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ORIGINAL PAPER

Banding patterns and chromosomal evolution in five species of neotropical Teiinae lizards (Squamata: Teiidae)

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Abstract Karyotypes of five species of South American teiid lizards from subfamily Teiinae: *Ameiva ameiva*, *Kentropyx calcarata*, *K. paulensis*, *K. vanzoi* ($2n = 50$, all acrocentric), and *Cnemidophorus ocellifer* ($2n = 50$, all biarmed), are herein described and compared on the basis of conventional and silver staining, and CBG and RBG banding patterns. Meiotic data are also included. Karyotypes of *K. paulensis*, *K. vanzoi*, and *C. ocellifer* are reported here for the first time. Inter-generic variability in Ag-NORs location was detected with NORs occurring at the end of long arm of pair 1 in *K. calcarata*, *K. paulensis*, and *K. vanzoi*; pair 5 in *C. ocellifer* and pair 7 in *A. ameiva*. The location of NORs, along with the karyological differences between *A. ameiva* and the Central American species (*A. auberi*), corroboretes the molecular-based hypothesis that the genus *Ameiva* is paraphyletic. Inter-populational heteromorphism in Ag-NORs size was detected between populations of *C. ocellifer*. RBG and CBG banding data demonstrated that the biarmed condition of the *C. ocellifer* chromosomes is due to multiple pericentric inversion events instead of addition of constitutive heterochromatin. Differential-staining techniques used here revealed valuable information about Teiinae karyotypic diversity and made it possible to compare these species, contributing to both the better comprehension of their chromosomal evolution and issues on taxa systematics.

Keywords Chromosomal evolution · Karyotype · Differential staining · Lizards · Teiidae

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Introduction

The family Teiidae is an exclusively New World group of lizards comprised of ten extant genera and about 120 species, ranging from the Northern United States, throughout Central America to the North of Argentina (Pough et al. 2001). Gorman (1970) suggested the split of Teiinae within two cytogenetical groups: the *Dracaena* group karyotype ($2n = 34–38$) is characterized by the presence of macro and microchromosomes and those of *Ameiva* group ($2n = 30–56$) that shows a gradual series of large to small chromosomes. Presch (1974, 1983), based on osteological characters, raised both groups to the tribes: Teiini, with the genera *Ameiva*, *Cnemidophorus*, *Dicrodon*, *Kentropyx*, and *Teius*, and Tupinambini including *Callopistes*, *Crocodilurus*, *Dracaena* e *Tupinambis*. Later, these categories were elevated to the status of subfamilies Teiinae and Tupinambinae, respectively (Estes 1983; Estes et al. 1988).

In spite of the unambiguous monophyly of both subfamilies, the phylogenetic relationships of teiid genera within subfamilies are still disputed. Among the five hypotheses proposed for the Teiinae (Gorman 1970; Presch 1974; Rieppel 1980; Denton and O'Neill

1995; Reeder et al. 2002), at least three are controversial, especially within the tribe Cnemidophorini (*Ameiva*, *Aspidoscelis*, *Cnemidophorus*, and *Kentropyx*, *sensu* Reeder et al. 2002). Recently Reeder et al. (2002), based on molecular and morphological data, found evidence of paraphyly for the genus *Cnemidophorus*; the Central and North American species were allocated in the resurrected genus *Aspidoscelis* and those from South America remained in *Cnemidophorus*. In the same paper they suggested that the genus *Ameiva* is paraphyletic.

The incongruence between alternative phylogenetic hypotheses for Teiinae is mostly due to an inadequate sampling and taxa identification, as well as lack of multiple data sets; these prevent the proposal of a robust phylogenetic hypothesis for the subfamily. Many new species have been described in the genus *Cnemidophorus* on a regular basis (Cole and Dessauer 1993; Markezich et al. 1997; Rocha et al. 1997, 2000; Feltrim and Lema 2000; Dias et al. 2002; Colli et al. 2003a, b; Soares et al. 2003), mainly those from South America, reflecting the need of extensive revisions and multidisciplinary studies involving species and populations from this geographic region.

The diploid chromosome numbers of Teiinae range from $2n = 46$ to 56 with the majority of chromosomes acrocentrics, except for those of *Aspidoscelis* and *Cnemidophorus*, many of which are biarmed. Gorman (1970) proposed a $2n = 50$ acrocentric ''*Ameiva/Kentropyx*-like ancestral karyotype'' for this group, which would have originated by multiple macrochromosomal fission events from a $2n = 36$ (12 macrochromosomes and 24 microchromosomes) Tupinambinae-like ancestral karyotype. Olmo (1986) considered that Robertsonian rearrangements must be involved in the differentiation of both subfamilies, but the lack of banding data for all species prevents the understanding of their chromosomal evolution.

