Neotropical Entomology (2023) 52:57–66
https://doi.org/10.1007/s13744-022-00997-0

SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

The Spittlebug *Mahanarva tristis* as a Senior Synonymy of Four Neotropical Species of *Mahanarva* (Hemiptera: Auchenorrhyncha: Cercopidae), and Considerations About *M. tristis* Subspecies

Christian Schöbel[1] · Gervásio Silva Carvalho[1] · Andressa Paladini[2] · Renato Augusto Teixeira[3]

Received: 9 November 2021 / Accepted: 3 October 2022 / Published online: 29 November 2022

Abstract
Mahanarva Distant, the neotropical spittlebug genus contains 48 species and many of them are only known from their original descriptions and one location. A group of species of this genus stand out due to their similarities and are studied here. Based on comparisons between 28 *Mahanarva tristis* (Fabricius) specimens and the original drawings of the other species, we demonstrate strong morphological similarities. Examinations of the tegmina showed a polymorphism with different dot and stripe patterns. Those patterns are not exclusive for one species and are found throughout the taxa. Again, studying the male genitals no species-specific characters can be found. Furthermore, differences of the parameres were explained by different angle positions of these genital plates which alter the resulting photos and drawings significantly. On the other hand, changes of the aedeagus can be explained due to its fragile structure and the resulting manipulations during handling. In addition, the overlapping known distribution of the taxa leads to the conclusion that the four species are in fact synonyms of *M. tristis* and that there is no evidence for the validity of the subspecies. We conclude that the New World spittlebug *M. tristis* is considered a senior synonym of *Mahanarva fraseri* (Distant) **n. syn.**, *Mahanarva mura* (China & Myers) **n. syn.**, *Mahanarva raripila* (Jacobi) **n. syn.**, and *Mahanarva trifissa* (Jacobi) **n. syn.** Aside from that, there was no evidence for the validity of the *M. tristis* subspecies *Mahanarva tristis guppyi* (Urich) **n. syn.**, *Mahanarva tristis monagasi* (Fennah) **n. syn.**, *Mahanarva tristis quadrimaculata* (Fennah) **n. syn.**, *Mahanarva tristis suffusa* (Walker) **n. syn.**, and *Mahanarva tristis walkeri* (Lallemand) **n. syn**. Unfortunately, it was not possible to conclude the taxonomic state of *Mahanarva tristis stalii* (Lallemand) because there are no known specimens or types available. So, the subspecies is considered a *species inquirenda*.

Keywords Paramere · Angles · Tegmina · Polymorphism · Taxonomics

Introduction

The Neotropical spittlebug genus *Mahanarva* contains a total of 48 species and is divided into the two subgenera *Mahanarva* (*Ipiranga*) Fennah and *Mahanarva* (*Mahanarva*) Distant. The type species of the genus is *M. indicata* Distant and all in this article analyzed species belong to *Mahanarva* (*Mahanarva*). Distant characterized the genus in 1909 by the size of the subtriangular head because the length is about the same as the breadth between the eyes. Furthermore, the ocelli are divided by the central longitudinal ridge but still placed close together. The convex and strongly inflated postclypeus possesses lateral grooves and reaches the procoxa. There is a short subcylindrical basal body on the third segment of the antennae and the rostrum reaches the mesocoxa. The pronotum's lateral edges are concave and the frontal edges straight. As all New World cercopids, the genus presents two spines on the posterior tibiae. Within this genus, the basal spine is smaller than the one located on the middle of tibia. On the hind tarsi, there are 20–30 apical spines arranged in three rows. The Pygofer presents a long, lateral process between the anal tube and the subgenital plates. Within the pygofer, the aedeagus is slender with dorsal processes on the shaft. Parameres have one or two subapical spines inserted laterally. The insect's relatively wide tegmina

Edited by Takumasa Kondo

Gervásio Silva Carvalho retired

✉ Christian Schöbel
cschoebel@hotmail.com

Extended author information available on the last page of the article

present a distinct Cu_1 vein and prominent apical veins with a net pattern (Schöbel and Carvalho 2021; Distant 1909).

There are known cases of wing color and pattern polymorphism which makes many species nearly indistinguishable if not for a comparison of the male genitals. Within *Mahanarva*, tegminal polymporphism is known for *Mahanarva fimbriolata* (Stal), *Mahanarva spectabilis* (Distant), and *M. tristis*. All three species can present a variety of black to reddish-colored tegmina with different spot and dot patterns (Borges et al. 2020; Paladini et al. 2018). Especially the identification of *M. spectabilis*, *M. fimbriolata* can be very challenging (Schöbel and Carvalho 2021).

But this is not only a characteristic of *Mahanarva*. *Deois incompleta* (Walker) and *Zulia pubescens* (Fabricius) also show color polymorphism in comparison to specimens from other regions (Paladini et al. 2018). Throughout Cercopidae, polymorphism is also common, and there are several studies describing the vast number of tegminal color variations especially of the widely distributed meadow spittlebug *Philaenus spumarius* (Linné) (Farish 1972; Thompson and Halkka 1973; Stewart 1996; Yurtsever 2000; Yurtsever et al. 2010). For detailed analyses of polymorphism, a vast amount of material must be studied. Unfortunately, this is difficult to achieve for the majority of *Mahanarva* species because for most of them there are only few specimens known.

Mahanarva tristis was first placed within *Cercopis*, then transferred to *Tomaspis* in 1869 by Stal, to *Delassor* in 1949 by Fennahand, finally to *Mahanarva* in 1968, again by Fennah. *Sphenorhina stellata* Walker, *Sphenorhina semifascia* Walker, and *Sphenorhina duodecimpunctata* Walker are three present synonyms of the species (Metcalf 1961).

