during the Holocene). These rocky outcrops represent the only natural open habitats among these river valleys, originally covered with seasonal forests. In addition, these river valleys and canyons retain milder climatic conditions in relation to the higher portions of the plateau. Despite the intense deforestation of the seasonal forests in southern Brazil, these populations have not expanded their occupation beyond the limits of the outcrops, pending in favor of the argument that the current climatic condition is unfavorable for the species expansion, at least in the Southern Brazilian Plateau. This situation is quite contrasting with the alleged opportunism of these lizards that, according to Rodrigues (1987), being good colonizers, would be expanding its distribution favored by deforestations (at least for the *torquatus* populations in the state of São Paulo). In fact, there is evidence to believe that the opposite is occurring in southern Brazil. Apparently, some populations have disappeared after the formation of reservoirs for hydroelectric dams on the Iguaçu River, in the state of Paraná (R.S. Bérnils, personal communication) and in the upper Uruguay Basin in the border of the states of Santa Catarina and Rio Grande do Sul (M. Borges-Martins, personal observation). Viability of populations of these saxicolous lizards could be conditioned to the maintenance of adequate habitats. In the surroundings of the Quebra-Queixo hydroelectric dam, on the Chapecó river (a large tributary of the Uruguay river), where rocks and crevices are very abundant, the

species is also still abundant. For populations from southwestern Rio Grande do Sul, expansion of *Eucalyptus* spp. plantations in the vicinities of the rocky outcrops could result in shading and affect the viability of some of these populations (personal observations; see Pillar *et al.* 2009 for a discussion on the conservation of the southern Brazilian “campos”).

It is worth considering that the mainly saxicolous habit of the populations from Southern Brazil, Argentina and Uruguay (Gudynas & Skuk 1983; Cei 1993; this study) differs in what Cei (1993) observed for populations from Corrientes (Argentina), allegedly more arboreal. Still, the Atlas of Alvarez *et al.* (2002) shows that these populations are also distributed exclusively along the Parana River and in the vicinities of the Paraguay River mouth, both rivers of the La Plata Basin, as are the remaining populations.

***Tropidurus torquatus* (Wied-Neuwied, 1820)**

(Figs. 18–20)

Stellio torquatus Wied-Neuwied, 1820: 106. Type locality: not given. Restricted to the coast of the State of Rio de Janeiro according to Rodrigues (1987), based on Wied’s itinerary. Neotype, MZUSP 54907, from Lagoa do Paulista, Restinga de Jurubatiba National Park, designated by Rodrigues (1987).

Agama operculata Lichtenstein, 1822: 243. Type locality: not given (fide Rodrigues 1987).

Agama brasiliensis Raddi, 1822: 59. Type locality: surroundings of the city of Rio de Janeiro.

Agama tuberculata Spix, 1825: 12. Type locality: States of Rio de Janeiro and Bahia. Lectotype, ZSMH 531/0, designated by Hoogmoed & Gruber (1983).

Trop[idurus] Tuberculata—Gray, 1831: 41 (*partim*).

Tropidurus torquatus—Wied-Neuwiedi, 1825: 139

Ecphymotes torquatus—Duméril & Bibron, 1837:344 (*partim*)

Tropidurus microlepidotus Fitzinger, 1843: 72. Type locality: not given. Restricted to the State of Rio de Janeiro, according to the itinerary of the frigate Novara (fide Rodrigues, 1987).

Taraguira darwini Gray, 1845: 220. Type locality: Abrolhos Archipelago.

Tropidurus torquatus torquatus—Cei, 1993: 316.

Neotype. MZUSP 54907; sex not informed; from Lagoa do Paulista, Parque Nacional da Restinga de Jurubatiba, north coast of the State of Rio de Janeiro (22°14’S e 41°33’W); collected 15 December 1979 by P. E. Vanzolini; designated by Rodrigues (1987).

Diagnosis. *Tropidurus torquatus* is diagnosable from all congeners, except those of the *torquatus* group, by lacking a middorsal scale row and by having imbricate and keeled dorsal scales. From those of the *torquatus* group, except for *T. catalanensis* and *T. imbituba* **sp. nov.**, it can be distinguished by having two mite pockets under the oblique neck fold, the upper pocket is well developed and the lower is poorly developed; two or three axillary pockets; and inguinal granular pocket present (type “A” *sensu* Rodrigues 1987). As presently recognized *T. torquatus* can be distinguished from *T. catalanensis* and *T. imbituba* only on the base of coloration characters which are best developed on adult males. From *T. catalanensis* it differs in not having yellow coloration on chest and mental region, while from *T. imbituba* it differs in not having orange-bronze coloration on the venter and sides of the trunk.

