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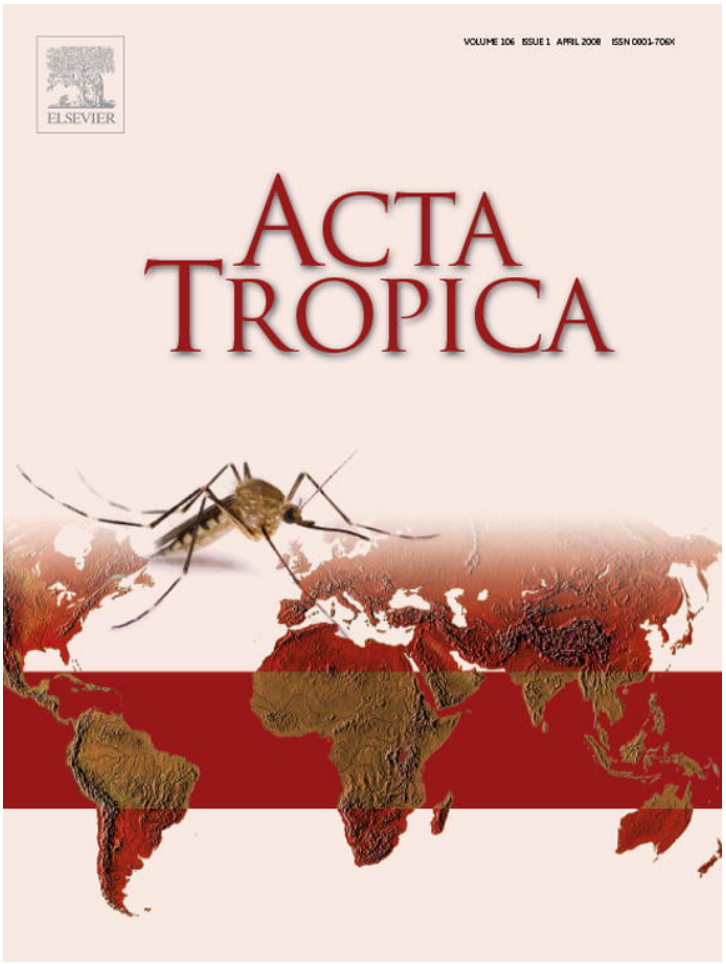

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Inferences about antennal phenotype: the "*Triatoma maculata* complex" (Hemiptera: Triatominae) is valid?

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Abstract

The "*Triatoma maculata* complex" is presently formed by two epidemiologically important species of Triatominae, *Triatoma maculata* and *Triatoma pseudomaculata*, which share morphologic and chromatic characteristics. In order to clarify the systematic status and infer the evolutionary relationships of these vectors of Chagas disease, we performed a comparative analysis of their antennal phenotype, taking also into account *Triatoma wygodzinskyi*, a possible sister species. The comparison was based on *sensilla* arrays on the three distal segments of the antenna. Our results show a close similarity between *T. pseudomaculata* and *T. wygodzinskyi* antennal phenotypes, and significant differences with *T. maculata*. The inter-population study reinforces the idea that *T. pseudomaculata* (arboricolous species) and *T. wygodzinskyi* (rupicolous species) would originate from a common ancestor.
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Keywords: *Triatoma maculata* complex; *Triatoma pseudomaculata*; *Triatoma maculata*; *Triatoma wygodzinskyi*; Antennal phenotype; *Sensilla*; Brazil

1. Introduction

Triatominae are the vectors of Chagas disease, which is caused by the protozoan parasite *Trypanosoma cruzi* (Chagas, 1909) and is ranked as one important parasitic disease for Latin America (WHO, 2006). In Brazil, the eradication program focused on *Triatoma infestans* (Klug, 1834), had as consequence the occurrence in dwellings of new potential vectors originally restricted to the sylvatic environment (Dias et al., 2002). In the northeast of Brazil, *Triatoma pseudomaculata* (Corrêa and Espínola, 1964), one of these potential vectors, is exhibiting a quick synanthropic process (Dias et al., 2000; Diotaiuti et al., 2000; Noireau et al., 2005). Because of their similar morphologic and chromatic characteristics, *T. pseudomaculata* was misidentified for many years as *Triatoma maculata* (Erichson, 1848), a species found in the Roraima State of Brazil, Venezuela, Colombia, Surinam, Guyana, French Guiana, and some Caribbean islands (Carcavallo et al., 1998a, 2000). Finally, *T. pseudomaculata* was formally described in 1964 from specimens collected in Sobral, Ceará State. According to the Schofield (1988) hypothesis about their origin, *T. maculata* and *T. pseudomaculata* would be the result of the evolution of two geographic populations issuing from a common ancestor by passive dispersion of nymphs associated to migratory birds.

