

## Comparative cytogenetic studies of eleven species of the *Tropidurus torquatus* group (Sauria, Tropiduridae), with banding patterns

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The chromosomes of 173 specimens representing eleven species of the *Tropidurus torquatus* group, from 33 localities in Brazil, were analysed after Giemsa staining, C-banding, NORs, and replication banding techniques. A karyotype with  $2n = 36$ , including 12 macrochromosomes and 24 microchromosomes (12 M + 24 m), and sex determination of the XY:XX type were found in *Tropidurus cocorobensis*, *T. erythrocephalus*, *T. etheridgei*, *T. hispidus*, *T. hygomi*, *T. montanus*, *T. mucujensis*, *T. oreadicus*, and *T. torquatus*. The two other species, *T. itambere* and *T. psammonastes*, presented  $2n = 36$  (12 M + 24 m) karyotype only in females while males had  $2n = 35$  (12 M + 23 m), due to the sex determination of the  $X_1X_2Y:X_1X_1X_2X_2$  type. Other interspecific differences as well as some intraspecific variation regarding the NORs and C-banding patterns have been observed, mainly in the microchromosome set. On the contrary, the macrochromosomes were highly conservative. Although consistent karyotypic diversity occurred in the *torquatus* group, the cytogenetic data obtained up to now did not allow us to clarify the phylogenetic relationships of the species. Nevertheless, the geographical distribution of the distinct cytotypes in *T. hispidus* and *T. torquatus* suggested that more than one species might be involved in each case.

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Until recently, the former genus *Tropidurus* was considered a natural assemblage of open formation lizards widely distributed throughout the South American continent and the Galapagos Islands. Several taxonomic revisions of *Tropidurus* species have been made over the last years (DIXON and WRIGHT 1975; ORTIZ 1980; CEI 1982; GUDYNAS and SKUK 1983; RODRIGUES 1981, 1984a, 1984b, 1986, 1987), and five relatively homogeneous species groups were accepted to belong to the genus: *occipitalis*, *melanopleurus*, *peruvianus*, *torquatus*, and *nanuzae* (RODRIGUES 1988). Although these studies improved the species level taxonomy of this complex and it remains largely accepted, the generic concept of *Tropidurus* has changed very recently.

FROST (1992) carried out an extensive phylogenetic analysis of *Tropidurus* and related genera, providing a new taxonomic scheme. According to

this analysis, the former western *Tropidurus* of the *occipitalis* and *peruvianus* groups were considered as *Microlophus* and *Plesiomicrolophus*, while the eastern species, previously included in the *melanopleurus*, *nanuzae*, and *torquatus* groups, the genus *Tapinurus*, and the species of the mainly forest genera *Plica*, *Strobilurus*, and *Uracentron* were grouped in a redefined genus *Tropidurus*, rendering it monophyletic. One of the points that remains obscure in the cladogram concerns the position and relationship of the former *torquatus* group. Once considered a monophyletic complex of species, based on the absence of a dorsal crest of scales, the group does not appear so in the cladogram. Although we think that this characteristic is synapomorphic for the group (including *Tapinurus*), much more data are necessary to firmly establish the relationships among the species.

Until 1978, only three species of the former *torquatus* group were recognized. RODRIGUES (1987), reviewing the forms occurring in regions south of the Amazon river, has shown the existence of eleven species currently known as: *T. cocorobensis*, *T. erythrocephalus*, *T. etheridgei*, *T. hispidus*, *T. hygomi*, *T. insulanus*, *T. itambere*, *T. montanus*, *T. mucujensis*, *T. oreadicus*, and *T. torquatus*. Later, the 12th species of the group, *T. psammonastes*, was described (RODRIGUES et al. 1988). *T. bogerti* from Venezuelan tepuis was not included in the analysis made by RODRIGUES (1987).

The first cytogenetic investigations of lizards identified as *Tropidurus torquatus* were made on conventionally stained chromosomes (GORMAN et al. 1967; BEÇAK et al. 1972). Later, cytogenetic analyses of two species assigned to the *torquatus* group, using banding techniques, showed some minor chromosome differences as well as distinct mechanisms of sex-determination (KASAHARA et al. 1983). Additionally, intraspecific geographical variation was revealed for some species as different populations were karyotyped (KASAHARA et al. 1987a; KASAHARA et al. 1988). These preliminary results prompted us to characterize the whole *torquatus* group, for a more accurate comparative chromosome analysis.

