

***Teletusa limpida* (SIGNORET): a Neotropical proconiine leafhopper that mimics megachilid bees (Hymenoptera: Apoidea), with notes on Batesian mimicry in the subfamily Cicadellinae (Hemiptera: Cicadellidae)**

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Abstract

Morphological comparisons and field studies carried out in the Brazilian State of Minas Gerais suggested that the proconiine leafhopper *Teletusa limpida* (SIGNORET) is a Batesian mimic of bees of the family Megachilidae. This leafhopper exhibits the following mimicry-related characteristics: (1) body densely covered by conspicuous hairs, especially developed on the face and mesoscutellum, (2) disc of frons forming an approximately right angle with the longitudinal axis of body, (3) fore- and hindwings almost entirely hyaline, (4) abdomen short and expanded laterally, and (5) overall coloration dark brown or black with yellow markings. These features are remarkably similar to those of four megachilid species that are sympatric with *T. limpida* in Minas Gerais (*Anthodioctes megachiloides* (HOLMBERG), *Hypanthidiodes subarenarium* (SCHWARZ), *Hypanthidiodes musciforme* (SCHROTTKY), and *Megachile meoxanthoptera* COCKRELL. Specimens of *T. limpida* are especially similar to those of *A. megachiloides*

and *M. meoxanthoptera*. Yellow areas on the leafhopper abdomen resemble the metasomal scopal hairs or the pollen carried on the scopa of the bees. The present case of mimicry is compared with the two other known cases of mimicry in leafhoppers of the subfamily Cicadellinae (genera *Propetes* WALKER and *Lissoscarta* STÅL), as well as with similar cases in the Auchenorrhyncha. The appearance of mimicry in the Cicadellinae is discussed in a phylogenetic context.

Key words

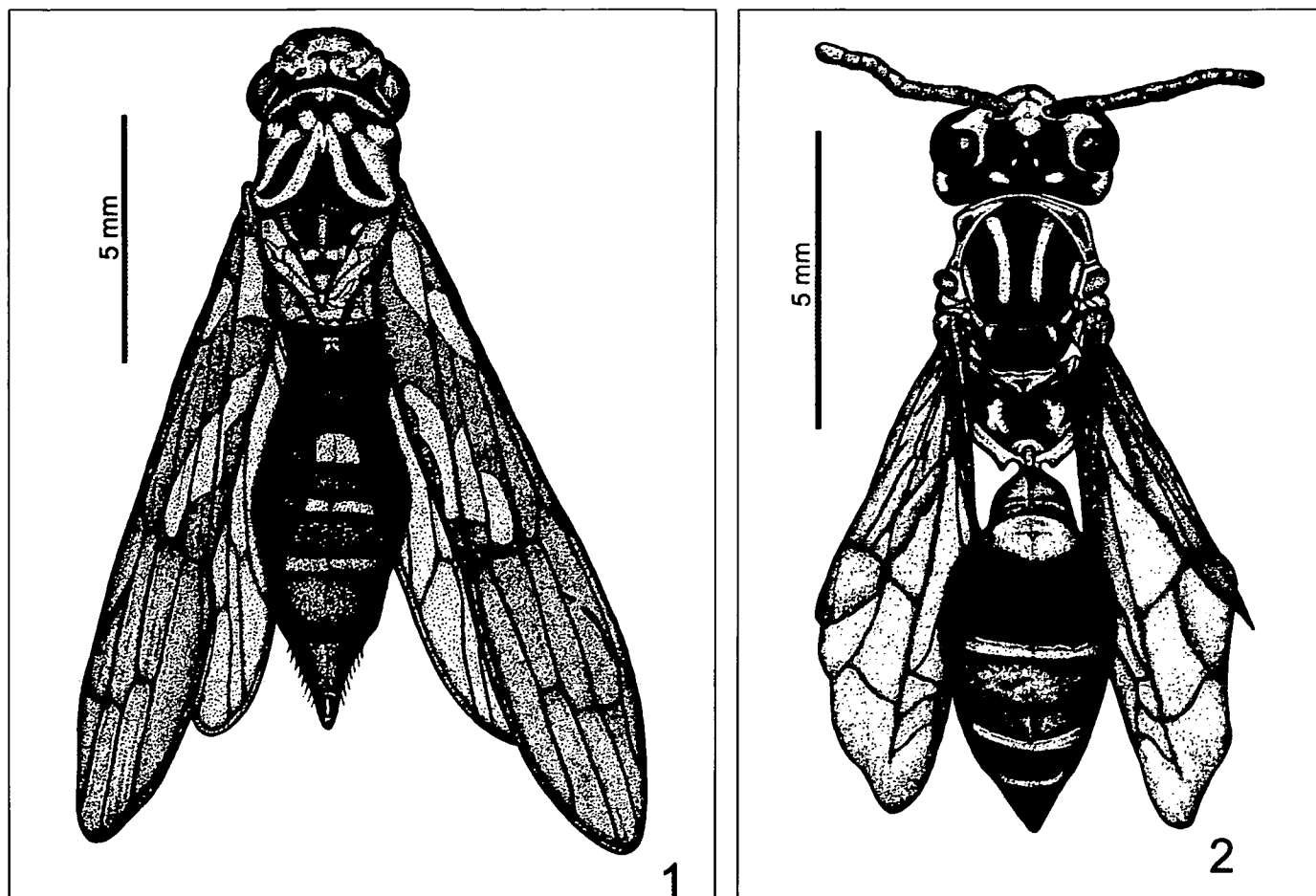
Proconiini, Cicadellini, mimetic species, morphology, phylogeny, Megachilidae, Vespidae.

