GEOGRAPHIC PATTERNS OF ABDOMINAL URTICATING SETAE TYPES IN NEOTROPICAL TARANTULAS (ARANEAE, THERAPHOSIDAE)

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ABSTRACT

We studied the geographic distribution of theraphosid abdominal urticating setae types to test the presence of biogeographical patterns. Setae types were mapped on area cladograms recently proposed for the regionalization of the Neotropical region. We found some patterns which agree with some historical biogeography events and also some ecological pressures are discussed to explain urticating setae distribution.

Keywords: biogeography, tarantulas, Theraphosidae, urticating-setae.

RESUMEN

Patrones biogeográficos de los tipos de setas urticantes abdominales en tarántulas neotropicales (Araneae, Theraphosidae). Estudiamos la distribución geográfica de los tipos de setas urticantes abdominales de arañas Theraphosidae para poner a prueba la existencia de patrones biogeográficos. Las setas fueron mapeadas en un cladograma recientemente utilizado para la regionalización de la región Neotropical. Encontramos algunos patrones que coinciden con algunas hipótesis de biogeografía histórica de la región y discutimos también las posibles presiones ecológicas que pueden explicar la distribución de las setas urticantes.

Palabras clave: biogeografía, setas urticantes, tarántulas, Theraphosidae.

INTRODUCTION

Theraphosid tarantulas show a remarkable defensive behavior that involve the releasing of urticating setae (Cooke *et al*., 1972). Although Theraphosidae are present in several tropical and subtropical regions of the world, urticating setae only evolved in New World tarantulas, and are present in more than 500 of the 600 species present in the continent (Bertani & Guadanucci, 2013). Representatives of Avicullariinae and Theraphosinae are the only subfamilies that present urticating setae; they are located on the dorsum of the abdomen in Theraphosinae and most Avicullariinae, or on prolateral palpal femur as in the Avicullariinae genus *Ephebopus* (Marshall & Uetz, 1990; Foelix, 2009). The Theraphosinae and *Avicularia versicolor* (Walckenaer,

1837) release their urticating setae by scratching the posterior legs against the setae patch on the abdomen (Cooke *et al*., 1972; Pérez-Miles & Prandi, 1991; Bertani *et al*., 2003; Bertani & Marques, 1996) while other Avicullariinae species transfer the urticating setae by direct contact of the abdomen against the target (Bertani & Marques, 1996). *Ephebopus* release urticating setae by scratching the palps against the basal segments of the chelicerae (Marshall & Uetz, 1990a; Foelix *et al*., 2009).

Cooke *et al.* (1972) described four types of urticating setae considering their morphological characteristics and numbered them I to IV. Type II is only present in some Avicullariinae, whereas types I, III and IV are present in most Theraphosinae. Marshall & Uetz (1990) described type V urticating setae on prolateral palpal femur of *Ephebopus* (Avicullariinae). Pérez-Miles (1998) described type VI urticating setae on the abdomen of *Hemirrhagus* (Theraphosinae). Recently Perafán *et al.* (*in press*) discovered another new type (VII) of urticating setae in an undescribed Theraphosinae genus.

Among Theraphosinae two different types can co-occur simultaneously on the same individual (I+III or III+IV) and it has been suggested that different types can be segregated in different areas of the abdomen (Cooke *et al*., 1972; Bertani & Guadanucci, 2013). Cooke *et al.* (1972) also suggested the use of urticating setae types in the taxonomy of the theraphosids and consequently they were incorporated as characters to a first phylogenetic analysis of the Theraphosinae (Pérez-Miles *et al*., 1996); in that cladogram type III setae were widespread in the subfamily; type IV occurred in a group including several old named Grammostolinae, and type I occurred in most other Theraphosinae genera. The increasing number of theraphosid genera described in recent years makes to regard the analysis of Pérez-Miles *et al.* (1996) as a limited taxon sample. Also exhaustive studies on morphology and function of urticating setae (Bertani & Guadanucci, 2013) improved the knowledge on this subject. Based on this important amount of information and informal observations carried on during more than three decades, we hypothesized that there is an association between the occurrence of urticating setae types in Theraphosinae and their geographic distribution. To test this hypothesis we study the occurrence of urticating setae types in Theraphosidae genera together with their geographic distribution and we mapped them on a general area cladogram of the Neotropical regionalization recently proposed by Morrone (2014a, 2014b). Our results strongly suggest the presence of geographic patterns of distribution for some urticating setae types. Considering Theraphosidae are biogeographically informative because their poor vagility, limited dispersal mechanisms and sedentary habits (Ferretti *et al*., 2012, 2014), those patterns are discussed in the light of historical biogeographical hypothesis.

MATERIAL AND METHODS

Urticating setae types were recognized following morphological characteristics given by Cooke *et al*., 1972; Marshall & Uetz, 1990; Bertani & Marques, 1996; Pérez-Miles, 1998; and Bertani & Guadanucci, 2013. The presence of urticating setae types in Theraphosidae genera was registered from direct examination of specimens during more than 30 years in different studies, and from the literature, especially original descriptions (Table 1). We considered

Table 1. Theraphosids genera considered in the study, presence of urticating setae and geographic distribution in the biogeographic units proposed by Morrone (2014b). AS = Antillean Subregion, MTZ= Mexican transition zone, MD= Mesoamerican dominion, PCD= Pacific dominion, BBD= Boreal Brazilian dominion, SBD= South Brazilian dominion, S-EAD= South-eastern Amazonian dominion; PRD= Parana dominion, CD= Chacoan dominion, SATZ= South American transition zone, mod=modified, ?= uncertain. *Examined material; other information taken from literature.