Around 65% of the Teiinae species were cytogenetically studied (Reeder et al. 2002), but most of these data are restricted to species of *Aspidoscelis*. Nevertheless, these contributions were based only on conventionally stained karyotypes; a method that does not establish homologies essential to properly understand chromosomal evolution and phylogenetic relationships of a group. Banded karyotypes were only described for around 8% of the Teiinae taxa (Bickham 1976; Bull 1978; Schmid and Guttenbach 1988; Porter et al. 1991, 1994; Veronese et al. 2003; Peccinini-Seale et al. 2004), with some reports controversial (Peccinini-Seale and Almeida 1986; Sites et al. 1990; Rocha et al. 1997) or not properly illustrated (Rocha et al. 1997; Veronese et al. 2003).

In this report, we describe and compare the karyotypes of five species of South American Teiinae: *Ameiva ameiva*, *Cnemidophorus ocellifer*, *Kentropyx calcarata*, *K. paulensis*, and *K. vanzoi*, on the basis of conventional and silver staining, and CBG and RBG banding. The use of differential staining techniques revealed valuable phylogenetic characters that may contribute to the better comprehension of their chromosomal evolution and shed light on systematic issues, as well as improve our knowledge on the karyotypic diversity within the Teiidae.

Materials and methods

Cytogenetic analyses were carried out on a total of 33 specimens of *A. ameiva*, *C. ocellifer*, *K. calcarata*, *K. paulensis*, and *K. vanzoi* from different Brazilian localities (Table 1). Voucher specimens were identified and their provisorial ID will be correlated with the herpetological collection ID of the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Chromosomal spreads were obtained from bone marrow, intestine, liver, and spleen according to Kasahara et al. (1987), or from fibroblast culture of caudal muscle following Yonenaga-Yassuda et al. (1988). Meiotic analyses were performed on testis preparations.

The diploid number and chromosome morphology were established after conventional staining. Mitotic chromosomes were analyzed after CBG and silver staining according to routine techniques. RBG banding was obtained on fibroblasts culture after treatment with 5-bromodeoxiuridine (5-BrdU) for about 16 h, followed by FPG staining (Dutrillaux and Couturier 1981).

Results

Conventional staining

All Teiinae studied presented a karyotype composed of 50 chromosomes in a series of a gradual size-changes, but in *A. ameiva* (Fig. 1a), *K. calcarata*, *K. paulensis*, and *K. vanzoi* (Fig. 1b) the chromosomes are all acrocentrics, whereas in *C. ocellifer* they are all biarmed (Fig. 1c). Secondary constrictions were observed at the end of the long arm of pair 5 in *C. ocellifer* and at the end of pair 1 in all species of *Kentropyx*. Heteromorphic sex chromosomes were not detected.

Table 1 Species, localities and specimens of Teiinae lizards sampled for this study

Species	Locality		Specimens and sex	ID number (LG)
Ameiva ameiva	Pimenteiras do Oeste, RO	(12°44′S, 60°08′W)	2 M	1062/1086
	Niquelândia, GO	(14°28′S, 48°27′W)	2 M e 1 F	1081/1082/1090
	Aripuanã, MT	(10°10′S, 59°27′W)	1 M	1196
	Lajeado, TO	(9°45′S, 48°21′W)	5 F	1816/1843/1891/1898/1917
Cnemidophorus ocellifer	Arinos, MG	(15°55′S, 46°06′W)	1 F	104
	Morro do Chapéu, BA	(11°33′S, 41°09′W)	1 M	488
	Santo Amaro das Brotas, SE	(10°10′S, 59°27′W)	1 M e 3 F	170/171/172/174
	Subaúma, BA	(12°14′S, 37°03′W)	1 M	511
Kentropyx calcarata	Aripuanã, MT	(10°10′S, 59°27′W)	1 M e 1 F	1175/1197
	Ilhéus, BA	(14°47′S, 39°02′W)	1 M	2054
	Lajeado, TO	(9°45′S, 48°21′W)	6 F e 2 M	1997/1998/1999/2015/2016/2021/2044/2045
Kentropyx paulensis	São José dos Campos, SP	(23°10′S, 45°53′W)	2 F e 1 M	502/1014/426
Kentropyx vanzoi	Vilhena, RO	(12°44′S, 60°08′W)	1 M	1176

ID numbers from the Laboratório de Citogenética de Vertebrados (IBUSP, São Paulo, Brazil)

F female, *M* male, *BA* state of Bahia, *MG* state of minas Gerais, *MT* state of Mato Grosso, *PA* state of Pará, *RO* state of Rondônia, *RR* state of Roraima, *SE* state of Sergipe, *TO* state of Tocantins, *SP* state of São Paulo

Analyses of meiotic cells performed in male specimens of *K. vanzoi*, *K. calcarata*, and *C. ocellifer* revealed 25 bivalents with terminal and interstitial chiasmata in diplotene cells (Fig. 2). Heteromorphic bivalents were not observed.