## Material and methods

A sample of 173 specimens representing eleven species of the *torquatus* group was obtained from different localities in Brazil (Table 1; Fig. 1). *T. insulanus* and *T. bogerti* were not available for cytogenetic analysis because their very restricted distribution did not allow collection of live specimens. All the specimens were deposited in the Museu de Zoologia, Universidade de São Paulo (MZUSP). Part of the present sample was referred previously in KASAHARA et al. (1983, 1987a, 1988), RODRIGUES et al. (1988), YONENAGA-YASUDA et al. (1988), and PELLEGRINO et al. (1994).

Chromosome spreads were obtained from bone marrow, liver, and spleen preparations (KASAHARA et al. 1987a) or from fibroblast cultures (YONENAGA-YASSUDA et al. 1988). Testes chromosome preparations were also made. Some specimens were submitted to in vivo or in vitro treatment with 5-bromodeoxyuridine (BrdU) and 5-fluorodeoxyuridine (FudR).

Chromosomes were studied after Giemsa staining, C-banding (SUMNER 1972), and NOR stain-

ing techniques (HOWELL and BLACK 1980). Replication R-banding was obtained following FPG staining (DUTRILLAUX and COUTURIER 1981).

## Results

### Conventional staining

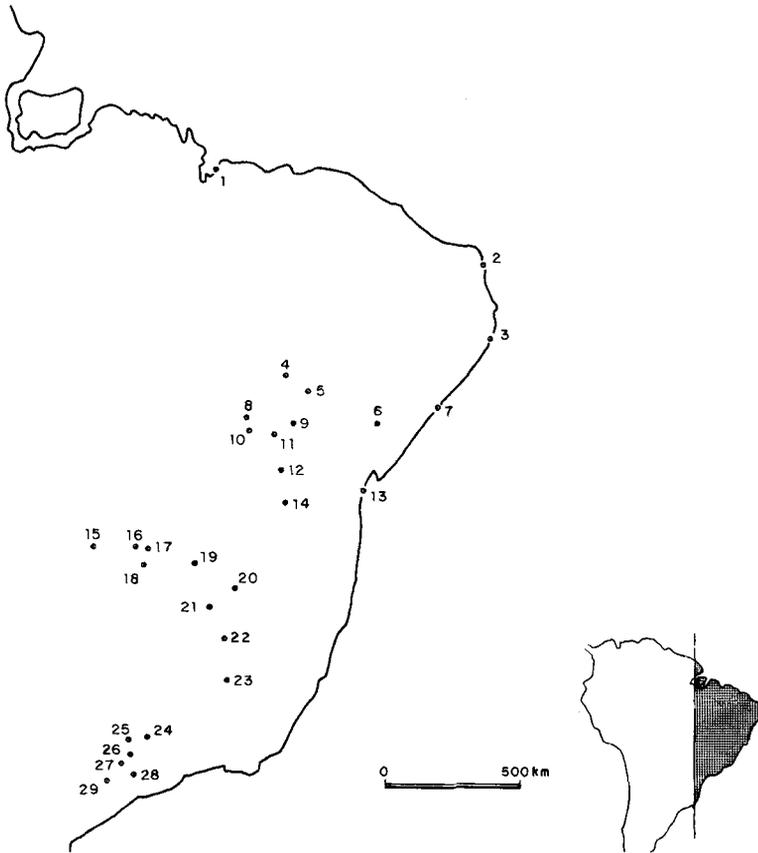
Nine species, *T. cocorobensis*, *T. erythrocephalus*, *T. etheridgei*, *T. hispidus*, *T. hygomi*, *T. montanus*, *T. mucujensis*, *T. oreadicus*, and *T. torquatus*, presented a  $2n = 36$  karyotype, including 12 macrochromosomes (M) and 24 microchromosomes (m), in males and females (Fig. 2a and b). The mechanism of sex determination was of the XY:XX type, the Y being a minute microchromosome and the X a non-identified microchromosome.

