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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências Biológicas, na Área de Zoologia.

Orientador: Prof. Dr. Silvio Shigueo Nihei

Co-orientador: Dr. Pedro Guilherme de Souza Dias

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Sumário

Resumo

A subfamília Landrevinae Gorochov, 1982 (*sensu* OSF) possui atualmente 194 espécies válidas, distribuídas em 40 gêneros e três tribos. A tribo Landrevini compreende 28 gêneros e 160 espécies, quase a totalidade da subfamília, enquanto Odontogryllini compreende cinco gêneros e 20 espécies, e Prolandrevini sete gêneros e 14 espécies. Essa subfamília é um grupo diverso de grilos de floresta, distribuídos especialmente em clima tropical nas regiões biogeográficas Neotropical, Afrotropical, Oriental e Australásia. Uma análise cladística é apresentada, incluindo 48 terminais e 106 caracteres morfológicos. A análise filogenética com pesagem igual resultou em 14 arvores mais parcimoniosas, com 483 passos. A subfamília Landrevinae foi recuperada como um clado monofiléticos, bem como Landrevini. A tribo Odontogryllini foi recuperada como um grupo polifilético, com Prolandrevini alocado dentro da tribo. Esse trabalho é o primeiro passo para um melhor entendimento desse complexo grupo de grilos.

Abstract

The subfamily Landrevinae Gorochov, 1982 (*sensu* OSF) currently includes 194 valid species, distributed in 40 genera and three tribes. The tribe Landrevini comprises 28 genera and 160 species, almost all the subfamily, while Odontogryllini comprises five genera and 20 species, and Prolandrevini has seven genera and 14 species. This subfamily is a diverse group of forest crickets distributed specially in tropical clime of the Neotropical, Afrotropical, Oriental and Australasian biogeographic regions. A cladistic analysis is presented including 48 terminals and 106 morphological characters. The phylogenetic analysis with equal weight resulted in 14 most parsimonious trees, with 483 steps. The subfamily Landrevinae was recovered as a monophyletic clade, as well as Landrivini. Odontogryllini was recovered as a paraphyletic group, with Prolandrevini nested inside. This work is the first step towards an improvement in understand this complex group of crickets.

1 Introduction

Orthoptera is the most diverse lineage among Polyneoptera, with more than 28000 described species (Cigliano *et al.*, 2020). It is divided in two suborders, Caelifera and Ensifera. Several morphological and molecular phylogenetic studies also support the monophyly of the order and its suborders (Gwynne, 1995; Flook & Rowell, 1997; Flook *et al.*, 1999; Rentz, 2000; Wheeler *et al.*, 2001; Desutter-Grandcolas, 2003; Grimaldi & Engel, 2005; Jost & Shaw 2006; Legendre *et al.*, 2010; Sheffield *et al.*, 2010; Zhou *et al.*, 2010; Song *et al.*, 2015). Some of these works support Gryllidea *sensu* Vickery (1977), a taxon comprising all crickets, as monophyletic and with infraordinal status (Song *et al.*, 2015; Chintauan-Marquier *et al.*, 2016). The study of Chintauan-Marquier *et al.* (2016) also supports the subdivision of Gryllidea into two clades with superfamily status: Gryllotalpoidea, including the families Gryllotalpidae and Myrmecophilidae, and Grylloidea with four families: Mogoplistidae, Trigonidiidae, Phalangopsidae and Gryllidae.

The family Gryllidae was divided into 12 subfamilies: Gryllinae, Gryllomiminae, Gryllomorphinae, Itarinae, Landrevinae, Sclerogryllinae, Euscyrtinae, Hapithinae, Pentacentrinae, Podoscirtinae, Eneopterinae and Oecanthinae (Chintauan-Marquier *et al.*, 2016; Cigliano *et al.*, 2020). Although this study strongly supports Gryllidae monophyly, internal relationships are unclear, and the traditional subfamilies have not recovered monophyletic groups. This occurred with Landrevinae, which was recovered as polyphyletic divided into three distinct Gryllidae clades (Chintauan-Marquier *et al.*, 2016).

The subfamily Landrevinae Gorochov, 1982 (*sensu* OSF) currently includes 194 valid species, distributed in 40 genera and three tribes. The tribe Landrevini comprises 28 genera and 160 species, almost all the subfamily, while Odontogryllini comprises five genera and 20 species, and Prolandrevini has seven genera and 14 species (Cigliano *et al.* 2020). This subfamily is a diverse group of forest crickets distributed specially in tropical clime of the Neotropical, Afrotropical, Oriental and Australasian biogeographic regions. These crickets are known by the common name bark crickets because they are found especially under the tree bark, although they are also found on trunks of living and dead trees, even as fallen logs (Otte, 1988; Gorochov, 2017). Nevertheless, this behavior does not apply to all members of the subfamily since the Neotropical group are found on the leaf litter inside the forests (de Mello, 1992).

These crickets are characterized by their general appearance similar to that of Gryllinae, with robust body and legs, color ranging from brown to dark brown and black. However, they have body usually dorsoventrally flattened and posterior tibia bearing dorsoproximal small spines, sometimes between the spurs (Gorochov, 2013). The differences between the genera are particularly given by the characters of the male genitalia and the tegmina, but often these differences are not very distinct and distinction between some genera could be difficult especially because some species have intermediate characters (Gorochov, 2017).

The genera currently allocated in Landrevinae (*sensu* OSF) are listed below:

- Landrevinae Gorochov, 1982
  - Landrevini Gorochov, 1982
    - *Landreva* Walker, 1869
      - synonym *Ectolandrevus* Saussure, 1877
      - synonym *Landrevus* Saussure, 1877
    - *Endolandrevus* Saussure, 1877
    - *Paralandrevus* Saussure, 1877
    - *Duolandrevus* Kirby, 1906
    - *Copholandrevus* Chopard, 1925
    - *Mjobergella* Chopard, 1925
      - synonym *Mjöbergella* Chopard, 1925
    - *Drelanvus* Chopard, 1930
    - *Lasiogryllus* Chopard, 1930
    - *Apiotarsoides* Chopard, 1931
    - *Hemilandreva* Chopard, 1936

Odontogryllodes Chopard, 1969

Ahldreva Otte, 1988

Ajorama Otte, 1988

Avdrenia Otte, 1988

Eleva Otte, 1988

Fijina Otte, 1988

Ginidra Otte, 1988

Jareta Otte, 1988

Kotama Otte, 1988

Papava Otte, 1988

Repapa Otte, 1988

Sigeva Otte, 1988

Solepa Otte, 1988

Vasilia Gorochov, 1988

Otteana Gorochov, 1990

Ectodrelanva Gorochov, 2000

Endodrelanva Gorochov, 2000

Sulawemina Gorochov, 2016

Odontogryllini de Mello, 1992

Odontogryllus Saussure, 1877

Brasilodontus de Mello, 1992

Valchica de Mello, 1922

Xulavuna de Mello & Campos, 2014

Yarrubura de Mello & Campos, 2014

Prolandrevini Gorochov, 2005

Gryllapterus Bolívar, 1912

Oreolandreva Chopard, 1945

Microlandreva Chopard, 1952

Prolandreva Gorochov, 2005

Creolandreva Hugel, 2009

Astriduleva Gorochov, 2016

Striduleva Gorochov, 2016

1.1 Systematic history of Landrevinae

The first work that brought together some genera that are currently allocated in Landrevinae was the catalog *Mélanges Orthoptérologiques - Cinquième Fascicule*, made by the Swiss entomologist Henri de Saussure (1877). Considered the first taxonomic and morphological study of Grylloidea, Saussure grouped the genera *Landreva*, *Odontogryllus* and *Gryllomorpha* in his category Légion des Gryllomorphites, under the Tribu des Grylliens and Famille des Gryllides. The genera *Paralandrevus, Endolandrevus* and *Ectolandrevus* as subgenera for *Landreva*. He defined the following characters for the recognition of *Landreva*: posterior tibia with serrulate basal half and armed with spurs in the distal half, ocelli arranged in triangle, apterous or with incomplete wings, head rounded, rostrum large and inclined, pronotum posterior border straight and lateral lobes angular forward, posterior basitarsi strongly serrulate.

Saussure (1877) also stated that this group contains two different morphotypes, one present in *Landreva* and *Odontogryllus*, which are related to that of the Grylliens, and other one in *Gryllomorpha* that could be more related to Phalangopsites. The first ones possess a stocky body and face that resembles crickets of the genus *Gryllus*, as well as another characteristics of Grylliens, like three apical spurs on anterior tibia, four apical spurs on middle tibia, posterior tibia robust, arched, with upper face flattened, a little widened posteriorly, with edges lined with fixed spines which are arranged regularly, the last outer spine being as large as the preceding, the superior-external spur being of the same size as these spines. However, the lower-inner spur is smaller than the outer one, contrary to what is observed in other Grylliens. For him, these characteristics which is seem in *Landreva* and *Odontogryllus* show that they belong without contested to the tribe of the Grylliens.

