Antennal Phenotype of *Triatoma dimidiata* Populations and Its Relationship with Species of *phyllosoma* and *protracta* Complexes

S. CATALÁ,[1] C. SACHETTO,[1] M. MORENO,[1] R. ROSALES,[2] P. M. SALAZAR-SCHETTINO,[3] AND D. GORLA[1]

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ABSTRACT *Triatoma dimidiata* (Latreille 1811) Reduviidae Triatominae is the main vector of Chagas disease in several countries of Latin America. As for other vector species, the characterization of *T. dimidiata* subpopulations within particular geographical regions or occupying different habitats could help in better planning of vector control actions. A first objective in this study was to evaluate the antennal phenotype as a phenetic marker to characterize populations of *T. dimidiata* collected in different geographic areas and domestic and sylvatic habitats. A second objective was to evaluate the phenetic relationships of *T. dimidiata* with other species of the *phyllosoma* complex: *longipennis*, *pallidipennis*, and *phyllosoma*. The antennal sensilla of *T. dimidiata* specimens collected in Mexico, Central America, and Colombia were analyzed and compared with the antennal sensilla of *T. longipennis*, *T. pallidipennis*, and *T. phyllosoma*. *T. barberi* was used as an outgroup in the analysis. For each specimen, the ventral side of the three distal segments of the antennae was drawn, identifying and counting four types of sensilla. In *T. dimidiata*, univariate and multivariate analysis showed differences between sexes, among populations collected in different habitats within the same region, and among populations collected in different geographic regions. Two types of antennal sensilla showed a latitudinal variation. Domestic specimens showed intermediate characteristics of the antennal phenotype, between sylvatic cave- and sylvatic forest-collected specimens. The antennal phenotypes show high similarities among *T. pallidipennis*, *T. phyllosoma*, and *T. longipennis*, with a better differentiation of *T. pallidipennis*. *T. dimidiata* is separated from the other members of the complex by a similar distance to *T. barberi*, of the *protracta* complex.

KEY WORDS antennal sensilla, *phyllosoma* group, *Triatoma dimidiata*, Triatominae, Chagas disease

Triatoma dimidiata (Latreille 1811) Reduviidae Triatominae is the main vector of Chagas disease in the southern region of Mexico, Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama) and regions of Colombia, Venezuela, Ecuador, and north of Perú (Zeledón 1981, Schofield 1994, Bustamante 2001) (Fig. 1). The species is found in a variety of sylvatic ecotopes, especially among rocks, bat caves, rodent or marsupial nests, and hollow trees, feeding on mammals, birds, and reptiles. It is able to colonize human dwellings, especially those built with adobe, hiding in the wall crevices (Schofield 1994). *T. dimidiata* has a good dispersal capacity and ability to occupy different habitats, although its colonization capacity of human dwellings is relatively low. Domestic colonies are rarely numerous (Monroy 2003).

T. dimidiata shows high morphological variability along its geographical distribution range. According to Lent and Wygodzinsky (1979), head length has a latitudinal variation, being shorter in specimens at the north of the distribution (south of Mexico) and longer at the south of the distribution in Colombia. Specimens from Ecuador and Peru have a disjunct distribution and show shorter heads, suggesting that these could have originated from Central American populations and been transported by human migrations. There also is variation in the body size and in relative measures of head and eyes (Bustamante 2001) and in the darkness of the hemilytra membrane (Lent and Wygodzinsky 1979).

The phenotypic plasticity of Triatominae seems a frequent adaptive response to new habitats (Dujardin et al. 2000a). Bilateral symmetry and sexual dimorphism are relaxed, and there is a general reduction of the body size as a response to domiciliation (adaptation to domestic habitat) (Dujardin et al. 2000a). The density of sensilla in the antennal pedicel decreases progressively in species living in stable habitats (Catalá 1997). Because morphology seems to be modulated by ecological factors, their effect may produce different morphological phenotypes in populations of the same species living in different geographic regions and/or habitats (Dujardin et al. 2000a). Characterization of subpopulations within particular geographical

[1] Centro Regional de Investigaciones Científicas y Transferencia Tecnológica (CRILAR), Anillaco-La Rioja, Argentina.
[2] Laboratorio de Entomología Aplicada y Parasitología, Escuela de Biología, FCQF, Universidad de San Carlos, Guatemala.
[3] Departamento de Parasitología y Microbiología, UNAM, Mexico.