Genus	Urticating setae types								Geographic area									
	only I	I mod	I+III	only III	III+IV	II	VI	VII	AS	MTZ	MD	PCD	BBD	SBD	S-EAD	PRD	CD	SATZ
*Avicularia**						x			x		x	x	x	x	x	x	?	
*Acanthoscurria**			x						x			x	x	x			x	?
*Agnostopelma**																		X
*Ami**		x	x									x	x	x				
*Aphonopelma**	x									x	x	x						
Bonnetina				x						x	x							
*Brachypelma**			x							x	x	x						
*Bumba**					x								x					
Catanduba					?											x	x	
Chromatopelma					x							x						
Citharacanthus		x	x						x	x	x							
Clavopelma	x									x	x	x						
Cotztletana	x									x	x							
Crassicrus	x										x							
Cubanana			x						x									
*Cyclosternum**				x							?	x		x				x
*Cyriocosmus**				x								x	x	x			x	x
*Cyrthopholis**	x								x									
Davus				x						x	x							
*Euathlus**					x													x
*Eupalaestrus**			x													x	x	
*Grammostola**					x											x	x	x
*Hapalopus**				x							x	x	x	x				
Hapalotremus				x										x				x
*Hemirrhagus**							x			x	x							
*Homoeomma**					x											x	x	
Iridopelma						x							x		?	x	x	
Kochiana				x												x		
*Lasiodora**			x													x	x	
Lasiodorides			x										x	x				
*Magulla**					x											x	x	
*Megaphobema**			x									x	x					
*Melloleitaoina**					x													x
*Metrioplema**	x									?	x	x						
*Munduruku**					x								x					
Neostenotarsus			x										x					

Table 1. *(Cont.)*

Genus	Urticating setae types								Geographic area									
	only I	I mod	I+III	only III	III+IV	II	VI	VII	AS	MTZ	MD	PCD	BBD	SBD	S-EAD	PRD	CD	SATZ
Nhandu *			x										x	x	x	x	x	
Pachistopelma						x										x		
Pamphobeteus *			x										?	x				x
Phormictopus *			x						x									
Phrixotrixhus *					x													x
Plesiopelma *					x											x	x	
Proshapalopus		x	x											x		x		
Pseudhapalopus			x															x
Pterinopelma	x		x														x	
Reversopelma			x											x				
Schizopelma *			x							x	x							
Sericopelma *			x							x	x	x						
Sphaerobothria *	x											x						
Theraphosa *				x									x					
Thrixopelma *					x									x				x
Tmesiphantes *					x											x	x	
Vitalius *			x													x	x	
Xenesthis *			x									x						
Undescribed genus. *									x				x					

urticating setae types present in representative species and we did not consider sexual dimorphism (lack of one type in one sex) because is not know in all species. The geographic distribution of the taxa bearing urticating setae was taken from collection sites and information from literature. Doubtful geographic references were not considered. To map the distribution of urticating setae types, we considered the regionalization and biogeographical units (Fig. 1) proposed by Morrone (2014b). The distribution map was produced using DIVA-GIS version 7.5.0 (http://www.diva-gis.org/) and we used the shapefile of the regionalization map of Morrone (2014a) provided by Löwenberg-Neto (2014). We used the general area cladogram of Morrone (2014a) and we traced character history for urticating setae types on it, with Mesquite (Maddison & Maddison, 2008), using parsimony ancestral state reconstruction. Considering the serial homology proposed for urticating setae types (Bertani & Guadanucci, 2013), we map them on Morrone's (2014a) cladogram codified as follows (Table 2): 1. urticating setae type I (only): absent (0), present (1); 2. co-occurrence of types I and III: absent (0), present (1); 3. type I modified (with area b longer than usual): absent (0), present (1); 4. type II: absent (0), present (1); 5. type III (only): absent (0), present (1), 6. co-occurrence of types III and IV: absent (0), present (1); 7. type VI: absent (0), present (1); 8. type VII: absent (0), present (1). Abbreviations: AS = Antillean subregion, MTZ= Mexican transition zone, MD= Mesoamerican dominion, PCD= Pacific dominion, BBD= Boreal Brazilian dominion, SBD= South Brazilian dominion, S-EAD= South-eastern Amazonian dominion; PRD= Parana dominion, CD= Chacoan dominion, SATZ= South American transition zone.

