
Systematic revision and phylogenetic analysis of the South American genus *Chlorus* (Orthoptera, Acridoidea, Melanoplinae)

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The South American grasshopper genus *Chlorus* (Melanoplinae, Dichroplini) from Bolivia, southern Brazil and Paraguay is revised. Cladistic analysis of morphological characters indicates that *Chlorus* constitutes a monophyletic group whose generic relationships remain unsolved. If the external morphology is considered, *Chlorus* showed to be related to *Dichromatos*, while characters from the male genitalia support the relationship between *Chlorus* and *Eurotettix*. Seven species are recognised for *Chlorus* with three of them described as new: *Chlorus spatulus*, *Ch. chiquitensis* and *Ch. attenuatus*. Keys to the species of the genus and a review of the morphological characters defining the taxa are provided.

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Introduction

Chlorus constitutes a monophyletic genera group of Dichroplini together with *Scotussa* Giglio-Tos, *Leiotettix* Bruner, *Atrachelacris* Giglio-Tos, *Ronderosia* Cigliano, *Eurotettix* Bruner, and *Dichromatos* Cigliano (Cigliano & Ronderos 1994; Cigliano *et al.* 1996; Cigliano 1997; Cigliano 2007). At present, *Chlorus* contains four described species from eastern Bolivia, southern Brazil and Paraguay. The distribution of the genus appears to be restricted to the Paranense, Cerrado and Yungas biogeographical provinces (following Cabrera & Willink's 1973 biogeographical scheme).

A recent study (Cigliano 2007) on the phylogeny of *Eurotettix* where the four species of *Chlorus* known at that time (*Chlorus vittatus*, *Ch. borellii*, *Ch. bolivianus* and *Ch. brunneus*) were chosen as outgroups showed that one of them, *Ch. vittatus*, grouped at the basal node of the ingroup.

The review of the literature shows that the descriptions of the genus and species as well as a few published additional studies offer limited information. Several trips to the distribution area of the genus and new material at hand rendered the discovery of three new species of *Chlorus*. A complete and comprehensive systematic revision is necessary in order to analyse the phylogenetic relationships.

In this study the status of *Chlorus* and the relationships within the species are elucidated through a reassessed phylogenetic study based on the analysis carried on for *Eurotettix* and *Dichromatos* (Cigliano 2007). In order to check for the monophyly of *Chlorus* the previous phylogenetic analysis (Cigliano 2007) was expanded and species representing the group of genera where the genus is included were added into this study. Besides, a review of the morphological characters defining the taxa and description of three new species for the genus is given.

Materials and methods

Morphological study

Terminology for external morphology and male genitalia follows Otte (1981) and Amédégno (1976), respectively. Descriptions of the species are mostly based on male specimens because Melanoplinae females are usually very difficult to discriminate and thus the identification is usually done by association with males collected at the same time and place. Measurements are given in millimetres; body length is measured from the apex of fastigium to the apex of hind femur.

Museum specimens were relaxed in a humid chamber and for speeding the process the abdomen terminalia were moistened

with ammonia. Genitalia were then pulled from the body using a finely hooked pin, cleared in potassium hydroxide and stored in glycerine.

Photographs were taken with a digital camera. Illustrations were made as pencil sketches using a camera Lucida on a stereomicroscope Nikon SMZ-U.

Specimens examined are deposited in the following institutions: Academy of Natural Sciences, Philadelphia, USA (ANSP); Museo de La Plata, Facultad de Ciencias Naturales, Universidad Nacional de La Plata, Argentina (MLP); Museu Nacional, Rio de Janeiro, Brazil (MR); Facultad de Ciencias, Universidad de la Republica, Uruguay (FCMON); United States National Museum of Natural History, Washington, D.C., USA (USNM).

Cladistic analysis

Phylogenetic analyses were performed on a matrix comprising 30 adult morphological characters and 27 taxa (Appendices 1 and 2). The list of characters was slightly modified from that one used in the analysis of the phylogenetic relationships of the species of *Eurotettix* and *Dichromatos* (Cigliano 2007). Morphological characters comprised structures from the head and thorax, male genitalia, female ovipositor and colouration patterns. Although colouration in Acrididae is known to be variable and sometimes affected by local environmental conditions, the characters on body colour used in this analysis are not variable at the intraspecific level and appear to be heritable. Tree searches were conducted in NONA (Goloboff 1999) run within WINCLADA version 1.00.08 (Nixon 2002) and in TNT (Goloboff *et al.* 2000). Heuristic searches were performed by tree bisection–reconnection (TBR) branch swapping on 5000 series of random-addition sequence replicates, tree search options of Hold 1000, Hold/1000, Mult* 5000 were used in NONA. Implicit enumeration option was used in TNT. All characters were considered to be of equal weight, multistate characters were treated as unordered. Support for individual nodes was assessed by calculation of absolute Bremer support values (Bremer 1994) performed in TNT.

Characters were polarised using the outgroup selection of *Scotussa impudica* (Giglio-Tos), *Leiotettix viridis* Bruner, *Atrachelacris unicolor* Giglio-Tos and *Ronderosia bergi* (Stål).

Results

Cladistic analysis

Parsimony analysis of the data matrix (Appendix 2) yielded five most parsimonious trees of length 75 (consistency index, 0.66; retention index, 0.88) in NONA, the same trees were recovered with the implicit enumeration algorithm implemented in TNT. The strict consensus tree (Fig. 1) was 90 steps long (CI = 0.55, RI = 0.80). The analysis consistently recovered the three genera (*Chlorus*, *Eurotettix* and *Dichromatos*) as monophyletic taxa; however, their relationships varied from

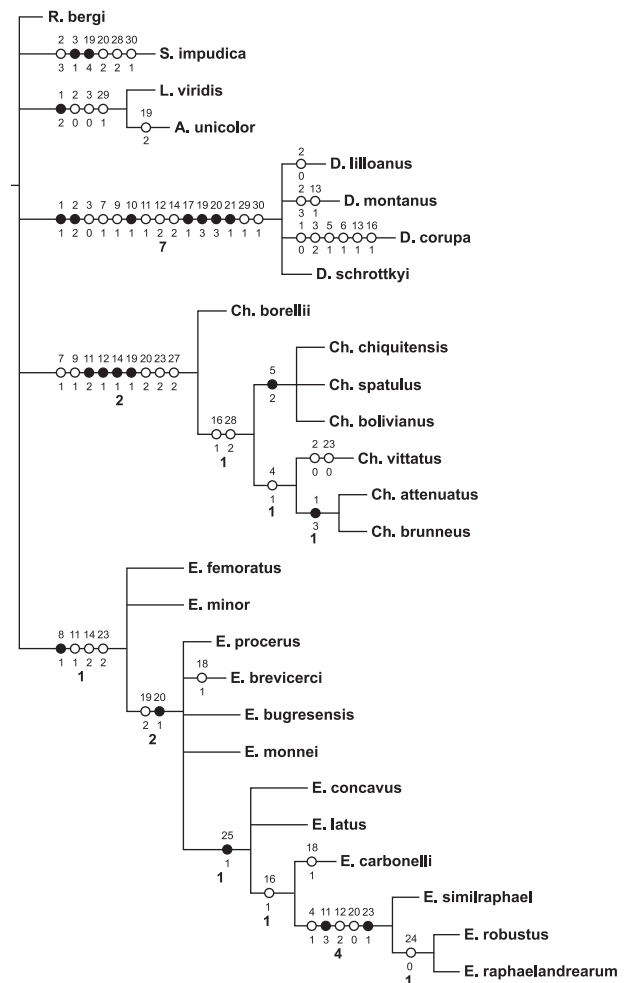


Fig. 1 Strict consensus tree of five equally parsimonious trees (length 75, consistency index = 0.66, retention index = 0.88) resulting from the cladistic analysis for the genus *Chlorus* of unordered morphological character dataset. Black circles indicate unique changes and white circles homoplasies. The numbers below the nodes are the absolute Bremer support values.

one tree to the other (Fig. 1). Two of the trees (Fig. 2B) showed *Chlorus* related to *Dichromatos* based on characters from the external morphology: pronotum gibbous in lateral view (7 : 1) and frontal costa produced in lateral view (9 : 1), while the remaining trees (Fig. 2A) showed *Chlorus* related to *Eurotettix* based on characters from the male genitalia: distal third portion of aedeagal valves of phallic complex straight (23 : 2) and sheath of aedeagus wide (27 : 2).