Variation. Head length 20–25% of SVL; tail 57–64% of total length. Frontal scales of the head generally flat, eventually concave and, in this case, most frequently in males from *Cerrado* and the mountain ranges of Rio de Janeiro. Number of scales between the nasals 2–4; rostral contacting nasals in 25.4% of the specimens from *Cerrado* and in 60.6% and 70.6%, respectively, of specimens from coast and from the mountain ranges of Rio de Janeiro; 9–15 scales between rostral and interparietal; 2–4 scale rows of enlarged supraoculars, generally three; 6–9 enlarged supraoculars in the first row of specimens from the coast and from the mountain ranges of Rio de Janeiro and 6–11 in specimens from *Cerrado* (examples of the supraocular scuttelation patterns in some populations are in Rodrigues 1987, p. 194, fig. 28C-H; Cei 1993, p. 319, fig. 49B; and Cei 2003, p. 135, fig. 2G); 4–7 supralabials to below the center of eye, generally 5, followed by 3–7 small elongated scales to the commissure of mouth; supralabials contacting subocular in 51.6% of specimens from the coast; in 82.4% of specimens from the mountain ranges of Rio de Janeiro; and in 41% of specimens from *Cerrado*; in the three cases, contact is generally with the 5th supralabial, or less frequently with the 4th, 6th or 7th; in some cases subocular is in contact with both 5th and 6th or 6th and 7th supralabials; 7–11 infralabials, generally 8–9; preauricular fringe with 5–8 spines (4–8

according to Rodrigues 1987), generally 6–7; 8–14 scales between the subocular and the preauricular fringe; mental generally triangular or polygonal in the coast and in the mountain ranges of Rio de Janeiro; mental generally presents a bell-like shape (laterally curved) in specimens of the *Cerrado* group of populations; 3–5 postmentals (3–4 in Rodrigues 1987); first postmentals contacting one another in 6.9% of specimens; 2–4 canthals, generally 3; 42–58 gular scales (51.1 ± 3.3 , $n=70$) in specimens from *Cerrado*, 49–63 (57.6 ± 4.6 , $n=16$) in those from the mountain ranges of Rio de Janeiro and 41–61 (49.4 ± 3.9 , $n=32$) in the coast.



FIGURE 18. *Tropidurus torquatus* from Arraial do Cabo, north coast of Rio de Janeiro. Adult male (UFRGS 5756; SVL 70 mm).



FIGURE 19. *Tropidurus torquatus* from Comendador Levy Gasparian, mountain ranges of Rio de Janeiro, near to the border with Minas Gerais. Adult male (UFRGS 5829; SVL 126.6 mm). Photo by Rafael Balestrin.



FIGURE 20. *Tropidurus torquatus* from Brasília National Park, Brasília, Distrito Federal, Central Brazil (not collected).

Two mite pockets under the oblique neck fold, the upper pocket is well developed and the lower is poorly developed; antehumeral fold present; two or three axillary pockets; inguinal granular pocket present; 26–35 subdigital lamellae on the fourth toe; 17–33 scales on the dorsum of tibia (20–33 in the coastal populations and 17–24 in those from *Cerrado* and the mountain ranges of Rio de Janeiro). Dorsals imbricate, mucronate and keeled, 95–140 (89–144 according to Rodrigues 1987); 95–125 in coastal populations (102–121 in males, 102–115 in females; we couldn't determine the sex of the specimen MHNCI 3648, a juvenile from Ilhéus, Bahia, which presents 95 dorsals, the lowest value considering all analyzed groups); 107–140 in the mountain ranges of Rio de Janeiro (107–128 in males, 124–140 in females); 100–136 in *Cerrado* (100–120 in males, 102–136 in females). 86–130 scale rows around midbody (76–143 according to Rodrigues 1987); 92–117 in coastal populations (92–117 in males, 102–117 in females); 100–130 in the mountain ranges of Rio de Janeiro (100–119 in males, 123–130 in females); 86–114 in specimens from *Cerrado* (86–105 in males, 91–114 in females). 70–97 smooth ventrals.