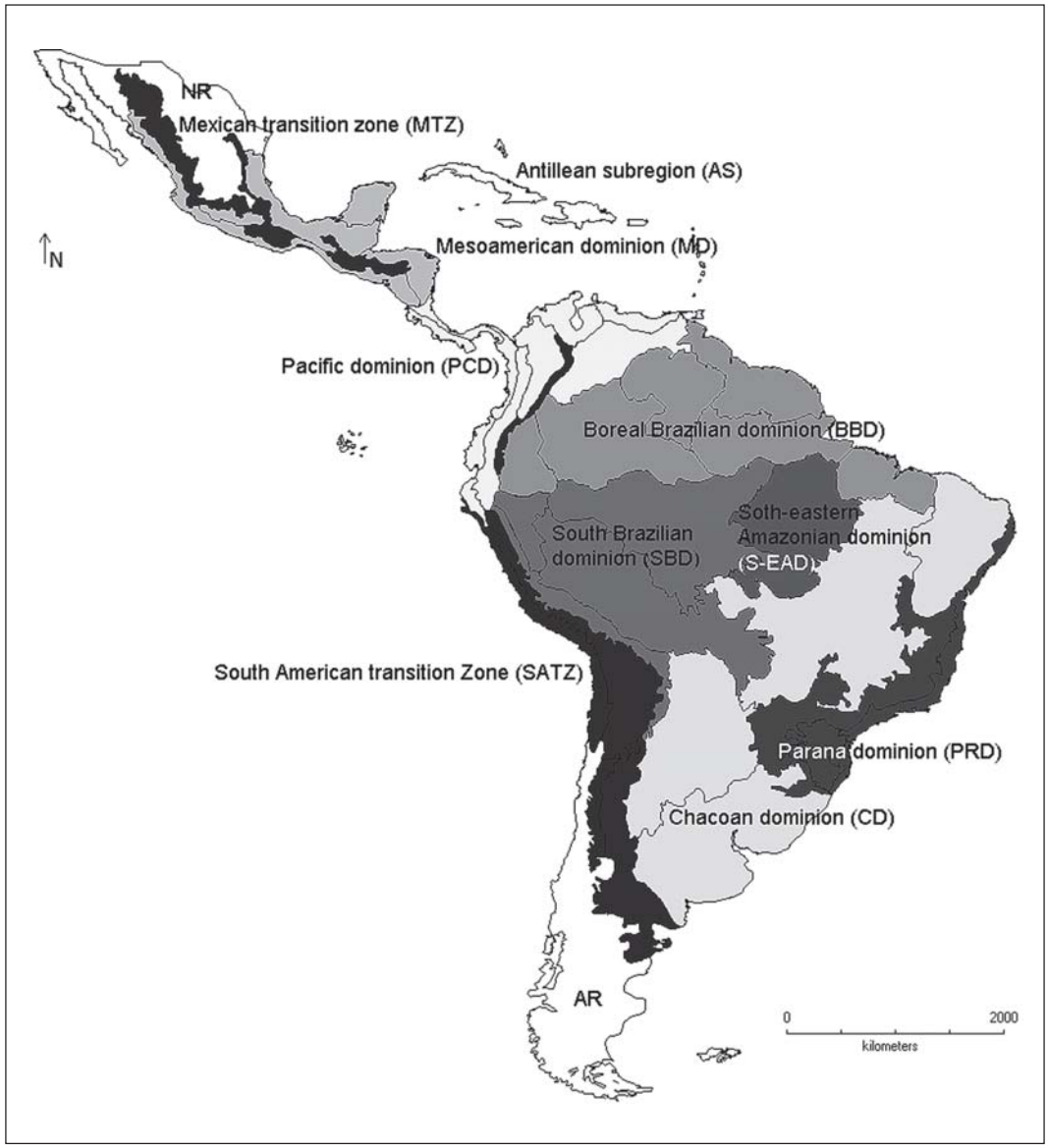

Fig. 1. Biogeographic regionalization map, redrawn from Morrone (2014b).

RESULTS

Type I urticating setae

Genera which only present type I urticating setae (Table 1) mainly occur in the northern area of South America, Mesoamerica, Antilles and also in the Neartic region. *Pterinopelma vitiosum* (Keyserling, 1891) is the only species present in the Chacoan dominion with type I urticating setae type alone but other species known of *Pterinopelma* have co-occurrence of types I and III. The pattern of distribution comprises the following biogeographical units: Chacoan, Pacific, and Mesoamerican dominions, Mexican transition zone, Antillean subregion (Fig. 2), and also in the Neartic region. Mapping type I urticating setae on the area cladogram, it show four steps (Fig. 2b). Modified type I urticating setae (with area b longer than usual) showed a slightly different and more restricted distribution; occur in Amazonia (Boreal Brazilian and South Brazilian dominions), northern South America (Pacific dominion) and Mesoamerican dominion (Fig. 3). In the area cladogram, modified type I present an unique change at the node of these areas being congruent with this clade (Fig. 3b). Only species of *Ami*, *Citharacanthus* and *Proshapalopus* have these modified urticating setae (Table 1).

Type II urticating setae

This type of urticating setae are present in the Avicullariinae *Avicularia*, *Pachistopelma* and *Iridopelma* (Table 1) and, with exception of *Avicularia versicolor*, is transferred by direct contact of the abdomen against the target. The geographic distribution of these setae comprises tropical areas of South and Central America, including: Chacoan, Parana, South Brazilian, Boreal Brazilian, South-

Table 2. Matrix used to trace characters on the general area cladogram of Morrone (2014a). Characters: 1. urticating setae type I (only): absent (0), present (1); 2. co-occurrence of types I and III: absent (0), present (1); 3. type I modified (with area b longer than usual): absent (0), present (1); 4. type II: absent (0), present (1); 5. type III (only): absent (0), present (1), 6. co-occurrence of types III and IV: absent (0), present (1); 7. type VI: absent (0), present (1); 8. type VII: absent (0), present (1).

Biogeographic unit	Characters							
	1	2	3	4	5	6	7	8
Antillean subregion	1	1	0	1	0	0	0	0
Mexican transition zone	1	1	0	0	1	0	1	0
Mesoamerican dominion	1	1	1	1	1	0	1	0
Pacific dominion	1	1	1	1	1	1	0	1
Boreal Brazilian dominion	1	1	1	1	1	1	0	0
South Brazilian dominion	0	1	1	1	1	1	0	0
South-eastern Amazonian dominion	0	1	0	1	0	0	0	0
Parana dominion	0	1	0	1	1	1	0	0
Chacoan dominion	0	1	0	1	1	1	0	0
South American transition zone	1	1	0	0	1	1	0	0
Neartic region	1	1	0	0	0	0	0	0
Andean region	0	0	0	0	0	1	0	0