About *Gryllomorpha*, Saussure mentioned that they have the body slenderer, anterior tibia with only two apical spurs, posterior tibia slender, rounded, straight, not dilated posteriorly and with mobile spurs, last outer spine smaller than the previous one, very close to the upper spur, which is even smaller than this spine. These characters are similar to those of the Phalangopsites, and indeed, *Gryllomorpha* could be classified as much in this group as well in Grylliens. They are on the boundary of the two groups, and Saussure place them among the Grylliens because their posterior tibia are not serrulate between the spines.

One year later, Saussure (1878) published the *Mélanges Orthoptérologiques - Sixième Fascicule* and made the first mention of a group based on *Landreva*, as a Légion Landrevites. The author concluded that *Gryllomorpha* is more related to Phalangopsites and moved the genus. Thereby, the author replaced the name Gryllomorphites with Landrevites, and limited the scope of the group to species that have the face of *Gryllus*, posterior tibia, slightly arched, slightly thicker towards the end, flattened above, armed with fixed spines thick and shorter than spurs.

In his work *Orthopterorum Catalogus*, Chopard (1967) followed first Saussure's proposition and united under the tribe Gryllomorphini (Gryllinae) those genera which resembles field crickets and possessed spines above subapical spurs on hind tibia. These genera are *Landreva*, *Duolandrevus*, *Endolandrevus*, *Paralandrevus*, *Drelanvus*, *Gryllapterus*, *Hemilandreva*, *Copholandrevus*, *Lasiogryllus*, *Mjobergella*, *Oreolandreva*, *Microlandreva*, *Odontogryllus*, *Odontogryllodes*, *Hymenoptila*, *Discoptila*, *Petaloptila*, *Acroneuroptila* and *Gryllomorpha*.

This classification changed when Gorochov (1982) described the subfamily Landrevinae after study some new material from Southeast Asia. According to the author, with new studies it is evident that these species have a great contrast with species of Gryllomorphinae and Gryllinae and therefore require a separate subfamily. He defined the subfamily with the following characters: body big, a little flat, more or less bright, similar to Gryllinae's body; head hypognatha, large, broad, somewhat flattened; ocelli developed, lateral ocelli located at the frontal sutures; males with metanotal gland; forewings developed but short, mirror sometimes developed sometimes absent; hindwings, when present, rudimentary; pseudoepiphallic sclerite large with protruding lateral lophi and less developed medial lophi; rami very close to pseudoepiphallic sclerite; pseudoepiphallic paramere small and not too separate from pseudoepiphallic sclerite; endophallic apodema well developed.

Gorochov (1982) moved to this new subfamily the genera *Landreva,* as well as some genera that were previously considered as *Landreva* synonyms: *Duolandrevus*, *Endolandrevus* and *Paralandrevus*. He also stated that the systematic position of *Drelanvus*, *Gryllapterus*, *Hemilandreva*, *Copholandrevus*, *Lasiogryllus*, *Mjobergella*, *Oreolandreva*, *Microlandreva*, *Odontogryllus* and *Odontogryllodes* were not very understandable, but they probably belong to Landrevinae.

In an almost concomitant and independent work, the monograph *Australian Crickets*, Otte & Alexander (1983) erected the tribe Landrevini (Gryllinae) to include the following genera formerly belonging to Gryllomorphini (*sensu* Chopard 1967): *Landreva*, *Duolandrevus*, *Endolandrevus*, *Paralandrevus*, *Drelanvus*, *Hemilandreva*, *Lasiogryllus*, *Odontogryllodes*, *Microlandreva*, *Copholandrevus*, *Mjobergella* and *Gryllitara*. The authors kept in Gryllomorphini the genera *Gryllomorpha*, *Discoptila*, *Hymenoptila*, *Petaloptila*, *Acroneuroptila*, *Odontogryllus*, *Oreolandreva*, *Gryllapterus* as well as added *Eurygryllodes* and *Malua*. These genera under Landrevini share two rows of spines above subapical spurs with Gryllomorphini, but according to the authors, they have the following differences of the genera maintained in the previous tribe: body flattened, upper lobe of clypeus not swollen, males and females with wings (sometimes very short), males of most species with stridulum, mirror sometimes present and sometimes absent, tympana variable, harp usually with at least five veins, frons without setae in vicinity of antennae, and males without spermatophore.

After study a male of *Pteroplistus,* Otte (1988) decided to expand the subfamily Pteroplistinae to include Landrevinae (*sensu* Gorochov, 1982) or Landrevini (*sensu* Otte & Alexander, 1983). Thereby, the subfamily proposed by the author would comprise two tribes, Pteroplistini (with *Pteroplistus* as the only representative) and Landrevini (with 28 genera, of which 13 were described in this paper).

The recognition of the subfamily Pteroplistinae (*sensu* Otte 1988) is due by the following characteristics: scape as wide as rostrum, head rather square in dorsal view, forehead angulate in lateral view, dorsum of head flattened, median ocellus positioned on dorsum of head, lateral lobes of pronotum with a distinctly slanted margin lowest at anterior border, pronotal margins with small bristles on leading margin, metanotum in most species with a large and shallow dorsal depression containing bristles, male forewings variable, forewings in singing species with short apical area (except Pteroplistini), Cu2 vein (stridulum) with a distinct bend, file with a small raised cluster of teeth, hindwings absent in all species (except Pteroplistini), foretibia with tympanal openings variable, front and middle tibia with 3/3 apical spurs in Landrevini and 2/2 in Pteroplistini, hind tibia with 4/4 subapical spurs in Landrevini and 2/3 in Pteroplistini, presence of short spines above subapical spurs on hind tibia, male genitalia elongated, epiphallus strongly bilobate, absence of arched spermatophore tube mold, ectoparameres not extending beyond epiphallus and virga wide with thin lateral flanges.

The author agreed with Gorochov (1982) that Landrevini were quite different from Gryllomorphini and are not even members of the subfamily Gryllinae, contrary to his previous proposal (Otte & Alexander, 1983). The author also suggested that they may have a close relationship with Oecanthinae and listed several shared characteristics, such as, the presence of a prominent knob in the stridulatory file proximal end, prognathous members, spines and spurs on the hind tibia, absence of a long arching spermatophore tube mold, epiphallus strongly bilobed, and scape much broader than the interantennal space. These two subfamilies (Pteroplistinae and Oecanthinae) could be related to Podoscirtinae and Eneopterinae, especially because of the metanotal gland present in these groups.

The Neotropical fauna received attention with the work of de Mello (1992). Following the classification proposed by Otte (1988), with Landrevinae (*sensu* Gorochov, 1982) as a tribe of Pteroplistinae, de Mello (1992) erected the new tribe Odontogryllini to include the Neotropical genus *Odontogryllus* as well as the new genera *Brasilodontus* and *Valchica* described in this paper.

The tribe Prolandrevini was erected by Gorochov (2005) to allocate the genera *Prolandreva,* which differs from all other representatives of Landrevinae in the presence of small spines between outer spurs in the posterior tibia, the widened second segment of posterior tarsi, and the very long pseudepiphallic sclerite.

The Neotropical tribe Odontogryllini was moved from Pteroplistinae to Landrevinae by Gorochov (2013), since the author had already presenting arguments showing that Pteroplistinae and Landrevinae are are not closely related to each other (Gorochov, 1990, 2000, 2001, 2004; Gorochov & Warchalowska-Sliwa, 2004)

In another study with Neotropical specimens, Campos & de Mello (2014) described two new monotypic genera, *Yarrubura* and *Xulavuna*, as well as five new species of *Brasilodontus*. The authors compared this new material with the *Odontogryllus*, *Valchica* and *Brasilodontus* previously described species and concluded that Odontogryllini is not a natural assemblage. Therefore, they decided to suppress the tribe Odontogryllini and transferred all Neotropical genera to Landrevini.

In an article summarizing his previous work with the group, Gorochov (2016) proposed some characters to differentiate the Landrevinae tribes. Firstly, the author undid the synonym made by Campos & de Mello (2014) and restore Odontogryllini, because for him, the action is insufficiently grounded, and some possible diagnostic characters of this tribe proposed by Gorochov (2013) were not discussed. He also moved the genera *Oreolandreva*, *Microlandreva* and *Creolandreva* from Landrevini to Prolandrevini.

Gorochov (2016) stated that Landrevini differs from Odontogryllini and Prolandrevini by the shape of the stridulatory file, presenting a S-shape or almost S-shape in the lateral part of the first tribe and straight or weakly arcuate in the later one. He also proposed that Landrevini and Odontogryllini differ from Prolandrevini in the absence of denticles between outer subapical spurs on posterior tibia that are present in Prolandrevini, and in the size of pseudepiphallic sclerite, which are much longer than the rami in Prolandrevini.