Color in life. The dorsal pattern in coastal populations is light gray with a very variable pattern of white and dark spots (Figure 18). In the populations from the mountain ranges of Rio de Janeiro and *Cerrado*, ground color is browner or greenish. Those from the mountain ranges of Rio de Janeiro are very dimorphic in coloration, adult males showing numerous black and cream spots (Figure 19), while females are almost uniform gray or brown, with few spots. A black antehumeral band occupying 5–15 scale rows in coastal populations, separated or not from the opposite one by up to 25 scales (mean $14,2 \pm 5,9$); this band occupies 5–13 scale rows in specimens from the mountain ranges of Rio de Janeiro and is separated or not from its opposite one by up to 18 scales ($11,5 \pm 6,3$); and 3–10 scale rows, separated or not from its opposite one by up to 18 scales ($10,2 \pm 5,4$) in specimens from *Cerrado*. Venter white or cream. Adult males whit femoral and preanal patches of black pigmented glandular scales. Presence of midventral patches variable in specimens of all populations analyzed but usually present in the largest males (Rodrigues 1987 stated that this condition was variable only in the coastal populations and always present in the “inland” populations). Adults with black gular patches, more developed in males. Chin white or cream, with dark reticulations enclosing white or cream blotches more evident in juveniles.

Distribution. From north and northwestern state of São Paulo, northward to the limits of the Cerrado formations in Tocantins. West to Mato Grosso and east it reaches the coast from the city of Rio de Janeiro to Bahia

(about 50 km south of Salvador, according to Rodrigues 1987). Recently the species was reported for the coast of São Paulo but it was considered a recent occupation as a result of the human expansion in areas along the coast (De Sena *et al.* 2008).

Remarks. At least three forms are included under *Tropidurus torquatus*. From east to west, a group of lizards inhabits mainly the coastal *restingas* from Bahia to Rio de Janeiro. This form corresponds to *Tropidurus torquatus strictu sensu*, since the species was described based on lizards from these populations. There is another form in the mountainous region in the border of Rio de Janeiro and Minas Gerais. This region was, originally, predominantly covered with Atlantic Rainforest and it is supposed that these populations were originally restricted to open enclaves in the midst of forests, such as large rock outcrops. Westward, in the Brazilian central plateau, there is a third set of populations inhabiting mainly the Cerrado domains.

Coastal populations from eastern Brazil seem to have a continuous distribution along the coastal *restingas*, where these lizards are very abundant. However, these populations are not morphologically homogenous as evidenced by tibia counts, which shows clinal variation, diminishing from south to north. Rodrigues (1987) provided a plausible explanation for the great variation found in the coastal populations, based on sea level fluctuations.

It is important to note that the coastal distribution of *torquatus* includes several islands and, there, most of the available habitats are rocks. One of these populations, from Abrolhos Archipelago, was described by Gray (1845) as *Taraguira darwinii*. A difference between the saxicolous populations, including the insular ones, and the coastal sand-dwelling populations is the shape of the claws, thick and strongly curved in the saxicolous forms and long and thin in the psammophilous forms. However, some specimens collected in the coast in habitats other than the *restingas* also presented thicker claws, although all other characteristics are still identical to those from the *restingas*. Therefore, it is a much variable characteristic with little value in understanding differentiation patterns, as already noted by Rodrigues (1987). Rodrigues found lizards with long and thin claws only in the coast. However, we found lizards with this character in our group from Central Brazil (*Cerrado* group). These populations are probably the most generalist form in relation to habitat use and seem to have a continuous distribution in this broad area, which can explain the relative homogeneity of this group. In many areas of Cerrado, *T. torquatus* uses tree trunks, termite mounds, and even urban areas as much as, or more frequently than rocks (Rodrigues 1987; Nogueira 2006; personal observations). According to Nogueira *et al.* (2005) and Nogueira (2006), the Cerrado populations of *T. torquatus* are associated with the border of gallery forests, where they use mainly tree trunks, rarely occurring in the large and continuous areas of open Cerrados (savannas).

Taxonomic and biogeographic comments. In the first taxonomic revision of the *Tropidurus torquatus* group, Rodrigues (1987) noted morphological differences between the coastal populations of *torquatus* and the remaining “inland” populations. However, as he could not find a geographic structure for all the variation found, he preferred to keep them as a single species. This author based his analysis on the sympatric occurrence of lizards with distinct fold and pocket patterns, delimiting very large and heterogeneous areas of sympatry, as he pointed out. Besides lacking a representative group of the southernmost populations attributable to *torquatus*, the joint analysis of morphologically distinct populations, grouped within large sympatry areas, may have prevented the recognition of geographic patterns.