Introduction

Batesian mimicry in the subfamily Cicadellinae

Two cases of Batesian mimicry in leafhoppers of the subfamily Cicadellinae have been reported in the literature. BOULARD (1978) and MEJDALANI & FELIX (1997) described morphological and behavioral features of the

the constriction at the base of the abdomen (data based so far only on field observations of *L. vespiformis* (FABRICIUS) and *L. beckeri* MEJDALANI & FELIX). This behavior, in which the mimic suddenly exposes characteristics that are similar to those of its model, is called "ostensible mimicry" (BOULARD 1978). It has not been observed in any other known leafhopper genus.

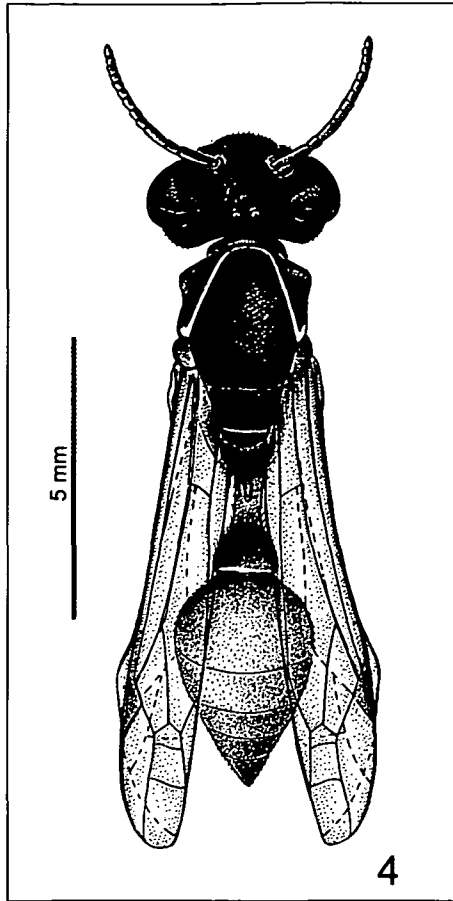
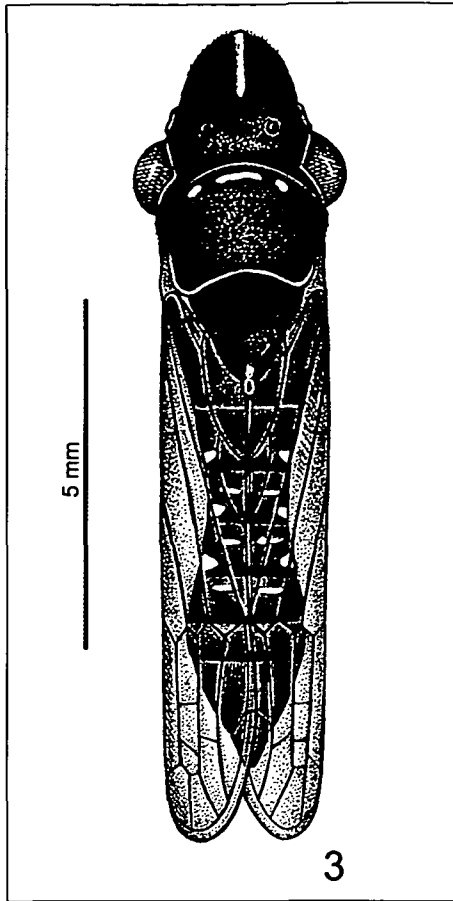


Figs 1 and 2.