Differential staining

A single NOR-bearing chromosome pair was detected in all species studied. In *A. ameiva* the Ag-NORs were located at the telomeric region of the long arm of pair 7 (Fig. 3a), whereas in all species of *Kentropyx*, it was observed at the secondary constriction at the telomeric region of the long arm of pair 1 (for an example, see pattern of *K. calcarata*, Fig. 3b). *C. ocellifer* showed Ag-NORs at the end of the long arm of pair 5 (Fig. 3c), but both specimens from Bahia state (Table 1) showed heteromorphism in Ag-NORs size: one homologue presented the NORs twice the size of the other in more than 90% of the cells analyzed (56 of 60 in LG 488, and 45 of 48 in LG 511, Fig. 3d).

Faintly stained heterochromatic blocks were observed at the centromeric and telomeric regions of most pairs of *A. ameiva*, *C. ocellifer*, and *K. paulensis* after C-banding (Fig. 4). The use of 5-BrdU in fibroblast cultures allowed us to unequivocally characterize each chromosome pair of *A. ameiva*, *C. ocellifer*, *K. calcarata*, and *K. vanzoi* and perform comparative analyses between their largest chromosomes on the basis of replication banding patterns (RBG banding). Pairs 1–13 of *A. ameiva*, *K. calcarata*, and *K. paulensis* are homeologous along their entire length. The comparison between these chromosomal pairs with the corresponding pairs of *C. ocellifer* suggests that the bi-armed condition of the latter species is probably due to multiple pericentric inversions events involving short proximal portions of the chromosomes (Fig. 5a, b).

Discussion

This paper is the first to use differential staining techniques to study karyotypes of a series of species of Teiidae and it reinforces the importance of this kind of approach for a better comprehension of the chromosomal evolution trends within this group of lizards.

Conventional staining

Ameiva ameiva presented the same diploid number ($2n = 50$) previously reported in the literature for specimens from other localities (Peccinini-Seale and Almeida 1986; Gorman 1970; Beçak et al. 1972; Schmid and Guttenbach 1988; Sites et al. 1990; Veronese et al. 2003). All these authors described the *A. ameiva* karyotype as composed by acrocentric macrochromosomes and microchromosomes. Because there is no clear separation in size between these two groups of chromosomes, we prefer to classify them here as a gradual series of acrocentric chromosomes. Veronese et al. (2003) found three small metacentric chromosome pairs in specimens from Santarém, state of Pará (Brazil), which led them to claim that ‘‘the presence of