The analysis recovered *Chlorus* as a monophyletic taxon (Fig. 1), that collapsed after two additional steps, based on tegmina widely ovate (11 : 2), apex of tegmina straight (12 : 1), tegmina veins strongly impressed (14 : 1), distal half of male cerci lamellate (19 : 1) and male cerci curved inwards mostly in a right angle, apex directed inwards (20 : 2), besides

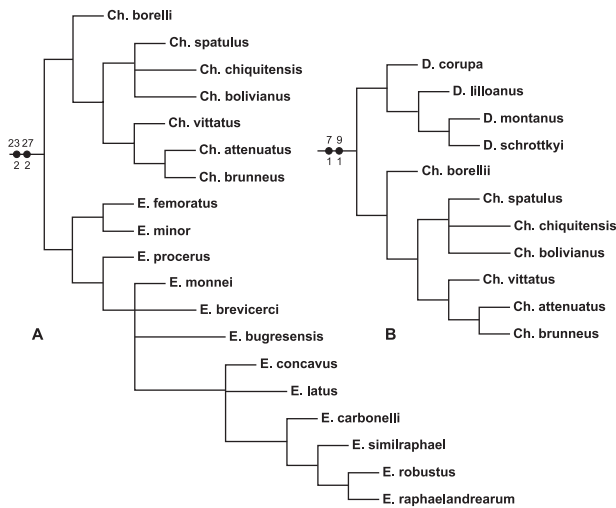


Fig. 2 A, B. Alternative topologies showing sister relationships between *Chlorus* and its closest genera. —A. Topology showing sister relationship between *Chlorus* and *Eurotettix*. —B. Topology showing sister relationship between *Chlorus* and *Dichromatos*.

the homoplasies that share with *Dichromatos* (7 : 1, pronotum gibouse; 9 : 1, frontal costa produced) and those shared with *Eurotettix* (23 : 2, distal portion of aedeagal valves of phallic complex straight; 27 : 2, sheath of aedeagus wide). Within the genus, two clades were depicted, that collapsed after one additional step, one constituted by *Ch. vittatus*, *Ch. attenuatus* and *Ch. brunneus* based on pronotal disk with two light bands on sides (4 : 1) where *Ch. attenuatus* and *Ch. brunneus* showed a sister relationship based on body colour ferrugineous (1 : 3), and the other constituted by *Ch. spatulus*, *Ch. chiquitensis* and *Ch. bolivianus* based on the colour of the lower mid half of pronotal lobes white (5 : 2). The two clades were related by tegmina with dorsal field lighter than lateral field (16 : 1) and middle lobe of sheath of aedeagus highly surpassing lateral lobes (28 : 2), *Ch. borellii* showed to be the ‘basal’ species of the genus.

The monophyly of *Eurotettix* is supported by one synapomorphy (8 : 1, posterior border of pronotum entire) and three homoplasies (11 : 1, tegmina ovate; 14 : 2, tegmina veins intermediately impressed; 23 : 1, distal third portion of aedeagal valves of phallic complex straight) collapsed after one additional step (Fig. 1). The monophyly of *Dichromatos* is supported by seven synapomorphies (1 : 1, body colour olive dark; 2 : 2, outer face of hind femur with a bright shiny area; 10 : 1, hind femur elongate; 17 : 1, sexual dimorphism in body colour present; 19 : 3, distal half of male cerci elbowed shaped; 20 : 3, male cerci curved inwards, apex directed upwards; 21 : 1, male subgenital plate with pointed apex) and eight homoplasies (3 : 0, dark post ocular band absent from pronotal lobes; 7 : 1, pronotum gibouse; 9 : 1, frontal costa produced; 11 : 1, tegmina ovate; 12 : 2, apex of tegmina subangulate; 14 : 2, tegmina veins intermediately impressed;

29 : 1, lophi of epiphallus without conical internal conical protuberance; 30 : 1 ovipositor valves robust and straight) with the highest Bremer value support of the trees (Fig. 1).

Taxonomy

Genus *Chlorus* Giglio-Tos, 1898

Chlorus Giglio-Tos, 1898: 50; Liebermann, 1939: 215, 1968: 28; Ronderos, 1985; Cigliano, 1997[1998]: 8; Cigliano 2007: 176; Eades *et al.*, 2006.

Type species: *Paradichroplus borellii* Giglio-Tos.

Redescription. Brachypterous, small to medium size insects (from about 17 mm in the smallest males of *Ch. borellii* to about 31 mm in the largest females of *Ch. bolivianus*). Body colour brown with dark brown postocular band extending on lateral lobes of pronotum and expanded behind the principal transverse sulcus, pronotal lobes with lower mid half usually dirty white. Epimeron dirty white. Hind femur with the upper half of outer medial area dark brown, lower half of outer medial area dirty white. Head with large prominent eyes; fastigium with margins distinct but low; fastigio-facial angle rounded; frontal costa a little prominent between eyes. Pronotum subcylindrical, with prozona a little higher than metazona in lateral view, with deep transverse sulci; metazona much shorter than prozona; pronotal disk curving roundly into lateral lobes, without lateral carinae; medio-longitudinal carina only faintly indicated on metazona; posterior margin of pronotal disk rounded. Tegmina broadly ovate, short, barely reaching the second abdominal tergite; broad at the base and with straight distal margin. Veins of tegmina strongly impressed. Hind femora robust. Ovipositor valves short, dorsal valves upcurved. Male subgenital plate with rounded apex. Male cerci curved inwards in acute angle, distal half lamelliform. Male internal genitalia: ectophallus with cingulum with wide rami and in some species with prominent lateral expansions. Sheath of aedeagus wide, with a pair of lateral lobes shorter than middle lobe; middle lobe with mid-longitudinal indentation. Valves of aedeagus stout, with sclerotisation reduced towards tips, arch of dorsal valves largely developed. Lophi of epiphallus with internal conical protuberance.

Relationships. Similar to *Eurotettix* and *Dichromatos*. *Chlorus* shares with *Eurotettix* characters from the male genitalia, but differs from it in the gibouse pronotum; tegmina broadly ovate with straight distal margin; male cerci curved inwards in acute angle with distal half lamelliform. *Chlorus* shares with *Dichromatos* characters from the external morphology (the shape of the head with frontal costa prominent, pronotum gibouse), but differs from it mainly in characters from the male genitalia (male cerci with distal half lamellate, aedeagal valves straight, sheath of aedeagus wide, epiphallus with lophi with internal conical protuberance).

Key to species of *Chlorus*

- 1 Body colour with two longitudinal dorsal light bands running from the back of eyes along the pronotal disk (Fig. 4I,K) ... 2
 1' Body colour dorsally homogeneous brown, without longitudinal light bands (Fig. 4H) 4
 2 First and second pair of legs green; hind femur with outer area homogeneously green (Fig. 3B); male cerci with distal half a little expanded, half moon shaped, apex acute (Fig. 4P,W); aedeagal valves slender, homogeneously sclerotised, with apices directed outwards (Fig. 5G,H)..... *Ch. vittatus*
 2' First and second pair of legs brown; hind femur with the upper outer medial area dark brown, and lower outer medial area cream (Fig. 3C–F); aedeagal valves very robust, highly sclerotised proximally and reducing the sclerotisation to the apices, with apices straight (Fig. 5L,M,Q,R) 3
 3 Hind femur with ventral and inner area bright red; hind tibiae yellow; male cerci with distal half broadly expanded lamelliform (Fig. 4Q,X); sheath of aedeagus wide with highly prominent lobes (Fig. 5L); aedeagal valves stout with blunt wide apices (Fig. 5L,M).....*Ch. brunneus*
 3' Hind femur with outer ventral area dark brown and inner ventral area bright red, inner medial area black; hind tibiae green bluish; male cerci slender (Fig. 4R,Y); sheath of aedeagus narrower, with lobes less prominent (Fig. 5Q); aedeagal valves concave in lateral view, with acute apices (Fig. 5P,Q).....*Ch. attenuatus*
 4 Pronotal lobes with lower mid half dirty white moulted with dark brown (Fig. 3A); face dark brown; male cerci slender, with distal half portion not expanded and truncate rounded apex (Fig. 4O,V); phallic complex with stout, short aedeagal valves (Fig. 5A,C); epiphallus with lophi and lateral plates largely developed (Fig. 5D,E)*Ch. borellii*
 4' Pronotal lobes with lower mid half homogeneously dirty white (Fig. 3E–G; face dirty white; male cerci broader with distal half portion expanded and pointed apex (Fig. 4Z,AA,AB) 5
 5 Male cerci with distal half portion highly expanded, subrectangular (Fig. 4T); hind femur with proximal area of inner face and ventral area bright red; hind tibiae red with tinges of green proximally; aedeagal valves stout with apices diverging caudally, ventrally concave at the apices (Fig. 5AB)*Ch. spatulus*
 5' Male cerci with distal half portion less expanded, subtriangular or sigmoid shape (Fig. 4Z,AB); hind femur and tibiae with other combination of colours; aedeagal valves straight and slender (Fig. 5W,AG)..... 6
 6 Male cerci with distal half portion sigmoid (Fig. 4AB); hind femur with the ventral area dark bluish-green and inner face dark bluish-green and yellow proximally; hind tibiae dark bluish-green; phallic complex as in Fig. 4AE–AI*Ch. chiquitensis*
 6' Male cerci with distal half portion subtriangular (Fig. 4Z); hind femur with the lower marginal area yellow, inner medial area black except proximal area yellow; hind tibiae yellow; phallic complex as in Fig. 5U–Y*Ch. bolivianus*