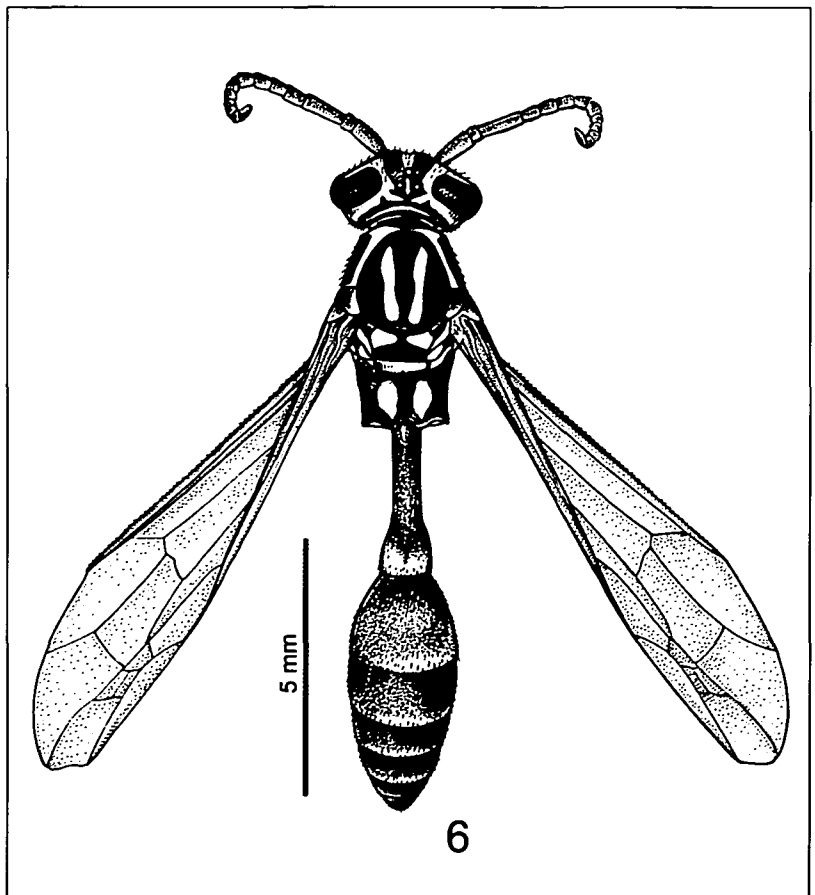
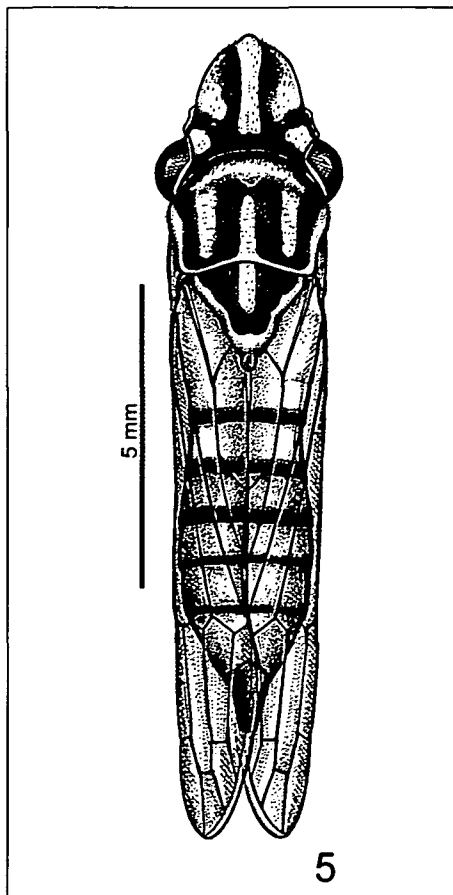
(Fig. 1) The cicadelline Batesian mimic *Lissoscarta beckeri* MEJDALANI & FELIX (female) and (Fig. 2) its epiponine wasp model *Agelaia fulvofasciata* (DEGEER), body in dorsal view (northern Brazil; from MEJDALANI & FELIX 1997). Mimic and model are approximately the same size.

cicadelline genus *Lissoscarta* Stål that enable its seven known species to mimic epiponine wasps (Vespidae: Polistinae) (Figs 1 and 2). The abdomen in *Lissoscarta* is strongly constricted at the base, the fore- and hindwings are elongate and hyaline, and the color pattern is remarkably similar to that of many epiponine wasps (crown, pronotum, and mesonotum yellow with dark maculae and stripes; abdominal terga yellowish-brown with a transverse yellow stripe on their posterior margins). When threatened, *Lissoscarta* leafhoppers spread their wings in a similar way to that of a wasp in the resting position, showing

TAKIYA et al. (1999) described morphological features of the proconiine genus *Propetes* WALKER related with the mimicry of epiponine wasps. Specimens of the two known species of *Propetes*, as those of *Lissoscarta*, have hyaline and elongate forewings and the abdomen is constricted basally. According to TAKIYA et al. (1999), the males of *P. schmidti* MELICHAR are mostly black with small yellow areas and stripes, while in the females these yellow markings are distinctly larger (Figs 3 and 5). The different color patterns of males and females suggested the existence of a dual, sex-limited Batesian mimicry. In this kind of mimicry each sex of the mimic has its own



Figs 3 and 4.
(Fig. 3) The proconiine Batesian mimic *Propetes schmidtii* MELICHAR (male) and (Fig. 4) its epiponine wasp model *Polybia rejecta* (FABRICIUS), body in dorsal view (southeastern Brazil; from TAKIYA et al. 1999). Mimic and model are approximately the same size.