Geographic distribution of most *Tropidurus* species, particularly those in the *torquatus* group, is strongly associated to the great South American diagonal of open formations (from northeast to southwest, respectively, the Caatinga, Cerrado and Chaco) (Vanzolini 1972, 1974; Rodrigues 1987; Zanella 2010). Some evidences suggest recent speciation processes in the genus. Harvey and Gutberlet (1998) described three new *Tropidurus* species from the Serranía de Huanchaca, Bolivia, an isolated mountain range overlapping the northeastern border of Bolivia and Brazil, in a transitional area between the Amazon and the Cerrado morphoclimatic domains. These authors suggested that their new species probably shared recent ancestors with *Tropidurus* currently distributed in open formations at low elevations along the Andes of Argentina and southern Bolivia, forming pairs of possible sister species (*T. etheridgei*–*T. chromatops*, *T. melanopleurus* Boulenger, 1902–*T. callathelys* Harvey & Gutberlet, 1998 and *T. spinulosus* [Cope, 1862]–*T. xanthochilus* Harvey & Gutberlet, 1998), and that a single historical event may account for the evolution of each species pair from common ancestors previously distributed across open formations of south-central South America. Relationship between the last two pairs, involving species of the *spinulosus* group, was later corroborated on the basis of molecular and morphological evidence (Harvey & Gutberlet 2000; Frost *et al.* 2001).

Rodrigues (1987) attributed the great variability of the coastal populations of *torquatus* to the events of marine transgressions and regressions occurred after the last glaciation. It is possible that these events have also been of great importance to the evolution of *T. imbituba*, since in the recent past the hill where these lizards are isolated was an island in the periods of marine transgressions, when the ocean was above the current level (Horn Filho 2003; Leal 2005; Vieira *et al.* 2009). As Rodrigues pointed out, the physiognomy of the South American landscapes was very different at the end of the last glaciation, when the climate was cooler and arid, and the emerged area of the continent was much larger as a consequence of marine regression. One could hypothesize that a common ancestor of the coastal *T. torquatus* and *T. imbituba* had, in this period, a broad distribution along the Brazilian coast. However, the fact that *imbituba* was not able to colonize the adjacent *restingas* suggests that his ancestor was already a saxicolous form that possibly inhabited the granitic slopes of the Serra do Mar and Serra Geral, currently covered by the Atlantic Rain Forest. With the gradual shift to a more humid climate and the expansion of forests, these lizards had their habitat drastically reduced. Thus, *T. imbituba* is probably more related to *T. catalanensis* or the “inland” populations of *T. torquatus* than to the psammophilous form of the eastern Brazilian coast (*T. torquatus stricto sensu*).

It is interesting to note that the *restingas* and sand dunes of the coastal plains of southern Santa Catarina share with the plains of Rio Grande do Sul and Uruguay typical faunistic elements of open areas of the Pampa Biome, while the hills and rocky seashores that break the continuity of these coastal plains present a typical fauna of the Atlantic Rainforest (Ghizoni *et al.* 2009; Kunz & Ghizoni 2011; Kunz *et al.* 2011). It seems that *T. imbituba* represents a relictual element of a period of semi-arid climate, when a typical open area fauna was able to occupy those hills, currently covered by forests. Other reptile species from open areas that inhabit these rocky seashores, like the skink *Aspronema dorsivittatum* (Cope, 1862) (Mabuyidae), are also able to occupy the sandy *restingas*.

Rodrigues (1987) found two diversity patterns in the *torquatus* group. In the first group, from eastern South America, there is a large amount of species with restrict geographic distributions. In the second group, there is a low diversity but the species have wide geographic distributions. According to Rodrigues, species of the second group are related to Central Brazil, noting that none can be treated, without restrictions, as an animal of the great South American diagonal of open formations. Still, from northeast to southwest, there is *T. hispidus* inhabiting mainly the Caatingas, *T. itambere*, *T. oreadicus* and the populations of *T. torquatus* from central Brazil with wide distributions in the Cerrado Domains (noting that the *torquatus* distribution in Central Brazil seems to be more related to gallery forests than to the extensive savanna-like formations in the Cerrado; see Nogueira *et al.* 2005 and Nogueira 2006), and *T. etheridgei* mainly in the Chaco Domains, with some populations in the Cerrado.