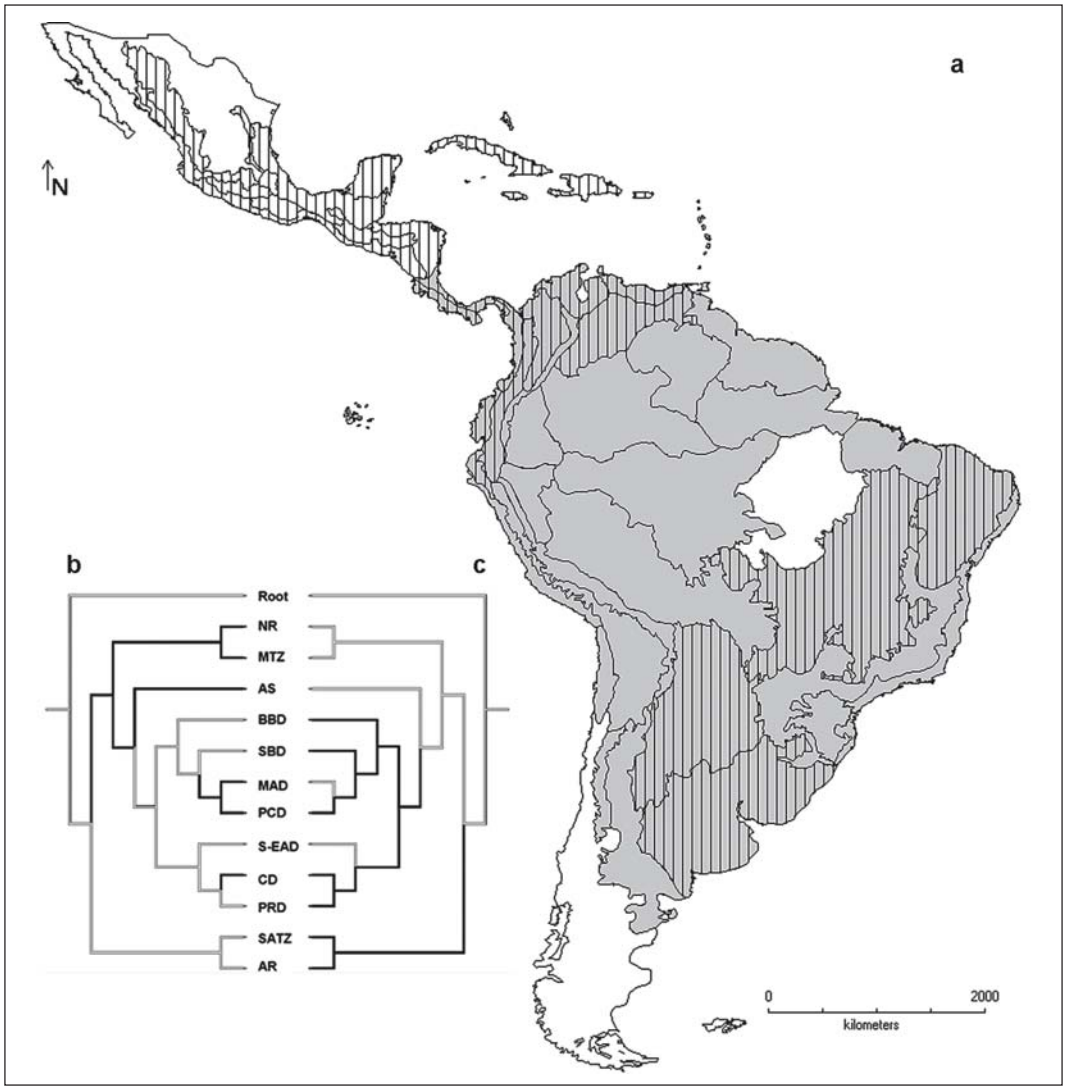

Fig. 2. a) Geographic distribution of the urticating setae types I (only) and III+IV, based on the biogeographical units of Morrone (2014b): grey=type III+IV, vertical fill= type I. b) and c) Traced history of urticating setae on the general area cladogram (Morrone, 2014a): b) only type I and c) III+IV. For abbreviations see Material and Methods.

eastern Amazonian, Pacific and Mesoamerican dominions, as well as Antillean subregion (Fig. 4). Type II setae only show one step at the node of these tropical areas in congruence with the topology of the area cladogram (Fig. 4b). In the Chacoan dominion only few species of *Avicularia* and