Two other species, *T. itambere* and *T. psammonastes*, presented the  $2n = 36$  (12 M + 24 m) karyotype only in females. Males had  $2n = 35$  (12 M + 23 m), due to a centric fusion between the Y and an autosomal microchromosome (Fig. 2c). The submetacentric chromosome derivative of this rearrangement was not always recognized, but the presence of a trivalent in diplotene and metaphase I cells confirmed unequivocally the occurrence of the  $X_1X_2Y:X_1X_1X_2X_2$  mechanism of sex determination.

The specimens of *T. hispidus* from 7 localities (São Luís, MA, Natal, RN, João Pessoa, PB, Alagoado, BA, Raso da Catarina, BA, Nova Soure, BA, and Santo Amaro das Brotas, SE) exhibited a very prominent secondary constriction at the distal region of the long arm of the macrochromosome pair 2, which corresponded to a nucleolar organizer region. This cytotype was referred to as Karyotype A in KASAHARA et al. (1987a). The specimens from Santo Inácio, BA, Morro do Chapéu, BA, and Mucujê, BA, presented Karyotype B, characterized by a slight secondary constriction in the long arm of pair 2, while those from Jacobina, BA, Grão Mogol, MG, and Diamantina, MG, had Karyotype C, with no secondary constriction in this pair. In both karyotypes, pair 2 is not the nucleolar organizer.

### NOR staining

The species of the *torquatus* group had, in general, two NORs which were located in the proximal centromeric region of an acrocentric pair of mi-



**Fig. 1.** Collection localities of *Tropidurus torquatus* species group in Brazil. 1. São Luís (Olho D'Água), MA; 2. Natal, RN; 3. João Pessoa, PB; 4. Alagoado, BA; 5. Raso da Catarina, BA; 6. Nova Soure, BA; 7. Santo Amaro das Brotas, SE; 8. Arraial do Paulista, BA, Ibiraba, BA; 9. Jacobina (Serra do Ouro), BA; 10. Santo Inácio, BA; 11. Morro do Chapéu, BA; 12. Mucuje, BA; 13. Guaibim, BA; 14. Pico das Almas, BA; Rio das Contas, BA; 15. Reserva Biológica de Águas Emendadas, N of Brasília, DF; 16. Buritis, MG; 17. Arinos, MG; 18. Unai, MG; 19. Mocambinho, MG; 20. Grão Mogol, MG; 21. Pedra Menina, MG; 22. Diamantina, MG; Gouveia, MG; São João da Chapada, MG; 23. Serra do Cipó, MG; 24. Poços de Caldas, MG; 25. São João da Boa Vista, SP; 26. Rio Claro, SP; 27. Piracicaba, SP; 28. Joanópolis, SP; 29. Sorocaba, SP.

crochromosomes (Fig. 3a). Nevertheless, some variations in the NOR patterns were observed. All male specimens of *T. itambere* and *T. psammomastes* had a single NOR metaphase (Fig. 3b) but its size is twice as large as each of the double NORs of the females. *T. hispidus* with Karyotype A had active NORs at the distal region of the long arm of the macrochromosome pair 2 (Fig. 3c).

Interpopulational variability was observed in *T. torquatus*. While the specimens from Guaibim, BA, Buritis, MG, Unai, MG, and Reserva Biológica de

Águas Emendadas, North of Brasília, DF, showed the usual single pair of acrocentric microchromosomes bearing NORs, those from Piracicaba, SP, had two pairs (Fig. 3d and e), and the sole specimen from Pedra Menina, MG, had only one microchromosome with active NOR in all metaphases.