Because they share many morphologic and chromatic characteristics, both species form the "*T. maculata* complex" (Carcavallo et al., 2000) or "*maculata* subcomplex" (Dujardin et al., 2000). A third Brazilian species, *Triatoma wygodzinskyi* (Lent, 1951), exhibits close morphological similarities with *T. pseudomaculata* (Carcavallo et al., 2000). *T. wygodzinskyi* has been described from a small number of specimens (5) obtained from a single sampling in the south of Minas Gerais State, Brazil.

T. maculata is commonly found in the wild environment in palms trees, associated with birds, bats, rodents and marsupials (Carcavallo et al., 1998b), but exhibits epidemiological importance when it colonizes synanthropic structures (Feliciangeli et al., 2003; Luitgards-Moura et al., 2005). *T. pseudomaculata* is not only found in hollow trees but also in rodent, marsupial and "armadillo" shelters (Lent and Wygodzinsky, 1979;

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Espínola, 1985; Dias-Lima et al., 2003). It is currently reported to be colonizing artificial structures (Silveira and Vinhaes, 1998) and may be considered as a synanthropic vector candidate. Finally, *T. wygodzinskyi* occurs exclusively in the cracks of stone located in southern Minas Gerais and northern São Paulo (Lent and Wygodzinsky, 1979; Carbajal de la Fuente, unpublished data).

According to Hypša et al. (2002) and Santos et al. (2007), *T. maculata* and *T. pseudomaculata* would pertain to distinct evolutionary lineages whereas *T. pseudomaculata* and *T. wygodzinskyi* would be closely related species. In order to confirm this hypothesis and to clarify the systematic status, we carried out an inter- and intra-specific comparative study of the antennal phenotype observed for *T. maculata*, *T. pseudomaculata* and *T. wygodzinskyi*. We also explored the existence of sexual dimorphism in the antenna of these species.

2. Material and methods

2.1. Insects

Brazilian populations of three species were compared: *T. maculata* (one population from Mucajaí, Roraima State); *T. pseudomaculata* (three populations from Itaobim, Minas Gerais; Curaçá, Bahía; and Sobral, Ceará) and *T. wygodzinskyi* (two population from Santa Rita de Caldas, Minas Gerais, and Vargem Grande do Sul, São Paulo) (Table 1). The insects analyzed were field specimens, except for *T. maculata* and the Sobral population of *T. pseudomaculata*, which originated from a first generation, obtained from the insectary of the Laboratório de Triatomíneos e Epidemiologia da Doença de Chagas, Instituto Rene Rachou, FIOCRUZ, Brazil. We currently consider that the triatomine populations from São Paulo State characterized as *Triatoma arthurneivai* (Lent and Martins, 1940), and studied by Hypša et al. (2002) and Paula et al. (2005) pertained in reality to the species *T. wygodzinskyi* (Santos et al., 2007). Unfortunately, we could not include specimens of *T. arthurneivai* in this analysis. The antennas of all the collection type specimens were damaged and recent collecting efforts in Serra do Cipó, Minas Gerais State, were unsuccessful.

Table 1
Characteristics of the different samples analyzed

Species	Code	Locality, State	Habitat	*N*	
				F	M
T. wygodzinskyi	TwyMG	Santa Rita de Caldas, MG	Rocks	5	5
	TwySP	Vargem Grande do Sul, SP		5	5
T. pseudomaculata	TpsCE	Sobral, CE	Peridomestic	5	5
	TpsBA	Curaçá, BA		5	5
	TpsMG	Itaobim, MG		0	5
T. maculata	TmaRR	Mucajaí, RR	Palm tree	5	5

MG: Minas Gerais; SP: São Paulo; CE: Ceará; BA: Bahía; RR: Roraima. *N*: Number of antennas, F: females, M: males.

2.2. Antennal preparations

One antenna per individual was removed using fine forceps, stored in 70% ethanol and diafanized in sodium hydroxide (10%). After neutralization with acetic acid (10%), each antenna was mounted on a slide in glycerine. *Sensilla* identification and counting were made on the ventral side of the three distal segments of the antenna: pedicel (P), flagellum first segment (F1), and flagellum second segment (F2), using optical microscopy (400×) and a drawing chamber (Carbajal de la Fuente and Catalá, 2002). *Sensilla* were classified in Bristles (BR), thin-walled trichoids (TH), thick-walled trichoids (TK) and basiconica (BAS) according to Catalá and Schofield (1994).