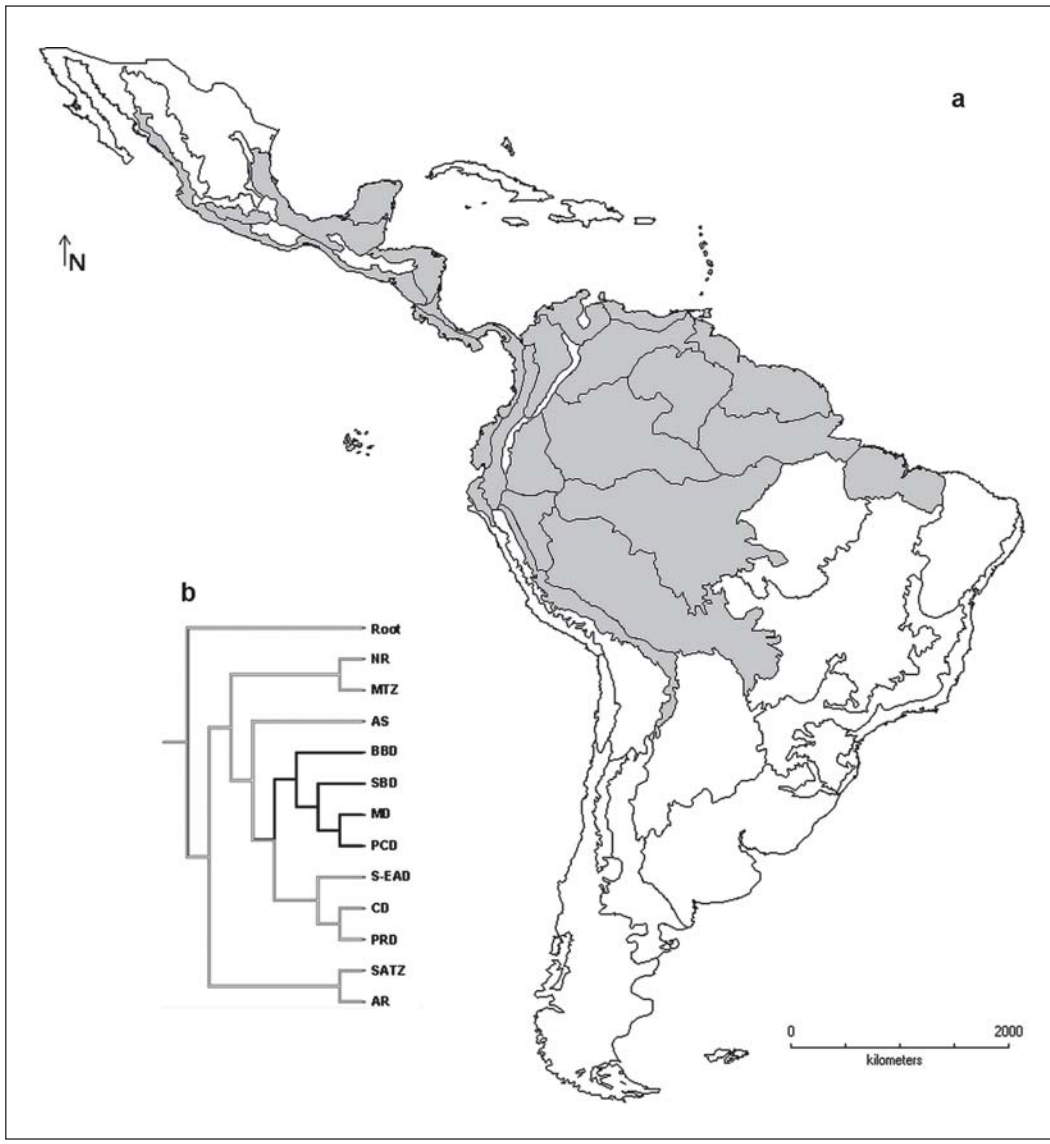

Fig. 3. a) Geographic distribution of the modified type I urticating setae, based on the biogeographical units of Morrone (2014b). b) Traced history of these setae on the general area cladogram (Morrone, 2014a). For abbreviations see Material and Methods.

Iridopelma are present and restricted to northern Caatinga and Cerrado provinces. These species are the only representatives with type II setae in open environments.

Type III urticating setae

Genera which only present type III setae (without type I or IV) are widely distributed in almost all areas considered with exception of Antillean subregion and South-eastern Amazonian dominion (Fig. 5 and Table 1). In the area cladogram, type III setae present four steps which could represent some losses or transformations to the combination I+III (Fig. 5b).

Type I + III urticating setae

The co-occurrence of types I and III urticating setae is widespread distributed throughout the Neotropical region and also in the Neartic region and is the most common urticating setae combination within the Theraphosinae genera (Fig. 5 and Table 1). Mapping types I + III on the area cladogram, they occurred on the in-group node with a secondary loss in the Andean region (Fig. 5c).

Type III + IV urticating setae

The co-occurrence of types III and IV urticating setae is strictly distributed in South American Neotropics, excepting South-eastern Amazonian dominion. The distribution comprises southern part of Pacific, Boreal Brazilian, South Brazilian, Chacoan and Parana dominions (Fig. 2, Table 1). This setae combination is also present in the Andean region. Mapping types III-IV on the area cladogram, they present four steps (Fig. 2c).

Types VI and VII urticating setae

Type VI urticating setae are only present in the Mexican endemic genus *Hemirrhagus* so their distribution is restricted to Mesoamerican dominion and Mexican transition zone (Table 1). Type VII was recently discovered in an undescribed Theraphosinae genus and seems to be transferred by direct contact (as type II). This new genus is located in Colombia so its distribution is only known from Sierra Nevada de Santa Marta on Pacific dominion (Fig. 4).

DISCUSSION

Bertani & Guadanucci (2013) proposed that urticating setae present a special homology called as homonomy. Homonoms are many copies of the homologue in one individual, which are expected to pass the similarity and congruence tests of homology, but not of conjunction, since the two supposed homologues are found in the same organism (Patterson, 1982).

In the transformation series of the urticating setae, Bertani & Guadanucci (2013) proposed the ancestral condition of type III, from which would derivate types I or IV.

The widespread distribution of type III setae occurring alone or in combination with other types of urticating setae clearly agree with that hypothesis, as also with the cladogram of Pérez-Miles *et al.* (1996) who proposed that type III setae would be a synapomorphy of Theraphosinae. The presence of type III setae in the Antilles suggest their early origin during Early Jurassic to Early Cretaceous (190-148 My), before the vicariant event between this region and the remaining