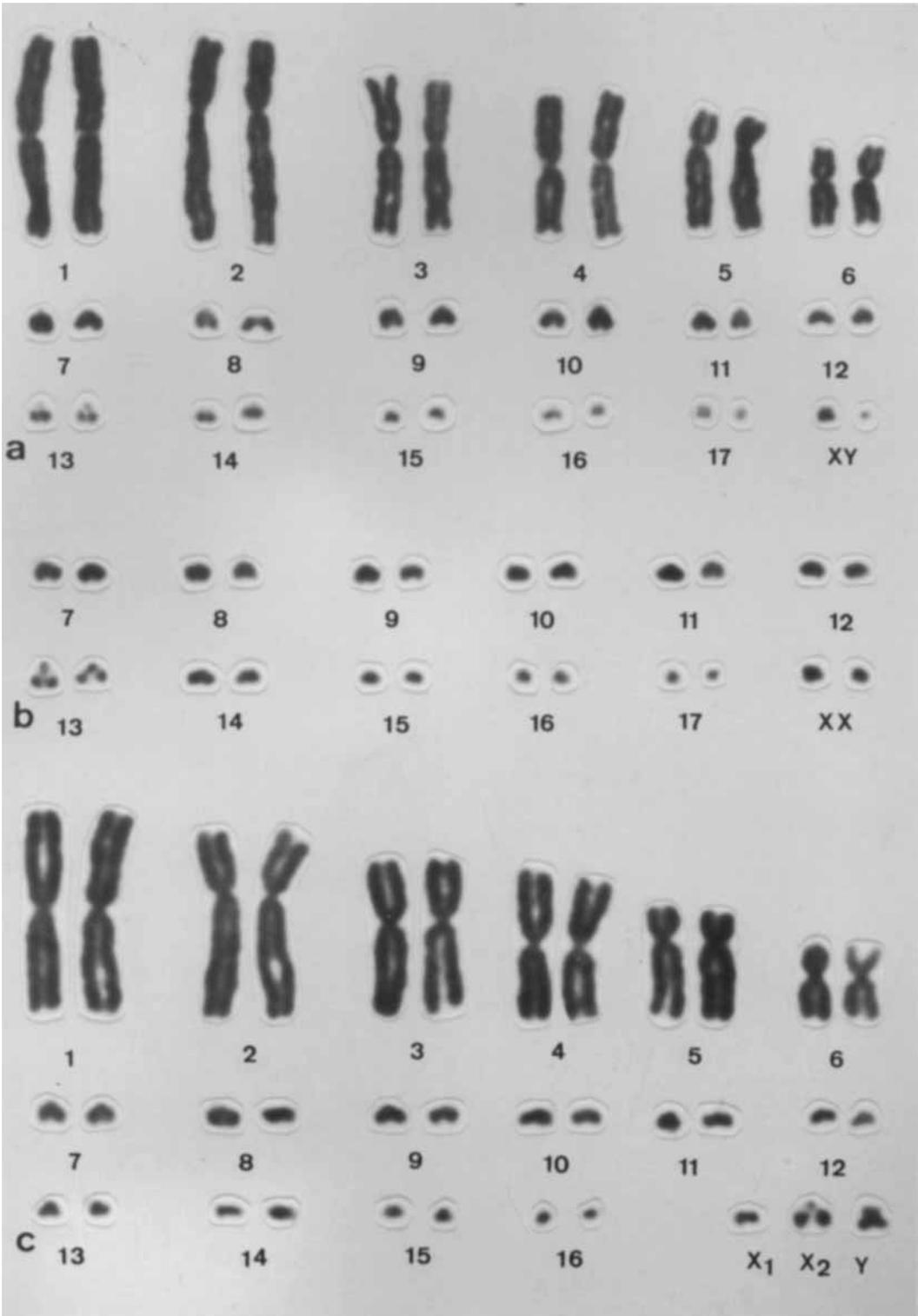
Intrapopulational variation was observed in *T. hygomi*, with the majority of the specimens showing two NORs, while the single female of the sample has only one active NOR per metaphase.