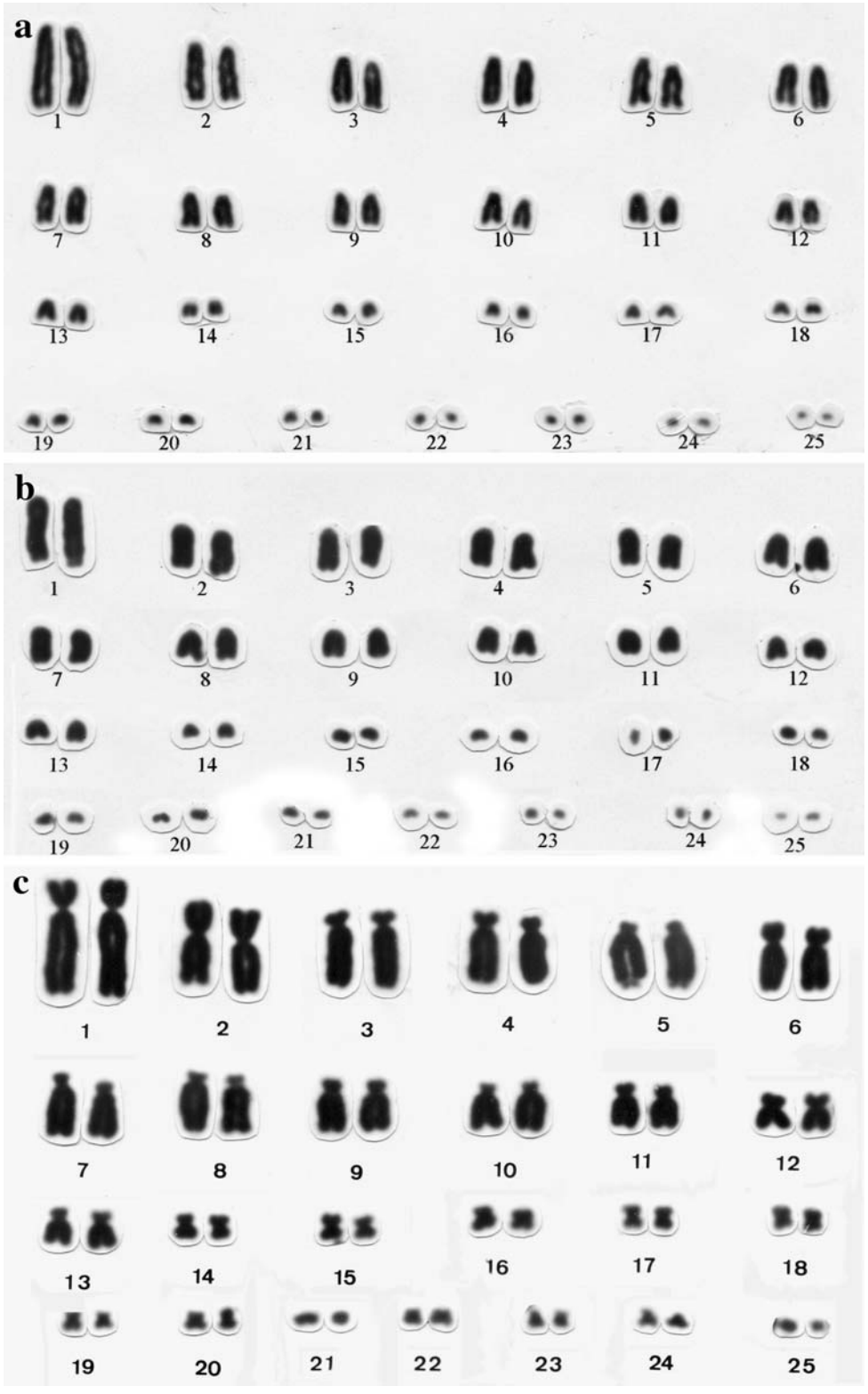

Fig. 1 Karyotypes of Teiinae species conventionally stained. (**a**) *Ameiva ameiva*, 2*n* = 50, female from Palmas, TO; (**b**) *Kentropyx vanzoi*, 2*n* = 50, male from Vilhena, RO, and (**c**) *Cnemidophorus ocellifer*, 2*n* = 50, male from Morro do Chapéu, BA

an average of three pairs of small metacentric chromosomes can therefore be suggested as a chromosomal marker for the whole family''. We consider this suggestion doubtful because some species of teiid lizards present all chromosomes acrocentric (e.g., *Kentropyx*), and the morphological classification for small elements

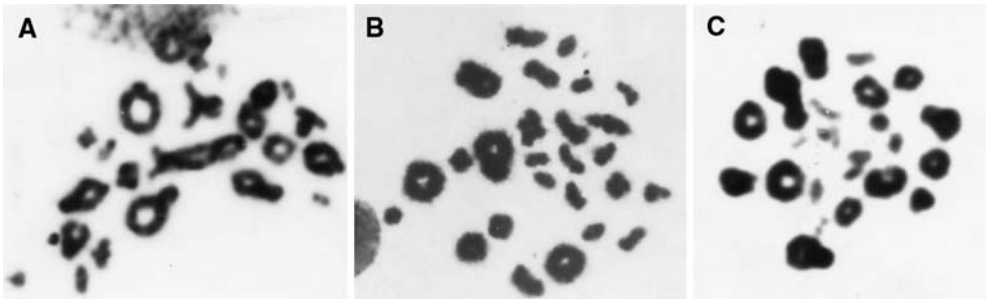

Fig. 2 Diplotene cells with 25 bivalentes after conventional staining of: (**a**) *Kentropyx vanzoi*; (**b**) *K. calcarata*, and (**c**) *Cnemidophorus ocellifer*

of the karyotype is very inaccurate. Besides, no homology between these small teiid chromosomes can be inferred in conventional or even RBG staining methods.