Currently, there are seven *M. tristis* subspecies: *M. tristis tristis*, *M. tristis guppyi*, *M. tristis monagasi*, *M. tristis quadrimaculata*, *M. tristis stalii*, *M. tristis suffusa*, *M. tristis walkeri*. *Mahanarva tristis guppyi* was first described within *Delassor* Fennah and then in 1961 listed as a subspecies of *M. tristis* (Metcalf 1961). The type of *M. tristis guppyi* is considered by Carvalho and Webb (2005) as missing, but the description of the tegminal coloration matches a female specimen from Trinidad and Tobago included in Urich's publication (1913) and deposited in the NHMUK. Therefore, it is plausible that this female specimen is the missing type. Both *M. tristis monagassi* and *suffusa* were posteriorly assigned to *Delassor* and in case of *M. t. suffusa* to *Sphenorhina* Amyot and Serville as well. *M. tristis walkeri* was a variant of *Sphenorhina suffusa* Walker which is now *M. tristis suffusa* as already mentioned. Unfortunately, there is no known type or specimen of *M. tristis stalii* which does turn the subspecies a *species inquirenda* and does not allow any judgment. Only the distribution in Argentina is known and matches with the known distribution of *M. tristis.*

Mahanarva fraseri was described within *Tomaspis*, placed into *Delassor* by Fennah (1949) and then into *Mahanarva*, again by Fennah (1968). *Mahanarva mura* was described within *Tomaspis* as the other species, then placed in *Delassor* by Fennah (1949) and afterwards in *Mahanarva* by Fennah (1968). *Mahanarva raripila* was placed originally in *Tomaspis* and then in 2005 transferred to *Mahanarva* by Carvalho and Webb (2005). The last species, *M. trifissa*, was first placed in *Tomaspis* in two different subgenera—originally in *T.* (*Sphenorhina*) and then in *T.* (*Tomaspis*)—by Lallemand (1912). Goding (1923) removed the subgenera and subsequently the species was placed in *Mahanarva* by Carvalho and Webb (2005).

After analyzing type specimens of several *Mahanarva* species, it was possible to observe that the species *M. fraseri*, *M. mura*, *M. raripila*, *M. trifissa*, and *M. tristis* share morphological similarities. Descriptions of the pygofers match between the species and there is a geographical overlap. Morphologically, all species possess two spines on the parameres, present an aedeagus with a lateral shaft process and upward inclined tips. Furthermore, the coloration and pattern of the tegmina is variable. The external morphology is identical except for the ocelli position, arista length, and postclypeus shape. Regarding occurrence, the type specimens are from Ecuador (*M. fraseri*, *M. raripila*, *M. trifissa*) or from North Brazil (*M. mura*, *M. tristis*). Unfortunately, it was not possible to extract and analyze the genitals of the type specimens and we have to work with existing drawings. The low amount of available material of the species impedes more in-depth analyses of the morphology, although through the obtainment of 26 specimens from Acre and two from Ecuador it was possible to test the hypothesis that assigned variations of the abovementioned species are results of the angle during examination of the parameres and that tegminal pattern variations are a polymorphism of the species.

Initial examination of the putative named species revealed strong morphological similarities, particularly in light of the known color pattern variation of the tegmina. Therefore, this article discusses the synonymization of *M. tristis* with *M. fraseri*, *M. mura*, *M. raripila*, and *M. trifissa* and analyzes the validity of the *M. tristis* subspecies.

There are different hypotheses regarding the taxonomy of the species. Morphological caracteristics (male genitals, tegminal color, and pattern) analyzed of this *M. tristis* group could result in three possible scenarios: (1) All specimens have the same morphology, so only *M. tristis* can be identified; or (2) the specimens exhibit many combinations of characteristics, so the species present intraspecific variation; or (3) the same shapes of male genitals are exhibited in specimens with consistent tegminal color and pattern, which would indicate that specimens correspond to different species ocurring in sympatry. The second scenario allows two possibilities: (a) the other species of *Mahanarva* with similar location are compared to *M. tristis* specimens and those fitting to observed variation are treated as synonymous; or

(b) the other *Mahanarva* species do not fit into the variation and, therefore, no taxonomic change can be proposed.

Material and Methods

It was possible to assess several types of the species in the NHMUK and the Senckenberg Naturhistorische Sammlung Dresden (SNSD) (Table 1). Additional specimens of *M. tristis*, *M. mura*, and *M. tristis suffusa* were inspected in the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCTP).

For a comparison between the species, drawings of the genitalia were compared to the other 28 M. *tristis* specimens of the MCTP of which 26 were collected in Acre and two in Ecuador. These 28 specimens were considered to belong to the same species because they were collected in similar habitats and in the same collecting events.

Genitals of the 28 mentioned specimens from Acre and Ecuador were extracted from the dried specimens and the paramere and aedeagus extracted from the pygofer. The extraction of genitals of museum specimens was not possible. The 28 M. *tristis* specimens from the MCTP museum were identified by Gervásio Carvalho using the available literature and a reference collection. Afterwards, the structures were photographed using the Leica M205 A stereomicroscope and Leica DMC 2900 camera. Photos of the male genitals are taken in different angles and visually compared between each other and with drawings of type specimens of the analyzed species and subspecies. The pictures and drawings were processed and arranged using GIMP v.2.10.12 (The GIMP Development Team 2021).

The description of *M. tristis* follows an already-published description of the species from 2018 in which the polymorphism was analyzed (Paladini et al. 2018). We updated this existing description with the results of this article. All specimens belong to the same collection events and were collected in two locations of Rio Branco (Acre–Brazil, $N=26$) and one place of Ecuador ($N=2$). The measures were taken from 15 specimens since the other specimens were damaged.

Results

The *M. tristis* specimens present some genital variation in the position of the spines on the parameres and the shape of the upper paramere edge. They also exhibit many shades and patterns on the tegmina. This variations fits with the second scenario (hypothesis 2) described above. Next, the comparison with other *Mahanarva* species (*M. fraseri*, *M. mura*, *M. raripila*, and *M. trifissa*) was made and the diagnosable characteristics (male genitalia, tegminal color, and pattern) of these species also fit with specimen variation of *M. tristis* (sustaining the scenario A). Addictional details are presented and discussed below.