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Fig. 1. Localities where *T. dimidiata* occur, as reported by several authors and unpublished data.

regions or in different habitats could help in a better planning of control actions.

According to Schofield (2000), *T. dimidiata* would group a series of relatively isolated subpopulations, with low gene flow between them. If this were true, it should be possible to control domestic populations and then analyze reinfestation sources with genetic and phenetic markers. Within this context, the study of genetic and phenetic markers that could be used in the identification of the most likely source of reinfesting populations is a priority for control programs (Bustamante 2001). For hematophagous insects in general, the antennal phenotype would reflect an ancestral pattern modulated by the needs of each particular species (McIver 1985). Number, type, and distribution of sensilla over the antennal segments constitute an antennal phenotype that represents a reliable phenetic marker in several Triatominae species (Catalá 1997, Catalá et al. 2001, Catalá and Dujardin 2001).

T. dimidiata is included in the *phyllosoma* complex. According to Dujardin et al. (2000b), members of this complex show several similarities, and under laboratory conditions some interspecific crossings give viable offspring. A *phyllosoma* group has been proposed by Dujardin and Schofield (2004), conformed by Mesoamerican and Caribbean species including those of the *flavida* complex (*T. bruneri*, *T. flavida*, and *T. obscura*) and those of the *phyllosoma* complex (*bassolsae*, *bolivari*, *brailovskyi*, *dimidiata*, *gomeznunezi*, *hegneri*, *longipennis*, *mazzottii*, *mexicana*, *pallidipennis*, *phyllosoma*, *picturata*, and *ryckmani*). Some controversies exist about these species, mainly because several are poorly known. According to Mazzotti and Osorio (1942), *longipennis*, *mazzottii*, *pallidipennis*, *phyllosoma*, and *picturata* are subspecies of *T. phyllosoma*, but Lent and Wygodzinsky (1979) considered them as a monophyletic group and elevated some subspecies to the species level.

This study has two main objectives. First, to use the antennal phenotype as a phenetic marker to characterize populations of *T. dimidiata* collected in different geographic areas and domestic and sylvatic habitats. Second, to evaluate the position of *T. dimidiata* in comparison with a group of species included in the *phyllosoma* complex (*longipennis*, *pallidipennis*, and *phyllosoma*).

Materials and Methods

Insects. In total, 103 *T. dimidiata* collected in different habitats from Mexico, Costa Rica, Guatemala, Honduras, and Colombia were studied (see details in Table 1). Besides the *T. dimidiata* specimens, 16 *T. phyllosoma*, 10 *T. longipennis*, and 11 *T. pallidipennis* were included as comparison with these species of the *phyllosoma* complex. In total, eight specimens of *T. barberi* (*protracta* complex) were used as an outgroup in the analysis (Table 1).

The specimens of *T. dimidiata* were collected in domestic habitats (within rooms of rural houses), peridomestic habitats (corrals for domestic animals located near the houses and store rooms where dogs and domestic birds sleep during the night) and two types of sylvatic habitats, that were considered separately: "sylvatic forest," collected in the forest of Petén (Guatemala), and "sylvatic cave," collected in lime stone caves located in Lanquin, Guatemala (Monroy 2003).