Cnemidophorus ocellifer is a convenience name used for a species complex (Rodrigues 1987; Rocha et al. 2000). Although some new species from this complex have been described, like *C. nativo*, *C. littoralis*, and *C. mumbuca*, several others remain unnamed. The karyotype of *C. ocellifer* here described differs in diploid number from those described for two other species of the *ocellifer* complex: *C. nativo* ($2n = 48$, Rocha et al. 1997) and *C. littoralis* ($2n = 46$, XY, Peccinini-Seale et al. 2004) both with, at least, five biarmed

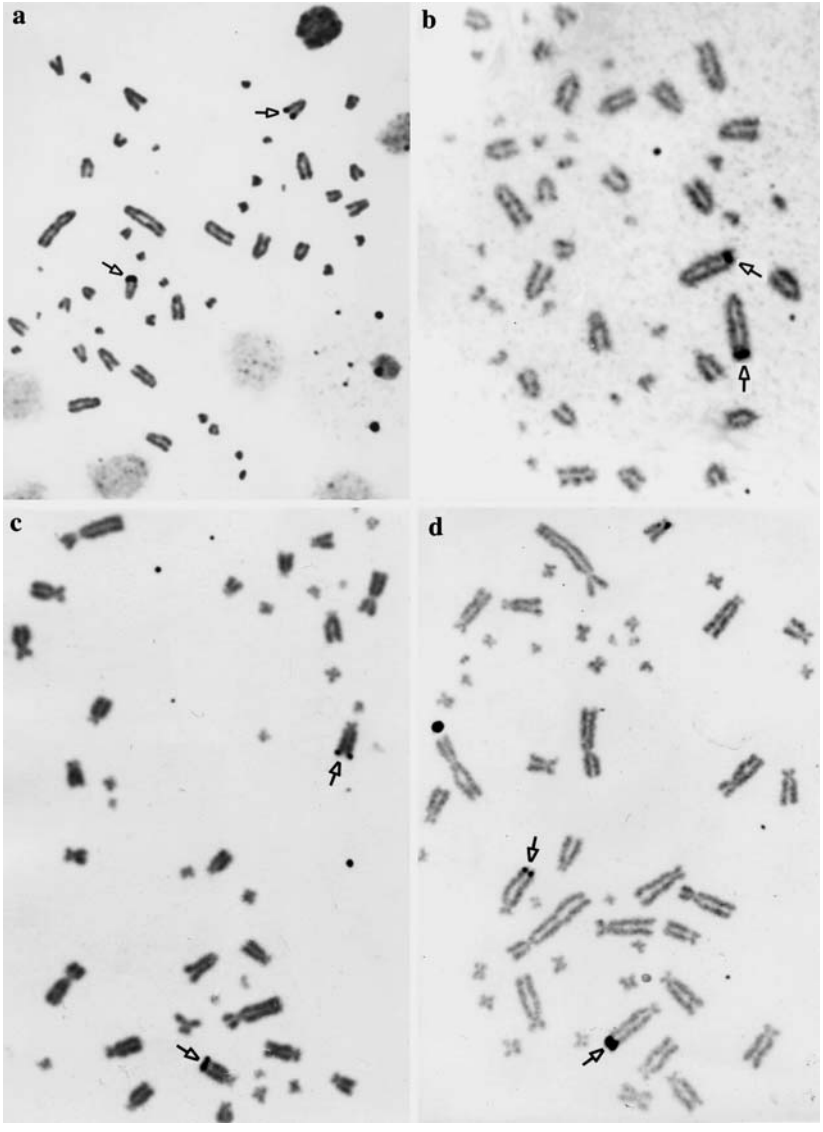

Fig. 3 Mitotic metaphases showing the Ag-NOR bearing chromossomes (*arrows*): (**a**) Pair 7 of *Ameiva ameiva*; (**b**) Pair 1 of *Kentropyx calcarata*; (**c**) Homomorphic pair 5 of *Cnemidophorus ocellifer* from Bahia and (**d**) Heteromorphic pair 5 of *C. ocellifer* from Sergipe and Minas Gerais, showing heteromorphism in size of NORs

