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Origin and clonal diversity of the parthenogenetic lizard *Aspidoscelis rodecki* (Squamata: Teiidae): chromosomal evidence

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Abstract

Origin and clonal diversity of the parthenogenetic lizard *Aspidoscelis rodecki* (Squamata: Teiidae): chromosomal evidence. We analyzed the karyotypes of individuals of two different populations of *Aspidoscelis rodecki* to investigate the origin and chromosomal diversity of this unisexual lizard. The karyotype of *A. rodecki* has a diploid number of 50 chromosomes, and exhibits a marked structural heteromorphism. The unique arrangement seems to have originated by Todd´s fission after the origin of parthenogenesis (hybridization between *A. angusticeps* and *A. deppii*). This pattern was observed in two populations of the species, which is endemic to the Yucatan Peninsula.

Keywords: chromosome fission, karyotype, parthenogenesis.

Resumen

Origen y diversidad clonal de la lagartija partenogenética *Aspidoscelis rodecki* (Squamata: Teiidae): evidencia cromosómica. Con el fin de conocer el origen y la diversidad cromosómica de *Aspidoscelis rodecki,* analizamos el cariotipo de individuos de dos poblaciones de esta lagartija unisexual. El cariotipo de *A. rodecki* presenta un número diploide de 50 cromosomas y muestra un marcado heteromorfismo estructural. El arreglo cromosómico parece haberse originado a través de fisiones de Todd, posteriores al origen de la partenogénesis (hibridación entre *A. angusticeps* y *A. deppii*). Este patrón fue observado en dos poblaciones de la especie, que es endémica de la Península de Yucatán.

Palabras Claves: cariotipo, fisión cromosómica, partenogénesis.

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Resumo

Origem e diversidade clonal do lagarto partenogenético *Aspidoscelis rodecki* (Squamata: Teiidae): evidências cromossômicas. Com a finalidade de investigar a origem e a diversidade cromossômica de *Aspidoscelis rodecki,* analisamos os cariótipos de indivíduos de duas populações diferentes desse lagarto unissexual. O cariótipo de *A. rodecki* possui um número diplóide de 50 cromossomos e exibe um heteromorfismo estrutural marcante. O arranjo cromossômico parece ter sido originado pela fissão de Todd após o surgimento da partenogênese (hibridização entre *A. angusticeps* e *A. deppii*). Esse padrão foi observado em duas populações da espécie, que é endêmica da Península de Yucatán.

Palavras-chave: cariótipo, fissão cromossômica, partenogênese.

Introduction

Parthenogenetic whiptail lizards of the genus *Aspidoscelis* were first identified from the Yucatan Peninsula almost 50 years ago by McCoy and Maslin (1962). The authors assigned the name *Cnemidophorus cozumelus* to the lizards, which previously had been known as *C. deppei cozumelus* (Gadow 1906). Based on color pattern and scutellation, the species was divided into two subspecies, *A. c. cozumela* and *A. c. rodecki. Aspidoscelis c. cozumela* occurs on Isla Cozumel, Isla del Carmen, and some mainland localities in Campeche and Quintana Roo, Mexico, and El Petén, Guatemala. *Aspidoscelis c. rodecki* included the parthenoforms from Isla Contoy, Isla Mujeres, and the adjacent mainland in northeastern Quintana Roo, Mexico. Fritts (1969) elevated *A. c. rodecki* to the species level and *A. cozumela* was divided into two subspecies—*A. c. cozumela* and *A. c. maslini.* Karyotypical and morphological data led Fritts (1969) to conclude that *A. c. maslini* had arisen from interspecific hybridization between individuals of two gonochoristic lizards from Yucatan, *A. angusticeps* and *A. deppii.* He only examined the karyotype of *A. c. maslini,* but hypothesized that the other two parthenoforms had the same origin because of their morphological similarities. Subsequent studies showed that *A. angusticeps* was the maternal species of the parthenogenetic lizards, although this involved two hybridization events (Moritz *et al.* 1992b, Hernández-Gallegos *et al.* 1998, Hernández-Gallegos *et al.* 2003), one of them giving origin to *A. rodecki* and the second to *A. c. maslini* and *A. c. cozumela.* The latter two were later recognized as different species (*A. maslini* and *A. cozumela*) because of their morphological differences (Taylor and Cooley 1995).