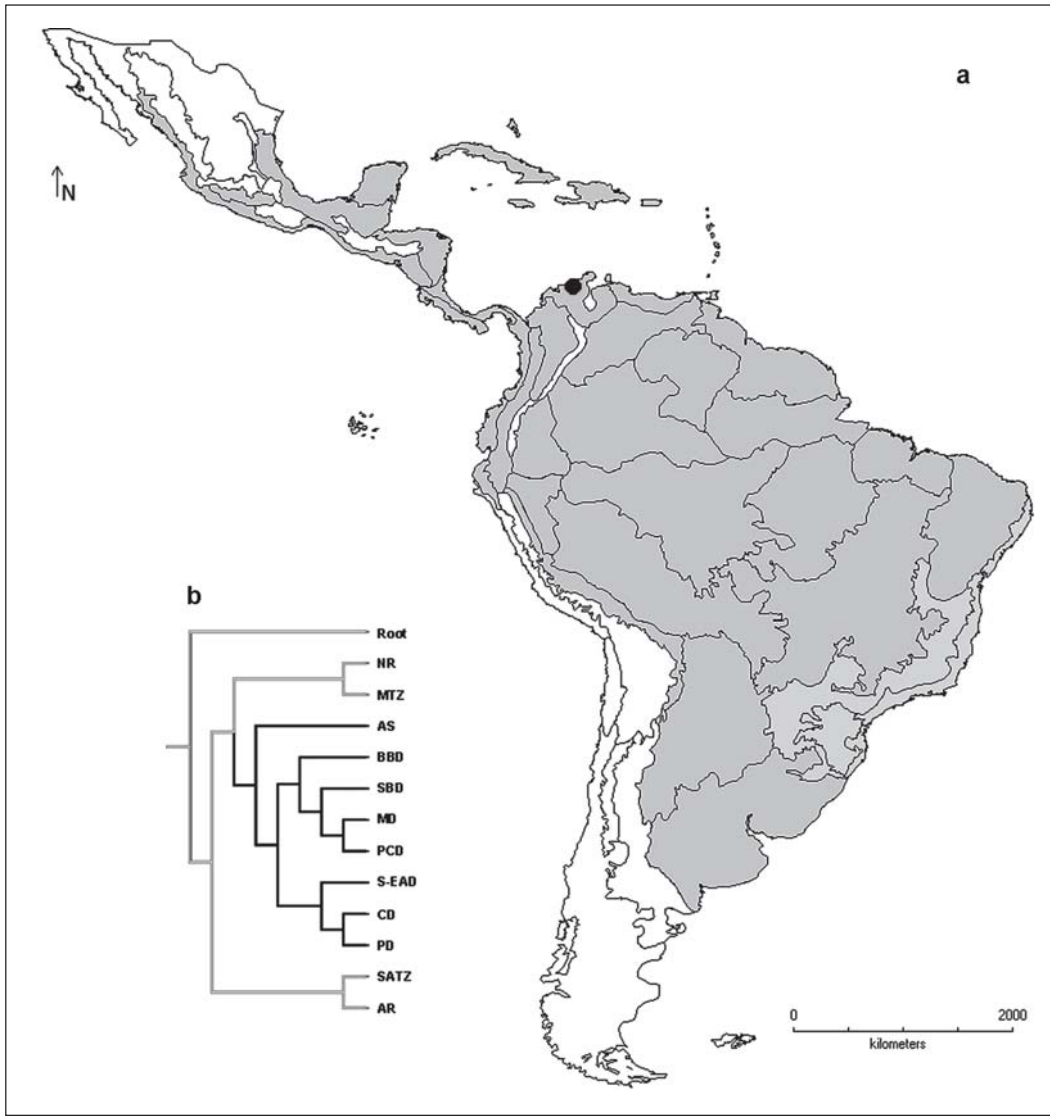

Fig. 4. a) Geographic distribution of the urticating setae type II, based on the biogeographical units of Morrone (2014b). b) Traced history of these setae on the general area cladogram (Morrone, 2014a). Black circle show the geographic distribution of the urticating setae type VII (Theraphosinae urticating setae of an undescribed genus). For abbreviations see Material and Methods.