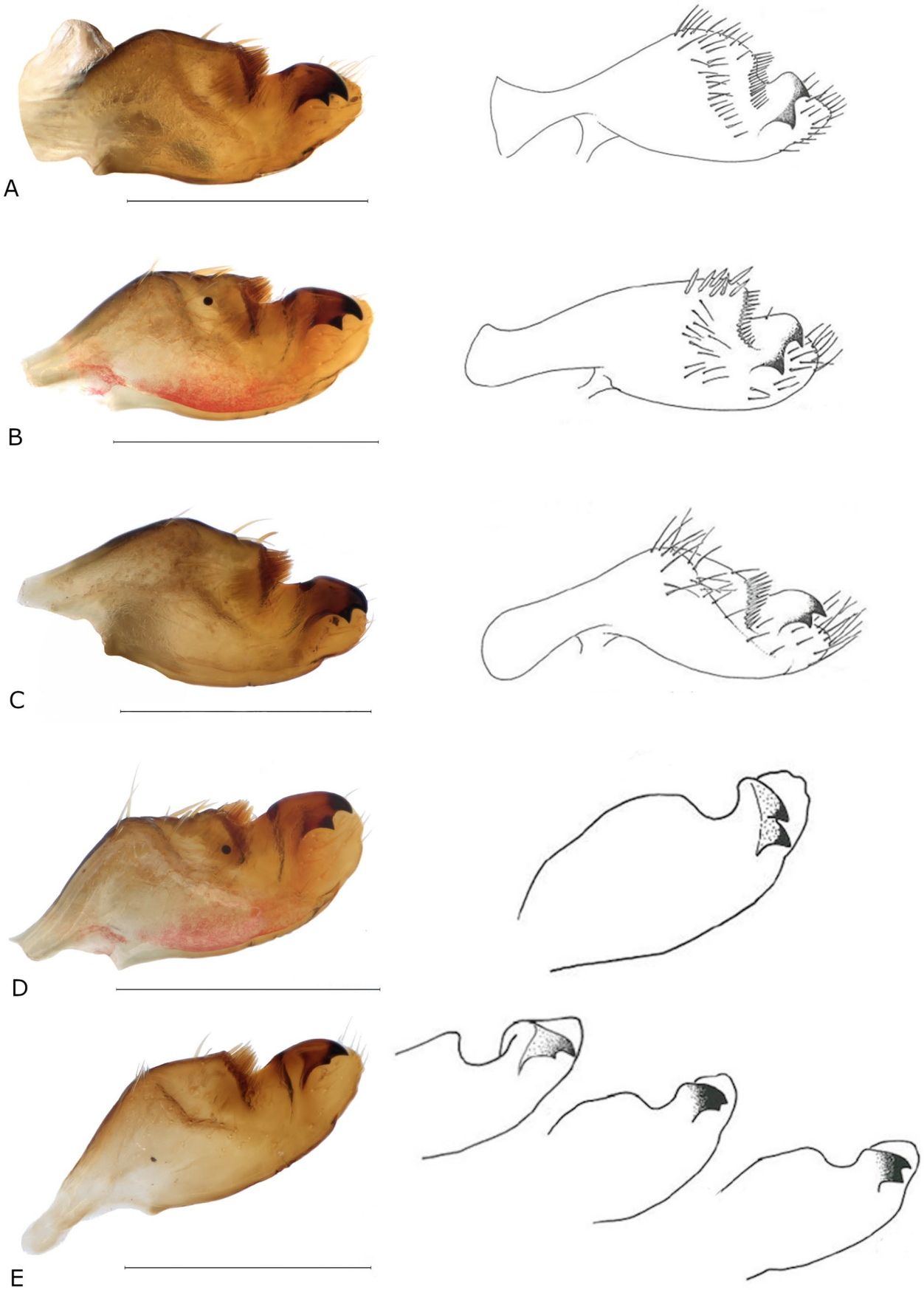
Morphological Comparison

Body

The morphology of the body of the putative species is very similar and there are only a few differences. The position of the ocelli of *M. mura* species is a bit further to the front of the head than in the other species. On their antennae, *M. raripila* and *M. trifissa*, *M. tristis walkeri*, *M. tristis monagasi*, and *M. tristis guppyi* possess arista which have the same length as the pedicel. *M. fraseri*, *M. mura*, *M. tristis*,

Table 1 Type museum, type location, known distribution, and kind of examination of the taxa. Occurrence records are taken from specimen labels. *NHMUK* Natural History Museum UK, *SNSD* Senckenberg Naturhistorische Sammlung Dresden, *AM* Amazonas, *PA* Pará, *AC* Acre, *RO* Rondônia

Taxon	Type museum	Type location	Other known distributions	Kind of examination
M. tristis	NHMUK	Brazil	Brazil: AM, PA, AC, RO; Argentina; British Guiana, Colombia; Ecuador; French Guiana; Peru; Suriname; Trinidad; Uruguay	In locus
M. tristis guppyi	Unknown	Unknown	Trinidad	In locus
M. tristis monagasi	NHMUK	Venezuela: S. Antonio	Brazil: RO	In locus
M. tristis quadrimaculata	NHMUK	Venezuela: Guanare	–	In locus
M. tristis stalii	Unknown	Unknown	Argentina	Not examined
M. tristis suffusa	NHMUK	Brazil	–	In locus
M. tristis walkeri	NHMUK	Brazil	Brazil: PA	By photo
M. fraseri	NHMUK	Ecuador	Ecuador; Bolivia	Not examined
M. mura	NHMUK	Brazil: AM	Brazil: AM, PA, RO	In locus
M. raripila	SNSD	Ecuador	–	In locus
M. trifissa	SNSD	Peru	Ecuador; Peru	In locus


A
B
C
D
E

◂**Fig. 1** *Mahanarva tristis* parameres (left) in comparison with drawings of 'other species' (Right). **A** *M. tristis*. **B** *M. fraseri*. **C** *M. mura*. **D** *M. raripila*. **E** *M. trifissa*. The drawings (on the right side) of *M. raripila* and *M. trifissa* are already published in Carvalho and Webb 2005. The other drawings are unpublished material but were created with the purpose to include them in the mentioned book (Carvalho, personal communication). On the left side of the figure, photos of five different parameres from *M. tristis* specimens from the MCTP collection are shown. The material belongs to the 28 analyzed specimens. All parameres are from the left side of the insect. Each scale bar 0.5 mm

and its subspecies *M. tristis quadrimaculata* and *M. tristis suffusa* have slightly smaller arista. And finally, the form of the postclypeus of *M. trifissa* and *M. tristis guppyi* is more rounded than the other species. Those are the only morphological differences of the insect's bodies between the species. Therefore, we conclude that these differences are polymorphous characters of *M. tristis*, nonetheless, because the rest of the body morphology is identical.