Individuals of *Aspidoscelis rodecki* from distinct populations are similar in size and color pattern (McCoy and Maslin 1962, Fritts 1969, Taylor and Cooley 1995, Hernández-Gallegos *et al.* 2003). A recent skin-graft analysis showed histocompatibility among individuals from Puerto Juárez and Isla Contoy (Hernández-Gallegos *et al.* 2003), although genetic differences have been found among them (Manríquez-Morán 2007). We analyzed the karyotypes from individuals of two different populations of *A. rodecki,* one from Puerto Juárez and the other from Isla Contoy (separated by about 35 km), to investigate the origin and chromosomal diversity of unisexual *A. rodecki.*

Materials and Methods

We collected specimens from approximately 1 km south of Puerto Juárez ($N = 20$) and around the Biological Research Station at Isla Contoy ($N = 14$), Quintana Roo, Mexico (Figure 1).

Voucher specimens are deposited in the Colección Herpetológica, CIB-UAEH.

We followed the technique of Baker *et al.* (1982) to obtain chromosome preparations. Lizards were injected with 0.2–0.3 ml of 0.05% colchicine 3 h before being sacrificed. We removed the femurs and crushed them in 6 ml of 0.075 M KCl immediately after the lizards were euthanized. Bone marrow cells were left in the solution for 30 min and then the cells were centrifuged and fixed in 3:1 methanol-acetic acid, washed in fresh fixative, and centrifuged two or three more times. Last, slides were made by blaze drying, and staining with 5% Giemsa. To determine the exact chromosome number, we examined 30 chromosomic groups from each individual. Karyotype (chromosomal arrangement) was established according to Cole (1970) and Lowe *et al.* (1970b).

Results

Analysis of chromosomes from the 34 individuals revealed that both populations of *Aspidoscelis rodecki* (Figure 2) have identical karyotypes, with a diploid number of 50 chromosomes (0 + 28 + 22). The karyotype lacked Set I chromosomes, but had 28 Set II macrochromosomes (10 subtelocentric and 18 telocentric) and 22 Set III microchromosomes (8 seeming to be biarmed and 14 uniarmed). The fifth telocentric macrochromosome has terminal satellites.

Discussion

Since the discovery of parthenogenesis in reptiles (Darevsky 1958), karyological studies have revealed that almost all of the parthenogenetic species originated through interspecific hybridization between gonochoristic species (Dawley and Bogart 1989, Vrijenhoek *et al.* 1989, Avise 2008). Similarly, Fritts (1969) presented morphological evidence that *Aspidoscelis rodecki* had its origin through the hybridization of *A. angusticeps* and *A. deppii.*

Lowe *et al.* (1970b) showed that among gonochoristic taxa of the genus *Aspidoscelis* there are three species groups based on morphology and karyology. Furthermore, their study revealed that several parthenogenetic lizards of this genus had arisen from intergroup hybridization. Species of the *A. sexlineata* Group have a karyotype of 46 (2 + 24 + 20) chromosomes, whereas species in the *A. deppii* Group have a diploid number of 52 (0 + 28 + 24). Therefore, the hybrids of *A. angusticeps* (*A. sexlineata* Group) and *A. deppii* (*A. deppii* Group) should have a karyotype of 49 chromosomes, as already was assigned to the *A. cozumela* Group as a perfect match (Lowe *et al.* 1970b). However, this expectation does not explain the absence of the metacentric macrochromosome characteristic of the *A. sexlineata* Group (Lowe *et al.* 1970b, Reeder *et al.* 2002).

Aspidoscelis rodecki has a diploid number of 50 chromosomes (0 + 28 + 22) with 28 subtelocentric and telocentric medium size chromosomes and 22 uniarmed and biarmed small chromosomes. In contrast to the hypothetical hybrid karyotype (*A. angusticeps* × *A. deppii:* 1 + 26 + 22), *A. rodecki* lacks five chromosomes—a Set I metacentric chromosome, two Set II subtelocentric chromosomes and probably two Set III biarmed chromosomes. However, it has six additional telocentric chromosomes. Contra the idea that the main source of chromosomic evolution in *Aspidoscelis* has been Robertsonian centric fusion, the karyotype of *A. rodecki* seems to be the result of Todd´s fission. This kind of fission, which seems to be the main mechanism of chromosomal evolution within unisexual *Aspidoscelis* (Fritts 1969, Lowe *et al.* 1970a, b, Cole 1979, Manríquez-Morán *et al.* 2000), also has been observed in several other gonochoristic species. It is responsible of chromosomal diversity in some groups of reptiles (*Liolaemus,* colubrid snakes), mammals (Canidae, Artiodactyla, Old World monkeys) and several invertebrates (Kolnicki 2000).