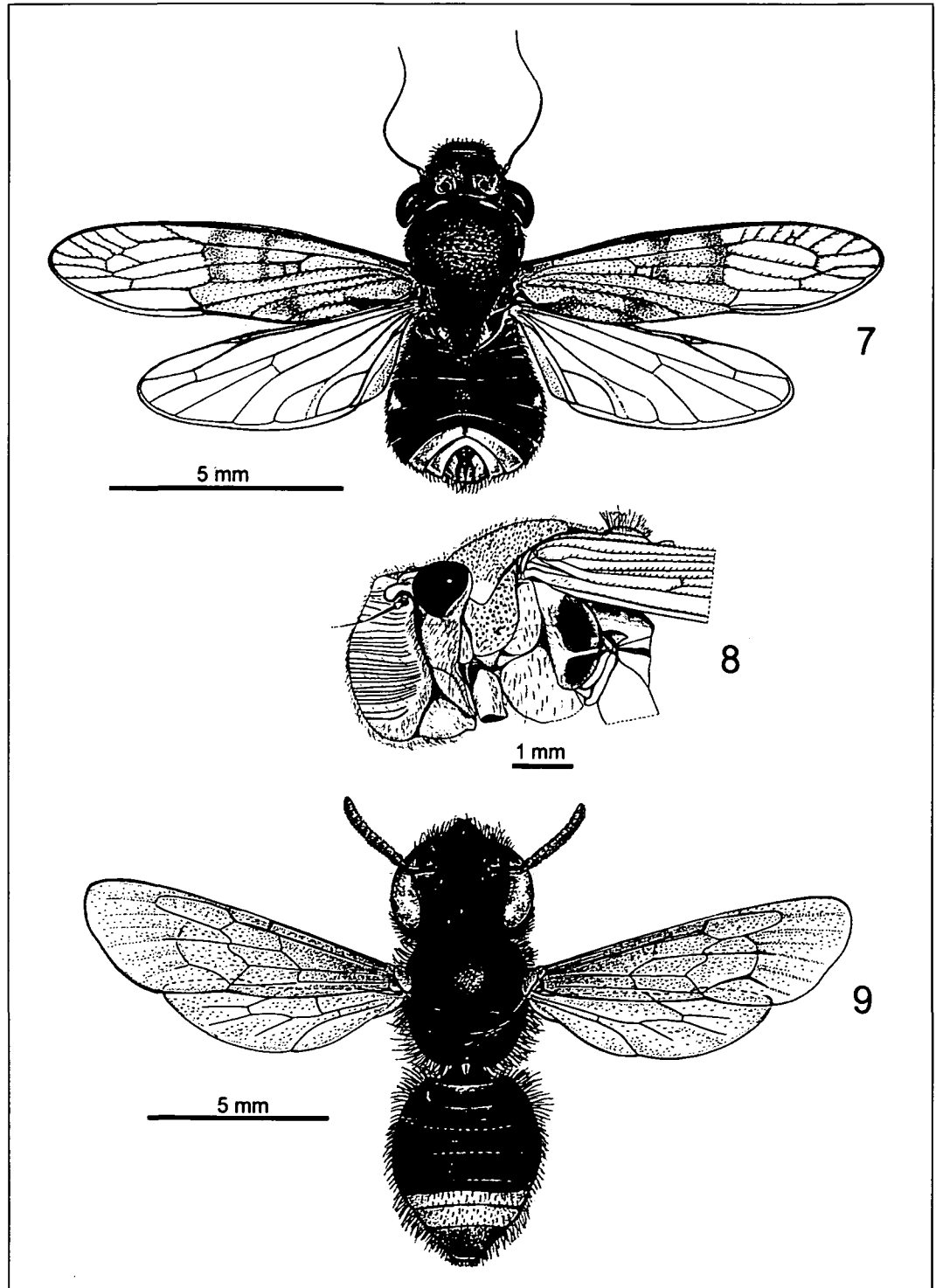


Figs 5 and 6.
(Fig. 5) The proconiine Batesian mimic *Propetes schmidtii* MELICHAR (female) and (Fig. 6) its epiponine wasp model *Mischocyttarus ypiranguensis* da FONSECA, body in dorsal view (southeastern Brazil; from TAKIYA et al. 1999). Mimic and model are approximately the same size.

models (VANE-WRIGHT 1976) (Figs 4 and 6). This is the only known case of dual-mimicry in the Auchenorrhyncha. According to VANE-WRIGHT (1976), this kind of mimicry occurs rarely in Lepidoptera and more commonly in Hymenoptera (e.g., EVANS 1968).

Using VANE-WRIGHT's (1976) terminology and analytic schemes, the mimicry cases of *Lissoscarta* and *Propetes* were considered re-

spectively by MEJDALANI & FELIX (1997) and TAKIYA et al. (1999) as belonging to class VI (antergic defensive). According to VANE-WRIGHT (1976), in this class the mimic simulates an organism in some way repellent to the operator, so avoiding attention it would otherwise receive. The presence of the mimic is a disadvantage to the model. Class VI includes H.W. Bates' original formulation of mimicry (Fig. 10).