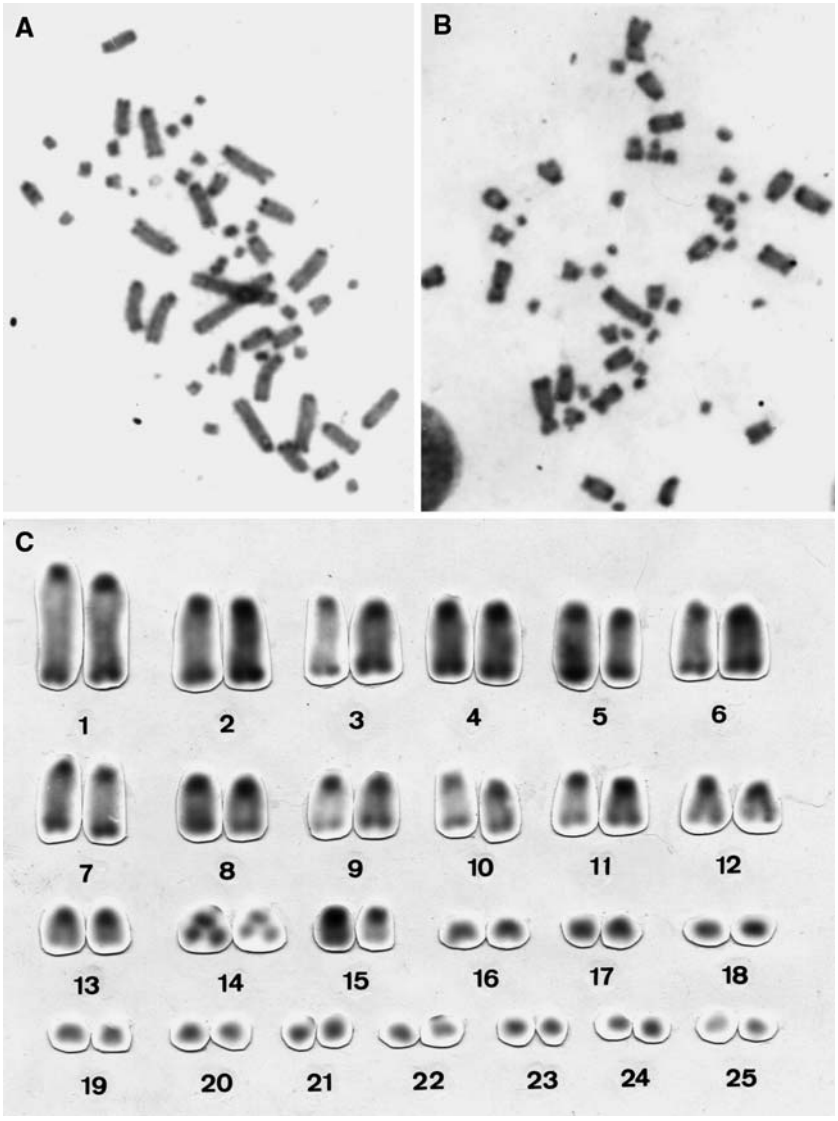

Fig. 4 C-banding metaphases of: (**a**) *Ameiva ameiva*; (**b**) *Cnemidophorus ocellifer* and (**c**) C-banding karyotype of *Kentropyx paulensis*, $2n = 50$

elements. Because chromosomal differentiation between both subfamilies of Teiidae probably evolved by multiple macrochromosomal centric fissions, resulting in an all acrocentric *A. ameiva*/*Kentropyx*-like karyotype, the occurrence of biarmed chromosomes might represent a synapomorphy of the *ocellifer* group, since *C. lemniscatus* (*lemniscatus* group) presents, in some populations, the single biarmed pair 1 (Lowe et al. 1970; Peccinini-Seale and Frota-Pessoa 1974) and the biarmed pairs 3 and 14–16 in *C. lacertoides* (*lacertoides* group, Cole et al. 1979; Veronese et al. 2003).

The karyotypes of *K. paulensis* and *K. vanzoi* are also reported here for the first time and they share the same diploid number ($2n = 50$) and chromosome morphology of those described for specimens of *K. calcarata* from Brazil (this study) and Suriname (Cole et al. 1995) and of *K. borckiana* and *K. striata* from Guyana (Cole et al. 1995).

Differential staining

In spite of the karyological similarities between *A. ameiva* and the *Kentropyx* studied here on the basis of conventional staining and C- and R-banding, both genera differ in Ag-NORs location.

All specimens of *A. ameiva*, sampled here from different Brazilian localities, show Ag-NORs exclusively at the telomeric end of the long arm of pair 7, in a agreement with the data found by Veronese et al. (2003) for specimens from Santarém, state of Para, and Schmid and Guttenbach (1988), the latter using fluorescent *in situ* hybridization (FISH) of ribosomal probes. However, Peccinini-Seale and Almeida (1986) and Sites et al. (1990) described inter-individual variation in number of NORs involving pairs 1, 2, 7, 16, 18, 19 and some small chromosomes for specimens from Santarém and Capanema, state of Pará, and Urucuri-