2.3. Data analysis

Means and standard deviations were calculated for each type of *sensilla* in each one of the antennal segments. Levene's test was used to check the homogeneity of variances. Variables were analyzed using ANOVA and mean values were contrasted using the LSD (least significant difference) test. Variables with significant differences were used for discriminant analysis between species using PADWIN software, version 81a (J.P. Dujardin, http://www.mpl.ird.fr/morphometrics). For population analysis, Mahalanobis distances and their statistical significance were calculated by permutation tests (1000 runs each) after Bonferroni correction. Cluster analysis based on Euclidean distances was used to build an UPGMA (unweighted pair-group method with arithmetic average) phenogram. This analysis was carried out with 12 variables using PAST software version 1.44 (http://www.folk.uio.no/ohammer/past).

3. Results

3.1. Analysis by species

T. maculata and *T. pseudomaculata* presented the four types of *sensilla* distributed on their pedicel and antennal segments. *T. wygodzinskyi* presented a low quantity (TwySP) or did not present (TwyMG) the P-TK *sensilla* type (Table 2). Interspecific univariate analysis (variables log transformed) showed significant differences in pedicel mechanoreceptor (P-BR) and chemoreceptor (P-TH, P-TK, P-BAS, F2-TH and F2-BAS) densities. The LSD test revealed that P-TH and F2-TH could separate the three species, and P-TK, P-BAS and F2-BAS separated *T. maculata* to the remaining species ($P < 0.01$). P-TK, P-BAS and F2-BAS did not exhibit significant differences between *T. pseudomaculata* and *T. wygodzinskyi*. For discriminant analysis, canonical factor 1 (CF1) separated *T. maculata* from the remaining species and demonstrated close proximity for *T. pseudomaculata* and *T. wygodzinskyi* (Fig. 1). The CF1 explained 92% of the variance while the CF2 explained 8%. The Mahalanobis distances between the three species were highly significant ($P < 0.001$). After 1000 permutations, 80% of *T. wygodzinskyi* specimens were correctly reclassified, while *T. maculata* and *T. pseudomaculata* had reclassification rates of 70% and 72%, respectively.

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Table 2
Average (standard deviation) of *sensilla* on each antennal segment of the populations examined

Species	Pedicel				Flagellum 1				Flagellum 2			
	BR	TH	TK	Bas	BR	TH	TK	Bas	BR	TH	TK	Bas
TwyMG	116.80 (16.62)	117.00 (42.93)	0	2.5 (2.27)	23.4 (3.47)	54.4 (15.79)	121.10 (24.00)	22.40 (7.79)	12.10 (3.69)	27.90 (11.25)	80.50 (14.83)	13.30 (3.56)
TwySP	121.70 (15.76)	144.30 (53.43)	0.40 (0.69)	2.90 (2.47)	24.80 (4.21)	61.60 15.53)	108.80 (22.67)	16.50 (2.50)	13.50 (4.22)	39.10 (13.68)	94.70 (21.26)	18.10 (4.99)
TpsMG	132.60 (16.82)	205.20 (57.75)	1.00 (2.23)	5.00 (1.87)	22.4 (3.78)	60.20 (17.99)	186.00 (15.55)	33.20 (18.97)	12.60 (2.60)	27.00 (3.53)	137.00 (20.85)	16.80 (11.21)
TpsBA	135.20 (20.61)	183.50 (49.59)	4.4 (6.18)	4.90 (1.91)	23.30 (2.83)	55.80 (15.24)	201.70 (34.29)	27.90 (6.29)	12.10 (3.66)	27.20 (10.49)	113.00 (34.30)	16.40 (8.08)
TpsCE	113.50 (15.28)	154.20 (55.41)	1.30 (1.77)	3.70 (2.45)	21.60 (2.63)	50.90 (14.78)	140.70 (28.55)	19.50 (7.83)	13.20 (3.79)	23.40 (6.56)	92.00 (19.45)	12.00 (4.44)
TmaRR	133.90 (14.88)	288.40 (106.04)	37.9 (35.59)	9.2 (5.59)	25.2 (2.94)	87.30 (13.38)	227.5 (33.43)	40.10 (15.09)	13.40 (2.31)	42.80 (7.88)	144.00 (18.48)	35.10 (10.35)

TwyMG and TwySP: *T. wygodzinskyi* from Minas Gerais and São Paulo States; TpsMG, TpsBA and TpsCE: *T. pseudomaculata* from Minas Gerais, Bahía and Ceará States; TmaRR: *T. maculata* from Roraima State. BR: Bristles; TH: thin-walled trichoids; TK: thick-walled trichoids; Bas: basiconics.