Preparation and Analysis of Antennae. Antennae were excised and processed with 4% sodium hydroxide and then neutralized with 5% glacial acetic acid. The antennae were mounted using glycerin. This procedure allowed cuticle diafanization and made possible the identification and counting of sensilla using a stereomicroscope at 400× and drawn using a camera lucida. For each specimen, the ventral side of the three distal segments of the antennae was drawn, identifying and counting the following receptors according to

Table 1. Site collection, habitat, and number of specimens used in this study

Species	Orgin	Habitat	No. of specimens
T. dimidiata	Mexico: Veracruz	D	10 F, 10 M
	Mexico: Hidalgo	D	3 F, 8 M
	Mexico: Yucatán	D	7 F, 8 M
	Guatemala: Petén	SS	6 F, 6 M
	Guatemala: Alta Verapaz (Lanquin)	SC	3 F, 3 M
	Guatemala: Quiché, Jutiapa, Sta. Rosa Honduras: Yoro	D	12 F, 12 M
	Costa Rica: Heredia, San José	PD	10 F, 10 M
	Colombia: Santander (San Joaquín)	D	3 F, 3 M
T. phyllosoma	Mexico, Oaxaca	D, PD	1 F, 15 M
T. longipennis	Mexico: Nayarit, Jalisco, Lab. Inst. Oswaldo Cruz	ND, L	4 F, 6 M
T. pallidipennis	Mexico: Morelos	D, PD ND	1 F, 10 M
T. barberi	Mexico: Oaxaca, Guanajuato	ND, D	4 F, 4 M

F, females; M, males; D, domestic; PD, peridomestic; SS, sylvatic from forest; SC, sylvatic from caves; L, laboratory reared; ND, not determined.

Catalá and Schofield (1994): bristles (BR), thin-walled trichoid (TH), thick-walled trichoid (TK), and basiconica (BA).

Data Analysis. Averages and standard deviations of sensilla number by type and antennal segment were calculated. The Levene test was used to determine homoscedascity. Variables with homogeneous variances were analyzed using analysis of variance (ANOVA). Variables showing heteroscedascity were analyzed using the nonparametric test of Kruskal–Wallis.

The data set was analyzed using PADWIN version 60, to estimate functions that identify the studied groups. PADWIN is a software developed by J.P. Dujardin (http://www.mpl.ird.fr/morphometrics) that performs discriminant analyses but estimates statistical significance (of Wilks value and of Mahalanobis distances values) in a nonparametric way, by permutation tests. The number of permutations used here, to estimate reported statistical significances, was 1000.

The discriminant analysis was carried out with the variables that produced the highest contribution to explain variability in the description of the studied populations. Using the Mahalanobis distances calculated in the discriminant analysis, an unweighted pair-group method with arithmetic average cluster analysis (Statistica, StatSoft, Inc. 2000) was carried out to analyze the grouping pattern of the populations.

For analysis of the latitudinal variation in *T. dimidiata*, linear correlations were calculated by using only the domestic specimens to avoid influence of different habitats.

Results

Analysis of *T. dimidiata* Populations. Antennae of *T. dimidiata* show all the sensillar types in the three distal antennal segments. The number of sensilla by type is shown in Table 2, grouped by collection site and habitat. Considering all specimens along range of the species distribution, the number of TH sensilla in the pedicel and flagellum one is significantly higher in males than in females ($P < 0.05$). There was no difference in the number of the other sensillar types among sexes.

Table 2. Antennal sensillar number for different populations of *T. dimidiata* (both sexes)