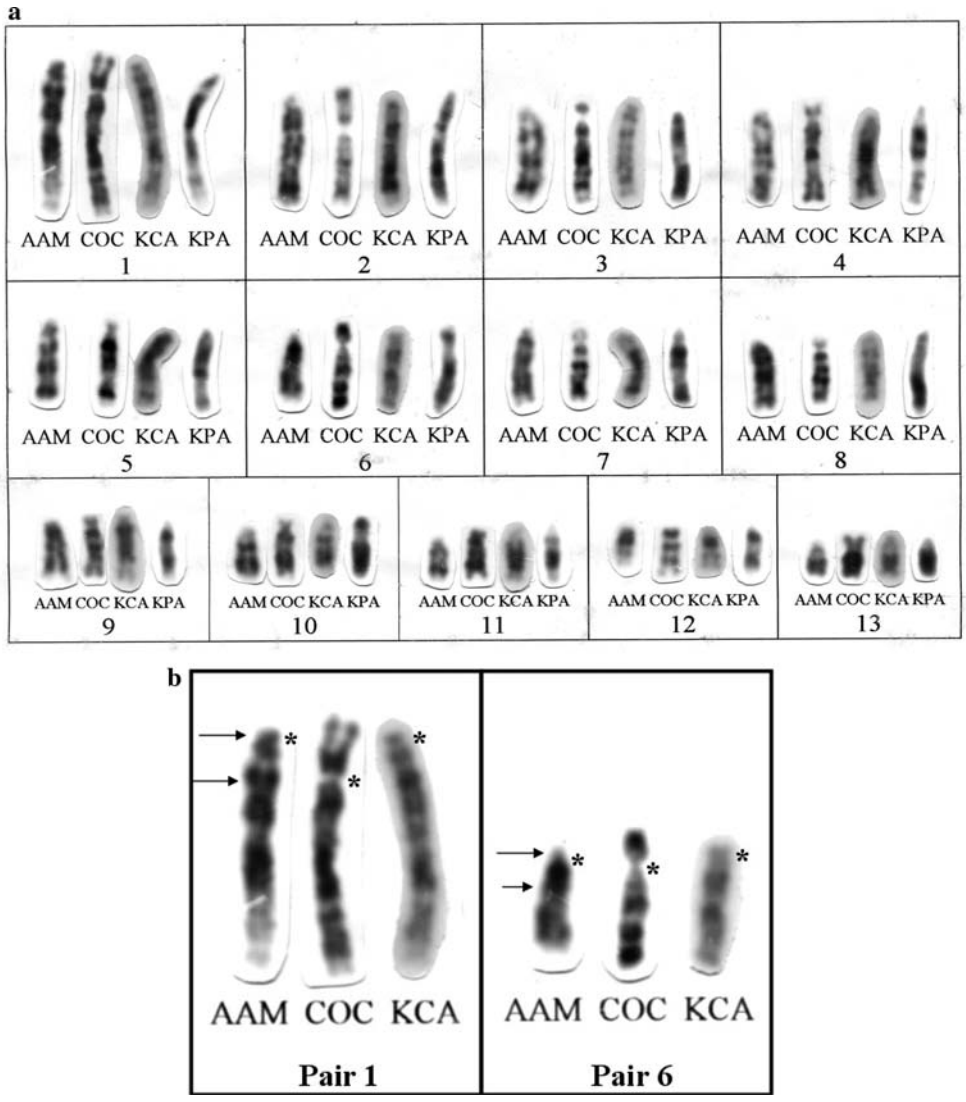

Fig. 5 Comparative replication RBG-banding patterns. (**a**) Homeologies among chromosomes 1–13 of *Ameiva ameiva* (*AAM*), *Cnemidophorus ocellifer* (*COC*), *Kentropyx calcarata* (*KCA*), and *K. paulensis* (*KPA*); (**b**) putative break points (*arrows*) and centromere position (*asterisk*) involved in the pericentric inversions, illustrated by pairs 1 and 6

tuba, state of Amazonas. We suspect that the majority of Ag-NOR signs observed by those authors are not true NOR sites, because in specimens from Santarém analyzed by Veronese et al. (2003), only a single Ag-NOR-bearing pair (pair 7) was described. Moreover, there is some uncertainty about the universality of silver staining method for detecting always active NORs, once this technique seems to reveal Ag-positive signals that do not correspond to rDNA sites like heterochromatin regions (Dobigny et al. 2002).

The karyotypes of *K. calcarata*, *K. paulensis*, and *K. vanzoi* exhibit Ag-NORs at the telomeric end of the long arm of pair 1, the same region of the conspicuous secondary constriction. Similarly, Cole et al. (1995) observed secondary constrictions at the same region for the South American species *K. calcarata*, *K. striata*, and *K. borckiana*.

Our findings about NOR location in the Teiinae are in agreement with Porter et al. (1991) who pointed out that the distribution of DNAr has changed many times during the Squamata evolution in spite of the conservative morphology of their chromosomes, indicating that NORs distribution could represent an important marker for Teiinae genera. In the closely related genera *Tupinambis* (Veronese et al. 2003) and *Crocodilurus* (Santos et al. in preparation) from the subfamily Tupinambinae, Ag-NORs occur at the region of the secondary constriction at the long arm of pair 2 observed in conventionally stained karyotypes. In spite of the lack of data on Ag-staining for the remaining genera *Callopistes*, *Dicrodon*, and *Dracaena*, the presence of the secondary constriction at pair 2 is also reported (Gorman 1970).