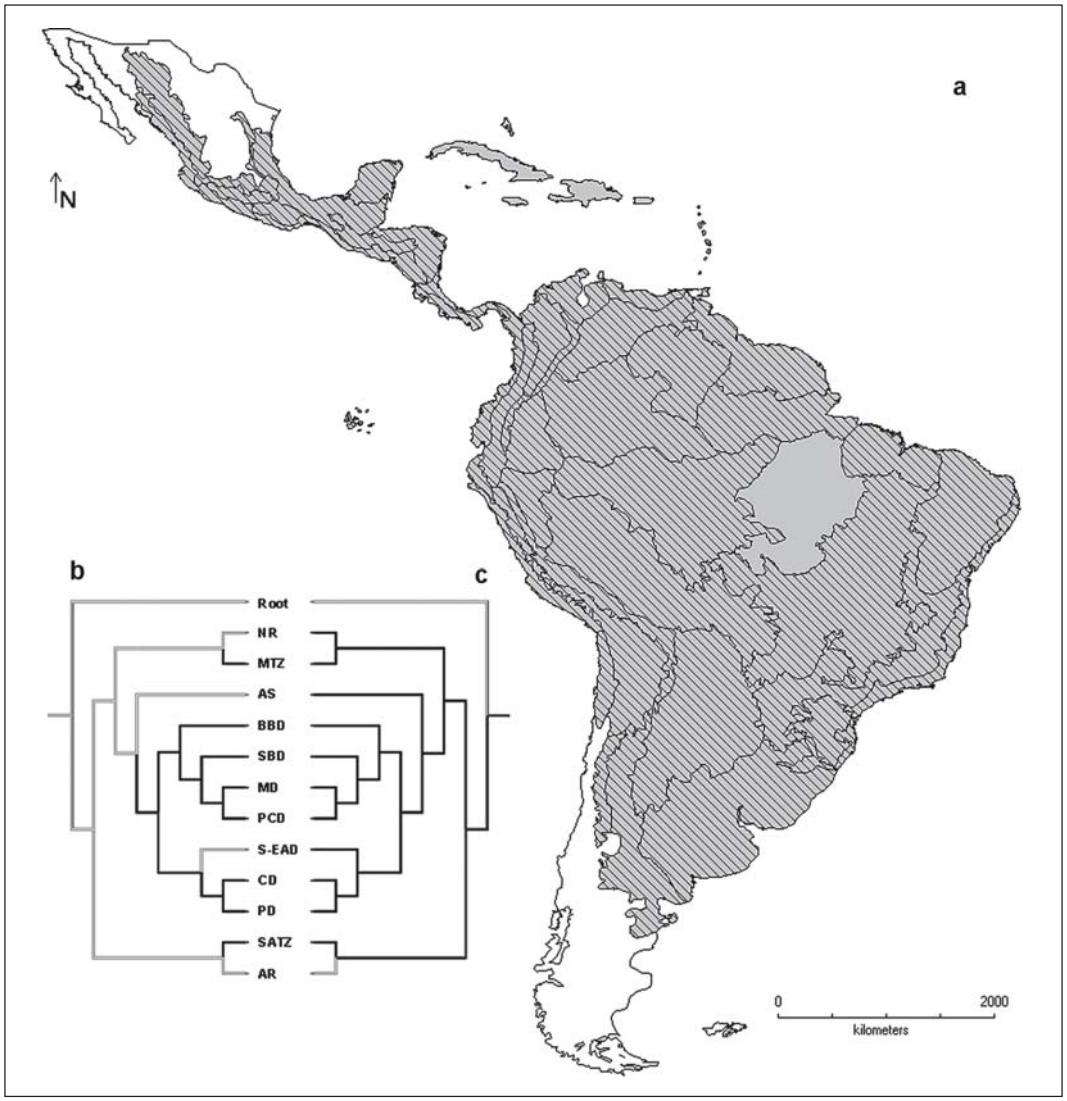

Fig. 5. a) Geographic distribution of the urticating setae types I+III and III (only), based on the biogeographical units of Morrone (2014b): grey= type I+III, upward diagonal fill= type III. b) and c) Traced history of urticating setae on the general area cladogram (Morrone, 2014a): b) only type III and c) type I+ III. For abbreviations see Material and Methods.

Neotropical region (Morrone, 2014). Although we did not include the Neartic region in our study, the presence of type III setae in this region (*Brachypelma* spp.) also agree with the ancient geodispersal of the Neotropical biota to North America and would explain the presence of ancient Neotropical elements in northern Mexico proposed by Halffter (1987) and Morrone (2005), during that period. The wide distribution of type III setae also agree with the plasticity in their function, since Bertani & Guadanucci (2013) proposed the use of these setae in passive defense against invertebrates as well as active defense against small vertebrates.

If type I setae are derived from type III as suggested by Bertani & Guadanucci (2013), their presence alone (with no co-occurrence of type III) could be explained as a secondary lost of type III setae. The lost of type III in favor of type I, mainly occurred in the northern part of South America and Mesoamerica as well as in the Neartic region. This pattern could reflect ecological pressures in these areas, because the effectiveness of the type I as passive defense against ants, phorids, and in general small invertebrates; only this type is massively incorporated on egg-sacs (Pérez-Miles & Costa, 1994; Bertani & Guadanucci, 2013). Type I setae easily get entangled with each other upon contact with barbed areas (Bertani & Guadanucci, 2013); this could help the spider to release them during incorporation of these setae to egg-sac. We observed that entangling is more conspicuous in modified type I setae which are confined to tropical areas. Tracing the modified type I setae on the cladogram (Fig. 3), we found this strictly agree with the monophyly of Amazonian subregion (Morrone, 2014a) and could be an additional evidence to support it.

With the exception of the presence of type I setae of *P. vitiosum* in the Chacoan dominion, the distribution of type I with the lost of type III, could be related with the Pliocene vicariant event between South-western Amazonia and North-western South America-Mesoamérica (Morrone, 2014a), where the setae occur. However, the presence of only type I setae, with loss of type III, in some genera of the Antilles is contradictory with that hypothesis, but could be explained by independent lost or by subsequent dispersal events.

Type IV urticating setae were also considered as derived from type III (Bertani & Guadanucci, 2013). In all species where type IV is present, they co-occur with type III. An exception of this trend is the sexual dimorphism found in some species in which one sex has only one type [e.g. females *Homoeomma uruguayense* (Mello-Leitao, 1946) only have type IV (Pérez-Miles, 2002)]. Type IV setae are restricted to South America and their origin could be posterior to a vicariant event between South America and Mesoamerica (Morrone, 2014a).

The distribution of type II setae comprises mainly tropical rainforest areas with few representatives in Caatinga and Cerrado (Bertani, 2012). This could be explained because these contact setae are present in arboreal species so their ecological dependence to forest or bromeliads seems to be clear. The distribution of these setae suggests an ancestral origin before the vicariance of the Antilles, Early Jurassic - Early Cretaceous (Morrone, 2014a). Probably type II setae was ancestrally widespread, and the present restricted distribution in the Chacoan dominion (absent in the southern area) would be explained by paleoecological changes which turn them to open areas. The presence of type II setae in few species of Caatinga and Cerrado could be relictual. In this sense, during Pliocene southern South America was dominated by grasslands, steppes and shrublands while rainforest were restricted to small areas in Brazil (Ortiz-Jaureguizar & Cladera, 2006). In agreement with this hypothesis, events of vicariance during Miocene/Pliocene were used to explain endemism for species of *Iridopelma* and *Pachistopelma* (Bertani, 2012). Tracing

type II setae in the area cladogram (Fig. 4), we found they clearly agree with the monophyly of the Neotropical region (Morrone, 2014a) and could constitute an additional evidence.