Pop	*n*		Pedicel				Flagellum 1				Flagellum 2			
			BR	TH	TK	BA	BR	TH	TK	BA	BR	TH	TK	BA
México, Veracruz. D	20	Avg	52.30	249.95	70.00	10.15	16.40	88.25	112.00	22.40	13.40	35.30	112.45	24.15
		SD	7.09	67.85	29.45	5.47	4.27	15.47	21.85	8.60	3.56	7.51	28.60	6.95
México, Hidalgo. D	11	Avg	50.82	301.91	79.09	13.27	15.45	92.72	111.36	25.18	10.82	46.45	95.45	29.91
		SD	10.15	41.65	22.90	5.24	3.36	21.52	17.05	5.91	2.56	8.86	10.51	7.08
México, Yucatán. D	14	Avg	56.21	282.00	70.79	17.79	16.29	94.29	91.00	32.64	8.57	45.93	83.79	27.71
		SD	6.05	45.26	13.25	11.74	4.95	14.62	15.44	7.32	2.79	10.86	11.47	7.58
Colombia, Santander. D	6	Avg	62.67	169.00	40.00	5.83	17.00	127.00	146.67	27.17	11.50	63.33	120.17	36.50
		SD	11.08	79.01	14.66	2.56	4.00	16.46	8.66	3.43	2.74	17.97	14.72	7.79
Costa Rica, Heredia and San Jose. PD	16	Avg	64.00	336.06	81.25	12.81	16.44	151.00	125.63	40.44	12.31	85.13	118.13	40.19
		SD	15.05	95.80	36.87	3.19	3.08	21.52	24.94	13.33	2.94	22.89	32.10	10.57
Guatemala; Quiché, Jutiapa, Sta. Rosa. Honduras, Yoro. D	24	Avg	41.38	192.83	106.50	12.00	16.75	95.38	144.92	57.88	10.79	43.38	119.08	49.00
		SD	7.96	52.65	36.97	5.39	3.76	28.86	32.95	21.06	3.43	19.78	34.17	17.37
Guatemala, Lanquin. SC	6	Avg	60.17	123.67	88.50	7.17	22.00	102.17	156.67	38.67	12.33	58.67	92.33	47.00
		SD	12.13	53.04	16.28	4.67	6.13	27.10	31.94	9.89	4.62	26.50	19.86	11.14
Guatemala, Petén. SS	6	Avg	40.17	226.67	106.67	19.17	13.00	98.67	77.33	49.33	9.00	34.67	86.50	43.67
		SD	4.58	51.75	10.58	5.19	2.76	20.78	23.12	15.47	1.26	12.50	17.50	18.38

D, domestic; PD, peridomestic; SS, sylvatic from forest; SC, sylvatic from caves; BR, bristle; TH, thin-walled trichoid; TK, thick-walled trichoid; BA, basiconica.

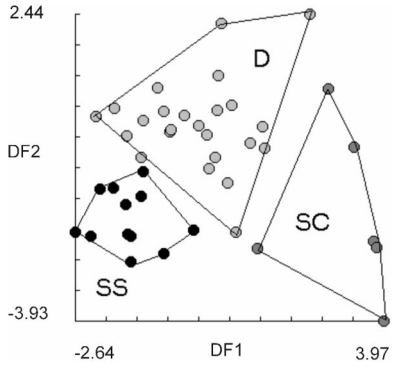

Fig. 2. Discriminant analysis of *T. dimidiata* collected in different habitats within Guatemala. D, domestic; SS, sylvatic forest, SC, sylvatic cave. DF1 and DF2 discriminant function 1 and 2, respectively.

Variations of Antennal Phenotype among Habitats. The antenna of the specimens collected in the habitats sylvatic forest, sylvatic cave, and domestic, all within Guatemala, were studied using a discriminant analysis (PADWIN). Specimens collected in other regions were excluded from the analysis to avoid confusion due to the geographic distance. The analysis produced functions that significantly discriminated the three groups. The first discriminant function explained 69% of the total variation, whereas the second function explained 31%. The Mahalanobis distances among the three groups were all significant. Distance between the domestic and sylvatic–cave habitats was the shortest, whereas the distance between the two sylvatic habitats was the longest distance (Fig. 2). The higher variation in the sensilla among habitats was observed in the TH of the pedicel and in the TK of flagellum 1. Specimens collected in the domestic habitats showed intermediate characteristics in the number of TK and TH.

Latitudinal Variation in TK and TH. Correlation between the number of the two chemoreceptors (TK and TH) and latitude of the collection site was analyzed to test the hypothesis of morphological changes of species along latitude as proposed by Lent and Wygodzinsky (1979). The number of TK in the flagellum one decreases with latitude increase ($r = -0.56$, $P < 0.001$, $n = 75$; Fig. 3A). Conversely, an increase of the pedicel TH was observed when latitude increases ($r = 0.58$, $P < 0.001$, $n = 75$; Fig. 3B).