Considering that the long arm of pair 2 is the largest arm of the Tupinambinae karyotypes, it is possible that the Ag-NOR-bearing chromosome pair 1 of the Teiinae *C. lemniscatus* and species of the genus *Kentropyx* may correspond to the Ag-NOR region of pair 2 in the

Tupinambinae. If this is the case, the Ag-NOR at pair 1 would represent a plesiomorphic character within Teiinae, and the NORs distribution would corroborate the paraphyletic state for the genus *Ameiva* as proposed by Reeder et al. (2002) based on molecular characters. This suggestion is reinforced by the fact that the Central and North American species *A. auberi* presents 30 chromosomes and the DNAr segment occurs in a microchromosome pair (Porter et al. 1991, 1994), whereas in the South American *A. ameiva* ($2n = 50$), the Ag-NOR bearing pair is the 7th of the karyotype.

Ag-NORs at the end of the long arm of pair 5 were found in *C. ocellifer* karyotype. They were heteromorphic in size in specimens from state of Bahia, whereas in other populations no difference was detected. Unfortunately, due to the difficulty in obtaining good quality metaphases in lizards, the NORs description for *C. nativo* (Rocha et al. 1997) and *C. littoralis* (Peccinini-Seale et al. 2004) is very doubtful. These regions were localized at the telomeres of pair 8, but considering that the size of the chromosomes 4–9 is very similar, specially those from intestinal epithelial cells presented in those articles, we do discard the hypothesis that the Ag-NORs occur at the pair 8 in these two species because of the poor quality of the chromosomal preparations presented by Rocha et al. (1997) and Peccinini-Seale et al. (2004). Future studies involving NOR location in larger sampling of *C. ocellifer* are needed to investigate this variation, but it seems that NOR location represents a diagnostic characteristic to study the differentiation of Teiinae. The recent description of new species of *Cnemidophorus* from the *ocellifer* group (Rocha et al. 1997, 2000; Dias et al. 2002; Colli et al. 2003a, b) confirm that *C. ocellifer* is indeed a complex of species and that the Ag-NOR variability detected may contribute to define species limits (for examples see Kasahara et al. 1987; Pellegrino et al. 2005). A better comprehension of these variation would be greatly enhanced with the use of FISH ribosomal probes to precisely locate the sites of rDNA.

Ameiva ameiva, *C. ocellifer*, and *K. paulensis* share very similar C-banding patterns characterized by positive bands at most pericentromeric and some telomeric chromosome regions. These results along with those from R-banding, indicates that the biarmed condition in *C. ocellifer* is not due to events of constitutive heterochromatin addition/deletion. Moreover, the absence of heteromorphism in the heterochromatin distribution between the homologous pairs corroborates meiotic data that do not revealed heteromorphic sex chromosomes in this species. On teiids, chromosomal sex determination (XX : XY) was reported for *Aspidoscelis tigris*; conventionally (Cole et al. 1969) and after C-banding (Bull 1978), and in *C. littoralis* on the basis of conventional staining (Peccinini-Seale et al. 2004).

R-banding patterns revealed complete homology among the pairs 1–13 of *A. ameiva*, *C. ocellifer*, *K. calcarata*, and *K. paulensis*, despite the remarkable differences in their Ag-NORs location. The comparative analyses of these four Teiinae species (Fig. 5) revealed that the biarmed condition of the *C. ocellifer* karyotype seems to be due to multiple pericentric inversions probably from an acrocentric ancestral karyotype similar to that of *Ameiva* or *Kentropyx*. This same process was suggested to take place into the differentiation between the karyotypes of the Brazilian gekkos *Phyllopezus periosus* and *P. pollicaris* (Pellegrino et al. 1997). R-banding patterns have been reported for a few species of lizards revealing a range of characters as fragile sites (Santos et al. 2003), sex chromosomes (Bertolotto et al. 2001), supernumerary chromosomes (Bertolotto et al. 2004) as well as longitudinal bands that contribute substantially for the comprehension of the chromosomal evolution especially within Gymnophthalmidae (Yonenaga-Yassuda et al. 1996, 2005; Pellegrino et al. 1999).

Finally, we reinforce the importance of improving the quality of chromosomal preparations for Neotropical species of Teiidae family. This is essential not only to understand its chromosomal evolution, or even propose phylogenetic hypotheses, but also to evaluate the species diversity within this group of lizards, especially within the *C. ocellifer* complex.

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