Aedeagus

Comparing the aedeagus of 28 M. *tristis* specimens, all show a triangular process at the tip of the aedeagus (Fig. 4B–D) and they all possess a thickening at the base. Only small differences on the aedeagus processes of *M. tristis* are visible. First of all, the angle of the processes is different but this can be explained by the thickness of the base of the processes. The whole aedeagus is sclerotized but the connection between the processes and the aedeagus itself is relatively thin. Extracting and aligning the aedeagus to take photos can easily alternate the angle of the processes or even break them. Therefore, this is not a useful character for species delimitation. Besides that, the tip of the aedeagus process is in some specimens more strongly aligned upwards (Fig. 4B). This can also be explained due to the slight sclerotization. Overall, it was not possible to detect significant differences on the aedeagus between the species and subspecies.

Paramere

The 28 analyzed *M. tristis* parameres show differences in regard to the upper edge of the paramere and the position of the two external spines nearly at the tip. There are parameres with a flat upper edge and others which are slightly bulged at the top. Comparing the parameres with the drawings of the different species, this is also visible. The drawings of the *M. tristis*, *M. mura*, *M. raripila*, and *M. trifissa*–type parameres (Fig. 1A, C, D, E) do not posses a flat upper edge. Only the drawing of *M. fraseri* (Fig. 1B) shows an opposite upper edge. But analyzing the images and drawings thoroughly, it shows that mostly the angle of the paramere during the drawing/photo process is responsible for these changes. The same applies to the angle and expression of the two spines. The drawings of the different species show differences in this regard. Inclining the parameres in different directions explains those differences. In case of *M. trifissa*, the angle of the paramere during the drawing was most likely slightly tilted downwards and therefore not enabling an ectal but slightly dorsal vision of the spines. Due to this angle, the second spine is less visible and less expressed in the drawing. This seems to be a common problem when drawing or photographing these insect genitals because the small parameres can be very movable under the microscope. Small tilts are difficult to notice and especially older drawings can contain these errors when microscopic technology was not as progressive as today. To visualize this problem, we create a figure in which the same paramere was photographed in slightly different angles. It is possible to see how the expression of the paramere's spines differ in the varying angles (Fig. 2A–I).

Besides, in this problem of exact illustrations, it was possible to find comparable *M. tristis* parameres for each of the species. Even the pattern of setae of the parameres is very similar (Fig. 1). In the case of *M. raripila* and *M. trifissa*, the horizontal inclination of the paramere showed similar structures as the drawings (Fig. 1D, E). Only the spines of the drawing of *M. raripila* seem to be less extended from the paramere than the other species and the analyzed photos of *M. tristis* specimens. This can be explained due to the angle of the paramere. Overall, there are no significant differences between the parameres of the different species. The observed changes are not sufficient to separate the species.

Tegmina

The analyzed *M. tristis* tegmina present a polymorphism in regard to the dot and mark pattern. At the base of the tegmina, it is possible to observe three dots, a combination of dots and stripes, three stripes, or no marks at all (Fig. 3). The size and thickness of the dots and stripes can vary. Furthermore, at about three-fourth of the tegmina's length, there are other marks present which can vary between dots in different sizes or a v/w-shaped stripe (Fig. 3). With the exception of the dotless tegmina form, all other forms are present throughout the 28 analyzed tegmina. The *M. tristis* subspecies differ from *M. tristis tristis* regarding their dot/stripe patterns on the tegmina. In the case of *M. t. walkeri*, *M. t. suffusa*, and *M. t. monagassi*, the dots and stripes are more pronounced and in the case of *M. t. guppyi* and *M. t. quadrimaculata*, there are no stripes and only dots are present (Fig. 3(A)). As the name suggests, *M. t. quadrimaculata* only has 4 dots at the apex of the tegmina and its base is unicolor. Despite the fact that all of the 28 analyzed *M. tristis* specimens had dots at the base of the tegmina, there is a specimen which only presents two stripes, one vertical