In his next work with Landrevinae, Gorochov (2017) changed the tribal position of some genera. He moved *Xulavuna* and *Yarrubura* from Landrevini to Odontogryllini, and *Gryllapterus* from Landrevini to Prolandrevini. He also moved *Vasilia*, *Otteana*, *Endodrelanva* and *Ectodrelanva*, that were considered as *incert sedis* and placed outside any tribe of Landrevinae, to Landrevini and state that their clearly belong to this tribe on the base of all their morphological characters. With these changes, all tribes were also separated in geographical distribution, so that Landrevini includes all genera from Oriental and Australasia regions, Odontogryllini includes the Neotropical genera and Prolandrevini the Afrotropical ones. The author also said that some genera, like

Paralandrevus, *Drelanvus*, and *Lasiogryllus* are not very understandable and may be synonyms or subgenera of any other genera.

Landrevinae was sampled with 6 terminals in the molecular phylogeny of Chintauan-Marquier *et al*. (2016) and recovered as polyphyletic. One of the Gryllidae clades groups the Neotropical genera *Odontogryllus* and *Brasilodontus* with *Hemygryllus* Saussure, 1877. Another clade is composed by *Creolandreva* and *Microlandreva* with *Pentacentrus* and *Orthoxiphus*. In the clade with largest number of terminals, two species of Landrevini appear as sister group of several genera, like *Anurogryllus*, *Gryllus*, *Miogryllus*, and others. Despite the polyphyly found by Chintauan-Marquier *et al*. (2016), the Orthoptera Species File still kept the subfamily as valid.

1.2 Objectives

The aim of this chapter is (1) to carry out a morphological study of the phallic complex and tegmina of Landrevinae aiming at the proposition of homology hypotheses and (2) to propose a phylogenetic relationships hypothesis based on morphological characters between the genera of Landrevinae.

2.Material and method

2.1 Examined material

This study was carried out with materials from the following institutions:

MZSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil, under the curatorship of Dr. Eliana Marques Cancello.

UBTU – Laboratório de Insetos, Departamento de Zoologia, São Paulo State University "Júlio de Mesquita Filho", Botucatu, Brazil, under the curatorship of Dr. Francisco de Assis Ganeo de Mello.

BPBM – Bernice Pauahi Bishop Museum, Honolulu, United States of America, under the curatorship of M.S. Jim Boone.

ZIN – Zoological Institute of Russian Academy of Science, Saint Petersburg, Russia, under the curatorship of Dr. Andrej Gorochov.

MNHN – Muséum national d'Histoire naturelle, Paris, France, under the curatorship of Dr. Laure Desutter-Grandcolas.

2.2 Taxonomic sampling

For the internal group composition 58 species were selected (Appendix 1) of Landrevinae, covering 27 different genera (18 species of Landrevini, 5 Odontogryllini and 4 Prolandrevini). Moreover, one undescribed genus of Odontogryllini was also included. Some genera of Landrevini (*Copholandrevus*, *Drelanvus*, *Eleva*, *Fijina*, *Hemilandreva*, *Jareta*, *Lasiogryllus*, *Mjobergella*, *Paralandrevus* and *Solepa*) were not included due to unavailability of material in the visited collections, as well as two genera of Prolandrevini (*Astriduleva* and *Striduleva*) that were described based on females only.

For the composition of the external group taxa possibly related to Landrevinae were selected, according to the relationship hypothesis of Chintauan-Marquier *et al*., (2016).

2.3 Characters and data matrix

This phylogenetic analysis was carried out based on external morphological characters of adult males, including their genitalia. Due to the high number of species with unknown females, their exclusive characters were not used.

The terminology used for general external morphology follows Otte & Alexander, 1982; Torre-Bueno, 1989; Snodgrass 1997. The terminology used to the male phallic complex follows Desutter (1987, 1990) as well as the recent modifications proposed by Desutter-Grandcolas (2003) and Souza-Dias (2015). The male tegmina terminology follows Desutter-Grandcolas *et al.* (2017). The criteria of homology adopted were the primary and secondary homology (De Pinna, 1991). The construction of characters follows Sereno (2007).

Some characters used in this study were proposed in previous phylogenetic works in Grylloidea (e.g., Robillard & Desutter-Grandcolas, 2004; Souza-Dias, 2015). However, most of the constructed characters are proposed here for the first time.

The data matrix was constructed on the software Mesquite 3.61 (build 927) (Maddison & Maddison, 2019). Inapplicable characters were encoded with “-“, and not observed characters with “?”.

2.4 Data analysis

The optimality criterion used for the phylogenetic inference was the Fitch parsimony (1971), considering all the characters as unordered and with equal weights. The tree rooting and character polarization were made following the outgroup method (Nixon & Carpenter, 1993). The search for trees was performed using the software TNT 1.5 (Goloboff *et al.*, 2015). The searches were made using the New Technologies, with 1000 replications, holding 100 trees by replicate, and using the followings searches algorithms: TBR; Drift, 200 substitutions per cycle; Tree-Fusing, 10 rounds; and Ratchet, 200 substitutions. The strict consensus tree was also obtained in TNT 1.5, as well as the Bremer support (Bremer, 1994). The resulting trees and characters were exported to the software Winclada (Nixon, 1994-2004), in which the consistency index (CI) (Kluge & Farris, 1969) and retention index (RI) (Farris, 1989) were calculated. Ambiguous characters were optimized through the algorithms ACCTRAN and DELTRAN (Farris, 1970; Swafford & Maddison, 1987). The resulting topologies were exported and edited in the software Adobe Illustrator CS6.

3 Results

3.1 Characters

Based on the morphological study performed, 106 characters were constructed, among which 10 from head, 9 from thorax, 9 from legs, 21 from wings and 57 from male genitalia. The characters proposed, their states and comments are presented below, as well as consistency index (CI) and retention index (RI) for each character.

Head

1. Head, vertex in lateral view (CI=20; RI=66):
    0, rounded
    1, flattened

2. Head, width, in relation to pronotum (CI=20; RI=42; ACCTRAN):
    0, wider
    1, equal
    2, narrower

3. Head, fastigium, development, side view (CI=50; RI=94):
    0, reduced
    1, developed

4. Head, fastigium, width in relation to scape (CI=50; RI=92):
    0, narrower
    1, wider

5. Head, coronal suture (CI=14; RI=53; ACCTRAN):
    0, visible
    1, not visible

6. Head, median ocellus, form:
    0, elliptical

1, rounded

7. Head, lateral ocelli, size in relation to median ocellus (CI=25; RI=57):
    - 0, smaller
    - 1, equal size
    - 2, bigger

8. Head, maxillary palpi, fifth palpomere, form (CI=33; RI=66; ACCTRAN):
    - 0, triangular
    - 1, clavated
    - 2, cylindrical
    - 3, spatulate

9. Head, maxillary palpi, fifth palpomere, coloration (CI=25; RI=75; ACCTRAN):
    - 0, uniform
    - 1, apex white

10. Head, maxillary palpi, fifth palpomere, apex, form (CI=50; RI=92):
    - 0, truncated
    - 1, rounded

Thorax

11. Pronotum, disc, bristles (CI=12; RI=63):
    - 0, absent
    - 1, present

12. Pronotum, disc, form (CI=50; RI=50):
    - 0, wider than long
    - 1, squared
    - 2, longer than wide

13. Pronotum, disc, anterior margin, form (CI=20; RI=50; ACCTRAN):
    - 0, concave
    - 1, straight
    - 2, convex

14. Pronotum, disc, anterior margin, bristles (CI=16; RI=66):
    0, presente
    1, absent

15. Pronotum, disc, anterior margin, wide in relation to posterior margin (CI=28; RI=16; DELTRAN):
    0, wider
    1, equal
    2, narrowed

16. Pronotum, disc, posterior margin, form (CI=16; RI=23; DELTRAN):
    0, concave
    1, straight
    2, convex

17. Pronotum, disc, posterior margin, bristles (CI=14; RI=73; ACCTRAN):
    0, presente
    1, absent

18. Pronotum, lateral lobes, border, orientation (CI=100; RI=100):
    0, straight
    1, diagonal

19. Metanotum, metanotal structures (CI=14; RI=57):
    0, absent
    1, present

Proposed by Otte (1988). The author states that metanotal glands are presents in Pteroplistinae, Oecanthinae, Podoscirtinae and Eneopterinae, suggesting a close relationship between these groups.

Legs

20. Tibia I, external tympanum (CI=14; RI=61):

0, absent
1, present

21. Tibia I, internal tympanum (CI=12; RI=65; DELTRAN):
0, absent
1, present

Otte (1988) proposed the following character: “Auditory tympana: 0, with neither; 1, with only inner; 2, with inner and outer tympana”. This form of codification does not respect the independence of the characters, since the internal and external tympana are independent and very variable in Landrevinae. These two previous characters where proposed by Souza-Dias (2015).

22. Tibia I, apical spurs, number (CI=100; RI=100):
0, 2 spurs
1, 3 spurs

23. Tibia II, apical spurs, number (CI=66; RI=92; DELTRAN):
0, 2 spurs
1, 3 spurs
2, 4 spurs

Otte (1988) proposed the following character: “Apical spurs in front/middle tibiae: 0, 3/3; 1, 2/2” and argued that this character distinguished the tribes in Pteroplistinae (*sensu* Otte, 1988), being 3/3 in Landrevini and 2/2 in Pteroplistini. Once again, the author does not respect the independence of the characters. These characters are proposed here separately, because they are independently from each other, as we can see in *Anurogryllus toledopizai*, which have 3 spurs on Tibia I and 4 spurs on Tibia II. These two previous characters were also proposed by Souza-Dias (2015).