Chlorus borellii (Giglio-Tos) (Figs 3A, 4A,H,O,V and 5A–E)

Paradichroplus borellii Giglio-Tos, 1894: 27.

Chlorus borellii Bruner, 1913: 498; Liebermann, 1939: 215, 1968: 28; Eades *et al.*, 2006; Cigliano 2007: 195.

Diagnosis. It is the most different species of the genus, without any certain sister species relationships. It can be easily distinguished from the remaining species of *Chlorus* by the pronotal lobes with mid lower half dirty white moulted with dark brown, eyes prominent and rounded, pronotum with distal margin of metazona extending caudally, male cerci with truncate rounded apex, and epiphallus with lophi and lateral plates largely developed.

Redescription. Body colour brown with dark brown post-ocular band extending onto lateral lobes of pronotum; pronotal lobes with lower mid half dirty white moulted with dark brown (Fig. 3A). First and second pair of legs ventrally green; hind femur with inner face black, except proximal area red, outer lower marginal area green, inner lower marginal area yellow; hind tibiae green. Tegmina homogeneously brown,

with the distal margin straight, most so in females. Eyes prominent and rounded on dorsal view (Figs 4H and 5G). Pronotum expanded on metazona, with the distal margin extending caudally, metazoan almost as long as prozona (Figs 4H and 5G). Male cerci slender sharply curved inwards, with distal half portion not expanded and truncate rounded apex (Fig. 4O,V). Phallic complex (Fig. 5A–E) with stout, short aedeagal valves; epiphallus with lophi and lateral plates largely developed.

Measurements. Body length 18.3 mm (17–20) males, 22.1 mm (21–22) females; femur III length 10.5 mm (10–11) males, 13.5 mm (13–14) females.

Material examined. BOLIVIA: 1 male, Villa Montes, Bol., Lind., D. Chaco Exped. (ANSP); PARAGUAY: 1 female, Horqueta, 45 km E Rio Paraguay, 23°N/57°W, IV-1934 (Schulze) (ANSP); 3 females, 1 male, Boqueron, 19 km N Tte. Montania to Tte. Martinez, S21°49'/W59°55', IV-2003 (Cigliano, de Wysiecki & Lhano) (MLP); 4 males, 6 females, Boqueron, Ruta Transchaco #9, 25 km W Filadelfia, Colonias

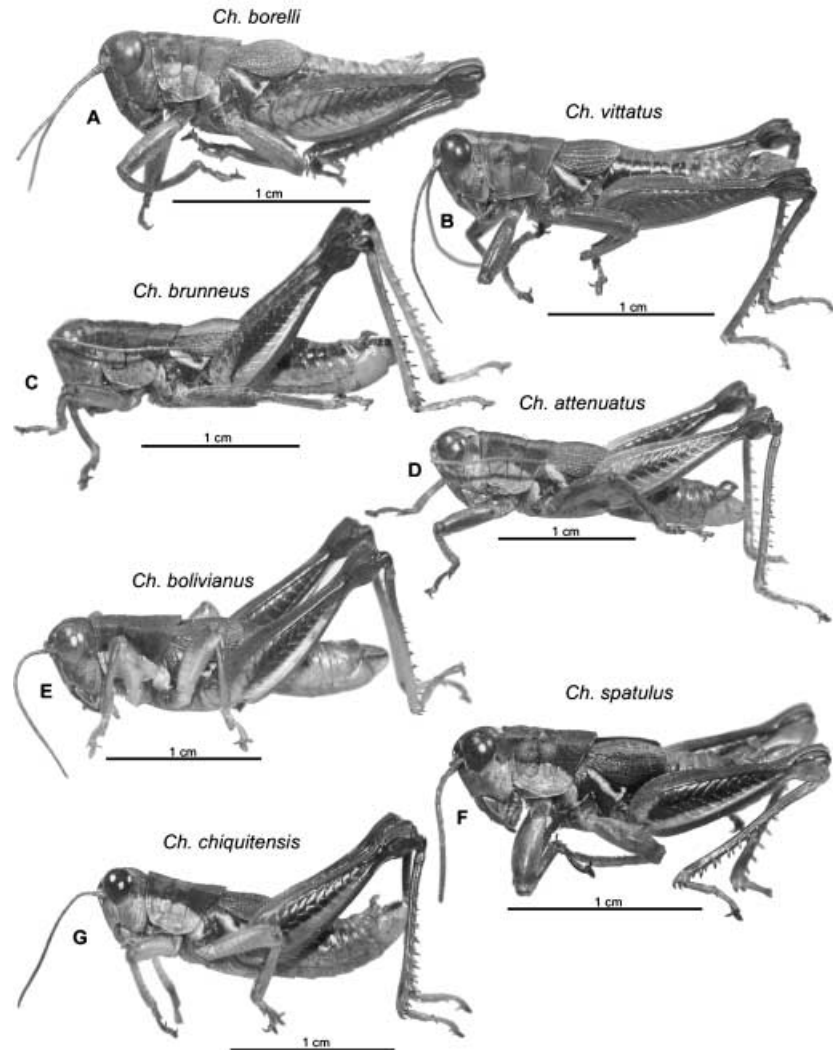


Fig. 3 A–G. *Chlorus* males, species as indicated. Habitus. Scale bar = 1 cm.

Menonitas, V-2002 (Cigliano & Lange) (MLP); 2 males, Parque Nacional Ybicuy, 328 m, S26°03'/W56°52', IV-2003 (Cigliano, de Wysiecki & Lhano) (MLP); 2 males, 1 female, 30 km N Filadelfia to Tte. Montania, S22°07'40'/W60°01'57' (Cigliano, de Wysiecki & Lhano) (MLP); 2 males, 2 females, 111 km N Filadelfia, S21°54'15'/W60°45'34' (Cigliano, de Wysiecki & Lhano) (MLP).

Distribution. Dry open forest in the Chaco biogeographical province (following the geographical scheme of Cabrera & Willink 1973) in eastern Bolivia and western Paraguay (Fig. 7).

***Chlorus vittatus* Bruner** (Figs 3B, 4B,I,P,W, 5F–J and 6B,H)
Chlorus vittatus Bruner, 1906: 690; Liebermann, 1939: 215, 1947: 391, 1968: 28; Eades *et al.*, 2006; Cigliano 2007: 195.

Diagnosis. Similar to *Ch. brunneus* and *Ch. attenuatus* from which it differs mainly in the colour of the legs wholly green, the sheath of aedeagus narrow with short lobes and valves of aedeagus slender.