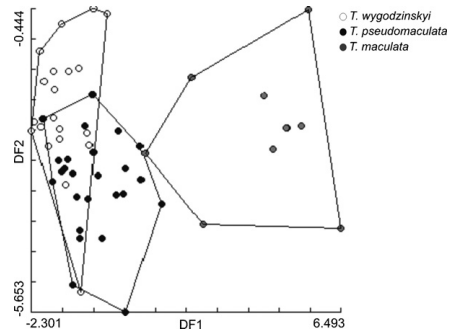

Fig. 1. Discriminant analysis based on 5 variables of the antennal phenotype of *T. wygodzinskyi* (Twy), *T. pseudomaculata* (Tps) and *T. maculata* (Tma). Distances between the three species are significant ($P < 0.01$).

3.2. Analysis by populations

Univariate analysis showed significant difference ($P < 0.05$) for the F2-BAS number between both *T. wygodzinskyi* populations. For P-BR, F1-TK and F2-TK *sensilla* types, significant differences were found among *T. pseudomaculata* populations. The TpsBA and TpsMG populations showed a greater number of P-BR ($P < 0.05$). For F1-TK, TpsCE had a smaller number for this type of *sensilla* and was significantly different from the others. Finally, TpsMG contained a F2-TK number that was significantly higher than other *T. pseudomaculata* populations. Cluster analysis clearly separated the two groups (Fig. 2): the first group included *T. wygodzinskyi* and *T. pseudomaculata* population from Ceará and the second group was contained the remaining *T. pseudomaculata* populations (TpsBA and TpsMG). Unassociated with these groups, we found the *T. maculata* pop-

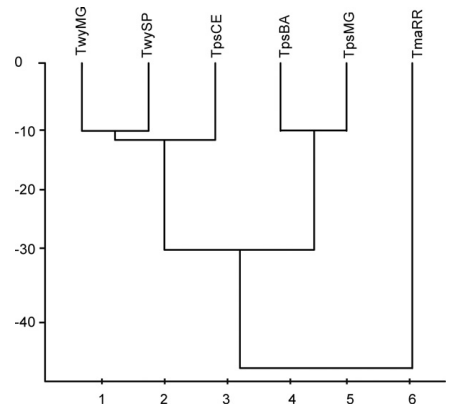

Fig. 2. Cluster analysis based on Euclidean distances of antennal phenotype (12 variables of *T. wygodzinskyi* from Minas Gerais State (TwyMG), São Paulo State (TwySP); *T. pseudomaculata* from Ceará State (TpsCE), Bahía State (TpsBA) and Minas Gerais State (TpsMG) and *T. maculata* from Roraima State (TmaRR)).

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Table 3
Average (standard deviation) of *sensilla* for five types of receptors among the four triatomine populations with sexual dimorphism ($P < 0.01$)

Species	P-BAS		F1-TH		F1-TK		F1-BAS		F2-TH	
	M	F	M	F	M	F	M	F	M	F
TwyMG	–	–	–	–	–	–	–	–	49.60 (10.06)	28.60 (6.65)
TpsBA	–	–	66.00 (8.36)	45.60 (13.88)	184.80 (19.14)	218.60 (39.57)	–	–	35.40 (2.70)	19.00 (8.51)
TpsCE	–	–	58.60 (15.58)	43.20 (10.03)	122.20 (19.42)	159.20 (24.52)	–	–	–	–
TmaRR	5.40 (4.50)	13.00 (3.74)	–	–	–	–	29.40 (13.24)	50.80 (7.15)	–	–

F1-TH: thin-walled trichoids on flagellum 1; F1-TK: thick-walled trichoids on flagellum; F1-BAS: basiconics on flagellum 1; F2-TH: thin-walled trichoids on flagellum 2; P-BAS: basiconics on pedicel. Twy: *T. wygodzinskyi*; Tps: *T. pseudomaculata*; Tma: *T. maculata*. CE: Ceará State; BA: Bahía State; MG: Minas Gerais State; RR: Roraima State.

ulation. Mahalanobis distances were only significant between *T. maculata* and the remaining populations. A low level of reclassification (10%) was obtained for specimens of *T. wygodzinskyi* from Minas Gerais, whereas 60% reclassification was obtained for the population from São Paulo. *T. pseudomaculata* populations from Ceará, Minas Gerais and Bahía State, were also poorly reclassified with 30%, 20% and 20%, respectively. *T. maculata* showed the best value of reclassification, with 70% of the specimens correctly classified.