Hugel (2009) states that *Microlandreva* and *Creolandreva* (both genera placed in Prolandrevini now) have two apical spurs on tibia I and II, a particular character that distinguished then to all other Oriental Landrevinae. This condition is also present in *Prolandreva*, although never mentioned in his descriptions.

24. Tibia III, subapical spines (CI=100; RI=100):
    0, absent
    1, present

Chopard (1967) united under the tribe Gryllomorphini (Gryllinae) those genera which looks like field cricket and have these subapical spines.

25. (24:1) Tibia III, subapical spines, position (CI=100; RI=100):
    0, only above spurs
    1, above and between spurs

Gorochov (2016) use this character to separate the tribes Landrevini and Prolandrevini.

26. Tibia III, external subapical spurs, number (CI=66; RI=80; ACCTRAN):
    0, 3 spurs
    1, 4 spurs
    2, 5 spurs

27. Tibia III, internal subapical spurs, number (CI=66; RI=80; ACCTRAN):
    0, 3 spurs
    1, 4 spurs
    2, 5 spurs

Hugel (2009) states that *Microlandreva* and *Creolandreva* have tibia III with 3 inner and 3 outer subapical spurs, distinguishing then of all other Oriental species that have 4 subapical spurs on each side.

28. Tibia III, size, in relation to basitarsus III (CI=33; RI=0):
    0, longer than basitarsus III
    1, same size of basitarsus III

Wings

Venation patterns and the structures responsible for stridulation make up a great source of characters for a phylogenetic study. These characters are informative for both high and lower level phylogenies. For example, Desutter-Grandcolas (2003) used 12 characters in his Ensifera phylogeny, Robillard & Desutter-Grandcolas (2004) used 33 characters in the Eneopterinae subfamily phylogeny, Souza-Dias (2015) used 17 in his Luzarinae work.

The forewings of crickets are tegmina type and they have several adaptations for sound production and transmission, although cases of regression and total loss of these structures are common (Walker & Masaki, 1988).

The forewing can be divided into two main parts. The lateral field covers the side of the abdomen and has longitudinal veins. The dorsal field is generally flat and with acoustic adaptations, of which the most important structures are the stridulatory file, responsible for the production of sound, in addition to the mirror and the harp, regions involved in the propagation (Otte & Alexander, 1983; Robillard & Desutter-Grandcolas, 2004).

29. Forewings, constitution (CI=14; RI=62; ACCTRAN):
0, coriaceous
1, pergameneous

The state “0, coriaceous” is characterized by a very reduced forewings with only few longitudinal veins, and the by the lack of any stridulatory structure. On the other side, a “1, pergameneous” forewing is clearly recognized by the presence of stridulatory structures. This character was firstly proposed by Souza-Dias (2015) and used by Campos (2016).

30. (29:0) Forewings, coriaceous, length:
0, covering the metanoto
1, covering first abdominal tergite

31. (29:0) Forewings, coriaceous, middle position (CI=33; RI=33; DELTRAN):
0, not touching each other

1, touching each other
2, overlapping

32. (29:0) Forewings, coriaceous, longitudinal venation (CI=33; RI=33; DELTRAN):
    0, absent
    1, present

33. (29:0) Forewings, coriaceous, lateral field (CI=25; RI=25; DELTRAN):
    0, absent
    1, present

34. (29:0 – 33:1) Forewings, coriaceous, lateral field, length in relation to dorsal field (CI=33; RI=60; DELTRAN):
    0, shorter
    1, equal
    2, longer

35. (29,0) Forewings, coriaceous, glandular structures (CI=100; RI=100):
    0, absent
    1, present

36. (29:1) Forewings, pergameneous, length (CI=40; RI=57; DELTRAN):
    0, covering only thorax
    1, covering the abdomen until tergite I
    2, covering the abdomen until tergite V
    3, covering all abdomen

37. (29:1) Forewings, pergameneous, vein A1 (stridulatory file) (CI=50; RI=50; DELTRAN):
    0, absent
    1, present

38. (29:1 – 37:1) Forewings, pergameneous, vein A1 (stridulatory file), shape (CI=33; RI=80; ACCTRAN):

0, curved once

1, curved twice (S-shape)

39. (29:1) Forewings, pergameneous, veins A2 and A3 (CI=40; RI=40; ACCTRAN):

    0, connected close to vein A1

    1, connected long before vein A1

    2, not connected

40. (29:1) Forewings, pergameneous, harp (CI=33; RI=50):

    0, absent

    1, present

41. (29:1 – 40:1) Forewings, pergameneous, harp, veins (CI=100; RI=100):

    0, connected direct to vein A1

    1, merged before connected to vein A1

42. (29:1 – 40:1 – 41:1) Forewings, pergameneous, harp, number of veins merged before reach vein A1 (ACCTRAN):

    0, harp veins 1 and 2 merged

    1, harp veins 1, 2 and 3 merged

43. (29:1) Forewings, pergameneous, mirror (CI=33; RI=71):

    0, absent

    1, present

44. (29:1) Forewings, pergameneous, apical area, development (CI=100; RI=100):

    0, reduced and without cells

    1, normal and with cells

45. (29:1) Forewings, pergameneous, lateral field, length in relation to dorsal field (CI=20; RI=33; DELTRAN):

    0, equal

    1, shorter

46. (29:1) Forewings, lateral field, posterior border, form (CI=16; RI=61; DELTRAN):
    0, semicircular
    1, transverse

47. (29:1) Forewings, lateral field, accessory veins, apex direction (CI=50; RI=83; DELTRAN):
    0, towards the border
    1, towards the dorsal field

48. Hindwings (CI=14; RI=40; DELTRAN):
    0, absent
    1, present

Proposed by Otte (1988). The author argued that this character distinguished the tribes in Pteroplistinae, being absent in Landrevini and present in Pteroplistini.

49. (48:1) Hindwings, development (CI=50; RI=50; DELTRAN):
    0, normal
    1, reduced

Genitalia

Characters from male genitalia are a good source of information to proposed hypotheses of homology (Song & Bucheli, 2010), and has been used as the main character font in cricket systematic (Desutter, 1987; Desutter-Grandcolas, 2003; Robillard & Desutter-Grandcolas, 2004; Souza-Dias, 2015)

The male genitalia of crickets (Fig. X) are a projective, non-intromittent organ whose function is related to spermatophore production and transfer during copulation. It has a remarkable dorsoventral asymmetry, with the highly sclerotized dorsal portion and the reduced ventral portion. Its basic structure is made up of three distinct parts, the pseudoepiphallus, ectophallic invagination and endophallus (Desutter-Grandcolas, 2003; Souza-Dias, 2015).

The pseudoepiphallus is formed in the distal portion by a long, flattened sclerite that dorsally covers most part of the genitalia. This sclerite may have medial and lateral lobes. Still in the distal portion are positioned the pseudoepiphalic parameres, paired and individualized structures responsible for attaching the copulatory papilla. In the basal portion are the *rami*, sclerites that delimit the genitalia laterally.

The ectophallic invagination has a pair of ectophallic apodemes, which can be connected to a sclerite that can have one or more projections, and their function is the movement of pseudoepiphallic parameres. One of these projections may be responsible to form the ectophallic arch. The ectophallic fold is a structure with varying degrees of development and sclerotization, located in the distal portion and close to the pseudoepiphallic parameres.

The endophallus is the innermost layer of the genitalia, with a centralized endophallic sclerite that may have simple or paired apodomes, as well as lateral projections.

Pseudepiphallus

50. Pseudepiphallus, rami, dorsal sclerites (CI=100; RI=100):

    0, absent

    1, present

Hugel (2009) says that *Microlandreva* and *Creolandreva* have rami with two sclerites. This state is also present in one species of *Prolandreva*.

51. (50:1) Pseudepiphallus, rami, dorsal sclerites, shape:

    0, thin and elongated

    1, triangular

52. Pseudepiphallus, rami, ramal plate:

    0, absent

    1, present

Character proposed by Robillard & Desutter-Grandcolas (2004) and Souza-Diaz (2015).