Redescription. Body colour dark brownish green with two longitudinal light brown bands running from the back of eyes along the pronotal disk; postocular dark band extending on lateral lobes of pronotum (Fig. 3B). Body ventral yellow with tinges of green, sides of abdomen black. Tegmina with dorsal field lighter than lateral field. First and second pair of legs green, hind femur with upper marginal area brown, outer and inner area green, inner lower marginal area yellow; hind tibiae green. Eyes sub oval in dorsal view (Figs 4I and 6H). Frontal costa a little prominent between eyes (Figs 4B and 6B). Pronotum with prozona twice the length of metazona. Male cerci

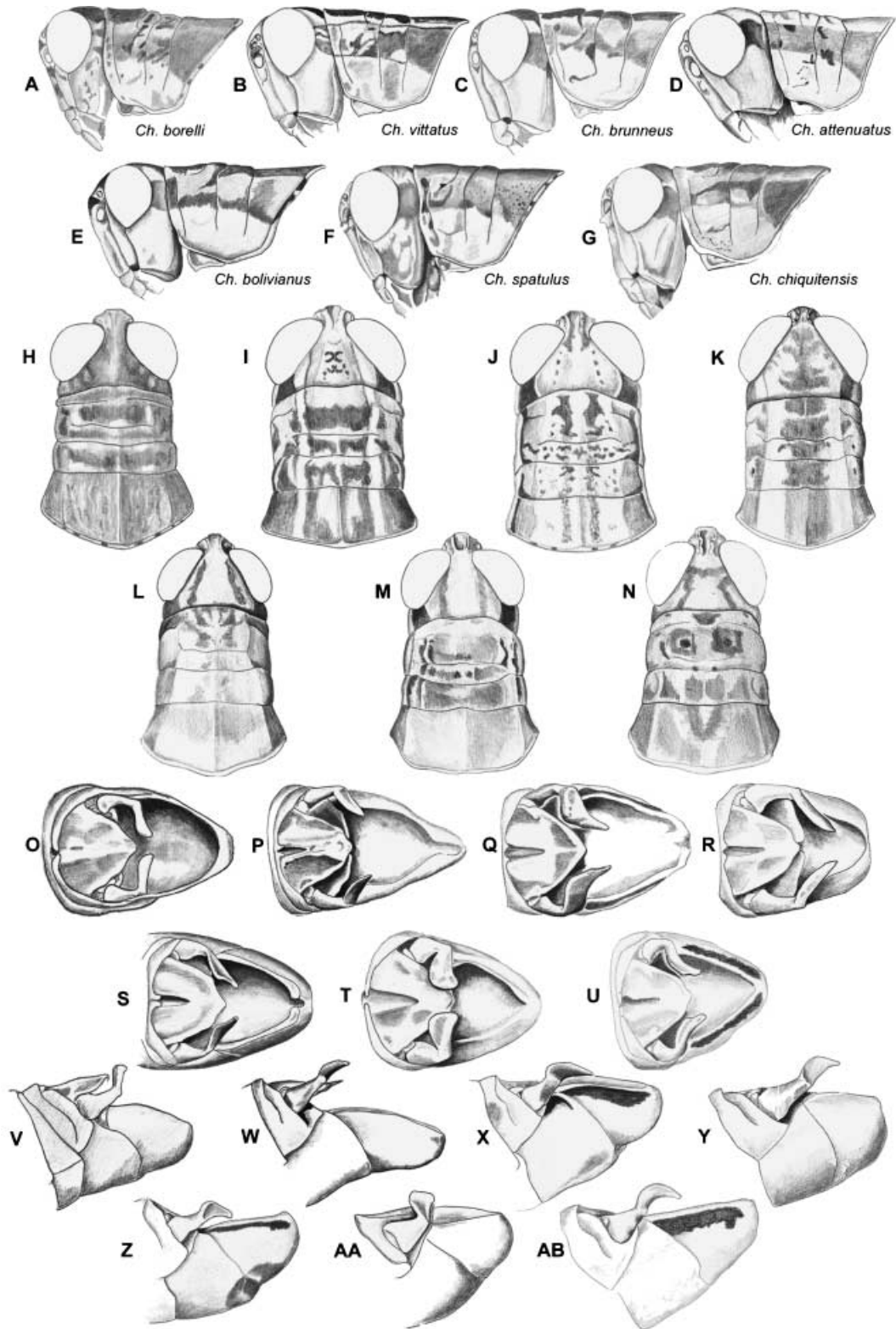


Fig. 4 A–AB. *Chlorus* males, species as indicated. —A–N. Head and pronotum lateral and dorsal view. —O–AB. Distal abdominal segments, dorsal and lateral view.

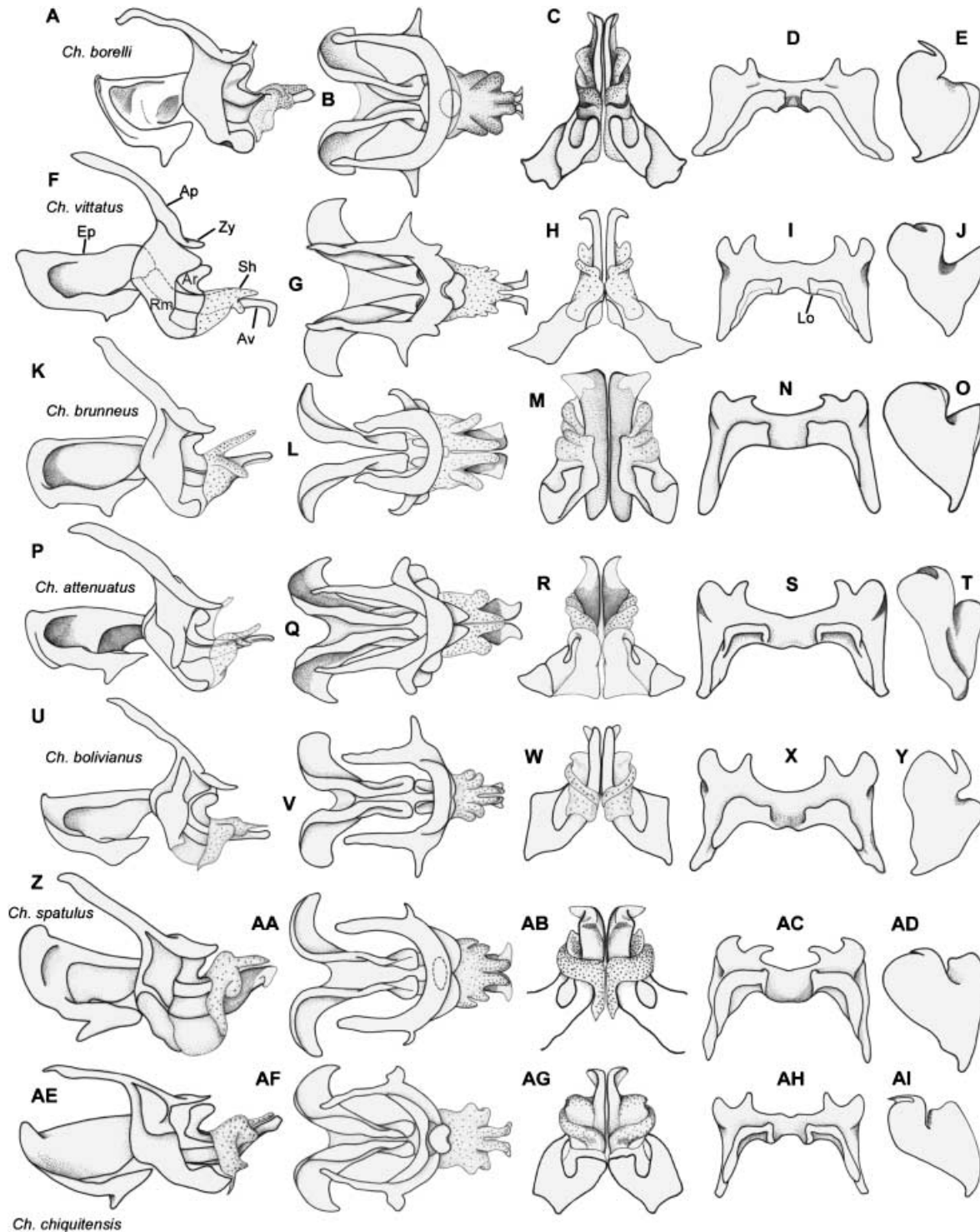


Fig. 5 A–AI. *Chlorus*, species as indicated. Phallic complex. —A, F, K, P, U, Z, AE. Endophallic plates, cingulum and aedeagal valves with sheath, lateral view; —B, G, L, Q, V, AA, AF. Endophallic plates, cingulum and aedeagal valves with sheath, dorsal view. —C, H, M, R, W, AB, AG. Distal portion of aedeagus, ventral view; —D, I, N, S, X, AC, AH. Epiphallus dorsal view; —E, J, O, T, Y, AD, AI. Epiphallus lateral view. Key to abbreviations: Ap, apodemes of cingulum; Ar, arch of dorsal valves; Av, aedeagal valves; Cg, cingulum; Ep, endophallic plates; Lo, lophi of epiphallus; Sh, sheath of aedeagal valves; Zy, zygoma.