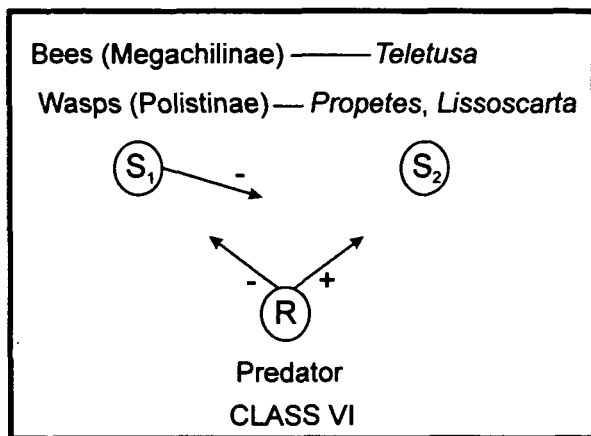
Figs 7-9.
(Fig. 7) The proconiine Batesian mimic *Teletusa limpida* (SIGNORET) (male) and (Fig. 9) its megachilinae bee model *Megachile neoxanthoptera* COCKERELL, body in dorsal view (southeastern Brazil). Mimic and model are approximately the same size. (Fig. 8) *T. limpida*, anterior portion of body in lateral view.

The proconiine genus *Teletusa*

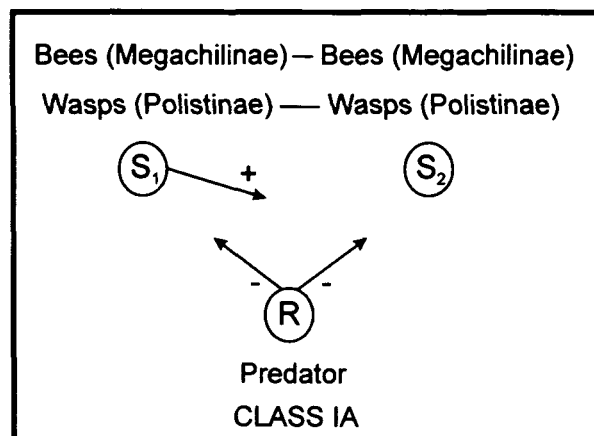
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YOUNG (1968) recognized a single valid species in the Neotropical genus *Teletusa*, *T. limpida* (SIGNORET), with six junior synonyms. He examined specimens of *Teletusa* from Amazonas in Brazil to Bolivia and to Paraguay and Argentina. The results of a phylogenetic analysis of the proconiine genera

Field studies carried out in the Brazilian State of Minas Gerais by one of the authors (DY) suggested that *T. limpida* could be a mimic of long-tongued solitary bees of the family Megachilidae (leafcutting bees). The morphological analysis of *T. limpida* leafhoppers and megachilid bees from the locality (Belo Horizonte) studied by DY confirmed the existence of such a mimicry relationship. The



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with the exposed posterior meron (MEJDALANI 2000) indicated that *Teletusa* is the sister group of a clade formed by the genera *Abana* DISTANT, *Acrobelus* STÅL, *Deselvana* YOUNG, and *Rhaphirrhinus* LAPORTE. The clade including the latter four genera and *Teletusa* is supported by two apomorphic features: (1) posterior region of crown with an elevated area between the ocelli and (2) apex of aedeagus with a pair of lateral lobes. *Teletusa* can be distinguished from the remaining genera of the clade by the following apomorphic characteristics: (1) body densely covered by conspicuous hairs, especially developed on the face and mesoscutellum (Fig. 8), (2) disc of frons forming an approximately right angle with the longitudinal axis of body (Fig. 8), (3) mesoscutellum swollen (Fig. 8), (4) forewings almost entirely hyaline (Fig. 7), and (5) abdomen short and expanded laterally (Fig. 7). YOUNG (1968) observed that *Teletusa* stands well apart from other genera in the tribe Proconiini in its very pubescent mesoscutellum and lower portion of the face, in the very short pygofer of the male, and in the broad, flattened, short abdomen.

bees examined, which belong to the subfamily Megachilinae, are *Anthodioctes megachiloides* (HOLMBERG), *Hypanthioides (Moureanthidium) subarenarium* (SCHWARZ), *Hypanthioides (Saranthidium) musciforme* (SCHROTTKY) (tribe Anthidiini), and *Megachile (Ptilosaroides) neoxanthoptera* COCKERELL (tribe Megachilini). We provide below an account of the characteristics of *T. limpida* that enable it to mimic the megachilid bees. These characteristics are compared with those of the proposed models. The present case of mimicry is compared with the two other known cases of mimicry in leafhoppers of the subfamily Cicadellinae, as well as with similar cases in the Auchenorrhyncha.

Material and methods

The specimens of *T. limpida* examined, which were determined by one of the authors (GM), are deposited in the following collections: Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro (MNR); Rio de Janeiro), Departamento de Zoologia, Museu Paraense Emílio

Figs 10 and 11.

(Fig. 10) Scheme showing the known Batesian mimicry (class VI) cases in the leafhopper subfamily Cicadellinae (based on VANE-WRIGHT 1976). In class VI, antergic defensive mimicry, the presence of the mimic is a disadvantage to the model. (Fig. 11) Müllerian mimicry (class IA) cases treated in the present study (based on VANE-WRIGHT 1976). In class IA, synergic warning mimicry, the model and mimic cooperate to produce a common defense signal that advertises their dangerous, nauseous or otherwise repellent features to the operator. S₁, model (signal transmitter); S₂, mimic (signal transmitter); R, operator (signal receiver); +, advantageous interactive role; -, disadvantageous interactive role.