53. Pseudepiphallus, rami, form of ramus (CI=50; RI=92):

0, cylindrical
1, flattened plate

54. (53:0) Pseudepiphallus, rami, ramus cylindrical, proximal portion of ramus sclerite, width (CI=20; RI=71):
    0, same width than the rest of sclerite (not dilated)
    1, wider than the rest of sclerite (dilated)

55. (53:1) Pseudepiphallus, rami, flattened plate, orientation of plate:
    0, dorso-ventral
    1, latero-lateral

56. Pseudepiphallus, rami, distal portion of ramus sclerite, orientation (CI=25; RI=77; ACCTRAN):
    0, straight
    1, slightly curved internally
    2, strongly curved internally

57. Pseudepiphallus, rami, apex of each ramus (CI=50; RI=75; ACCTRAN):
    0, not connected to each other
    1, connected to each other

58. Pseudepiphallus, rami, longitudinal orientation of each ramus (CI=20; RI=76):
    0, parallel
    1, internal
    2, external

59. Pseudepiphallus, rami, orientation, side view (CI=25; RI=76):
    0, straight
    1, curved ventrally

60. Pseudepiphallus, rami, connection with pseudepiphallic sclerite (CI=33; RI=33; ACCTRAN):
    0, membranous connection

1, ramus connect directly to the pseudoepiphallic sclerite

61. Pseudepiphallus, rami, connection with pseudepiphallic sclerite, position (CI=33; RI=60):
    0, at the base of pseudepiphallic sclerite
    1, at the lateral of pseudoepiphallic sclerite

62. Pseudepiphallus, rami, size in relation to pseudepiphallic sclerite (CI=15; RI=57; ACCTRAN):
    0, shorter
    1, equal
    2, longer

63. Pseudepiphallus, pseudepiphallic sclerite, distal portion, width in relation to proximal portion (CI=16; RI=66; DELTRAN):
    0, narrower
    1, equal

64. Pseudepiphallus, pseudepiphallic sclerite, dorsal sclerotization (CI=40; RI=66; ACCTRAN):
    0, completely absent
    1, reduced
    2. completely sclerotized

65. Pseudepiphallus, pseudepiphallic sclerite, dorsal sclerotization, ventral face, enhanced longitudinal sclerotization (CI=33; RI=50; ACCTRAN):
    0, absent
    1, present

66. Pseudepiphallus, pseudepiphallic sclerite, dorsal, medial lobes (CI=16; RI=73; ACCTRAN):
    0, absent
    1, present

67. (66:1) Pseudepiphallus, pseudepiphallic sclerite, dorsal, medial lobes, number of lobes (CI=16; RI=44; DELTRAN):
    0, one
    1, two

68. (66:1) Pseudepiphallus, pseudepiphallic sclerite, dorsal, medial lobes, direction of apex (CI=40; RI=40; DELTRAN):
    0, straight
    1, dorsally curved
    2, inwards curved

69. (66:1 – 67:1) Pseudepiphallus, pseudepiphallic sclerite, dorsal, median lobes, notch between medial lobes, deepness (CI=50; RI=75):
    0, not transpassing the level of pseudepiphallic sclerite
    1, below the level of pseudepiphallic sclerite

70. Pseudepiphallus, pseudepiphallic sclerite, lateral lophi, number of projections (CI=33; RI=50):
    0, one
    1, two

71. Pseudepiphallus, pseudepiphallic sclerite, lateral lophi, main projection, direction (CI=25; RI=57; DELTRAN):
    0, straight
    1, ventrally curved
    2, dorsally curved

72. (70:1) Pseudepiphallus, pseudepiphallic sclerite, lateral lophi, dorsal projection, direction (CI=100; RI=100; DELTRAN):
    0, straight
    1, dorsally curved

73. Pseudepiphallus, pseudepiphallic sclerite, dorsum, bristles (CI=16; RI=61):
    0, absent

1, present

74. Pseudepiphallus, pseudepiphallic sclerite, lateral lophi, bristles (CI=11; RI=52; DELTRAN):
    0, absent
    1, present

75. (74:1) Pseudepiphallus, pseudepiphallic sclerite, lateral lophi, bristles, position (CI=40; RI=25; DELTRAN):
    0, external
    1, internal
    2, both

76. Pseudepiphallus, pseudepiphallic parameres (CI=100; RI=100):
    0, absent
    1, present

77. (76:1) Pseudepiphallus, pseudepiphallic parameres, size in relation to lateral lophi (CI=28; RI=61; ACCTRAN):
    0, shorter
    1, equal
    2, longer

78. (76:1) Pseudepiphallus, pseudepiphallic parameres, position in relation to endophallic sclerite (CI=16; RI=44; ACCTRAN):
    0, medial
    1, lateral

79. (76:1) Pseudepiphallus, pseudepiphallic parameres, position in relation to the base of pseudepiphallic sclerite (CI=25; RI=25):
    0, basal
    1, distal

80. (76:1) Pseudepiphallus, pseudepiphallic parameres, connection to pseudepiphallic sclerite, development (CI=28; RI=78):
    - 0, not connected
    - 1, membranous
    - 2, fused

81. (76:1) Pseudepiphallus, pseudepiphallic parameres, membranous connection with ectophallic ventral projection, lenght (CI=50; RI=95):
    - 0, short, sclerites almost touching
    - 1, long, sclerites very distant

82. (76:1) Pseudepiphallus, pseudepiphallic parameres, membranous connection with ectophallic fold (CI=11; RI=55):
    - 0, absent
    - 1, present

83. (76:1) Pseudepiphallus, pseudepiphallic parameres, apex, form (CI=18; RI=62; ACCTRAN):
    - 0, rounded
    - 1, thin
    - 2, lamella

84. (76:1) Pseudepiphallus, pseudepiphallic parameres, apex, direction (CI=25; RI=62; DELTRAN):
    - 0, inward
    - 1, outward
    - 2, posterrad

Ectophallic invagination

85. Ectophallic invagination, ectophallic apodemes, size in relation to rami (CI=25; RI=64; ACCTRAN):
    - 0, shorter
    - 1, equal
    - 2, longer

86. Ectophallic invagination, ectophallic apodemes, orientation (CI=25; RI=75; ACCTRAN):
    - 0, parallel
    - 1, divergent

87. Ectophallic invagination, ectophallic apodemes, form:
    - 0, simple
    - 1, bifurcated

88. Ectophallic invagination, ectophallic medial projections (CI=20; RI=55):
    - 0, absent
    - 1, present

89. (88:1) Ectophallic invagination, ectophallic medial projection, direction (CI=14; RI=45; DELTRAN):
    - 0, transversally
    - 1, laterally

90. (88:1) Ectophallic invagination, ectophallic medial projection, size in relation to ectophallic apodemes (CI=100; RI=100):
    - 0, shorter
    - 1, longer

91. (88:1) Ectophallic invagination, ectophallic medial projection, apex position in relation to endophallic sclerite (CI=25; RI=25; DELTRAN):
    - 0, posterior
    - 1, underlapping

92. (88:1) Ectophallic invagination, ectophallic medial projection, membranous connection with ectophallic fold (CI=50; RI=83):
    - 0, absent
    - 1, present

93. Ectophallic invagination, ectophallic ventral projection (CI=20; RI=55):
    0, absent
    1, present

94. (93:1) Ectophallic invagination, ectophallic ventral projection, direction (CI=14; RI=40):
    0, straight
    1, outwards directed

95. (93:1) Ectophallic invagination, ectophallic ventral projection, size in relation to ectophallic apodemes (CI=16; RI=28; ACCTRAN):
    0, shorter
    1, longer

96. (93:1) Ectophallic invagination, ectophallic ventral projection, membranous connection with ectophallic fold (CI=12; RI=53; DELTRAN):
    0, absent
    1, present

97. Ectophallic invagination, ectophallic fold, form (CI=60; RI=89; DELTRAN):
    0, two projection that form medially two short lamellas connected
    1, very long fold that ends with two lammelas
    2, short and wide flattened plate
    3, elongate sclerite

Endophallus

98. Endophallus, endophallic sclerite, position in relation to basal portion of pseudepiphallic sclerite (CI=16; RI=64; DELTRAN):
    0, anteriorly
    1, medially
    2, posteriorly

99. Endophallus, endophallic sclerite, width (CI=33; RI=71):
    0, large

1, thin

100. Endophallus, endophallic sclerite, length in relation to ectophallic fold (CI=22; RI=50; ACCTRAN):
    0, shorter
    1, longer
    2, equal

101. Endophallus, endophallic sclerite, form (CI=33; RI=83; DELTRAN):
    0, cylindric
    1, ventrally concave

102. (101:0) Endophallus, endophallic sclerite, openings (CI=16; RI=64; ACCTRAN):
    0, none
    1, posterior opening
    2, anterior and posterior openings (tubular)

103. Endophallus, endophallic sclerite, apex, form (CI=28; RI=50):
    0, rounded
    1, thin

104. Endophallus, endophallic apodemes (CI=50; RI=75):
    0, absent
    1, present

105. (104:1) Endophallus, endophallic apodemes, number (CI=33; RI=75):
    0, simple
    1, paired

106. (104:1) Endophallus, endophallic apodemes, length in relation to endophallic sclerite (CI=50; RI=66):
    0, shorter
    1, equal
    2, longer

3.2 Analysis

The phylogenetic analysis with equal weight resulted in 14 most parsimonious trees, with 483 steps, consistency index 0.27 and retention index 0.65. The strict consensus obtained is presented with Bremmer support (Fig. 1), as well as one of the most parsimonious trees with optimized characters (Fig. 2) and with clades witch characters are discussed (Fig. 3).