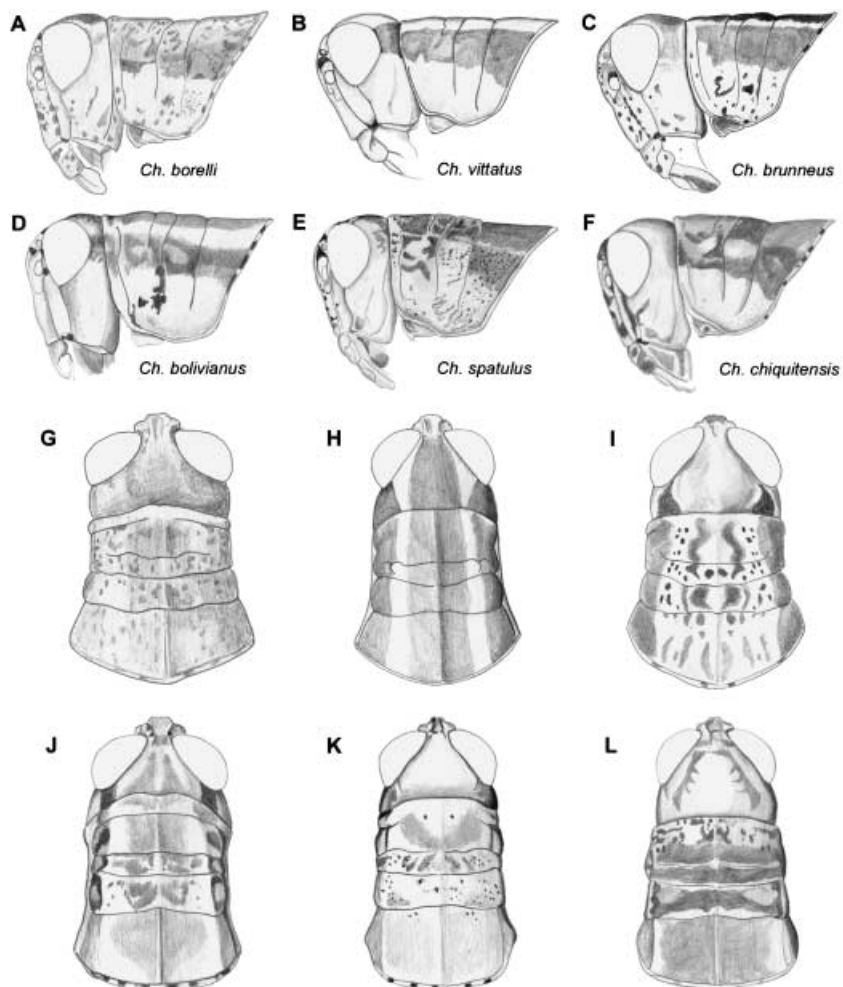


Fig. 6 A–L. *Chlorus* females, species as indicated. —A–F. Head and pronotum, lateral view. —G–L. Head and pronotum, dorsal view.

with distal half a little expanded half moon shaped, apex acute (Fig. 4P,W). Phallic complex (Fig. 5F–J) with slender aedeagal valves with apices diverging caudally, sheath of aedeagus narrow with short lobes; cingulum with highly developed arch.

Measurements. Body length 24 mm (23.5–24.5) males, 29.3 mm (29–31) females; femur III length 13 mm male, 15.7 mm (15.5–16) females.

Observations. The species shows intraspecific variation in the width of male cerci.

Material examined. One syntype male, PARAGUAY, Sapucay (USNM). PARAGUAY: 7 males, 6 females, Paraguari, Sapucay, III-1965 (Carbonell, Mesa & Monne) FCMON; 2 males, 8 females, Paraguari, Paraguari, III-1965 (Carbonell, Mesa & Monne) FCMON; 1 female, Sapucay, II-1905 (Foster) (ANSP); 1 male, Pque. Nac. Ybicuy, 328 m, S

26°03′/W56°52′, IV-2003 (Cigliano, de Wysiecki & Lhano) (MLP).

Distribution. Thick bush areas with weeds and scattered low trees, sometimes palm trees in the Paranaense biogeographical province (Cabrera & Willink 1973) in eastern Paraguay (Fig. 7).

***Chlorus brunneus* Bruner** (Figs 3C, 4C, J, Q, X, 5K–O and 6C–I)

Chlorus brunneus Bruner, 1911: 137; Liebermann, 1939: 215, 1965: 215, 1968: 28; Eades *et al.*, 2006; Cigliano 2007: 195.

Diagnosis. Similar to *Ch. attenuatus* from which it differs in the red colour of the inner area of hind femur, hind tibiae yellow, male cerci robust, the sheath of aedeagus wider with longer lobes, stout aedeagal valves with blunt apices.

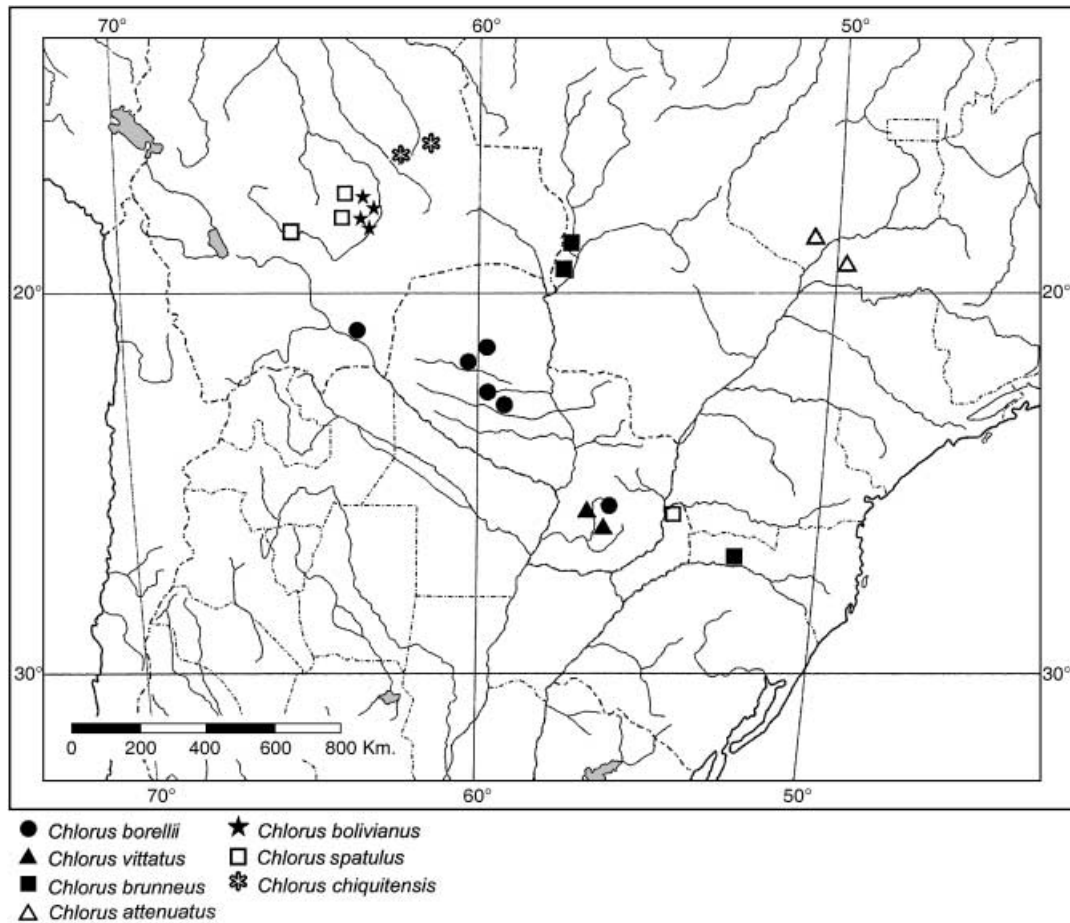


Fig. 7 Geographic distribution of the species of *Chlorus*. Symbols indicate localities of collection of specimens examined.