Characterization of *T. dimidiata* Domestic Populations. A discriminant analysis of domestic populations was carried out to test the ability of the antennal phenotype to identify domestic populations of different geographical origins. This analysis used the four variables with the highest contribution to the description of the populations: TH of the three antennal segments and TK of the flagellum 1. The discriminant analysis was significant (Wilks = 01765, $P < 0.001$); the derived Mahalanobis distances among populations were used in a unweighted pair-group method with arithmetic average cluster analysis (Fig. 4) that showed two main branches and three groups: one

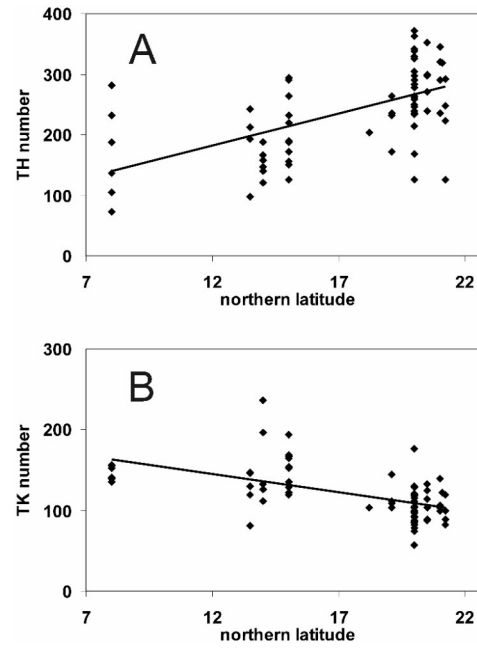

Fig. 3. Latitudinal variation of the thin-walled trichoids (TH) (A) and the thick-walled trichoids (TK) of the flagellum one (B) in both sexes of domestic *T. dimidiata* (all localities).

branch with the three populations of Mexico and the other branch with two groups: Colombia separated from Guatemala + Honduras populations. Distances between these three main groups were significant ($P < 0.05$).

Phenotypic Similarity within *phyllosoma* Complex. The similarity of the antennal phenotype of the four species of the *phyllosoma* group was analyzed using a nonparametric discriminant analysis with eight antennal variables (Table 3). The proportional contribution to the total variance of the two first functions were 0.69 and 0.28, respectively. Figure 5 shows the location of each specimen in the space defined by the first two discriminant functions. All distances were significant ($P < 0.05$). The antennal phenotype shows high similarity between *T. pallidipennis*, *T. phyllosoma*, and *T. longipennis*, with a better differentiation of *T. pallidipennis*. *T. dimidiata* is well separated from the other three species of the group.

Discussion

Intraspecific Variation of *T. dimidiata*. The sensilla of the triatomine antennae has been shown to be a reliable marker of sex, species, genera, and population within a species (Catalá and Schofield 1994, Catalá 1997, Gracco and Catalá 2000, Carbajal de la Fuente and Catalá 2002, Catalá et al. 2004). Triatominae species living in different habitats show many chemoreceptor sensilla of three different types in the antennal pedicel, whereas those adapted to one or few stable habitats (as a human house or a palm crown) show