3.3. Sexual dimorphism

The three species showed sexual dimorphism of their antennal phenotype (Table 3). *T. wygodzinskyi* males (TwyMG population) exhibited significantly more F2-TH than females. *T. pseudomaculata* showed sexual dimorphism for F1-TH and F1-TK (2 populations) and F2-TH (only TpsBA population). Males had a higher number of TH in F1 and F2 than females, although the contrary was observed for F1-TK. *T. maculata* females had a significantly higher density of P-BAS and F1-BAS than males.

4. Discussion

The close external similarities between *T. maculata* and *T. pseudomaculata* were always noted by the specialist. In a large study, Lent and Wygodzinsky (1979) noted that both species are hardly to separate using external features such as color pattern. They also stated that the male genitalia (mainly the endosomal processes) offered the best characteristics for an effective differentiation between them. These similarities were responsible for the establishment of "*T. maculata* complex" comprising exclusively these two species (Carcavallo et al., 2000; Dujardin et al., 2000). Nevertheless from enzymatic, cytogenetic and morphometric data, Santos et al. (2007) suggest the formation of a different group containing *T. pseudomaculata* and *T. wygodzinskyi*, excluding *T. maculata* to a distinct evolutionary lineage. In accordance with these results, our study demonstrates significant similarity between *T. pseudomaculata* and *T. wygodzinskyi* antennal phenotypes, and significant differences with *T. maculata*. Our results are also consistent with molecular studies performed by Hypša et al. (2002) and Paula et al. (2005), who show a high genetic difference between *T. maculata* and *T. pseudomaculata* and a close relationship between *T. pseudomaculata* and *T. wygodzinskyi* (formerly *T. arthurneivai* from São Paulo State; Santos et al., 2007). In contrast, they disagree with the analyses of 12S and 16S sequences performed by Sainz et al. (2004), which suggest that *T. maculata* and *T. pseudomaculata* are closely related species. This discordance could be attributed to a misidentification of Sainz's specimens from Sergipe (Brazil), included in the analysis as *T. maculata*. According to Lent and Wygodzinsky (1979) and Carcavallo et al. (1998a) who studied the geographic distributional range of Triatominae species, those individuals should be *T. pseudomaculata* because *T. maculata* is only found in Roraima State. Finally, it is highly probable that Sainz et al. (2004) have in fact specimens of a single species. Therefore, their conclusion

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about the phylogenetical proximity between *T. pseudomaculata* and *T. maculata* is doubtful, as pointed out by Santos et al. (2007).

The inter-population study reinforces the idea that *T. pseudomaculata* and *T. wygodzinskyi* could be sister species. Nevertheless, multivariate analysis shows the populations distributed in two clusters. The first cluster grouped both *T. wygodzinskyi* populations and *T. pseudomaculata* from Ceará, and the second one with *T. pseudomaculata* from Bahía and Minas Gerais. Both clusters are clearly separated from *T. maculata*. These facts demonstrate the phenotypic proximity of both *T. wygodzinskyi* populations, which originate from close collecting sites.

Even without significant differences in Mahalanobis distances between *T. wygodzinskyi* and *T. pseudomaculata* populations, it is interesting to point out the cluster formed by the *T. pseudomaculata* population from Ceará and *T. wygodzinskyi* populations (Fig. 2). The three populations present high similarity in their antennal phenotype. If we considered *T. wygodzinskyi* and *T. pseudomaculata* as sister species, two possible hypotheses could explain the phenogram topology. In the first, if we consider the antennal phenotype of the Ceará population as plesiomorphic, the phenogram reflects that the group formed by *T. wygodzinskyi* and *T. pseudomaculata* from Ceará shows less phenotypical differentiation from the common ancestor (Fig. 3a). In the second, we considered the antennal phenotype of *T. pseudomaculata* from Minas Gerais to be more plesiomorphic. In this case, the phenogram reflects that the group composed of *T. wygodzinskyi* and *T. pseudomaculata* from Ceará shows the highest phenotypic differentiation from the common ancestor (Fig. 3b). The assumption of Gaunt and Miles (2000), which suggests that genus *Triatoma* has evolved predominantly in rocky habitats, would favor the first hypothesis. Nevertheless, in order to test these hypotheses, further phylogenetic analyses will be necessary to determine the sister group/species of *T. pseudomaculata* and *T. wygodzinskyi*.

