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Release of urticating hairs by *Avicularia versicolor* (Walckenaer, 1837) (Araneae, Theraphosidae)

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Summary

The behaviour of releasing urticating hairs is described for the theraphosid spider *Avicularia versicolor*, a species endemic to the islands of Martinique, Guadeloupe and Dominica. In this species, the urticating hairs are thrown from the abdomen dorsum by movements of the tip of tarsus IV against the urticating hair field. Thus, it can be distinguished from other avicullariines, which transfer the urticating hairs through direct contact of the abdomen with the potential predator; instead, it approximates with theraphosines, which throw urticating hairs by using the spines on the ventral surface of metatarsus and tibia of leg IV to dislodge them. Morphological comparisons of typical urticating hairs of other avicullariines released by contact, airborne hairs of theraphosines, and airborne hairs of *A. versicolor* showed that, despite sharing their general morphology with other avicullariines, *A. versicolor* urticating hairs can be distinguished by the presence of well-developed barbs and their overall narrow shape. These characteristics approximate to those of airborne theraphosine urticating hairs. It is proposed that *A. versicolor* urticating hairs are derived from the typical urticating hairs released by contact found in other avicullariines and the characteristics that allow them to be airborne represent a homoplastic character shared with theraphosine species.

Introduction

Reports on the defensive use of urticating hairs by New World spiders of the family Theraphosidae have been known for many years (Bates, 1863), but only after the paper of Cooke *et al*. (1972) has the morphology of urticating hairs been investigated. These authors described four morphological types of urticating hairs found on the spiders' abdomen, three types (I, III, and IV) for species which are currently included in the subfamily Theraphosinae, and one type (II) for the genus *Avicularia* Lamarck, 1818 (Avicullariinae). More recently, Marshall & Uetz (1990a) described a further type (V) found on the prolateral surface of the pedipalps of *Ephebopus* Simon, 1892 (Avicullariinae) species, and Pérez-Miles (1998) found type VI on the abdomen of the holotype of *Hemirrhagus cervinus* (Simon, 1891) (Theraphosinae). Whereas most theraphosine species easily flick hairs off the abdomen dorsum when suffering even a slight disturbance, and *Ephebopus* spp. shed hairs from the pedipalps by scratching the urticating hair field

against the basal segments of the chelicerae, no aviculariine species has been seen throwing urticating hairs, apart from an anecdotal report on *Avicularia versicolor* (Walckenaer, 1837) by Eckardt (1992). While investigating the morphology of type II urticating hairs found in the aviculariine genera *Avicularia*, *Pachistopelma* Pocock, 1901, and *Iridopelma* Pocock, 1901, as well as the behaviour of rubbing the abdomen dorsum against an external stimulus, Bertani & Marques (1996) proposed that type II hairs were morphologically modified to be released through direct contact with a potential predator, being too heavy to be airborne. Furthermore, species of the genus *Avicularia* lack leg spines, which are used by theraphosine species to dislodge abdominal urticating hairs (Cooke *et al*., 1972; Bertani & Marques, 1996), making it even more difficult for an *Avicularia* sp. to throw urticating hairs.

However, further observations carried out by two of the authors (TB and YE) on *Avicularia versicolor* specimens throwing hairs led us to investigate the morphology of urticating hairs found in this species, as well as the mechanism used by the spider to dislodge the hairs from the abdomen. The results were compared with those for species known either to throw or to rub-in urticating hairs.

Material and methods

Material examined for the morphological study is deposited in the American Museum of Natural History, New York (AMNH, N. Platnick) and Instituto Butantan, São Paulo (IBSP, R. Bertani).

For the morphology of urticating hairs the following specimens were studied: *Avicularia* sp. (probably *A. avicularia* (Linnaeus, 1758)), 1♂ (IBSP 8565) and 1♀ (IBSP 8848), U. H. E. Tucuruí, Tucuruí, Pará, Brazil; *Grammostola actaeon* (Pocock, 1903), 1♂ (IBSP 4604), Camanducaia, Minas Gerais, Brazil; *Lasiodora* sp., 1♀ (IBSP 6379), Pindamonhangaba, São Paulo, Brazil; *Avicularia versicolor*, 1♂ (AMNH), Beatty col., 1967, Martinique, 2♂ (AMNH), Morne Carbet, forest trees, H. Beatty col., 18 March 1967, Martinique, 1 immature ♂ (AMNH) from trees in forest, Dr H. Perronnete (Lamontin) on behalf of Mrs Florange Grandjouan col., Martinique, 1♀ exuviae (IBSP 9633), probably Martinique, 2 exuviae of immature ♂ and ♀ (IBSP 9634), probably Martinique, 2♀ exuviae (IBSP 9635), probably Martinique, 2 immatures (IBSP 9636), probably Martinique.