Goeldi (MPEG; Belém), Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (DZR); Rio de Janeiro), and Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná (DZUP; Curitiba). The megachilid specimens studied are deposited in the Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais (UFMG; Belo Horizonte). They were determined by the Drs. F. A. Silveira (UFMG) or D. Urban (DZUP). The sexes and locality data of all studied specimens are as follows:

(1) *Teletusa limpida*. Brazil: State of Amazonas: 1 male, São Gabriel da Cachoeira Municipality (MNRJ); 1 male, Maturacá [São Gabriel da Cachoeira Municipality] (MPEG); 1 male and 3 females, Manaus Municipality (MNRJ); State of Pará: 1 male, Serra Norte [Parauapebas Municipality] (MPEG); State of Rondônia: 1 male, Vilhena Municipality (MNRJ); State of Mato Grosso: 1 male, Chapada dos Guimarães Municipality (MPEG); State of Goiás: 8 males, Campinas [Goiânia Municipality] (MNRJ); State of Minas Gerais: 2 males, Belo Horizonte Municipality (MNRJ); State of São Paulo: 3 males, Ilha Seca [Andradina Municipality] (MNRJ); 1 male and 1 female, Bebedouro Municipality (DZUP). Peru: Department of Loreto: 1 male, Aguas Calientes [?] (DZR).

(2) *Anthodioctes megachiloides*. Brazil: State of Minas Gerais: 3 males and 5 females, Belo Horizonte Municipality (UFMG).

(3) *Hypanthioides subarenarium*. Brazil: State of Minas Gerais: 1 male and 1 female, Belo Horizonte Municipality (UFMG); 2 males and 1 female, Catas Altas Municipality (UFMG).

(4) *Hypanthioides musciforme*. Brazil: State of Minas Gerais: 1 male, Belo Horizonte Municipality (UFMG); 2 males and 1 female, Sabará Municipality (UFMG).

(5) *Megachile neoxanthoptera*. Brazil: State of Minas Gerais: 5 males and 3 females, Belo Horizonte Municipality (UFMG); 1 male, Ponte Nova Municipality (UFMG).

The techniques for preparation of the male genital structures, which were dissected to confirm the identification of *T. limpida* sensu YOUNG (1968: 164, Fig. 151), follow those of OMAN (1949). The dissected parts are stored in microvials with glycerin. The leafhopper morphological terminology adopted herein follows mainly MEJDALANI (1998, 2000), while the bee morphological terminology follows mainly MITCHELL (1980) and MICHENER (1944). The body length (in mm) of leafhoppers and bees was taken from the apex of head to the apex of abdomen in dorsal view. The mimicry concepts, terminology, and analytic schemes used herein follow mainly the work of VANE-WRIGHT (1976).

Results

Megachilid bees

Males and females of the four studied bee species vary in length, respectively, from 5.6 to 8.1 mm and from 6.0 to 9.9 mm (see details on Table 1). The body in these bees has a mostly black, nonmetallic ground color, and is thickly beset with hairs (more conspicuously developed in *Megachile neoxanthoptera*) on the head, thorax, and abdomen (Fig. 9). The contour of the face, in lateral view, forms an approximately right angle with the longitudinal axis of body. The fore- and hindwings are mostly hyaline. The abdomen (metasoma) has an ellipsoidal form, or is somewhat rounded (males of *M. neoxanthoptera*). Terga on the posterior half of the metasoma are covered by yellow pubescence (*M. neoxanthoptera*), or possess conspicuous transverse yellow stripes (*Anthodioctes megachiloides*, *Hypanthioides subarenarium*, and *H. musciforme*). The pollen-collecting scopa is on the metasoma, not on

Table 1. Body length (in mm) of males and females of the leafhopper *Teletusa limpida* (SIGNORET) and of the megachilid bees *Anthodioctes megachiloides* (HOLMBERG), *Hypanthioides subarenarium* (SCHWARZ), *Hypanthioides musciforme* (SCHROTTKY), and *Megachile neoxanthoptera* COCKERELL. The number (n) of specimens measured is given inside parentheses.

	Males	Females
<i>Teletusa limpida</i>	6.2-7.2 (n = 13)	7.1-8.7 (n = 4)
<i>Anthodioctes megachiloides</i>	5.6-6.2 (n = 3)	6.8-7.9 (n = 5)
<i>Hypanthioides subarenarium</i>	6.4-6.7 (n = 3)	6.0-6.3 (n = 2)
<i>Hypanthioides musciforme</i>	6.3-7.5 (n = 3)	6.7 (n = 1)
<i>Megachile neoxanthoptera</i>	6.5-8.1 (n = 6)	9.4-9.9 (n = 3)

the hindlegs as in most bees. It occupies most of the metasomal sternum, being formed by long, robust, densely distributed hairs. The sting is well developed.