Tropidurus catalanensis has a parapatric distribution in relation to *T. etheridgei* (which occurs exclusively west of the Paraná Basin), with a more continuous distribution and less restricted to the river valleys in the Pampa Domains of southwestern Rio Grande do Sul and northwestern Uruguay, reaching marginally the Chaco Domains in the vicinities of the Paraná and Paraguay rivers (in the border of Argentina and Paraguay) and restricted to the river valleys and canyons of the Paraná-Uruguay Basin in the Paranaense Forest (*sensu* Morrone, 2001).

The distribution patterns of *T. catalanensis* and *T. imbituba* **sp. nov.** seem to corroborate the two distribution patterns found by Rodrigues, and these can be strengthened with the recognition of specific status for the *torquatus* populations from the mountain ranges of southeastern Brazil (with probably restricted distribution) and for those from Central Brazil (with a broader distribution). However, further conclusions on the relationship of the species associated with the *Tropidurus torquatus* complex and their distributional patterns must await ongoing phylogenetic and phylogeographic studies of the *Tropidurus torquatus* group.

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APPENDIX I. Material examined.

Countries are given in bold capitals, states in plain capitals, municipalities in plain text, and localities in italics.

Tropidurus torquatus

BRASIL: BAHIA: Ilhéus, *área da CEPLAC* (MHNCI 3648); ESPÍRITO SANTO: Vila Velha, *Ilhas Itatiaia* (MCP 6643); GOIÁS: Caldas Novas, *UHE Corumbá* (MCP 8646-55); Minaçu, *UHE Serra da Mesa* (MCP 9343-44); Niquelândia, *UHE Serra da Mesa, margem esquerda do rio Bagagem* (MCP 4759); São Miguel do Araguaia, *rio Araguaia–São Francisco* (MHNCI 1867); São Simão, *Fazenda São Vicente* (MHNCI 12102); MINAS GERAIS: Cascalho Rico (MCP 4620-22, MHNCI 7125); Ituiutaba, *PCH Jacu* (MHNCI 12269-70); Uberlândia (MCP 4623-32), *Fazenda do Gloria* (MCP 3548-50); MATO GROSSO: Poconé, *Base Pantanal do IBAMA* (MHNCI 987, 989); PERNAMBUCO: Petrolina (MHNCI 8219); RIO DE JANEIRO: Arraial do Cabo (UFRGS 5753-56); Maricá, *Barra de Maricá* (CHUFSC 531, 533); Comendador Levy Gasparian, *Afonso Arinos* (5829-35); Macaé (MZUSP 10170-71, 10174, 10176-77); Rio de Janeiro, *Ilha do Governador* (MCN 7099-7100), *Jacarepaguá* (MZUSP 36423-24, 36426, 36428, 36430-32, 36435-40, 36444-45), *Praia do Grumari* (UFRGS 2469-70), *São Cristóvão* (MCN 7101); Três Rios, *Anta* (MZUSP 5091-98, 5100-01); SÃO PAULO: Araçatuba (MZUSP 5084); *Nova Niponia* (MZUSP 6844); Castilho (MZUSP 10179, 10193-94, 10197, 10199, 10202-09, 13598); Itajobi (MZUSP 75174-75), *Fazenda Águas Claras* (MZUSP 75167-70, 75199); Pereira Barreto, *rio Tietê–UHE Três Irmãos* (MHNCI 2603, 2605, 4514); Santa Fé do Sul, *Cachoeira da Onça* (MZUSP 8245-46); São José do Rio Preto (MZUSP 12269, 75179-80); São Simão (MZUSP 98589); Taubaté (MZUSP 80164); TOCANTINS: Porto Nacional, *Fazenda Nossa Senhora da Conceição* (MCP 3153, 3155).