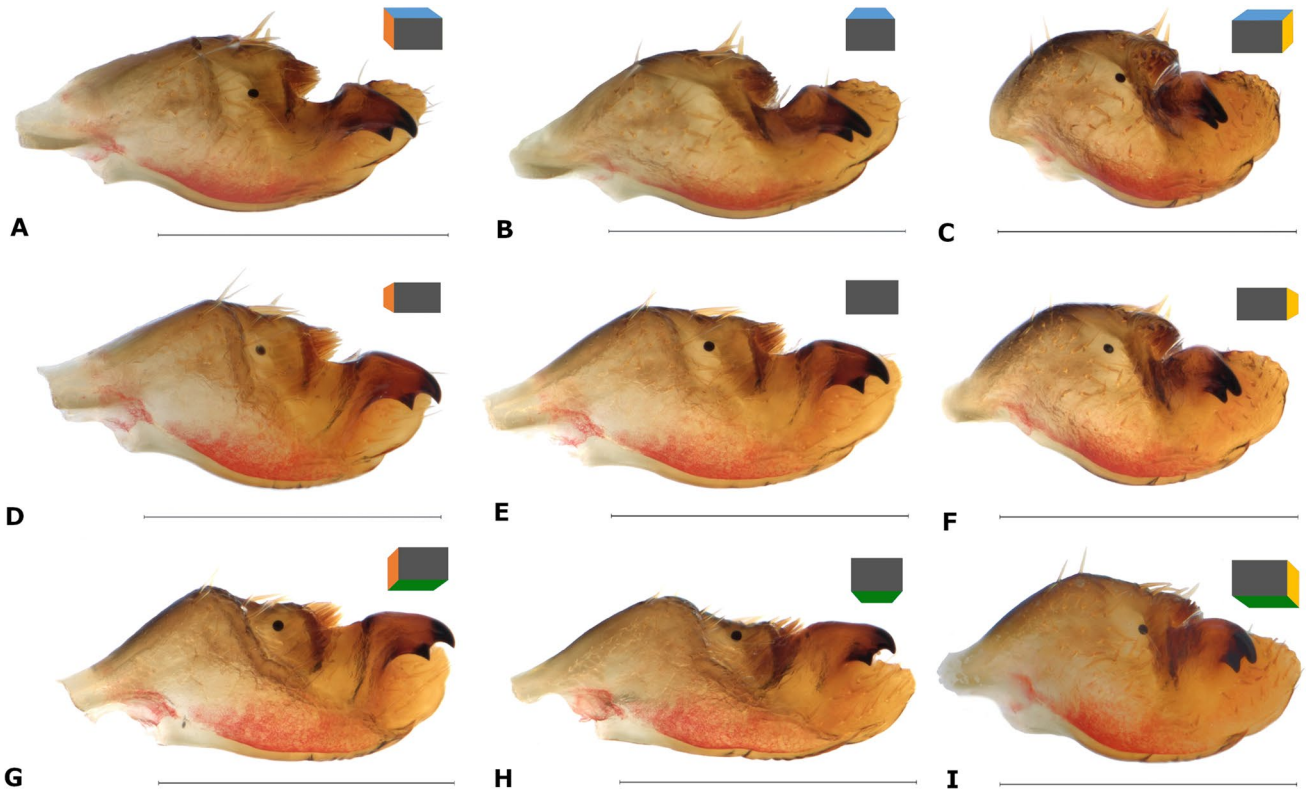


Fig. 2 *Mahanarva tristis* parameres in different angles with illustrational boxes above to indicate the angle. **A** Dorsal-basal; **B** dorsal; **C** dorsal-apical; **D** basal; **E** ectal; **F** apical; **G** ventral-basal; **H** ventral; **I** ventral-apical. All photos were taken from one paramere in different angles. The paramere belongs to one of the 28 analyzed specimens. Each scale bar 0.5 mm

and one inclined (Fig. 3(B)). *M. t. guppyi* also presents dots at the base of the tegmina. The types of *M. tristis*, its synonyms, and *M. mura* present only dots on their tegmina (Fig. 3(A)). In contrast, the syntypes of *M. fraseri* and *M. raripila* possess stripes at the base and dots at the tip of the tegmina (Fig. 3(C)). The analyzed types of *M. trifissa* show stripes at the base and at the tip as well a v/w-shaped stripe (Fig. 3(D)). Comparing the tegmina of all analyzed species, it is clear that for each wing pattern of the species or subspecies, there is a comparable one within *M. tristis* specimens. Therefore, it is not possible to determine differences between the species as this is clearly a case of polymorphism.

The coloration of the tegmina surface throughout all analyzed specimens ranges between darker and clearer brownish tones (Fig. 3(a)). The coloration of the dots and stripes as well varies between a reddish to yellowish coloration (Fig. 3(b)). This suggests that there is an intraspecific variation of the tegminal coloration but those variations can also be accounted by the different collection and storing methods. Collecting specimens with alcohol or using other methods as well as the specimen storage in different alcohol concentrations or within more or less light-protected drawers has a big influence on the coloration of the specimens. As we observed different colorations between the species and subspecies but also between different specimens of *M. tristis*, it is not reliable to separate the specimens due to their coloration. Each scale bar 2.0 mm.

Geographical Distribution

Of all the putative species, *M. tristis* has the widest known distribution throughout South and Central America (Table 1). Comparing this distribution with the other species and subspecies, it shows that there is a complete overalp. None of the other putative taxa have a known distribution outside the area where *M. tristis* is known to appear. Moreover, *M. tristis* occurs in British and French Guiana, Suriname, and Uruguay where there is no record of the other species (Table 1). The comparison of these intraspecific variations supports the hypothesis that these taxa are synonyms and therefore *M. tristis* will be placed as the senior synonym. Considering that all material was collected in similar habitats and in the same collecting