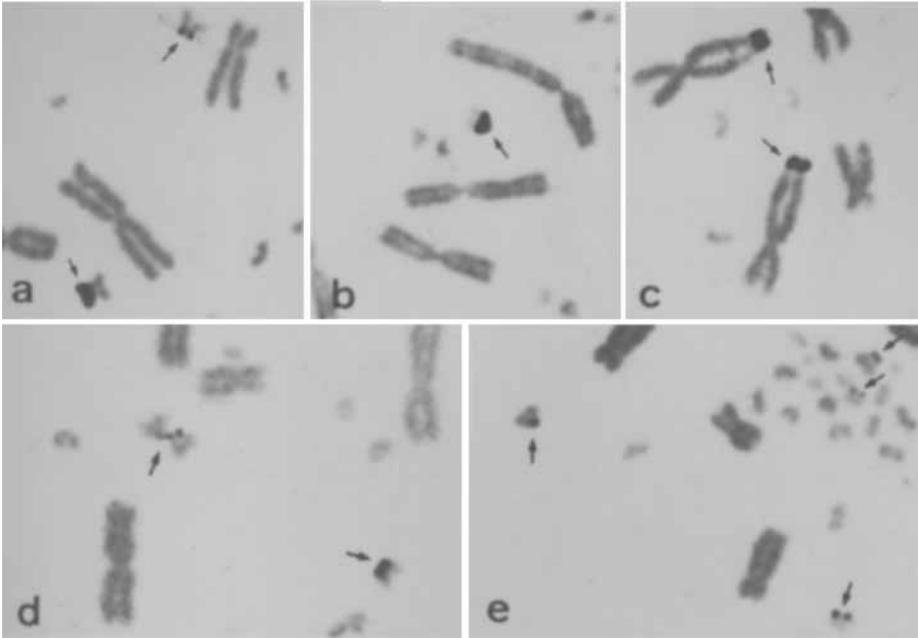
Table 1. Collection localities, sample size, sex, and C-banding pattern of the specimens of *Tropidurus torquatus* species group

Species	Sample size and sex		Localities	C-banding pattern
	Male	Female		
<i>T. cocorobensis</i>	4	2	Raso da Catarina, BA	type I
<i>T. erythrocephalus</i>	1	1	Santo Inácio, BA	not observed
	11	3	Morro do Chapéu, BA	type I
<i>T. etheridgei</i>	3	6	Arinos, MG	type II
	1		Mocaminho, MG	not observed
<i>T. hispidus</i>	1	1	São Luís (Olho D'Água), MA <sup>c</sup>	type I
	1	1	Natal, RN	not observed
	3	2	João Pessoa, PB <sup>b</sup>	type I
	4	3	Alagoado, BA	not observed
	3		Raso da Catarina, BA <sup>b</sup>	type I
	1	1	Nova Soure, BA	type I
	1	3	Santo Amaro das Brotas, SE <sup>b</sup>	type I
	2	3	Santo Inácio, BA <sup>b</sup>	type I
	3		Morro do Chapéu, BA <sup>b</sup>	type I
	4		Mucujê, BA <sup>b</sup>	type I
		1	Jacobina (Serra do Ouro), BA <sup>c</sup>	type I
		3	Grão Mogol, MG <sup>a</sup>	type I
		Diamantina, MG	type I	
<i>T. hygomi</i>	4	1	Santo Amaro das Brotas, SE	type I
<i>T. itambere</i>	2	1	Poços de Caldas, MG	type II
	2		São João da Boa Vista, SP	type II
		2	Rio Claro, SP <sup>a</sup>	not observed
		1	Joanópolis, SP	type II
	3	3	Sorocaba, SP <sup>a</sup>	type II
<i>T. montanus</i>	1	1	Pico das Almas, BA <sup>c</sup>	type II
		1	Rio das Contas, BA <sup>c</sup>	type II
	1		Buritis, MG	type I
	2	3	Grão Mogol, MG	type I
	1		Diamantina, MG	type I
	1	1	Gouveia, MG	not observed
	1	1	São João da Chapada, MG	not observed
	4	2	Serra do Cipó, MG	not observed
<i>T. mucujensis</i>	4	3	Mucujê, BA <sup>c</sup>	type II
<i>T. oreadicus</i>	2	1	Buritis, MG	type I
<i>T. psammonastes</i>	1		Arraial do Paulista, BA	not observed
	7	6	Ibiraba, BA	type II
<i>T. torquatus</i>	4	2	Guaibim, BA	type I
	1	2	Reserva Biológica de Aguas Emendadas, N of Brasília, DF	not observed
	3	4	Buritis, MG	type II
	4	6	Unai, MG	type II
		1	Pedra Menina, MG	type II
	2	2	Piracicaba, SP	type II
	Total	99	74	