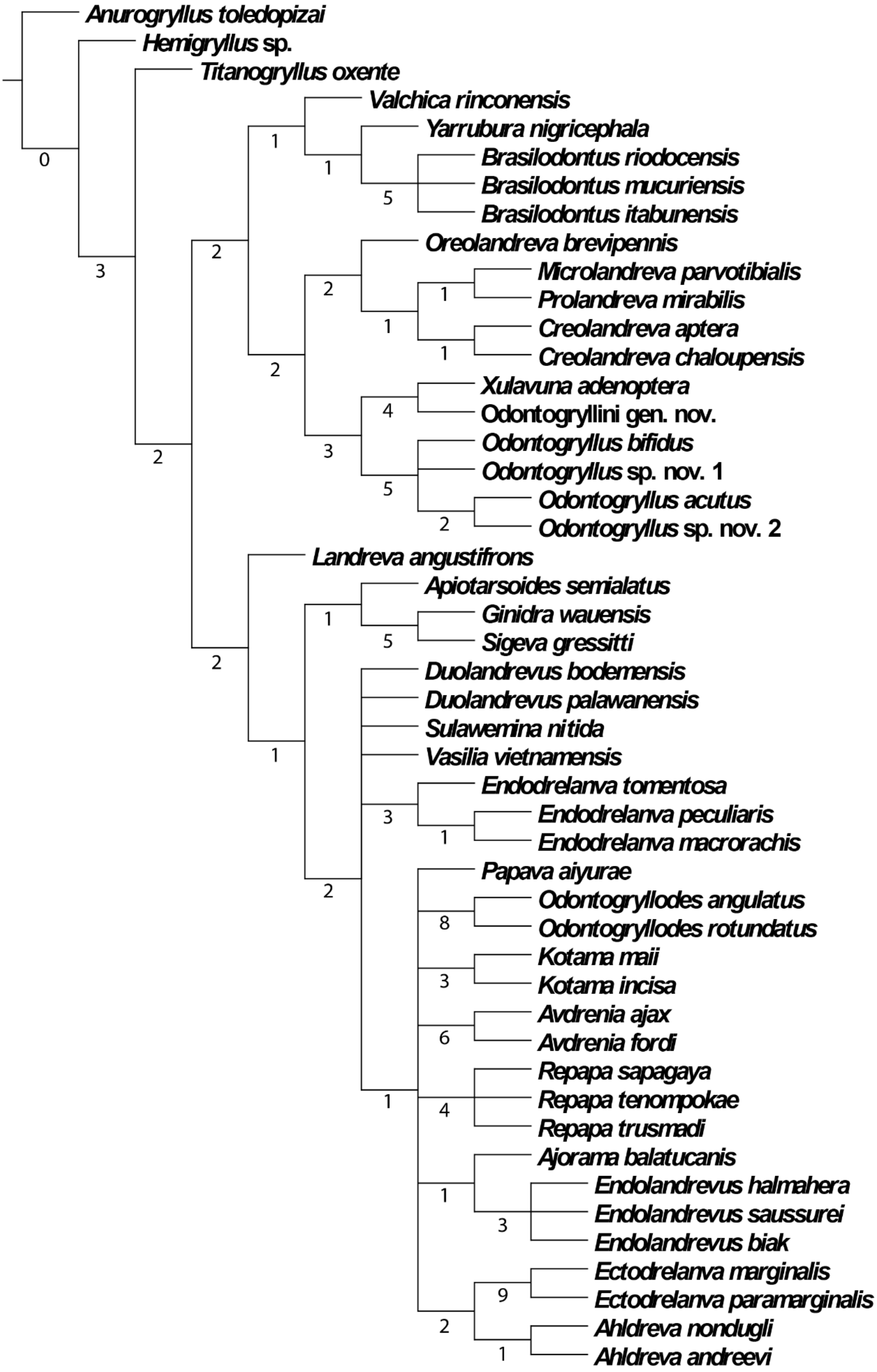

Figure 1 - Strict consensus tree of 14 most parsimonious trees with Bremmer support values.

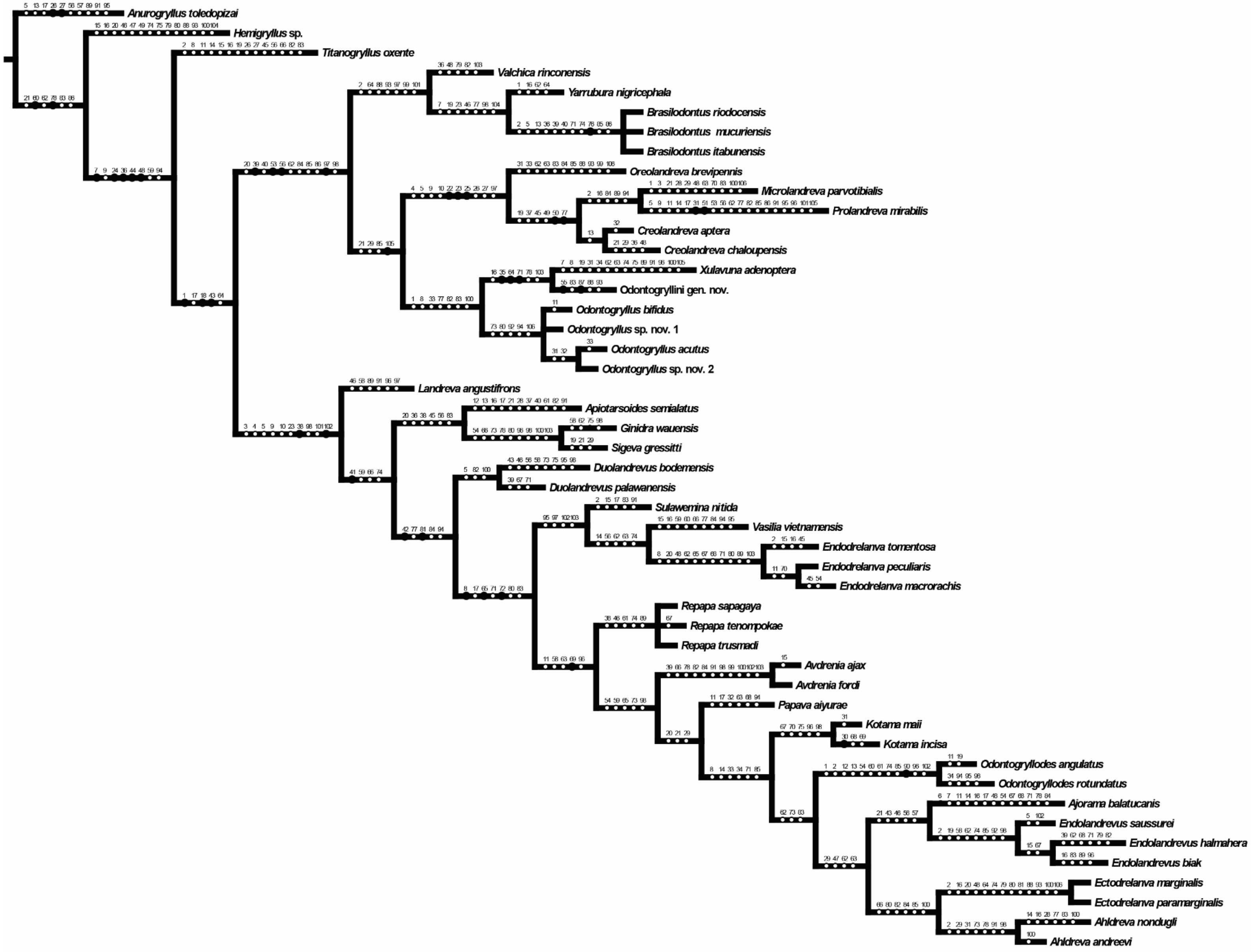

Figure 2 - One of 14 most parsimonious trees with characters optimized. White circles indicate homoplastic synapomorphies, black circles exclusive synapomorphies. L= 483.

Figure 3- One of 14 most parsimonious trees with some clades indicated

4 Discussion

The subfamily Landrevinae was recovery monophyletic in the clade A, with all 45 terminals from internal group. This clade is sustained by three exclusive synapomorphies, (1:1) vertex flattened, (18:1) pronotum with lateral lobes border in diagonal and (43:1) forewings pergamenous without mirror. Moreover, this clade also has two homoplastic synapomorphies, (17:1) pronotum posterior margin with bristles and (64:2) pseudepiphallic sclerite with dorsum completely scletotized.

The clade B gathered Odontogryllini and Prolandrevini, sustained by three exclusive synapomorphies and five homoplastic synapomorphies. The exclusive ones are (53:1) rami like a flattened plate, (56:0) distal portion of ramus sclerite straight and (97:3) ectophallic fold as a elongated sclerite. The homoplastic are (20:0) tibia I without external tympanum, (40:0) forewings pergamenous without harp, (62:0) rami shorter than pseudepiphallic sclerite, (84:0) pseudepiphallic parameres inward directed, (85:1) ectophallic apodemes with same size than rami, and (86:0) ectophallic apodemes parallels.