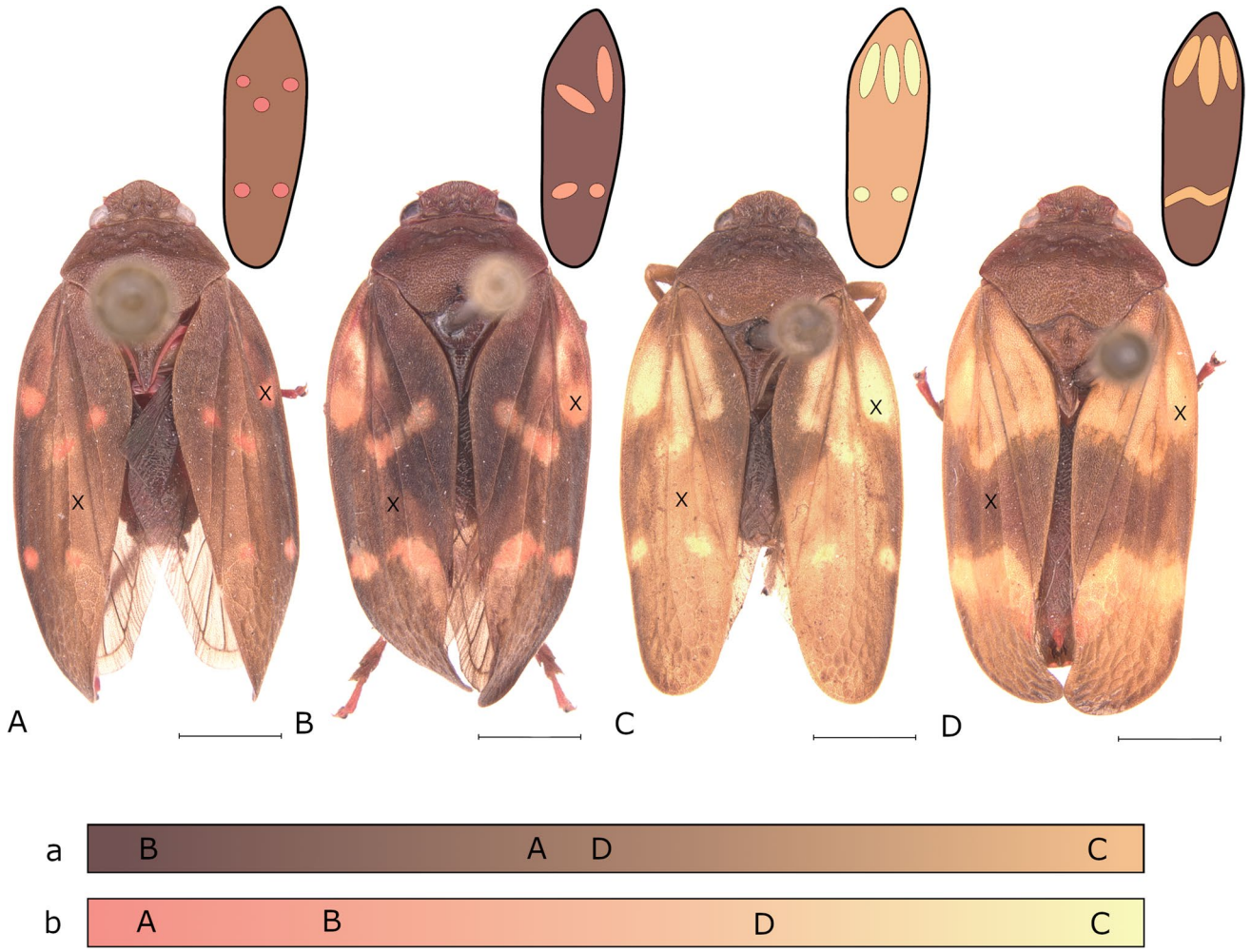


Fig. 3 Four different wing patterns of *Mahanarva tristis* with illustrational drawings. (A) Wing pattern with dots; (B) wing pattern with dots and one lateral stripe; (C) wing pattern with stripes and dots; wing pattern with stripes and v/w-shaped stripe near the tip. (a) Color gradient of the wing surface; (b) color gradient of the dots/stripes. X markers on the photos indicate which spot was selected to create the color gradients. Letters inside the gradients show the relative coloration of each wing pattern type. The photos were taken from the 28 analyzed specimens. The photos belong to both male and female specimens as it was unable to detect a gender bias regarding tegminal coloration or patterns

events, the observed variation can be considered intraspecific variation which is frequently influenced by the different angles in which images are taken.

Taxonomy

Mahanarva (*Mahanarva*) tristis (Fabricius 1803)

M. fraseri (Distant 1909) **n. syn.**, *M. mura* (China and Myers 1934) **n. syn.**, *M. raripila* (Jacobi 1908) **n. syn.**, *M. trifissa* (Jacobi 1908) **n. syn.**, *M. tristis guppyi* (Urich 1913) **n. syn.**, *M. tristis monagasi* (Fennah 1949) **n. syn.**, *M. tristis quadrimaculata* (Fennah 1953) **n. syn.**, *M. tristis suffusa* (Walker 1851) **n. syn.** and *M. tristis walkeri* (Lallemand 1912) **n. syn.**, *M. tristis stalii* (Lallemand 1912) ***sp. inq.***

Measurements (in mm) ♂/♀ ($N = 10/5$): head length, 1.1/1.4; head width, 2.5 /2.9; ocellus diameter, 0.1/0.1; interocelar distance, 0.2/0.2; ocellus-eye distance, 0.5/0.5; ocellus-tilo distance, 0.1/0.1; ocellus-posterior margin distance, 0.3/0.3; interocular distance, 1.5/1.9, tilo length, 0.4/0.5; tilo width, 0.8/1.0; posclypeus length, 1.5/1.9; posclypeus width, 1.1/1.4; pronotum length, 2.2/2.8; pronotum width, 3.9/4.7; scutellum length, 2.1/2.4; scutellum width, 1.6/1.8; tegmina length, 9.3/9.8; tegmina width, 3.4/4.0; total length, 11.4/12.4.

Description:

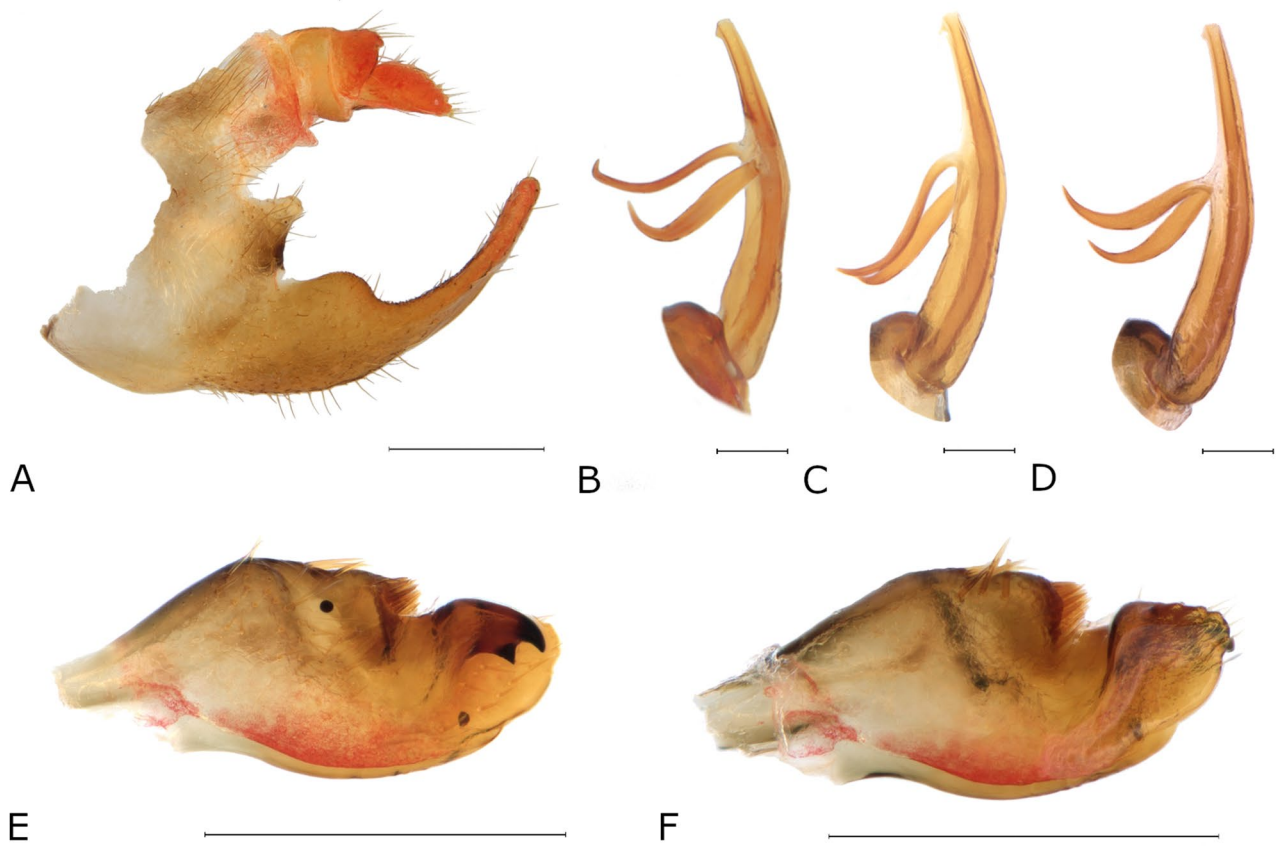


Fig. 4 Male genitalia of *Mahanarva tristis*. **A** Lateral view of the pygofer. **B**–**D** Aedeagus in three slightly different angles. **E** Paramere in ectal view. **F** Paramere in mesal view. Photos were taken from the 28 analyzed specimens. The parameres belong to one specimen and are from the insect's left side. The aedeagus of three different specimens are shown. The paramere does not correspond to the paramere from Fig. 2. Scale bar in the figures **A**, **E** and **F** with 0.5 mm, and figures **B**, **C** and **D** with 0.1 mm

The rounded eyes are arranged transversally, and the smooth rectangular vertex possesses a prominent median carina. The ocelli are placed closer to each other than to the eyes. As the vertex, the tylus is smooth and rectangular as well presenting a prominent median carina. On the antenna, the pedicel is lightly covered in small setae and the oval-shaped basal body of the flagellum contains one arista which is as long as the pedicel. In profile view, the postclypeus is angular and inflated and again contains a prominent longitudinal carina. Laterally, the postclypeus is marked by clear-cut lateral grooves and the rostrum is extending up to the mesocoxae. The hexagonal and curved pronotum contains a slightly visible median carina. Pronotum margins are straight on the front- and the lateral-anterior sides. But the lateral-posterior edges are lightly convoluted, and the posterior margin is grooved. In the middle of the scutellum, there is a low concavity and overall, there are horizontal grooves. The tegmina can possess up to three dots or stripes at the base up until the first third. At about two-thirds of the tegmina, two dots or a curved stripe is present. The Cu1 vein is not thickened at the base and the vein's apical plexus is present. On the posterior tibia, there are two spines. One at the base which is similar sized as the small spines forming the two rowed apical crowns of the tibia. The second spine on the tibia is significantly larger than the first one. The three rows of spines are covering the basitarsus. Those spines are furthermore covered by long setae. Between the claws, there is a triangular subungueal process.

The color of the whole insect may vary between black and brownish tones and the dots and stripes on the tegmina can show between reddish to yellowish colors. On the tegmina, there are only dots present (pattern as Fig. 3(A)) which are reddish colored.

On the male genitals, the pygofer contains a rounded process between the anal tube and the subgenital plates (Fig. 4A). The subgenital plates on the other hand are long and at the base rounded. Parameres present two spines

directed downwards near at the apical end and the dorsal margin is more or less rounded. In the middle part of the paramere, there are about three longer setae and right before the spines there is a comb of smaller setae arranged horizontally (Fig. 4E). Looking at the parameres in mesal view, the spines are not visible but the apical part is slightly emerging (Fig. 4). At the middle, the long and slender aedeagus holds a pair of lateral processes which are pointing anteriorly. Their tip is slightly bend upwards. The base of the aedeagus is thickened and thins out up to the tip which possesses a small triangular process (Fig. 4B–D).

Conclusion

Based on morphology and geographical distribution, *M. fraseri*, *M. mura*, *M. raripila*, and *M. trifissa* are synonyms of *M. tristis*. In addition, there was no evidence of the validity of the analyzed *M. tristis* subspecies. Body morphology is identical among them, with exception of the position of the ocelli, the length of the arista, and the form of the postclypeus. The male genitals show some differences among the nominal subspecies, but these are mainly related to different viewing angles during the analysis, and, in the case of the aedeagus, flexible parts which can be inadvertently distorted during handling of the specimens. The tegmina are polymorphic for variable patterns of dots and stripes which are not exclusive to subspecies but are present as intraspecific variation in *M. tristis*. In addition, coloration is influenced by capture and storage methods. These results are consistent with earlier recognition that tegminal patterns are variable and that the subspecies are questionable Carvalho and Webb (2005). Geographical distribution also supports a single, variable species. All the other nominal taxa analyzed occur within the known distribution of *M. tristis*.