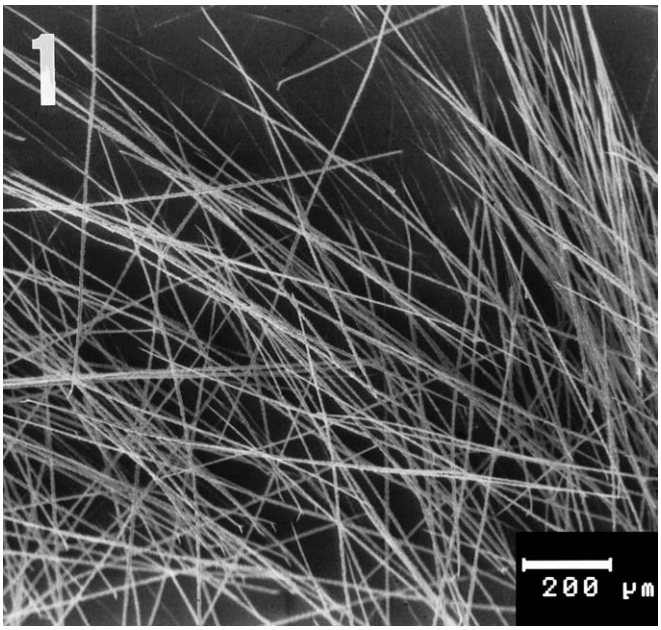
For measurements of urticating hairs, a sample of hairs was taken from exuviae of a female and an immature male of *A. versicolor* (IBSP 9634), a male and a female of *A. avicularia* (IBSP 8565 and 8848), a male of *Grammostola actaeon* (IBSP 4604), and a female *Lasiodora* sp. (IBSP 6379). Thirty hairs from each sample were measured under a compound microscope with the aid of an ocular micrometer, and relations between width and length were compared.

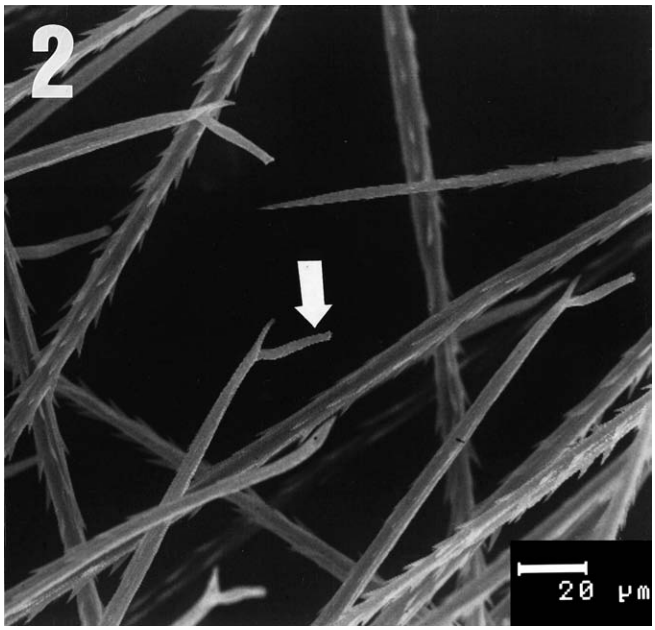
Micrographs were made with a Zeiss DSM 940 scanning electron microscope from the Instituto de Biociências da Universidade de São Paulo and with a LEO 440 from the Museu de Zoologia da Universidade de São Paulo.

For the behavioural study 4 females and 2 immatures of *A. versicolor* were stimulated by touching them with forceps (Bertani & Marques, 1996). The specimens were captive-bred and kept by TB in Denmark and YE in France. The stock probably came originally from Martinique.

Results and discussion

Behaviour: All six specimens of *A. versicolor* tested exhibited hair-flicking behaviour. None tried to rub the abdomen against the stimulus as is usually seen in other *Avicularia* species. Specimens of *A. versicolor* dislodge





Figs. 1–2: *Avicularia versicolor*. **1** Type II urticating hairs; **2** Detail of urticating hairs showing basal perforating tip; some hairs had the stalk (arrow) which attaches the hair to the cuticle retained.