Tropidurus catalanensis

ARGENTINA: CORRIENTES: Capital, *Barrio Lomas* (MHNCI 5845); Puente Pexoa (UFRGS 2708); **BRAZIL:** MATO GROSSO DO SUL: Naviraí, *rio Paraná - Porto Felipe (antigo Porto Caiuá)* (MHNCI 67–78); PARANÁ: Boa Vista da Aparecida, *rio Grapia* (MHNCI 8551), *rio Tormenta* (MHNCI 8763); Candói, *rio Jordão* (MHNCI 12439); Capitão Leônidas Marques, *rio Iguaçú–UHE Salto Caxias* (MHNCI 9028, 9030, 9051, 9067, 9078, 9086, 9088); Cruzeiro do Iguaçú, *Foz do Chopim* (MHNCI 8552, 8839, 8872, 8875-76); Diamante do Norte (MHNCI 9250, 11685), *Estação Ecológica do Caiuá* (MHNCI 7856-57); Foz do Iguaçú, *Parque Nacional do Iguaçú—sede* (MHNCI 87-90, 92, 95), *rio Paraná - Itaipu Binacional* (MHNCI 9317), *rio Paraná—Porto Meira* (MHNCI 10780); Foz do Jordão, *margem do rio Jordão* (MHNCI 9841, 9845); Guaíra (MHNCI 2725), *rio Paraná—extinto Parque Nacional de Sete Quedas* (MHNCI 79-82, 85, 96); Londrina, *área urbana* (MHNCI 7471); Mangueirinha, *Piscicultura da COPEL* (MHNCI 8172), *rio Iguaçú—Estância Hidromineral Vigor* (MHNCI 5212), *rio Iguaçú—foz do rio Morro Verde* (5213-14); Nova Prata do Iguaçú, *rio Iguaçú—foz do rio Vorá* (MHNCI 8764), *rio Canguçu* (MHNCI 8773); Porto Rico, *rio Paraná—fazenda Caracu* (MHNCI 3909); Reserva do Iguaçú, *Empresa Trombini de Celulose* (MCP 7217), *Estrada de acesso Vila Copel* (MCP 7221, 7224, 7232, 7238, 7243-46), *rio Jordão—antiga captação da Usina Lucher* (MHNCI 5048-49, 5051, 5058); Santo Antônio do Caiuá (MHNCI 10177); Três Barras do Paraná, *rio Adelaide* (MHNCI 8549), *rio Iguaçú—Barra Bonita* (MHNCI 8550); Vila Alta, *rio Paraná - Ilha Grande* (MHNCI 7425); RIO GRANDE DO SUL: Alegrete *Cerro da Lagoinha* (UFRGS 5385), *Cerro do Tigre* (UFRGS 5338-39, 5383); Aratiba, *UHE Itá* (UFRGS 5557, 5573-84); Esmeralda (MCN 15784-85, 15802, 15804, 15807-09, 15812, 15816); Pinhal da Serra (MCN 16152, 16183); Porto Vera Cruz (MCP 11577, 11757-59); Quarai (MCN 4749-52, 4754-61, 4769, 4774), *Cerro do Jarau* (UFRGS 4608, 4705); Santo Cristo (MCP 11666); São Francisco de Assis, *Areal Joaquim Paz* (UFRGS 5365), *Fazenda Taquari* (UFRGS 5324-37); Vacaria (MCN 16135, 16142-51, 16153, 16182, 16184-85, 16194, 16236); SANTA CATARINA: Anita Garibaldi (MCN 15792); Campos Novos (CHUFSC 1100-02, UFRGS 5306, 5309, 5311-13, 5315-16, 5544), *rodovia BR-470 - km 354, próximo à divisa SC/RS* (MCP 2859-61, 2864); Celso Ramos (MCN 16525-27), *margem do rio Canoas* (UFRGS 5537, 5539-43); Ipuaçú, *rio Chapecó—UHE Quebra-Queixo* (CHUFSC 594-95, UFRGS 5442-66); SÃO PAULO: Teodoro Sampaio, *Parque Estadual Morro do Diabo* (MHNCI 6868); **PARAGUAY:** ÑEEMBUCU: Pilar, *área urbana* (MHNCI 6161); **URUGUAY:** ARTIGAS: *1 km ESE of route n° 30 and Arroyo Catalán Grande* (MNHN 3489; holotype); *pantheon near route n° 30 and Arroyo Catalán Grande* (MNHN 3475; paratype).

Tropidurus imbituba sp. nov.

BRASIL: SANTA CATARINA: Imbituba, *Morro do Farol* (holotype: UFRGS 5932; paratypes: MCP 18944-49; UFRGS 5043-45, 5092-93, 5164-65, 5203, 5205-07, 5225, 5302, 5354, 5357-58, 5545-46).