See also: <sup>a</sup> KASAHARA et al. (1983), <sup>b</sup> KASAHARA et al. (1987a), <sup>c</sup> PELLEGRINO et al. (1994)

Fig. 2a–c. Chromosomes after conventional staining. a Karyotype ( $2n = 36$ ) of *Tropidurus oreadicus* male with XY sex chromosomes. b Microchromosomes of *Tropidurus oreadicus* female with XX sex chromosomes. c Karyotype ( $2n = 35$ ) of *Tropidurus itambere* male with  $X_1X_2Y$  sex chromosomes.





**Fig. 3a–e.** Partial metaphases after NOR staining. **a** NORs of different sizes in a pair of microchromosomes (arrows) of *Tropidurus torquatus* from Unai, MG. **b** NOR in one microchromosome (arrow) of *Tropidurus itambere* male. **c** NORs in the macrochromosome pair 2 (arrows) of *Tropidurus hispidus* with Karyotype A. **d and e** Three and four microchromosomes (arrows) with NORs in *Tropidurus torquatus* from Piracicaba, SP.

### C-banding

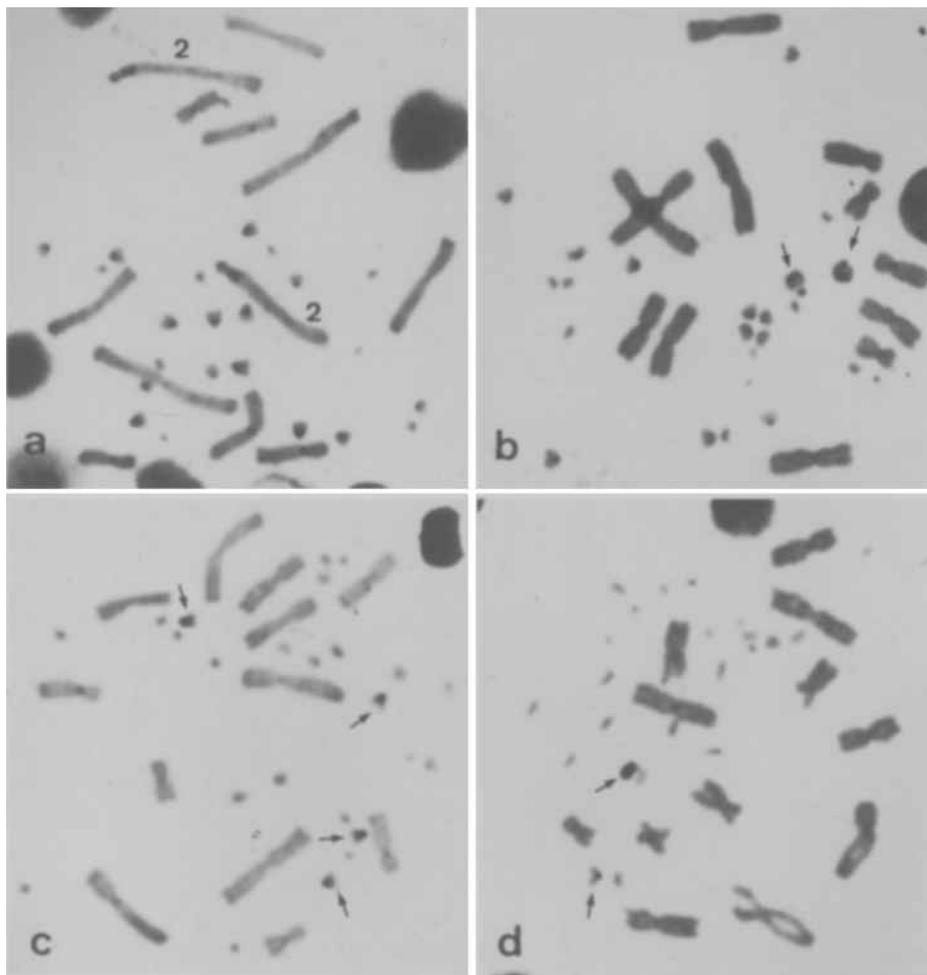
C-banding obtained in all eleven species from the majority of the collection localities revealed two main patterns. One of them (type I) was characterized by positive bands in the centromeric region of a variable number of microchromosomes, between 10 and 14 (Table 1; Fig. 4a and b). In some populations of *T. hispidus*, as those from João Pessoa, PB, Santo Amaro das Brotas, SE, Santo Inácio, BA, Mucujê, BA, Grão Mogol, MG, and Diamantina, MG, these bands appeared as very conspicuous blocks so that the two classes of microchromosomes, with and without C-positive bands, were clearly identified (Fig. 4a). The specimens of *T. torquatus* from Guaibim, BA, had an additional C-positive segment at the distal end of the microchromosomes bearing the NORs (Fig. 4b). For this reason, the size of these chromosomes was considerably larger than that of the other microchromosomes.