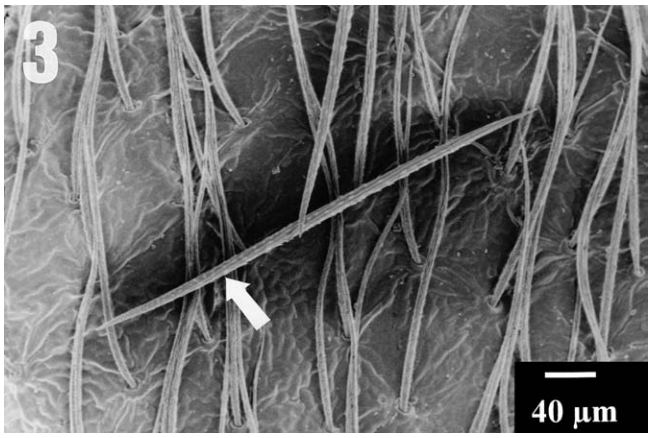


Fig. 3: *Avicularia avicularia*. Typical type II urticating hair (arrow) free from the stalk/cuticle.

the hairs by 2–4 kicks of one leg IV, and the region that contacts the hair field is the claw tuft, which is well-developed in avicularine species. This contrasts with the behaviour seen in theraphosines, where the spinose ventral areas of metatarsus and tibia IV are used to comb off the urticating hairs (Cooke *et al*., 1972; Bertani & Marques, 1996). However, no differences in either claw tuft or tarsus morphology were detected between *A. versicolor* and other *Avicularia* species. Also, there was no sign of hairs becoming stuck to the dense setae of the claw tufts. Whereas urticating hairs are normally seen stuck to the leg spines of tibia and metatarsus IV of theraphosines, it seems that claw tufts and scopula hairs rarely retain particles, so that the urticating hairs also do not get stuck. The absence of a more efficient way of dislodging the hairs would help to explain why a large part of the released hairs of *A. versicolor* tend to go off in clusters, instead of in a hair cloud as seen in theraphosines.

In one individual of *A. versicolor* the incorporation of urticating hairs into the silk used in egg sac construction was observed. After completion of the egg sac she clearly had a bald spot (10.0 × 7.0 mm) on the abdomen. Incorporation of urticating hairs into the moulting web as well as in the silk used for egg sacs has been reported for *Theraphosa blondi* (Latreille, 1804) (Marshall & Uetz, 1990b) and *Acanthoscurria atrox* Vellard, 1924 (Pérez-Miles & Costa, 1994) and it was proposed that this would protect the adult spider and/or the egg sac against fly larvae (Diptera, Phoridae) (Marshall & Uetz, 1990b).

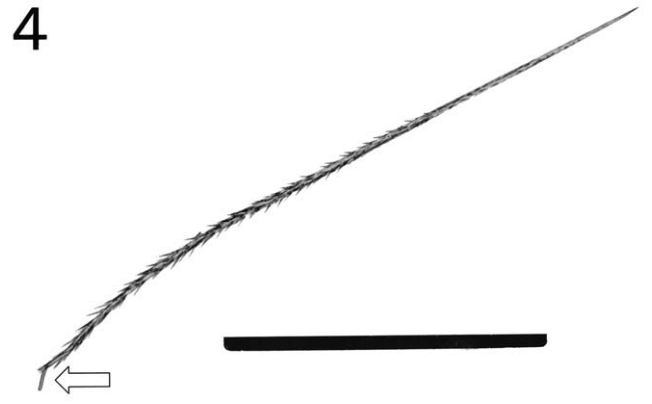


Fig. 4: *Lasiodora* sp. Type III urticating hair. The basal stalk which attaches the hair to the cuticle has been retained (arrow). Scale bar = 500 µm.

Morphology: The urticating hairs of *A. versicolor* (Figs. 1–2) are long (800–1370 µm) and narrow (5–10 µm), pointed at both ends and have a basal penetrating tip, well-developed, distally oriented barbs, and a stalk just before the penetrating tip, with which the hair is attached to the spider's abdomen. They can be easily removed from the spider's abdomen in tufts with forceps, in a similar way to theraphosine type III hairs. They fit the description of type II urticating hairs (Fig. 3) given by Cooke *et al*. (1972) rather well by being pointed at both ends, having a basal perforating tip, distally oriented barbs, and by the presence of a stalk just before the perforating tip. Other hairs having a basal perforating tip and distally oriented barbs (types V and VI) lack a stalk and are attached in sockets on the cuticle (Marshall & Uetz, 1990a; Pérez-Miles, 1998). Type III hairs (Fig. 4) have a distal perforating tip, basally oriented barbs, and are attached to the spider abdomen via a stalk.