Type VI is only present in some *Hemirrhagus* species and consequently endemic to Mexico, they were known from fossil representatives of Chiapas amber at Early-Middle Miocene (García-Villafuerte, 2008).

In conclusion, we detected the occurrence of biogeographic patterns in the distribution of theraphosid abdominal urticating setae which seem to be caused by both historical and ecological factors. These patterns additionally agree with the polarization proposed for types I, III and IV urticating setae and suggest a branched transformation series. Types I and IV seems to be derived from type III (Bertani & Guadanucci, 2013). Probably in one branch some of them derived in type I (co-occurrence of type I+III) and secondary the completely lost of type III (genera with only type I). In the other branch some type III setae derived in type IV (co-occurrence of type III+IV). The absence of intermediate forms between I and IV (Bertani & Guadanucci, 2013) and the absence of co-occurrence of these types in any genus suggest at least two independent acquisitions in different hypothetical ancestors.

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REFERENCES

Bertani R. & Marques O. A. V. 1996. Defensive behaviors in Mygalomorph spiders: Release of urticating hairs by some Avicullariinae (Araneae, Theraphosidae). Zoologisher Anzeiger, 234: 161-165.

Bertani R. 2012. Revision, cladistic analysis and biogeography of *Typhochlaena* C. L. Koch, 1850, *Pachistopelma* Pocock, 1901 and *Iridopelma* Pocock, 1901 (Araneae, Theraphosidae, Aviculariinae). Zookeys, 230: 1-94.

Bertani R., Boston T., Evenou Y. & Guadanucci J. P. L. 2003. Release of urticating hairs by *Avicularia versicolor* (Walckenaer, 1837) (Araneae, Theraphosidae). Bulletin of the British Arachnological Society, 12: 395-398.

Bertani R. & Guadanucci J. P. L. 2013. Morphology, evolution and usage of urticating setae by tarantulas (Araneae: Theraphosidae). Zoologia, 30: 403-418.

Cooke J. A., Roth V. D. & Miller F. 1972. The Urticating Hairs of Theraphosidae. American Museum Novitates, 2498:1-43.

Ferretti N., González A. & Pérez-Miles F. 2012. Historical biogeography of mygalomorph spiders from the peripampasic orogenic arc based on track analysis and PAE as a panbiogeographical tool. Systematic and Biodiversity, 10:179-193.

Ferretti N., González A. & Pérez-Miles F. 2014. Identification of priority areas for conservation in Argentina: quantitative biogeography insights from mygalomorph spiders (Araneae: Mygalomorphae). Journal of Insect Conservation, DOI 10.1007/s10841-014-9718-5.

Foelix R. F., Bastian R. & Erb B. 2009. Palpal urticating hairs in the tarantula *Ephebopus*: fine structure and mechanism of release. Journal of Arachnology, 37: 292-298.

García-Villafuerte M. A. 2008. Primer registro fósil del género *Hemirraghus* (Araneae, Theraphosidae) en ámbar del Terciario, Chiapas, México. Revista Ibérica de Aracnología, 16:43-47.

Goloboff P. A., Farris J. S. & Nixon K. C. 2008. TNT: Tree analysis using new technology version 1.1. Willi Hennig Society Edition. Program and documentation. http://filogenetica.org/TNT.htm

Halffter G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annual Review of Entomology, 32: 95-114.

Löwenberg-Neto, P. 2014. Neotropical region: a shapefile of Morrone's (2014) biogeographical regionalisation. Zootaxa, 3802: 300-300.

Maddison W. P. & Maddison D. R. 2015. Mesquite: a modular system for evolutionary analysis. Version 3.04 http://mesquiteproject.org

Marshall S. D. & Uetz G. W. 1990. The pedipalpal brush of *Ephebopus* sp. (Araneae, Theraphosidae): Evidence of a new site for urticating hairs. Bulletin of the British Arachnological Society, 8: 122-124.

Morrone J. J. 2005. Hacia una síntesis biogeográfica de México. Revista Mexicana de Biodiversidad, 76: 207-252.

Morrone J. J. 2014a. Cladistic biogeography of the Neotropical region: Identifying the main events in the diversification of the terrestrial biota. Cladistics, 30: 202-214.

Morrone J. J. 2014b. Biogeographical regionalisation of the Neotropical region. Zootaxa, 3782: 001-110.

Patterson C. 1982. Morphological characters and homology. Pp. 21-74. *In:* Joysey K. A. & Friday A. E. (Eds). Problems of Phylogenetic Reconstruction. Systematics Association Special Volume. Academic Press, London.

Pérez-Miles F. & Prandi L. 1991. El comportamiento de emisión de pelos urticantes en *Grammostola mollicoma* (Araneae, Theraphosidae): un análisis experimental. Boletín de la Sociedad Zoológica del Uruguay (2ª época), 6: 47-53.

Pérez-Miles F. & Costa F. G. 1994. *Acanthoscurria atrox* incorporates urticating hairs into its shedding mat. The Forum of the American Tarantula Society, 3: 63-64.

Pérez-Miles F. 1998. Notes on the systematics of the little known Theraphosid spider *Hemirrhagus cervinus*, with a description of a new type of urticating hair. Journal of Arachnology, 26: 120-123.

Pérez-Miles F. 2002. The occurrence of abdominal urticating hairs during development in Theraphosinae (Araneae, Thraphosidae): Phylogenetic implications. Journal of Arachnology, 30: 316-320.

Pérez-Miles F., Lucas S. M., da Silva Jr. P. I. & Bertani R. 1996. Systematic revision and cladistic analysis of Theraphosinae (Araneae: Theraphosidae). Mygalomorph, 1: 33-68.

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