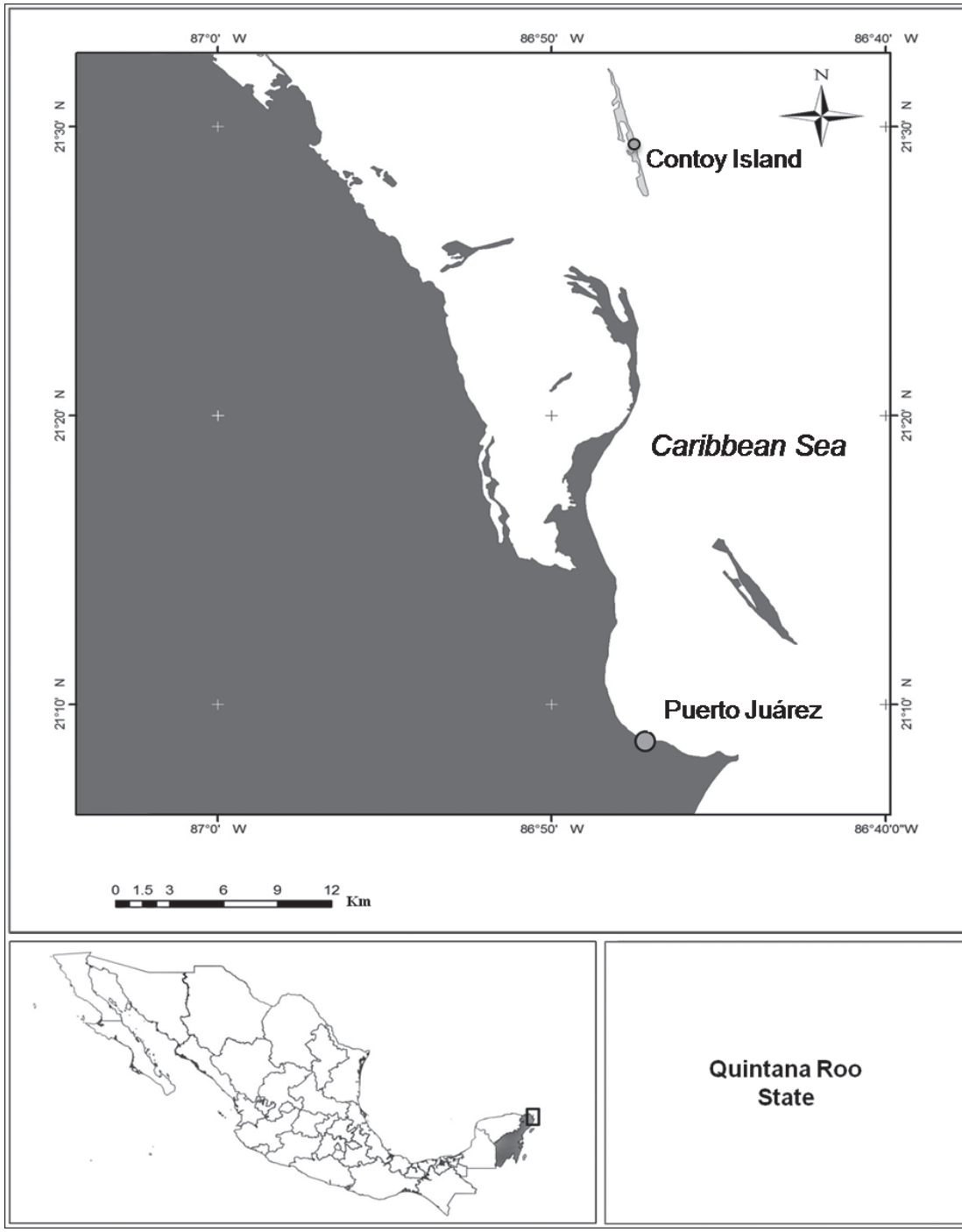

Figure 1. Gray circles indicate populations of the parthenogenetic lizard *Aspidoscelis rodecki* studied in the state of Quintana Roo, Mexico.