The main differences between *A. versicolor* type II hairs and those found in other avicularines are: (a) the easier way in which they can be released, as other type II hairs must be scraped from the spider's abdomen (Bertani & Marques, 1996); (b) the presence of well-developed barbs (Fig. 2), whereas typical type II hairs have only very short barbs resembling scales (Fig. 3); and (c) the overall shape, which is narrower in *A. versicolor* (Fig. 1) and stouter in other avicularine hairs (Fig. 3). Concerning hair dimensions, Table I shows the relation between length and width in *A. versicolor* and *A. avicularia* hairs (both having type II hairs), and compares them with *Lasiodora* sp. and *Grammostola actaeon* (both having type III hairs). All airborne hairs (theraphosine type III (Fig. 4) and *A. versicolor* type II (Figs. 1–2)) are narrow, mean width ranging from 6 to 7 µm, whereas type II hairs released by contact are stouter (Fig. 3), mean width ranging from 15 to 22 µm.

Species Urticating hair type	Length range (mean ± SD)	Width range (mean ± SD)	Length/width
***Lasiodora* sp.**	540–700	5–7	98.3
Female (type III)	(590 ± 30)	(6 ± 1)	
Grammostola actaeon	1170–1400	5–7	208.3
Male (type III)	(1250 ± 40)	(6 ± 1)	
Avicularia versicolor	800–1010	5–8	130.0
Immature male (type II)	(910 ± 50)	(7 ± 1)	
Avicularia versicolor	840–1370	5–10	174.2
Female (type II)	(1220 ± 140)	(7 ± 1)	
Avicularia avicularia	930–1110	20–25	46.8
Male (type II)	(1030 ± 40)	(22 ± 1)	
Avicularia avicularia	510–610	15–17	37.3
Female (type II)	(560 ± 20)	(15 ± 0.6)	

Table 1: Measurements (n = 30 in each category) of type II and III urticating hairs. *Lasiodora* sp. and *Grammostola actaeon* (type III, airborne), *Avicularia versicolor* (type II, airborne) and *A. avicularia* (type II, released by contact). All measurements in µm.

The length/width ratio in airborne hairs ranges from 98.3 to 208.3 whereas in hairs released by contact the range is 37.3 to 46.8. Interestingly, although the length of airborne hairs can show great variation (590–1250 μm) this is not accompanied by an increase in width, the mean of which varies only from 6 to 7 μm. An explanation could be that while increase in length will result in increase in total hair surface, aiding the hair to be airborne, increase in width will result in only a small increase in hair surface but a large increase in hair volume and consequently in hair mass, making it more difficult to be carried by the air. On the other hand, an increase in hair width might be advantageous to hairs which are transferred by contact, as is the case with typical type II hairs, because they would be harder to break while being inserted into a predator's skin.

Although there is no phylogenetic study of relationships among aviculariine genera, the presence of typical type II urticating hairs in the genera *Iridopelma* and *Pachistopelma*, probable sister groups of *Avicularia* (R. Bertani, pers. obs.), as well as in other *Avicularia* species (Bertani & Marques, 1996), leads us to believe that this is the plesiomorphic state for the avicularine genera *Avicularia*, *Iridopelma* and *Pachistopelma*. Thus, it is more parsimonious to consider *A. versicolor* airborne type II urticating hairs as representing a derived state from the plesiomorphic "released by contact" urticating hairs found in other avicularine genera. The distinct morphology of these airborne urticating hairs and the behaviour of flicking them using the claw tuft are considered autapomorphies for *A. versicolor*.

Well-developed barbs and long and narrow shape were considered by Bertani & Marques (1996) as necessary conditions for a hair to become airborne. The discovery of *A. versicolor* type II urticating hairs convergently having the above conditions strengthens that idea.

Unfortunately, the almost complete absence of data on biological aspects of *A. versicolor*, a species endemic to the islands of Martinique, Guadeloupe and Dominica in the West Indies, prevents a better understanding of this fascinating evolutionary convergence. It would be very interesting to know if the three isolated populations have the same modifications as described above, and what are the selective pressures acting on those populations.

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