Redescription. Body colour brown with two longitudinal light brown bands running from the back of eyes along the pronotal disk (Fig. 4C); postocular dark band extending on lateral lobes of pronotum (Fig. 3C). Body ventrally yellow. Tegmina dorsally light brown, laterally dark brown. Hind femur with the upper outer medial area dark brown, and lower outer medial area cream, ventral and inner area bright red. Hind tibiae yellow. Sides of abdomen black. Male subgenital plate with dark brown band on upper edge (Fig. 4Q,X). Male cerci with distal half curved inwards broadly expanded lamelliform with acute apices (Fig. 4Q,X). Phallic complex with cingulum with prominent lateral expansions, sheath of aedeagus wide, aedeagal valves short and very robust highly sclerotised proximally and reducing the sclerotisation to the wide blunt apices (Fig. 5L–M).

Measurements. Body length 23.5 mm (23–24) males, 30 mm (29–31) females; femur III length 13.3 mm (13–14) males, 16 mm (14–16) females.

Material examined. BRAZIL: holotype female, Corumba (ANSP); 3 females, 2 male, Mato Grosso, Urucum, Corumba, 23–29-XII-1919, Cornell University Expedition (ANSP) (MLP); 2 females, Santa Catarina, Nova Teutonia, S27°-11'/W52°-23', 300–500 m, II-1963 (Plaumann) (ANSP); 3 males, 1 female, Mato Grosso, Corumba, VII-1979, Silva (MR).

Distribution. Mato Grosso and Santa Catarina, Brazil, in the biogeographical provinces of Cerrado and Paranense (Cabrera & Willink 1973), respectively (Fig. 7).

***Chlorus attenuatus* sp.n.** (Figs 3D, 4D,K,R,Y and 5P–T)

Holotype. Male, BRAZIL, Goiás, Rio Verde, II-1979 (Roppa & Silva) (MR).

Paratypes. 1 male, same data as holotype; 2 male paratypes, BRAZIL, Minas Gerais, 30 km W Ituiutaba, 4-III-1980 (Roppa, Carbonell & Roberts) (MR).

Etymology. *Attenuatus* (L.) means thin, slender, referring to the shape of the male cerci.

Diagnosis. Similar to *Ch. brunneus* but differing in the colour of the inner area of hind femur black, hind tibiae green bluish, male cerci slender, and sheath of aedeagus narrower with shorter lobes and valves of aedeagus concave in lateral view and with acute apices.

Description. Body colour brown with two longitudinal light brown bands running from the back of eyes along the pronotal disk (Fig. 4K); postocular dark band extending on lateral lobes of pronotum (Figs 3D and 4D). Body ventrally yellow. Tegmina dorsally light brown, laterally dark brown. Hind femur with the upper outer medial area dark brown, and lower outer medial area cream, outer ventral area dark brown and inner ventral area bright red, inner medial area black. Hind tibiae green bluish. Sides of abdomen black. Male subgenital plate without dark brown band on upper edge (Fig. 4Y). Male cerci as in *Ch. brunneus* but with distal half slender (Fig. 4R,Y). Phallic complex with cingulum with lateral expansions, aedeagal valves largely developed, with sclerotisation reduced to the apices, with distal portion concave in lateral view and acute apices. Female, unknown.

Measurements. Body length 22.5 mm (19–24), femur III length 12 mm.

Observations. The species shows intraspecific variation in body size (the specimens from Ituiutaba is comparatively smaller, body length 19 mm), male cerci are more slender and longer, and aedeagal valves of phallic complex less sclerotised.

Distribution. Minas Gerais and Goias, Brazil (Fig. 7), in the Cerrado biogeographical province (Cabrera & Willink 1973).

***Chlorus bolivianus* Bruner** (Figs 3E, 4E,S,Z, 5U–Y and 6D,J)
Chlorus bolivianus Bruner, 1913: 498; Liebermann, 1950: 136, 1965: 215; Cigliano, 2007: 195; Eades *et al.*, 2006.

Diagnosis. Similar to *Ch. spatulus* differing in the colour of the internal page of the hind femur with inner lower marginal area yellow, inner medial area black except proximal area yellow; hind tibiae yellow; male cerci with distal half portion subtriangular and narrower sheath and valves of aedeagus.

Redescription. Body colour brown with dark brown postocular band extending onto lateral lobes of pronotum; pronotal lobes with lower mid half dirty white, extending onto episternum (Fig. 3E). Epimeron dirty white. Tegmina with lateral field dark brown almost black, dorsal field light brown. Hind

femur with the upper half of outer medial area dark brown, lower half of outer medial area dirty white, external lower marginal area olive green, inner lower marginal area yellow, inner medial area black except proximal area yellow. Hind tibiae yellow. Body yellow ventrally. Male cerci with distal half portion subtriangular (Fig. 4S,Z). Phallic complex with aedeagal valves straight and slender (Fig. 5V,W) with sheath of aedeagus comparatively narrow (Fig. 5V).

Measurements. Body length 22.07 mm (19–25) males, 27 mm (19–31) females; femur III length 12.5 mm (11–13) males, 15.6 mm (15–17) females.

Material studied. Holotype male, BOLIVIA, Santa Cruz de la Sierra (ANSP). BOLIVIA 2 males, 1 female, Santa Cruz, Naranjales, IV-1962 (Mesa), FCMON; 2 females paratypes, Santa Cruz de la Sierra, 450 m (Steinbach) (ANSP); 7 males, 4 females, Santa Cruz, 18 km SW Santa Cruz, 400 m, Social Club, 16-II-1976 (Ronderos, R.B., E.H., H.R. Roberts) (ANSP); 9 males, 7 females, Santa Cruz, 8–10 km SE Santa Cruz, 400 m, 8–9-III-1976 (Ronderos, R.B., E.H., H.R. Roberts) (ANSP); 2 males, topotypes, Santa Cruz de la Sierra, 10–20-I-1922, Steinbach (ANSP); 1 male, 1 female, Santa Cruz, Santa Cruz, Rio Piray, Botanical Garden, 400 m, 17-II-1976 (Ronderos, R.A., E.H., H.R. Roberts) (ANSP); 3 males, 3 females, Santa Cruz, 57–77 km W Santa Cruz to Cochabamba, 6–800 m, 22-II-1976 (Ronderos, R.A., E.H., H.R. Roberts) (ANSP); 1 male, 1 female, Santa Cruz de la Sierra, II-1922, Steinbach (ANSP); 1 male, Santa Cruz btw Buena Vista and San Carlos, Cacao forest, 350 m, 21-II-1976 (Ronderos, R.A., E.H., H.R. Roberts) (ANSP); 3 females, Santa Cruz, 20–34 km S Santa Cruz rd to Yacuiba, 500 m, 24-II-1976 (Ronderos, R.B., E.H., H.R. Roberts) (ANSP); 2 females, Santa Cruz, 82 km S Santa Cruz rd to Yacuiba, 500 m, 24-1976 (Ronderos, R.A., E.H., H.R. Roberts) (ANSP); 4 males, 2 females, Prov. Sara, 400 m, Steinbach (ANSP); 3 males, 4 females topotype, Provincia de Sara, II-1922 (Steinbach) (ANSP); 2 males, 1 female, Prov. Sara, Depto Santa Cruz, 500 m, II-1922 (Steinbach) (ANSP); 2 males, Santa Cruz de la Sierra, II-1922 (Steinbach) (ANSP); 1 male, Provincia de Sara, II-1922 (Steinbach) (ANSP); 1 male, 1 female, Santa Cruz, Rio Seco, II-1962 (ANSP); 14 females, 14 males, Santa Cruz e/Sta. Cruz de la Sierra-Samaipata, Angostura, II-2003 (Cigliano & Lange) (MLP); 6 females, 6 males, Santa Cruz Samaipata, II-2003 (Cigliano & Lange) (MLP); 7 females, 4 males, Santa Cruz e/Sta. Cruz de la Sierra y Samaipata, Achiras, II-2003 (Cigliano & Lange) (MLP); 3 females, 3 males, Santa Cruz, Samaipata, Achiras, II-2003 (Cigliano & Lange) (MLP).