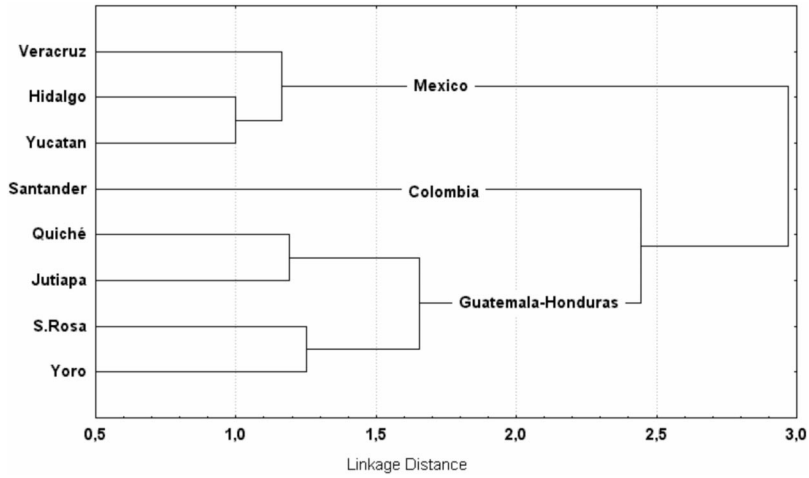

Fig. 4. Cluster analysis derived from Mahalanobis distances among the studied populations (unweighted pair-group method with arithmetic average method).

none or few chemoreceptors in the antennal pedicel (Catalá 1997). This study shows that *T. dimidiata* has many chemoreceptors of the three different types in the antennal pedicel, suggesting good capacity for dispersal and invasion of different habitats. Sexes were readily distinguished by the higher number of TH on the pedicel and first segment of the flagellum of males, coinciding with similar findings in other Triatominae (Catalá et al. 2000, Carbajal de la Fuente and Catalá 2002).

The antennal phenotype of the studied specimens varies according with very different habitats, particularly in the chemoreceptor trichoids TH and TK. The higher number of TK in cave and domestic specimens of *T. dimidiata* than in the sylvatic specimens of the Petén forest could be related with stability in the availability of food, mates, and refuge in the first-mentioned group. Cave specimens, which are big and pale with small eyes, showed more TK sensilla in the flagellum than the specimens of the other habitats. They probably show the extreme of a phenotype range because they occupy the most particular habitat, similar to a domestic habitat. Another highly domestic species of the southern cone of South America (*T. infestans*), shows more TK in the flagellum in the domestic population than the sylvatic populations found in the Cochabamba valleys of Bolivia, giving support to the idea that the abundance of this sensillum increases with the habitat stability and could constitute a good marker of domiciliation (Catalá and Dujardin 2001). The function of the TK is unknown, although it may be related with the detection of a pheromone by contact.

Characterization of populations collected in different habitats based on the antennal phenotype coincides with the findings of Bustamante (2001), Bustamante et al. (2004), and Calderón Fernandez et al. (2005) for the Guatemala populations, based on head and wing morphometry and cuticular hydrocarbons that allowed the characterization of the domestic, Petén sylvatic forest and Lanquin sylvatic cave phenotypes. The Lanquin cave specimens are phenotypically more similar to the domestic specimens. The antennal phenotype showed intermediate characteristics in domestic specimens, indicating a wide phenotypic range and high morphological plasticity of the species. This would represent a difficult problem for the control of this species, as peridomestic structures

Table 3. Number of antennal sensilla by type and segment in species of the *phyllosoma* complex and *T. barberi* (*rubrofasciata* complex)

Species	*n*		Pedicel				Flagellum 1				Flagellum 2			
			BR	TH	TK	BA	BR	TH	TK	BA	BR	TH	TK	BA
T. phyllosoma	16	Avg	81.25	122.38	45.31	5.19	15.25	76.44	225.19	22.69	9.91	40.64	199.45	32.27
		SD	11.96	27.66	16.68	1.97	3.96	16.85	25.69	10.96	1.45	9.15	31.61	11.99
T. longipennis	10	Avg	93.10	189.20	32.60	3.90	16.60	79.10	200.10	22.00	11.33	30.83	140.00	28.83
		SD	8.79	46.33	13.79	2.13	2.63	17.86	29.23	8.33	2.16	8.04	34.25	10.36
T. pallidipennis	11	Avg	97.27	221.27	44.73	5.45	15.91	90.55	296.00	28.27	9.36	33.18	205.64	36.27
		SD	7.77	43.61	17.99	1.21	2.34	16.46	41.00	13.41	2.84	4.79	25.79	15.70
T. dimidiata	103	Avg	52.47	246.40	83.00	12.51	16.58	104.62	121.01	37.91	11.21	50.33	107.11	36.26
		SD	12.57	86.44	33.10	6.95	4.23	30.11	32.99	18.49	3.39	22.86	28.99	14.99
T. barberi	8	Avg	97.13	120.50	0.63	2.13	13.13	40.63	89.00	15.86	7.75	17.88	104.75	20.88
		SD	10.15	64.36	1.19	1.81	3.27	17.86	20.28	6.94	1.28	6.03	5.90	5.33