The alternative C-banding pattern (type II) was characterized by a reduced amount of constitutive heterochromatin in the microchromosome set (Table 1; Fig. 4c and d). Only those bearing NORs

had C-positive bands, but two or three other microchromosomes in the karyotype occasionally showed faint centromeric C-bands. A variant pattern was shown by the specimen of *T. torquatus* from Pedra Menina, MG, whose metaphases always exhibited four microchromosomes with remarkable centromeric C-band (Fig. 4c).

A C-band polymorphism was found in *T. itambere*. Two specimens, one from São João da Boa Vista, SP, and the other from Joanópolis, SP, had one almost completely heterochromatic microchromosome in the karyotype (Fig. 4d). One male from Poços de Caldas, MG, was a homozygote having two of these chromosomes, but the second specimen from São João da Boa Vista, SP, and two specimens from Sorocaba, SP, did not show this variant heterochromatic microchromosome at all.

The macrochromosomes had less definite C-banding pattern, characterized by slight centromeric bands, not always observed in all karyotypes. On the other hand, in *T. hispidus* and sporadically in *T. torquatus* and *T. hygomi*, heavy positive blocks were seen in the centromeric region



**Fig. 4a-d.** Metaphases with type I (a and b) and type II (c and d) C-banding patterns. **a** *Tropidurus hispidus* from João Pessoa, PB, with centromeric C-bands in 13 microchromosomes. Observe C-positive staining bordering the secondary constriction in pair 2. **b** *Tropidurus torquatus* from Guaibim, BA, with additional C-positive segment in a pair of microchromosomes (arrows). **c** *Tropidurus torquatus* from Pedra Menina, MG, with centromeric C-bands in four microchromosomes (arrows). **d** *Tropidurus itambere* from São João da Boa Vista, SP, with centromeric C-bands in one microchromosome (arrow) and one almost completely heterochromatic microchromosome (arrow).

of the 5th and, less frequently, of the 2nd pair of macrochromosomes. The most generalized C-banding pattern in the macrochromosome set of the *torquatus* group was the positive staining of the distal region of the long arm of the 2nd pair (Fig. 4a and c), although not observed in all C-banded metaphases.

### R-banding

Clear replication R-banding patterns were obtained in the species of the *torquatus* group, with

exception of *T. cocorobensis*, allowing the homologous pairing of the macrochromosomes (Fig. 5). In prometaphases some microchromosomes also showed replication bands but their precise identification was not possible due to their small size.

### Discussion

Although all the eleven species of the *torquatus* group shared the same basic karyotype, a certain



**Fig. 5.** R-banding patterns after BrdU incorporation in the macrochromosomes of *Tropidurus torquatus* male. Observe the pair 2 with R-negative staining in the distal region of the long arms.

amount of chromosome variability occurred at intra and interspecific levels.

In the present study, the geographical karyotypic variation in *T. hispidus* was confirmed through the analysis of specimens collected in new localities, totalling 13 different populations karyotyped up to now. No correlation could be established between each of the three different cytotypes and morphological traits of the animals but, as advanced in KASAHARA et al. (1987a), some association with habitat is still possible: while the Karyotype A is characteristic of sandy habitats on the plains, the Karyotypes B and C are limited to rocky habitats in mountainous areas, near or above 900 meters of altitude. These data on the geographical distribution of the distinct cytotypes are consistent with the hypothesis that more than one species might, in fact, be included under the name *hispidus*.