Distribution. Forest openings in the Yungas biogeographical province (Cabrera & Willink 1973) of Bolivia (Fig. 7).

***Chlorus spatulus* sp. n.** (Figs 3F, 4G, MT, AA, 5Z–AD and 6E,K)

Holotype. Male, BOLIVIA, Santa Cruz, Samaipata, Pque. Nac. Amboro, 1714 m, 18°07'46.0"/63–48'27.9', IV-2004 (Cigliano & Lange) (MLP).

Paratypes. BOLIVIA: 1 female, 2 males, Santa Cruz, 57–77 km W Santa Cruz to Cochabamba, 6–800 m, II-1976 (Ronderos, R.B., E.H., H.R. Roberts) (ANSP); 2 males, 3 females, Santa Cruz, Samaipata, Pque. Nac. Amboro, 1714 m, 18°07'46.0"/63–48'27.9', IV-2004 (Cigliano & Lange) (MLP); 3 males, 2 females, Santa Cruz, Samaipata, 5 km from Achiras to Pque. Nac. Amboro: Los Paredones, II-2003 (Cigliano & Lange) (MLP); 1 male, Santa Cruz, Samaipata, Achiras, II-2003 (Cigliano & Lange). ARGENTINA: 1 male, 2 females, Misiones, Posadas, V-1971 (Contreras).

Etymology. Spatula (L) means a broad flat tool for stirring, referring to the shape of the male cerci.

Diagnosis. Similar to *Ch. bolivianus* differing in the colour of the hind femur with ventral and proximal area of inner face bright red, hind tibiae red with tinges of green proximally, the male cerci with distal half expanded, subrectangular, and aedeagal valves larger, ventrally concave at the diverging apices.

Description. Body colour as in *Ch. bolivianus* except for the colour of the hind femur with ventral and proximal area of inner face bright red; hind tibiae red with tinges of green proximally. Male cerci with distal half highly expanded, subrectangular (Fig. 4T,AA). Phallic complex rami of cingulum with lateral globose expansions (Fig. 5Z), and dorsal cuplike expansions (Fig. 5AA), sheath of aedeagus broadly developed (Fig. 5AA); aedeagal valves stout with apices diverging caudally, ventrally concave at the apices (Fig. 5AA,AB); epiphallus with largely developed lophi (Fig. 5AC,AD).

Measurements. Body length 19.25 mm (18–19) males, 27.30 mm (27–28) females.

Distribution. Most of the examined material was collected in forest openings in the Yungas biogeographical province (Cabrera & Willink 1973) at higher elevations than *Ch. bolivianus* in Bolivia (Fig. 7). Three specimens examined are from Argentina, Misiones, deposited at the MLP. However, the authors have done several trips to Misiones and the species was never collected there. If the locality label is correct, then *Ch. spatulus* shows an interesting vicariant distribution also present in the Paranense biogeographical province of Argentina.

***Chlorus chiquitensis* sp. n.** (Figs 3G, 4G,K,U, AB, 5AE–AI and 6E,L)

Holotype. Male, BOLIVIA, Santa Cruz, Mnes. Jesuíticas, 40 km S. d San Javier 263 m, 16°34'22.8"/62°29'32.6', IV-2004 (Cigliano & Lange) (MLP)

Paratypes. BOLIVIA, 4 males, 4 females, Santa Cruz, San Javier, 16°20'S/62°40'W, 535 m, III-1976 (Ronderos, R.A., E.H., H.R. Roberts) (ANSP); 4 males, 3 females, Santa Cruz, Mnes. Jesuíticas, 40 km S. d San Javier 263 m, 16°34'22.8"/62°29'32.6', IV-2004 (Cigliano & Lange) (MLP); 11 males, 3 females, Santa Cruz, 4 km N. de San Javier a Concepción, 576 m 16°21'07.5"/62°09'28.2", IV-2004 (Cigliano & Lange) (MLP); 3 females, Santa Cruz, 25 km O. Concepción, Las Piedras, 579 m, 16°12'29.7"/62°13'30.4", IV-2004 (Cigliano & Lange) (MLP).

Etymology. Referring to its geographical distribution in the Chiquitano forest from Bolivia.

Diagnosis. Similar to *Ch. bolivianus* but differing mainly in the colour of the femur and tibiae of the third pair of legs and in the shape of male cerci with distal portion sigmoid shape.

Description. Body colour as in *Ch. bolivianus* but differing in the colour of hind femur with the ventral area dark bluish-green and inner face dark bluish-green and yellow proximally; hind tibiae dark bluish-green. Male cerci with distal half portion sigmoid. Aedeagal valves straight (Fig. 5AF–AG), a little diverging distally (Fig. 5AG); sheath of aedeagus wide (Fig. 5AF).

Measurements. Body length 22.12 mm (20–24) males, 27 mm (25–29) females.

Distribution. In openings of dry forest with palm trees in the dry 'Chiquitano' forest (Navarro & Maldonado 2002) in the transition between the 'Chaqueño' and Amazonian biogeographical provinces (Cabrera & Willink 1973) in Bolivia (Fig. 7).

Discussion

The phylogenetic analysis conducted in this study showed that *Chlorus* is a monophyletic genus.

The inclusion in the analysis of species that represent the generic group where *Chlorus* is classified helped to define the monophyletic status of the genus. Within the genus, two clades were depicted based on characters from the external morphology. *Chlorus borellii* showed to be the 'basal' and most divergent species of the genus. Differences among the species of each group are mostly based on the colour of hind legs and the shape of male cerci and male genitalia. The analysis also showed that the relationships of *Chlorus* to its closest genus were not solved. If characters from the external morphology are considered, *Chlorus* is more related to *Dichromatos*. On the

other hand, if characters from the male genitalia are considered, *Chlorus* is related to *Eurotettix*. Because morphological characters showed not to be enough to resolve general relationships, molecular data, of a completely independent marker, not associated with morphological changes (e.g., mtDNA) should be used to discriminate between the two hypotheses.

Within the South American Melanoplinae, the tribe Dichroplini is the most diversified group (23 genera and 132 species). The taxonomic diversity within the tribe Dichroplini is accompanied by great morphological uniformity, except in the divergent male genitalia. Genitalia are not universally highly divergent in grasshoppers. In many large groups they are rather uniform and not useful for distinguishing species. Their divergence in the Melanoplinae appears to be associated with the mode of courtship — or rather the almost complete lack of precontact courtship — females are unaware of males until they have been jumped on (Otte 1976). At this point tactile stimuli appear to assume great importance (Otte 1976). Historically, diversification of mating structures has been attributed to selection for prezygotic isolation mechanisms that prevent hybridisation. The reproductive isolation hypothesis has two main predictions. First, if the diversification of mating structures results from selection for reproductive isolation, there should be species-specific fits of male and female mating structures. Second, there should be more diversification of mating structures in sympatry than in allopatry. A few systems are consistent with these predictions (Eberhard 1985). However, there are many systems for which there is no evident species-specific fit between male and female mating structures; in these species, female structures do not prevent intromission by males of other species (Eberhard 1985). Such seems to be the case in *Chlorus* species, where there is an apparent absence of corresponding female genitalic specificity; certainly they appear to be much more similar to one another than males.

Eberhard (1996) also argued that genitalic differences evolve outside the context of reproductive isolation and that diversity of male genitalia is shaped by cryptic female choice. If *Chlorus* females can judge male performance by postcopulatory courtship, Eberhard's argument holds consistent.

Taxonomists and ecologists (Lockwood 1989, 1996; Cohn 1994) have debated the value of genitalic differences in insect systematics using this same complex of grasshoppers (Melanoplinae) to make their points. Lockwood (1989, 1996) considered that genitalia may have low utility, while Cohn (1994) defended the position that without them grasshopper taxonomy can go nowhere. Whether the diversification of mating structures observed in *Chlorus* results from selection from reproductive isolation or is a result of sexual selection is out of the scope of this study. However, the differences found in the characteristics of the male genitalia among the new species of *Chlorus* are equivalent to those found in most of the

species of Dichroplini and we believe they justify the description of these new taxa.