Acknowledgements We would like to thank Dr. Mick Webb (NHMUK), Dr. André Reimann (SNSD), and Dr. Christian Schmidt (SNSD) for their help and hospitality during the institutional visits. Furthermore, we want to thank the three anonymous reviewers who very much improved the quality of the manuscript with their comments.

Author Contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Christian Schöbel, Gervásio Silva Carvalho, Andressa Paladini, and Renato Augusto Teixeira. The first draft of the manuscript was written by Christian Schöbel and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior–Brasil (CAPES)–Finance Code 001–and CNPq–Process: 88887.177172/2018–00 Protax-II.

Declarations

Conflict of Interest The authors declare no competing interests.

References

Borges RA, Auad AM, Fonseca MDG et al (2020) Coloration patterns of the tegmina of *Mahanarva spectabilis* (Hemiptera: Cercopidae): biological, morphological and genetic bases. Florida Entomol 103:376–383. https://doi.org/10.1653/024.103.0310

Carvalho GS, Webb M (2005) Cercopid spittle bugs of the New World (Hemiptera, Auchenorrhyncha, Cercopidae). Pensoft, Bulgaria, pp 1–271

China WE, Myers JG (1934) Critical notes on some neotropical species of Tomaspis (Homoptera, Cercopidae). Ann Mag Nat Hist 14:448–466

Distant WL (1909) XXII. - Rhynchotal notes-XLVI. J Nat Hist Ser 8(3):187–213

Fabricius JC (1803) Rhyngota. Systema Rhyngotorum, secundum ordines, genera, species, adiectis synonymis locis, observationibus, descriptionibus. Brunsvigae, pp 1–314

Farish DJ (1972) Balanced polymorphism in North American populations of the meadow spittlebug, Philaenus spumarius (Homoptera: Cercopidae). 1. North American Morphs. Ann Entomol Soc Am 65:710–719

Fennah RG (1949) New genera and species of neotropical Cercopidae (Homoptera). Ann Mag Nat Hist 1:605–620

Fennah RG (1953) Revisionary notes on neotropical Monecphorine Cercopoidea (Homoptera). Ann Mag Nat Hist 6:337–360

Fennah RG (1968) Revisionary notes on the new world genera of Cercopid froghoppers (Homoptera: Cercopoidea). Bull Entomol Res 58:165–190. https://doi.org/10.1017/S0007485300055954

Goding FW (1923) Sinopsis de los Cercopidae de Ecuador. Rev Del Col Nac Vicente Rocafuerte 5:45–52

Jacobi A (1908) Neue Cercopiden des Andengebietes. Sitzungsberichte der Gesellschaft natur- forschender Freunde, Berlin 8:200–215

Lallemand V (1912) Homoptera Fam. Cercopidae. Bruxelles, pp 1–167

Metcalf ZP (1961) General catalogue of the Homoptera. Fascicle VII. Cercopoidea Part 2 Cercopidae. North Carolina State College, Raleigh, pp 1–607

Paladini A, Domahovski AC, Krinski D, Foerster LA (2018) Reports of new wing color polymorphism and taxonomic information to cercopids (Auchenorrhyncha: Cercopidae) from upland rice crop, Pará state, Brazil. Brazilian J Biol 78:728–735. https://doi.org/10.1590/1519-6984.175519

Schöbel C, Carvalho GS (2021) The "State of Art" of *Mahanarva* (Hemiptera: Cercopidae) research An economically important New World spittlebug genus. Appl Entomol Zool. https://doi.org/10.1007/s13355-021-00744-8

Stal C (1869) Hemiptera Fabriciana. Fabricianska Hemipterarter, efter de Köpenhamn och Kiel förvarade typexemplaren granskade och beskrifne. 2. Handlingar. Kongliga Sven Vetenskaps Akad 8:1–130

Stewart AJA (1996) The colour/pattern polymorphism of *Philaenus spumarius* (L.) (Homoptera: Cercopidae) in England and Wales. Philos Trans R Soc B Biol Sci 351:69–89. https://doi.org/10.1098/rstb.1996.0005

The GIMP Development Team (2019) GIMP. Retrieved from https://www.gimp.org. Accessed 10 Oct 2021

Thompson V, Halkka O (1973) Color polymorphism in some North American *Philaenus spumarius* (Homoptera: Aphrophoridae) populations. Am Midl Nat 89:348–359

Urich FW (1913) The sugar cane froghopper (*Tomaspis varia* Fabr.) and biological notes on some Cercopids of Trinidad. Trinidad Tobago Dep Agric 9:1–46

Walker F (1851) List of homopterous insects. In: Gray JE (ed) List of the specimens of Homopterous insects in the collection of the British Museum Part I. Order of the Trustees, London, pp 637–907

Yurtsever S (2000) On the polymorphic meadow spittlebug, *Philaenus spumarius* (L.) (Homoptera: Cercopidae). Turkish J Zool 24:447–459

Yurtsever S, Akdeniz N, Karahalil B (2010) The colour/pattern polymorphism of *Philaenus spumarius* (Hemiptera: Cercopidae) in the north-western Black Sea region of Turkey. Biologia (bratisl) 65:309–315. https://doi.org/10.2478/s11756-010-0022-x

Authors and Affiliations

Christian Schöbel[1] · Gervásio Silva Carvalho[1] · Andressa Paladini[2] · Renato Augusto Teixeira[3]

Gervásio Silva Carvalho
gcarvalho2010@gmail.com

Andressa Paladini
andri.paladini@gmail.com

Renato Augusto Teixeira
renato.teixeira@pucrs.br

[1] PUCRS, Escola de Ciências da Saúde e da Vida, Programa de Pós-Graduacão em Ecologia e Evolução da Biodiversidade, Lab de Entomologia, Rio Grande do Sul, Porto Alegre, Brazil

[2] Depto de Ecologia e Evolução, Univ Federal de Santa Maria, Rio Grande do Sul, Santa Maria, Brazil

[3] PUCRS, Escola de Ciências da Saúde e da Vida, Programa de Pós-Graduacão em Ecologia e Evolução da Biodiversidade, Lab de Aracnologia, Rio Grande do Sul, Porto Alegre, Brazil