The clade C grouped the genera *Valchica*, *Yarrubura* and *Brasilodontus*. It is supported only by homoplastic synapomorphies, (2:2) head narrower than pronotum, (64:1) pseudepiphallic sclerite with dorsal sclerotization reduced, (88:0) ectophallic medial projections absent, (93:0) ectophallic ventral projection absent, (99:1) endophallic sclerite thin, and (101:0) endophallic sclerite cylindrical.

The clade D is composed by Prolandrevinae as a sister group of *Odontogryllus*, Odontogryllini gen. nov. and *Xulavuna*. Is supported by one synapomorphie, (105:1) endophallic apodemes paired, as well as four homoplastic synapomorphies, (21:0) tibia I without internal tympanum, (29:0) forewings coriaceous, (85:2) ectophallic apodemes longer than rami, (93:2) endophallic sclerite positioned posteriorly to the basal portion of pseudepiphallic sclerite.

The clade E is Prolandrevini, supported by three exclusive synapomorphies, (22:0) tibia I with two apical spurs, (23:0) tibia II with two apical spurs, and (25:1) tibia III with subapical spines between spurs. This presence of spines, sometimes tiny, between the spurs was used by Gorochov (2016) to separate Prolandrevini from Landrevini. Besides, the clade is also supported by six homoplastic synapomorphies, (4:0) fastigium narrow than scape, (5:1) coronal suture not visible, (9:0) maxillary palpi fifth palpomere with uniform coloration and (10:0) truncated, (26:0) tibia III with three internal subapical spurs and (27:0) three external.

The clade F is composed by *Odontogryllus*, *Xulavuna* and Odontogryllini gen. nov., supported by one synapomorphies, (97:2) ectophallic fold like a short and wide flattened plate, as well as seven homoplastic synapomorphies: (1:0) vertex rounded, (8:2) maxillary palpi fifth palpomere cylindrical, (32:0) forewings coriaceous with lateral field, (77:0) pseudepiphallic parameres shorter than lateral lophi, (82:1) pseudepiphallic parameres with membranous connection to ectophallic fold, (83:0) pseudepiphallic parameres with rounded apex, and (100:1) endophallic sclerite longer than ectophallic fold.

Within clade F, the relation between *Xulavuna* and Odontogryllini gen. nov is well supported by three exclusive synapomorphies, (32:1) forewings coriaceous with glandular structures, (64:0) pseudepiphallic sclerite with dorsal sclerotization completely absent, and (71:1) pseudepiphallic sclerite lateral lophi main projection ventrally curved.

The clade G is composed by Landrevini, sustained by two synapomorphies: (38:1) stridulatory file curved twice (S-shaped) and (102:1) endophallic sclerite with one posterior opening. The first one was used by Gorochov (2016) to differentiate Landrevini from Odontogryllini and Prolandrevini. However, many genera in these tribes do not have developed wings with stridulatory file. The second one is not comment in any literature, which is surprising since it would be interesting to know what function this opening has. This clade is also supported by eight homoplastic synapomorphies: (3:1) fastigium developed, (4:0) fastigium wider than scape; (5:1) coronal suture not visible, (9:0) maxillary palpi fifth palpomere with uniform coloration, (10:0) maxillary palpi fifth palpomere truncated, (23:1) tibia II with three apical spurs, (98:0) endophallic sclerite positioned anteriorly than the pseudepiphallic sclerite and (101:0) endophallic sclerite cylindrical.

With *Apiotarsoides*, *Ginidra* and *Sigeva*, the clade H is not sustained by any exclusive synapomorphies, but only by six homoplastic synapomorphies. They are (20:0) tibia I without external tympanum, (36:1) forewings pergameneous covering the abdomen until tergite I only, (38:0) forewings pergameneous with stridulatory file curved once, (45:0) forewings pergameneous lateral field same size as dorsal field, (56:2) distal portion of ramus sclerite strongly curved internally, (83:0) pseudepiphallic parameres with rounded apex.

The clade I is composed by several genera and supported by one exclusive synapomorphies, (69:0) notch between medial lobes not transpassing the level of pseudepiphallic sclerite. Furthermore, they also have four homoplastic synapomorphies, (20:0) pronotum disc without bristles, (58:1) rami curved ventrally, (63:1) pseudepiphallic sclerite distal portion same wide than proximal portion, (96:1) membranous connection between ectophallic ventral projection and ectophallic fold present.

5 Conclusions

The results show Landrevinae as a monophyletic group. Although the internal relationships are almost resolved (the consensus tree is satisfactory), the support of most clades are low and can collapse with few steps.

The tribe Landrevini was also recovered as monophyletic, but the internal nodes are not solved in the consensus tree. Odontogryllini was recovered as paraphyletic, with Prolandrevini as monophyletic and nested inside Odontogryllini. These clade in recovered in the consensus tree.

This work is the first step towards a better understanding of this group of crickets. The taxonomic work also needs to move forward, since several Landrevinae genera need revision, whether monotypic or inflated genera. Access to genetic material data can also help to clarify some points, especially when more taxa are sequenced.

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Appendix

Appendix 1 - Examined material. Abbreviations: BPBM, Bernice Pauahi Bishop Museum; IB-USP, Laboratório de Sistemática e Biogeografia de Insecta, USP; MHNH, Muséum national d'Histoire naturelle; MZSP, Museu de Zoologia da Universidade de São Paulo; UBTU, Laboratório de Insetos, UNESP Botucatu; ZIN, Zoological Institute of Russian Academy of Science.

Taxon	**Analyzed material**	**Collection**
Ahldreva andreevi Gorochov, 1996 Locality: New Guinea	Holotype (male)	ZIN
Ahldreva nondugli Otte, 1988 Locality: New Guinea, NE, Ahl Valley, Nondugl	Holotype (male)	BPBM
Ajorama balatukanis Otte, 1988 Locality: Philippines, Misamis Oriental, Mount Balatukan	Holotype (male)	BPBM
Apiotarsoides semialatus Chopard, 1931 Locality: Maluka, Kai Island	Syntype (male)	MNHN
Avdrenia ajax Otte, 1988 Locality: Solomon Island, Kolombangarae, Pepel	Holotype (male)	BPBM
Avdrenia fordi Otte, 1988 Locality: Bismarck Archipelago, New Ireland: southwest	Holotype (male)	BPBM
Duolandrevus (Jorama) bodemensis (Otte, 1988) Locality: New Guinea, Irian Jaya, Bodem	Holotype (male)	BPBM
Duolandrevus (Jorama) palawanensis (Otte, 1988) Locality: Philippines, Palawan	Holotype (male)	BPBM
Ectodrelanva marginalis Gorochov, 2000 Locality: Thailand, Phetchaburi, Kaeng Krachan National Park	Holotype (male)	ZIN
Ectodrelanva paramarginalis Gorochov, 2000 Locality: Cambodia, Rattanakiri Province, Banlung	Holotype (male)	ZIN
Endodrelanva macrorachis Gorochov, 2016 Locality: Borneo, Sabah, Mount Trus Madi	Holotype (male)	ZIN
Endodrelanva peculiares Gorochov, 2016 Locality: Borneo, Sabah, Mount Trus Madi	Holotype (male)	ZIN
Endodrelanva tomentosa juara Gorochov, 2016 Locality: Malaya, Peninsular Malaysia, Pahang, Tioman Island	Holotype (male)	ZIN
Endolandrevus biak Gorochov, 2016 Locality: New Guinea, Biak Island	Holotype (male)	ZIN
Endolandrevus halmahera Gorochov, 2016 Locality: Malesia, Maluka, Halmahera Island	Holotype (male)	ZIN
Endolandrevus saussurei Gorochov, 2016 Locality: Malesia, Maluka, Halmahera Island	Holotype (male)	ZIN

Ginidra wauensis Otte, 1988 Locality: New Guinea, Papua New Guinea, Morobe Province	Holotype (male)	BPBM
Kotama incisa Gorochov, 2016 Locality: Maluka, Halmahera Island, near Wasile Bay	Holotype (male)	ZIN
Kotama maai Otte, 1988 Locality: Borneo, British, Tenompok	Holotype (male)	BPBM
Landreva angustifrons Chopard, 1936 Locality: Sri Lanka, Labugama	Holotype (male)	MNHN
Odontogryllodes angulatus Gorochov, 2016 Locality: Malaya, Peninsular Malaysia, Pahang, Tioman Island	Holotype (male)	ZIN
Odontogryllodes rotundatus Gorochov, 2016 Locality: Malesia, Sumatera, Bengkulu Province	Holotype (male)	ZIN
Otteana truncicola Gorochov, 1996 Locality: Vietnam, Gia Lai Province	Holotype (male)	ZIN
Papava aiyurae Otte, 1988 Locality: New Guinea, East Highlands	Holotype (male)	BPBM
Repapa sapagaya Otte, 1988 Locality: Borneo, Sabah, Sandakan	Holotype (male)	BPBM
Repapa tenompokae Otte, 1988 Locality: Borneo, Sabah	Holotype (male)	BPBM
Repapa trusmadi Gorochov, 2016 Locality: Borneo, Sabah, Mount Trus Madi	Holotype (male)	ZIN
Sigeva gressitti Otte, 1988 Locality: New Guinea, Mt. Suckling	Holotype (male)	BPBM
Sulawemina nítida Gorochov, 2016 Locality: Sulawesi, Bogani Nani Wartabone National Park	Holotype (male)	ZIN
Vasilia vietnamensis Gorochov, 1988 Locality: Vietnam	Holotype (male)	ZIN
Odontogryllini gen. nov. 1 Locality: Brazil, Mato Grosso, Cotriguaçu		MZSP
Brasilodontus itamarajuensis de Mello & Campos, 2014 Locality: Brazil, Bahia, Itamaraju, Parna Histórico Monte Pascoal	Holotype (male) Topotypes	MZSP UBTU
Brasilodontus mucuriensis de Mello, 1992 Locality: Brazil, Bahia, Mucuri, Fazenda Farol	Holotype (male) Topotypes	MZSP UBTU
Brasilodontus riodocensis de Mello, 1992 Locality: Brazil, Espírito Santo, Linhares, Reserva Natural Vale	Holotype (male) Topotypes	MZSP UBTU
Odontogryllus acutus de Mello, 1992 Locality: Brazil, Amazonas, Humaitá	Holotype (male)	MZSP
Odontogryllus bifidus de Mello, 1992	Holotype (male)	MZSP