Chlorus belongs together with *Eurotettix*, *Dichromatos*, *Atrachelacris*, *Scotussa*, *Leiotettix* and *Ronderosia* to the group of genera referred to as 'Paranense-Pampeano' (Ronderos & Cigliano 1990). Following Cabrera & Willink (1973) biogeographical scheme the group is distributed in the following provinces of the Neotropical Region: Pampas, Chaqueño (Chacoan province of Morrone 2006), Cerrado, Yungas, Paranense (Cerrado, Parana Forest, Yungas, and *Araucaria angustifolia* Forest of Morrone 2006). *Chlorus* shows some biogeographical overlap with its closest genera, *Eurotettix* and *Dichromatos*, but has a wider distribution being present also in the Yungas and Chaqueño provinces. The greatest diversity of *Eurotettix* is recorded from the Cerrado and Paranense biogeographical provinces in southcentral Brazil and southcentral Paraguay, while *Dichromatos* is mostly represented in the Paranense biogeographical province in south-eastern Brazil, eastern Paraguay and north-eastern Argentina. The Cerrado formation is characterised by low open forests with thick understory of bushes and thick gramineous strata with tall weeds. While the vegetation of the Paranense province is characterised by tropical forest, some tall grass savannas and some scattered *Araucaria* forests found on the Brazilian planalto and north-eastern Argentina corresponding to the biogeographical province of *A. angustifolia* forest (following Morrone 2006's biogeographical scheme) that occur at an altitude between 600 and 1800 m. The greatest diversity of *Chlorus* is western to the distribution of the other two genera, reaching the Yungas province of Bolivia. Within the genus the most basal species, *Ch. borellii* is distributed in the Chaqueño and Paranense biogeographic provinces. One of the clades depicted within the genus (*Ch. vittatus*, *Ch. attenuatus*, *Ch. brunneus*) is distributed in the Paranense and Cerrado provinces of Paraguay and Brazil, and the other one (*Ch. spatulus*, *Ch. chiquitensis*, *Ch. bolivianus*) is present in the Yungas and the Chaqueño provinces (mostly in the 'Chiquitano' arid forest of Navarro & Maldonado 2002). The Yungas is characterised by a cloudy forest that can reach altitudes between 1700 and 2500 m in the Andes. The Chaqueño (= Chacoan of Morrone 2006) subregion is closely related to the Amazonian and Parana subregions. The development of the Chacoan subregion during the Tertiary split the former continuous Amazonian–Parana forest, representing an example of dynamic vicariance (Morrone 2006). Certain insect taxa reflect the Amazonian–Paranense disjunction while others, which probably evolved later, are found in both the Chacoan and Paranense subregions (Morrone 2006), such would be the example of the basal species of *Chlorus* (*Ch. borellii*). A phylogeographical analysis of small mammal species showed that central Brazil gallery and dry forests play an important role as present and past habitats for forest species from the

Amazonian and Parana subregions. Population of Chaqueño mammals have their closest relatives in the Amazonian subregion, in the Parana subregion, or are basal to both regions (Morrone 2006).

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Appendix 1.

List of characters

Head and thorax

- 1** Body colour: brownish (0); olive dark (1); green (2); ferrugineous (3)
2 Colour of outer face of hind femur: homogeneously coloured (0) (Fig. 3B); with a white band in the lower half of medial outer area (1) (Fig. 3F); with a bright shiny area (2); brightly coloured (3)
3 Dark brown post ocular band on pronotal lobes: absent (0); present, not expanding distally (1); present, expanding distally (2) (Fig. 3G)
4 Colour of pronotal disk: homogeneous (0) (Fig. 6G); with two light bands on sides (1) (Fig. 6H)
5 Lower mid half of pronotal lobes: homogeneous (0); yellowish white (1) (Fig. 3C); white (2) (Fig. 3G)
6 Colour of epimeron: same as body (0); whitish (1) (Fig. 3F)
7 Pronotum, lateral view: flat (0); gibouse (1) (Fig. 4D)
8 Posterior border of pronotum: crenulate (0); entire (1)
9 Shape of frontal costa: not produced in lateral view (0); produced in lateral view (1) (Fig. 4A)
10 Hind femora: robust (0); elongate (1)
11 Tegmina shape: elongate (0); ovate (1); widely ovate (2) (Fig. 3A); elongately ovate (3)
12 Apex of tegmina: rounded (0); straight (1) (Fig. 3B); subangulate (2)
13 Tegmina dorsally: touching each other or slightly separated (0); widely separated (1)
14 Tegmina basal width: normal (0); wide (1) (Fig. 3A); narrow (2)
15 Tegmina length: macropterous (0); brachypterous (1)
16 Tegmina, colour: homogeneous (0); with dorsal field lighter than lateral field (1) (Fig. 3C); with dorsal field brightly coloured (2)
17 Sexual dimorphism in body colour: absent (0); present (1)
18 Abdomen with a series of black dots on sides of mid-longitudinal carina: absent (0); present (1)

Male genitalia

- 19** Male cerci, shape of distal half: little compressed (0); lamellate (1) (Fig. 4T); tapering towards the apex (2); cylindrical with acute apex (3); globed shaped (4)
20 Male cerci: bent inwards (0); curved inwards gradually, apex directed inwards (1); curved inwards mostly in a right angle, apex directed inwards (2) (Fig. 4Q); curved inwards, apex directed upwards (3)
21 Male subgenital plate, apex: rounded (0) (Fig. 4X); pointed (1)
22 Aedeagal valves of phallic complex, length of distal two thirds: long (0) (Fig. 5F); intermediate (1); very short (2)

23 Distal third portion of aedeagal valves of phallic complex: gradually diverging outwards (0) (Fig. 5G); diverging in a right angle (1); straight (2) (Fig. 5W)

24 Apex of aedeagal valves in ventral view: not elbowed shaped (0); elbowed shaped (1)

25 Section of aedeagal valves: entire (0); with internal furrow (1)

26 Proximal hump of sheath of aedagus: absent (0); present (1)

27 Sheath of aedeagus: intermediate (0); narrow (1); wide (2) (Fig. 5L)

28 Middle lobe of sheath of aedeagus: as long as the lateral lobes (0) (Fig. 5A); a little surpassing lateral lobes (1); highly surpassing lateral lobes (2) (Fig. 5K)

29 Lophi of epiphallus: with internal conical protuberance (0) (Fig. 5I); without internal conical protuberance (1)

Female genitalia

30 Ovipositor valves: curved (0); robust and straight (1)

Appendix 2.

Data matrix for the phylogenetic analysis of *Chlorus*. Numbers of characters according to Appendix 1.

	0000000011111111111122222222223 123456789012345678901234567890
<i>Ronderosia bergi</i>	012011000000000000000000000000
<i>Scotussa impudica</i>	0310000000000000000000420000010201
<i>Leiotettix viridis</i>	2000000000000000000000000000010010
<i>Atrachelacris unicolor</i>	20000000000000000000000000000010010
<i>Chlorus attenuatus</i>	312111101021011100120020002200
<i>Chlorus chiquitensis</i>	012021101021011100120020002200
<i>Chlorus spatulus</i>	012021101021011100120020002200
<i>Chlorus bolivianus</i>	012021101021011100120020002200
<i>Chlorus vittatus</i>	002111101021011100120000002200
<i>Chlorus brunneus</i>	312111101021011100120020002200
<i>Chlorus borellii</i>	012011101021011000120020002000
<i>Eurotettix femoratus</i>	012011010010021000000220001100
<i>Eurotettix minor</i>	012011010010021000000220001100
<i>Eurotettix robustus</i>	012111010032021100200110102200
<i>Eurotettix raphaelandrearum</i>	012111010032021100200110102200
<i>Eurotettix similiraphael</i>	012111010032021100200111102200
<i>Eurotettix carbonelli</i>	012011010010021101210121102200
<i>Eurotettix concavus</i>	012011010010021000210121102200
<i>Eurotettix latus</i>	012011010010021000210121102200
<i>Eurotettix procerus</i>	012011010010021000210120002200
<i>Eurotettix bugresensis</i>	012011010010021000210121002200
<i>Eurotettix brevicerci</i>	012011010010021001210121001200
<i>Eurotettix monnei</i>	012011010010021000210121002200
<i>Dichromatos lilloanus</i>	100000101112021010331000010011
<i>Dichromatos montanus</i>	130000101112121210331000010011
<i>Dichromatos corupa</i>	022011101112121110331000010011
<i>Dichromatos schrottkyi</i>	120000101112021210331000010011