Teletusa limpida

The above-mentioned characteristics of the megachilid bees are apparently mimicked by *Teletusa limpida* (Figs 7-9). Males and females of this leafhopper vary in length, respectively, from 6.2 to 7.2 mm and from 7.1 to 8.7 mm (Table 1). The body has a dark brown or black ground color and is remarkably covered by hairs (Figs 7 and 8), being very similar to that of the bees, especially *A. megachiloides* and *M. neoxanthoptera* (Fig. 9). The hairs are strongly developed on the mesoscutellum and face; the contour of the latter, in lateral view, also forms an approximately right angle with the longitudinal axis of body (Fig. 8). The abdominal sterna, laterotergites, terga vii and viii, and the pygofer (tergum ix) are variably marked with yellow. These yellow areas resemble the scopal hairs or the pollen carried on the scopa, as well as color markings or hairs on other metasomal areas of the bees. The fore- and hindwings are, as in the proposed models, mostly hyaline. The abdomen is short, broad, and slightly flattened dorsoventrally, clearly resembling the metasoma of the bees. Its lateral areas are visible at the sides when the wings are at rest position.

Discussion

The aforementioned autapomorphic features of *Teletusa*, which clearly distinguish it from other related proconiine genera (YOUNG 1968, MEJDALANI 2000), are apparently mimicry-related, with the single exception of the expanded mesoscutellum. The hairy body, perpendicular frons, short and laterally expanded abdomen, and hyaline forewings (as well as hindwings), along with the dark brown or black overall coloration with yellow markings, give *T. limpida* (Figs 7 and 8) an appearance remarkably similar to the megachilids studied, especially *A. megachiloides* and *M. neoxanthoptera* (Fig. 9). The hairs and the peculiar aspect of the frons and abdomen are unique within the tribe Proconiini (MEJDALANI 2000). The hyaline forewings, on the other hand, arose

independently in the clade that includes the genus *Propetes*, the wasp-mimic proconiine (TAKIYA et al. 1999, MEJDALANI 2000) (Figs 3 and 5). Interestingly, this feature also arose independently in the wasp-mimic cicadelline *Lissoscarta* (BOULARD 1978, MEJDALANI & FELIX 1997, FELIX 1999, MEJDALANI 2000) (Fig. 1). The hyaline hindwings, which are also mimicry-related, are common in the Cicadellidae, being a plesiomorphic trait in the hymenopteran-mimic leafhoppers. The fore- and hindwings of *Teletusa*, *Propetes*, and *Lissoscarta* (Figs 1, 3, 5, and 7) clearly resemble those of bees or wasps (Figs 2, 4, 6, and 9). In addition to this important role, the hyaline aspect possibly allows an easier visualization by the predators (operators) of the leafhopper abdomen, which is short and expanded laterally (*Teletusa*, Fig. 7) or has a distinct constriction (*Lissoscarta* and *Propetes*, Figs 1, 3, and 5).

Leafhoppers of the genus *Teletusa*, as well as those of the genera *Propetes* and *Lissoscarta*, are very poorly represented in collections. They are apparently rare insects, an aspect that supports the hypothesis of Batesian mimicry (class VI, antergic defensive, of VANE-WRIGHT 1976) (Fig. 10). The predators (operators) from which the Batesian mimicry in *Propetes* and *Lissoscarta* affords protection are unknown. Thus, it was not possible to determine whether such mimicry cases are disjunct (mimic, model, and operator are different species) or bipolar (model and operator are the same) (MEJDALANI & FELIX 1997, TAKIYA et al. 1999). In the *Teletusa* case the predators are also unknown. This case, however, is certainly disjunct, since the model bees are not predators.

At least two other cases of class VI mimicry have been reported in the Auchenorrhyncha, both in the planthopper family Fulgoridae. HOGUE (1984) suggested that "lantern bugs", *Fulgora* spp., avoid predation by mimicking lizards. He observed that individuals of *Fulgora* typically rest during the day on the trunks of large trees. They position themselves vertically, the head with its great anterior protuberance uppermost and elevated at an angle away from the substratum. This posturing is similar to that assumed by certain species of arboreal lizards, e.g., *Plica plica* (LIN-

NAEUS) (Iguanidae). HOGUE (1984) described similarities in the size, overall form, and general color pattern of "lantern bugs" and lizards, as well as remarkable points of resemblance in their heads (posture, shape, and color markings) (Fig. 12). ZOLNEROWICH (1992) described a nymph of *Amycle* sp. that mimics jumping spiders (Salticidae). He observed that the nymph has four smooth, polished dark

because the conspicuous spines on its pronotum would keep predators away. Thus, the vespid mimetic signal would be reinforced. He did not mention whether *H. flavolineatus* is a Batesian or Müllerian mimic of ants. Personal observations by DY revealed that *Heteronotus* treehoppers are particularly similar to eumenine vespids. These wasps are typically black and yellow, with a doubly-constricted metasoma. The membracids are similarly marked, with a greatly elongated pronotum with two strong posterior constrictions, giving them the same size and proportions as the eumenine wasps.