The high phenotypical amplitude of *T. pseudomaculata* could be related to biogeographic areas and transition zones in Latin America. Morrone (2006) considers the bioregion from which TpsCE comes as "Para region". In accordance, TpsCE was the only population analyzed that originates from this region, while the two remaining *T. pseudomaculata* populations come from the savanna regions formed by the "cerrado" and "caatinga".

In the inter-populational analysis, we observe a low percentage of *T. wygodzinskyi* and *T. pseudomaculata* specimens correctly reclassified. This is not observed for *T. maculata*, pointing out again the high phenotypic similarities between *T. wygodzinskyi* and *T. pseudomaculata*.

Sexual dimorphism in the antennal *sensilla* pattern was recorded for several triatomine species: *T. infestans* (Catalá and Dujardin, 2001), *T. pseudomaculata* and *T. sordida* (Carbajal de la Fuente and Catalá, 2002), *T. dimidiata* (Latreille, 1811) (Catalá et al., 2005) and *Mepraia spinolai* (Porter, 1934) (Moreno et al., 2005). Our study confirms these results for *T. pseudomaculata* (Carbajal de la Fuente and Catalá, 2002) and reports for the first time sexual dimorphism in the antennal phenotype of *T. maculata* and *T. wygodzinskyi*.

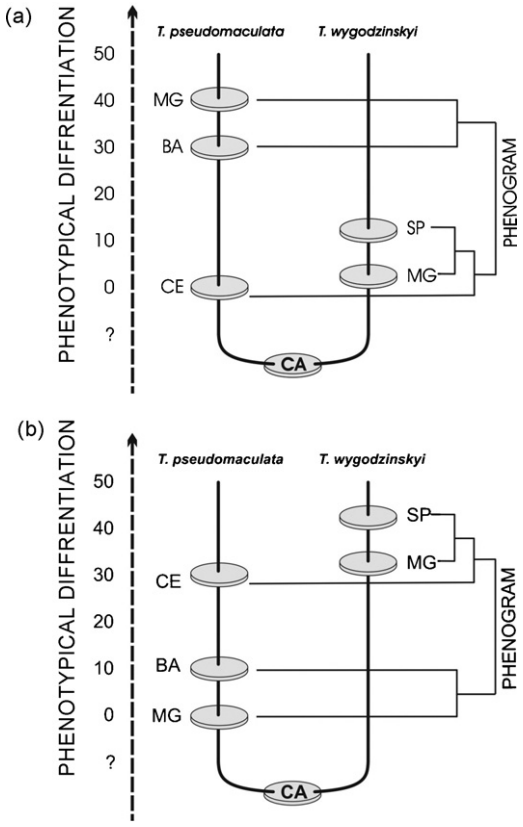

Fig. 3. Hypothesis to explain the phenogram topology of Fig. 2. (a) Considering the antennal phenotype of the Ceará population of *T. pseudomaculata* to be closer to a hypothetical common ancestor (CA) of *T. pseudomaculata* and *T. wygodzinskyi*. (b) Considering the antennal phenotype of the Minas Gerais population of *T. pseudomaculata* to be closer to a hypothetical common ancestor of *T. pseudomaculata* and *T. wygodzinskyi*.

Evidences of this study and previous works (Hypša et al., 2002; Paula et al., 2005; Santos et al., 2007) allow us to propose formally the recomposition of the "*T. maculata* complex". In conclusion, our antennal phenotype data clearly indicate a differentiation between *T. maculata* and *T. pseudomaculata*. In contrast, the latter species and *T. wygodzinskyi* are close species, confirming recent results obtained using geometric morphometry (Carbajal de la Fuente et al., unpublished data). The antennal phenotype reflects the exquisite adaptation of insects to their habitat. Several papers on Triatominae and other insect groups showed this effect very clearly (Lane and Crosskey, 1993; Gracco and Catalá, 2000; Catalá and Torres, 2001). However, the antennae, as a vital essential organ of the insects, have suffered, along their evolutionary history, strong selective pressures reflecting at one and the same time environmental and genetic changes. This work also confirms the high discriminating capacity of antennal phenotype analysis.

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