BR, bristle; TH, thin-walled trichoid; TK, thick-walled trichoid; BA, basiconica.

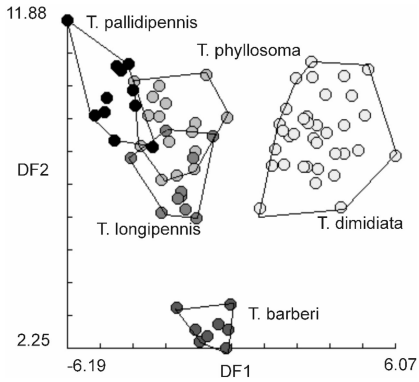

Fig. 5. Location of individuals of the four species of the *phyllosoma* group and *T. barberi* of the *rubrofasciata* group, in the space defined by discriminant function 1 (DF1) and discriminant function 2 (DF2). See text.

and/or the domicile could be invaded from sylvatic habitats after the application of insecticide, situations already reported by Monroy (2003) and Dumonteil and Gourbiere (2004).

T. dimidiata is considered a species with a genotype able to express different morphologies, physiological status and/or behavior responding to different environmental conditions (Bustamante 2001, Calderón-Fernandez et al. 2005). There is evidence that this species, showing a wide distribution range, has a high morphological and behavioral variability. This variability has lead many researchers to describe some variants as subspecies or even as different species. The antennal phenotype analyzed in this study allowed the identification of different geographic populations and agrees with the existence of a wide phenotypic variation of *T. dimidiata.* The proposed idea that the Yucatan population is a different species (Marcilla et al. 2001) was not confirmed by our results, but the studied specimens are not the same.

Although the peridomestic specimens, exclusively collected in Costa Rica, were excluded from the multivariate analysis, it is worth mentioning that they showed a particularly high number of TH in the three antennal segments (Table 2). Future studies should consider the analysis of larger specimen samples to compare the sensilla pattern among different habitats of the same region.

Besides the high phenetic variability, *T. dimidiata* also shows a variable ability to colonize the domestic habitat. In addition to the latitudinal variation in the head size reported by Lent and Wygodzinsky (1979), our study shows a latitudinal variation on the number of TK and TH trichoid sensilla. As latitude decreases, there is a decrease in the TH and an increase in the TK, suggesting that areas nearer the equator could represent more stable conditions for the domiciliation of the species. These findings also suggest that some morphological characters, such head size and form, are linked to the antennal phenotype and could be used together as strong morphological indicators for domiciliation and dispersion studies.

Interspecific Relationships. The identity of the species that are presently included in the *phyllosoma* group has been strongly discussed (Lent and Wygodzinsky 1979) and *T. pallidipennis* and *T. longipennis* have been considered subspecies of *T. phyllosoma* by Usinger (1944). The antennal phenotypes analyzed in this study support the idea that *T. phyllosoma* is very similar to *T. longipennis,* and *T. pallidipennis* is the most different to *T. dimidiata.* The position of *T. dimidiata* as a phenotypically different entity is clear. A similar clustering of these species was also demonstrated in sequence analysis of the mitochondrial large subunit rRNA and cytochrome *b* (Lyman et al. 1999) and of ITS-2 (Marcilla et al. 2001). Similarly, a cytogenetical analysis reported by Dujardin et al. (2000b) shows the proximity of the members of this species complex.

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