VANE-WRIGHT (1976) observed that the models in class VI mimicry are often members of Müllerian mimicry groups (class IA, synergic warning) (Fig. 11). According to him, in class IA the model and mimic co-operate to produce a common defense signal that advertises their dangerous, nauseous or otherwise repellent features to the operator. This is the classic situation originally described by F. Müller. One example of such Müllerian groups, or rings, are the epiponine wasps that are mimicked by *Lissoscarta* and *Propetes* leafhoppers (RICHARDS & RICHARDS 1951, BOULARD 1978, MEJDALANI & FELIX 1997, TAKIYA et al. 1999) (Figs 2 and 6). Our conclusion that members of two tribes of the subfamily Megachilinae could be models for *T. limpida* is apparently in accordance with the observation of VANE-WRIGHT (1976) that the models in class VI often belong to Müllerian groups. As described before, the body in the four studied bees has a very similar color pattern. It is mostly black, nonmetallic, with the tergal posterior half of the metasoma mainly yellow (Fig. 9). Interestingly, the yellow metasomal area in *M. neoxanthoptera* (Megachilini) and those in *A. megachiloides*, *H. subarenarium*, and *H. muscifforme* (Anthidiini) are not homologous. In the former species the yellow area is formed by pubescence, while in the latter three it is formed by transverse, colored integumental stripes. Such non-homologous conditions suggest that these bees belong to a Müllerian ring. Their sting, along with the hairy body, would teach predators to keep away. This suggestion of a Müllerian ring is corroborated by field observations in Belo Horizonte (Minas Gerais). In this area *T. limpida* appears to belong to a diverse group



Fig. 12. The „lantern bug“ *Fulgora* sp. (Fulgoridae), head, thorax, and part of wings in lateral view (northern Brazil). According to HOGUE (1984), „lantern bugs“ are possibly Batesian mimics of arboreal lizards. The mimics are similar to the proposed models in the size, overall form, and general color pattern, including remarkable points of resemblance in their heads (posture, shape, and color markings).

areas on its metathorax and hindwing pads that resemble the anterior eyes of jumping spiders. The middle- and hindlegs, which project posteriorly and have flattened femora and tibiae, are moved in an up and down manner similar to those of salticid legs and pedipalpi during courtship or aggression displays. In the cases reported by HOGUE (1984) and ZOLNEROWICH (1992) the model and operator were considered the same (bipolar).

Other cases of mimicry in the Auchenorrhyncha, which so far have not been classified according to the concepts of VANE-WRIGHT (1976), occur in the treehopper genus *Heteronotus* LAPORTE (Membracidae) (BOULARD 1999, DY, personal observations). BOULARD (1999) reported the occurrence of mimicry of ants and wasps by species of *Heteronotus*. He observed that individuals of *H. flavolineatus* LAPORTE are apparently ant-mimics. They are usually found with these hymenopterans, being sedentary and gregarious. On the other hand, individuals of *H. abcisus* WALKER are solitary and more active fliers, being possibly wasp-mimics. According to him, the latter species could belong to a Müllerian ring,

of palatable and unpalatable mimics that includes wasps (Sphecidae and Vespidae), bees (Apidae, Colletidae, and Megachilidae), moths (Arctiidae), flies (Syrphidae), and beetles (Cerambycidae) (DY, personal observations).

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Zusammenfassung

Morphologische Befunde und Freilandstudien in Minas Gerais (Brasilien) zeigen, dass Gestalt und Färbung der Zwergzikade *Teletusa limpida* (SIGNORET) aus der Unterfamilie Cicadellinae (Tribus Procimiini) als Batesische Mimikry der Bienenfamilie Megachilidae zu interpretieren sind. Dies ist auf fünf Merk-

malskomplexe der Zikade zurückzuführen: (1) eine auffällige und dichte Behaarung des Körpers, insbesondere im Gesicht und am Mesoscutellum, (2) die Platte der Frons steht im rechten Winkel zur Körperlängsachse, (3) Vorder- und Hinterflügel sind fast zur Gänze transparent, (4) das Abdomen ist kurz und lateral verbreitert, und (5) die Färbung ist dunkelbraun bis schwarz mit gelben Flecken. Diese Merkmale sehen jenen von vier Megachiliden-Arten, die mit *T. limpida* in Minas Gerais sympatrisch vorkommen (*Anthodioctes megachiloides* (HOLMBERG), *Hypanthiodes subarenarium* (SCHWARZ), *H. musciforme* (SCHROTTKY) und *Megachile neoxanthoptera* COCKERELL), sehr ähnlich. Individuen von *T. limpida* sehen vor allem *A. megachiloides* und *M. neoxanthoptera* sehr ähnlich. Die gelben Flecken am Abdomen der Zikade ähneln den Haaren der Scopa der Bienen oder Pollen, auf der Scopa transportiert wird. Die hier beschriebene Mimikry wird mit zwei anderen Fällen von Mimikry bei Zikaden (Gattungen *Propetes* WALKER und *Lissoscarta* STÄL; beides Cicadellinae) verglichen. Abschließend werden phylogenetische Aspekte des Auftretens von Mimikry bei Zikaden diskutiert.

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