*Tropidurus torquatus* also showed geographical differentiation of the karyotypes. The most remarkable discrepant karyotype was that found in the sample from Guaibim, BA, which exhibited

type I C-banding pattern and a pair of large microchromosomes, not observed in the karyotypes with the type II C-banding pattern of the other five populations. According to RODRIGUES (1987), who examined characteristics of the external morphology of *T. torquatus* from several localities of its wide distribution area, there are evidences of geographical and ecological differentiation when coastal and inland populations are compared. Considering that Guaibim, BA, is a locality in the coast while the other five are far from the coast, our data are suggestive that conspicuous karyotypic differences also distinguish the population of *T. torquatus*. This fact indicates that cytogenetic analyses, if extended to a greater number of populations, might elucidate an early hypothesis of RODRIGUES (1987) that the coastal and inland populations of *T. torquatus* would be indeed two different species.

The C-banding patterns of *T. montanus* from five localities were of type I or of type II. Although more cytogenetic data are necessary to characterize this variability, it is interesting to note that there

are evidences that *T. montanus* shows geographical variations in morphological traits.

At present, we have no means to infer a phylogenetical differentiation pattern of the species of the *torquatus* group based on the NORs or C-banding, but these data may be useful in further comparative analysis with other tropidurid lizards because our previous studies of some of the species, as *T. semitaeniatus*, *T. plica*, and *T. umbra* (KASAHARA et al. 1986), *T. nanuzae*, *T. amathites*, and *T. divaricatus* (KASAHARA et al. 1987b), *T. strobilurus* (RODRIGUES et al. 1989), *T. spinulosus*, and *Uranoscodon superciliosus* (PELLEGRINO et al. 1994), suggested consistent differences.

The most conspicuous interspecific difference within the *torquatus* group was related to the mechanisms of sex determination which clearly distinguished a major group of species with XY:XX sex chromosomes and another group, including *T. itambere* and *T. psammonastes*, with  $X_1X_2Y:X_1X_1X_2X_2$ . Considering that in previous studies RODRIGUES (1987) could not establish any evidence of relationship between these two species, their multiple sex chromosomes have more probably evolved independently, from XY:XX mechanism. Although three other species of *Tropidurus*, *T. nanuzae*, *T. amathites*, and *T. divaricatus*, included in the *nanuzae* group, also presented the  $X_1X_2Y:X_1X_1X_2X_2$  sex chromosomes (KASAHARA et al. 1987b), there are no phylogenetic grounds to interpreting this pattern. Furthermore, the *nanuzae* group did not share the distribution of constitutive heterochromatin and NOR localization with *T. itambere* and *T. psammonastes*, but it is worth to mention that there is an interesting geographic correlation involving these species: *T. psammonastes*, *T. amathites*, and *T. divaricatus* are restricted to the same sand dune fields of São Francisco River, in the State of Bahia, while *T. itambere* and *T. nanuzae* occur along the Espinhaço range. Although the *nanuzae* group is, according to FROST (1992), the first out-group for the species of the *torquatus* group, the phylogenetic relationships in the *torquatus* group remain unsolved.

It is interesting to remark that almost the whole of the chromosome variation showed by the species of the *torquatus* group involved the microchromosomes. In fact, with few exceptions the macrochromosomes were highly conserved. This conservatism was confirmed by comparing their R banding patterns, which are very similar, if not identical, in all ten species studied of the group, even at the high

resolution level. Additionally, there are strong banding homologies between the macrochromosome sets of the *torquatus* group and of other species of *Tropidurus*, previously karyotyped by us (KASAHARA et al. 1986, 1987b; RODRIGUES et al. 1989).

The present comparative cytogenetic investigation makes an important contribution to the characterization of almost the totality of the species of *Tropidurus* included in the *torquatus* group. In spite of consistent karyotypic differences, the cytogenetic data are not sufficient for elucidating the phylogenetic relationships of the species. Much more data covering the geographical ranges of the species are needed for a correct interpretation of the chromosome variations.

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