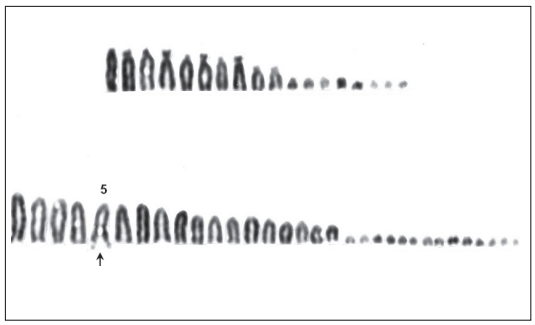

Figure 2. Diploid karyotype of *Aspidoscelis rodecki*. Arrow points out the terminal satellite of the telocentric chromosome number 5.

The evolution of the karyotype of *Aspidoscelis rodecki* seems to have followed the origin of parthenogenesis. Apparently, five chromosomes of the F_1 karyotype underwent fission to form 10 telocentric elements. Four of them are members of the Set II, and two of the Set III. The other elements might have been eliminated, as commonly happens with small arms after a chromosomic fission (Kolnicki 2000). As implied by histocompatibility studies (Hernández-Gallegos *et al.* 2003), the karyological data suggest that the two populations of *Aspidoscelis rodecki* represent a single clone. Although karyotypic variation has been documented within some unisexual *Aspidoscelis* (Fritts 1969, Lowe *et al.* 1970b, Cole 1979), individuals of *A. rodecki* are karyologically identical. In addition to *A. rodecki,* several unisexual species exhibit karyotypic homogeneity throughout their geographic range (Darevsky *et al.* 1985).

In contrast to the karyotypic homogeneity and histocompatibility, variation in morphology (Taylor and Cooley 1995) and color pattern (Hernández-Gallegos *et al.* 2003) has been reported among individuals from different populations of *A. rodecki.* Hernández-Gallegos *et al.* (2003) suggested that intraspecific variability might result from environmental factors. However, this observation also can be explained by genetic variation that skin-grafting does not reveal. An analysis of two mitochondrial DNA genes (cytochrome *b* and ND4) showed a genetic distance of 0.27% between individuals of Puerto Juárez and Isla Contoy (Manríquez-Morán 2007).

Low intraspecific variation is typical of unisexual lizards (Moritz *et al.* 1989, Fu *et al.* 2000) because of their young age (Moritz *et al.* 1989, Fu *et al.* 2000) and genetic, ecological, and phylogenetic constrains (Moritz *et al.* 1989, Vrijenhoek *et al.* 1989). Some authors have pointed out that intraspecific divergence is related to the time of origin of unisexual species (Abuhteba *et al.* 2000). Analysis of allozymes and mtDNA (Moritz *et al.* 1992a, Moritz *et al.* 1993, Murphy *et al.* 1997, Fu *et al.* 1999, Fu *et al.* 2000) suggest that all unisexual lizards appeared relatively recently, although estimated ages vary among different groups (Fu *et al.* 2000). Within the *Aspidoscelis cozumela* complex, *A. rodecki* is the least intraspecifically variable (Manríquez-Morán 2007). This suggests that its origin was more recent than that of other species in the complex.

A younger age for *Aspidoscelis rodecki* is supported by the lower degree of divergence with its maternal species. The average genetic distance between *A. maslini* and *A. cozumela* relative to *A. angusticeps* is 1.46% and 1.43%, respectively; *A. rodecki* differs 1.27% from its maternal ancestor (Manríquez-Morán 2007). Although this difference is small, it is congruent with biogeographic evidence; *A. maslini* is more widely distributed, probably because it is older (Hernández-Gallegos *et al.* 2003).

In contrast to mtDNA sequences, the karyological data indicate that within the *Aspidoscelis cozumela* complex, there has been more chromosomic change in *A. rodecki* than in other members of the complex. In spite of its wider geographical distribution, *A. maslini* has the exact hybrid karyotype between *A. angusticeps* and *A. deppii* (Fritts 1969). Because both populations of *A. rodecki* that we studied have the same modified karyotype, the chromosomal changes probably occurred in their common

ancestor. Hernández-Gallegos *et al.* (2003) suggested that the original populations of the *A. cozumela* complex might have originated on the mainland beaches on the Yucatan Peninsula. This is supported by the absence of the parental species in the islands. *Aspidoscelis rodecki* could have arisen in the northern part of the peninsula, because individuals of this species have a similar haplotype to that of *A. angusticeps* from Celestún, Yucatan, where both parental species were found recently in sympatry (pers. comm.). Later, the individual that underwent Todd´s chromosomal fissions invaded the adjacent islands, although this species is probably extinct at Isla Mujeres, its type locality.

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