Locality: Brazil, Amazonas, Humaitá		
Odontogryllus sp. nov. 1 Locality: Brazil, Amazonas, Parque Nacional do Jaú		MZSP
Odontogryllus sp. nov. 2 Locality: Brazil, Pará, Belterra		MZSP
Valchica rinconensis de Mello, 1992 Locality: Costa Rica, Osa Peninsula, Rincon	Holotype (male)	UBTU
Xulavuna adenoptera de Mello & Campos, 2014 Locality: Brazil, Amazonas, Reserva Florestal Adolpho Ducke	Holotype (male) Topotypes	MZSP UBTU
Yarrubura nigricephala de Mello & Campos, 2014 Locality: Brazil, Amazonas, Reserva Florestal Adolpho Ducke	Holotype (male) Topotypes	MZSP UBTU
Creolandreva aptera Locality: Reunion, Saint-Philippe, Basse Vallée	Holotype (male)	MNHN
Creolandreva chaloupensis Locality: Reunion, Ravine de la Grande Chaloupe	Holotype (male)	MNHN
Microlandreva parvotibialis Hugel, 2009 Locality: Reunion	Holotype (male)	MNHN
Oreolandreva brevipennis Chopard, 1945 Locality: Cameroon, Mt Cameroon	Holotype (male)	MNHN
Prolandreva mirabilis Gorochov, 2010 Locality: Southern Africa, KwaZulu, Vernon Crookes Nature Reserve	Holotype (male)	ZIN
Anurogryllus toledopizai (de Mello, 1988) Locality: Brazil, Rio Grande do Sul, Canguçu		MZSP
Hemygryllus sp. Locality: Brazil, Amazonas, Tarumã-mirim		UBTU
Titanogryllus oxente Souza-Dias & de Mello, 2018 Locality: Brazil, Bahia		MZSP

Appendix 2 - Data matrix: terminals and characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Anurogryllus toledopizai	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1
Hemigryllus sp.	0	1	0	1	0	0	1	1	0	1	1	0	0	1	2	2	0	0	1	0
Titanogryllus oxente	0	0	0	1	0	0	2	2	1	1	0	0	0	0	0	2	0	0	0	1
Odontogryllus acutus	0	1	0	1	0	0	2	2	1	1	1	0	0	1	1	1	1	1	1	0
Odontogryllus bifidus	0	1	0	1	0	0	2	2	1	1	0	0	0	1	1	1	1	1	1	0
Odontogryllus sp. nov. 1	0	1	0	1	0	0	2	2	1	1	1	0	0	1	1	1	1	1	1	0
Odontogryllus sp. nov. 2	0	1	0	1	0	0	2	2	1	1	1	0	0	1	1	1	1	1	1	0
Brasilodontus riodocensis	1	1	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0
Brasilodontus mucuriensis	1	1	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0
Brasilodontus itabunensis	1	1	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0
Valchica rinconensis	1	2	0	1	0	0	2	1	1	1	1	0	0	1	1	1	1	1	1	0
Yarrubura nigricephala	0	2	0	1	0	0	1	1	1	1	1	0	0	1	1	2	1	1	0	0
Xulavuna adenoptera	0	1	0	1	0	0	1	1	1	1	1	0	0	1	1	0	1	1	0	0
Odontogryllini gen. nov.	0	1	0	1	0	0	2	2	1	1	1	0	0	1	1	0	1	1	1	0
Ahldreva nondugli	1	0	1	0	1	0	2	1	0	0	0	0	0	1	1	0	0	1	1	0
Ahldreva andreevi	1	0	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	0
Ajorama balatucanis	1	1	1	0	1	1	1	1	0	0	1	0	0	1	1	2	1	1	1	0
Apiotarsoides semialatus	1	1	1	0	1	0	2	1	0	0	1	1	1	1	1	2	0	1	1	0
Avdrenia ajax	1	1	1	0	1	0	2	0	0	0	0	0	0	1	2	1	0	1	1	1
Avdrenia fordi	1	1	1	0	1	0	2	0	0	0	0	0	0	1	1	1	0	1	1	1
Duolandrevus bodemensis	1	1	1	0	0	0	2	1	0	0	1	0	0	1	1	1	1	1	1	1
Duolandrevus palawanensis	1	1	1	0	0	0	2	1	0	0	1	0	0	1	1	1	1	1	1	1
Ectodrelanva marginalis	1	2	1	0	1	0	2	1	0	0	0	0	0	0	1	2	0	1	1	1
Ectodrelanva paramarginalis	1	2	1	0	1	0	2	1	0	0	0	0	0	0	1	2	0	1	1	1
Endodrelanva peculiares	1	1	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	0
Endodrelanva tomentosa	1	2	1	0	1	0	2	1	0	0	1	0	0	0	2	2	0	1	1	0
Endodrelanva macrorachis	1	1	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	0
Endolandrevus halmahera	1	0	1	0	1	0	2	1	0	0	0	0	0	0	2	1	0	1	0	0
Endolandrevus saussurei	1	0	1	0	0	0	2	1	0	0	0	0	0	0	1	1	0	1	0	0
Endolandrevus biak	1	0	1	0	1	0	2	1	0	0	0	0	0	0	2	2	0	1	0	0
Ginidra wauensis	1	1	1	0	1	0	2	1	0	0	1	0	0	1	1	1	1	1	1	0
Kotama maii	1	1	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	0
Kotama incisa	1	1	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	0
Landreva angustifrons	1	1	1	0	1	0	2	1	0	0	1	0	0	1	1	1	1	1	1	1
Odontogryllodes angulatus	0	2	1	0	1	0	2	1	0	0	1	1	1	0	1	1	0	1	0	0
Odontogryllodes rotundatus	0	2	1	0	1	0	2	1	0	0	0	1	1	0	1	1	0	1	1	0
Papava aiyurae	1	1	1	0	1	0	2	0	0	0	1	0	0	1	1	1	1	1	1	0
Repapa sapagaya	1	1	1	0	1	0	2	0	0	0	0	0	0	1	1	1	0	1	1	1
Repapa tenompokae	1	1	1	0	1	0	2	0	0	0	0	0	0	1	1	1	0	1	1	1
Repapa trusmadi	1	1	1	0	1	0	2	0	0	0	0	0	0	1	1	1	0	1	1	1
Sigeva gressitti	1	1	1	0	1	0	2	1	0	0	1	0	0	1	1	1	1	1	0	0
Sulawemina nítida	1	0	1	0	1	0	2	0	0	0	1	0	0	1	0	1	1	1	1	1
Vasilia vietnamensis	1	1	1	0	1	0	2	0	0	0	1	0	0	0	2	2	0	1	1	1
Creolandreva aptera	1	1	0	0	1	0	2	1	0	0	1	0	1	1	1	1	1	1	0	0
Creolandreva chaloupensis	1	1	0	0	1	0	2	1	0	0	1	0	1	1	1	1	1	1	0	0
Microlandreva parvotibialis	0	0	1	0	1	0	2	1	0	0	1	0	0	1	1	2	1	1	0	0
Oreolandreva brevipennis	1	1	0	0	1	0	2	1	0	0	1	0	0	1	1	1	1	1	1	0
Prolandreva mirabilis	1	0	0	0	0	0	2	1	1	0	0	0	0	0	1	2	0	1	0	0

Appendix 2 - Data matrix: terminals and characters (continuation).

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Anurogryllus toledopizai	0	1	2	0	-	2	2	0	1	-	-	-	-	-	-
Hemigryllus sp.	1	1	2	0	-	1	1	0	1	-	-	-	-	-	-
Titanogryllus oxente	1	1	2	1	0	0	0	0	1	-	-	-	-	-	-
Odontogryllus acutus	0	1	2	1	0	1	1	0	0	0	1	0	0	-	0
Odontogryllus bifidus	0	1	2	1	0	1	1	0	0	0	0	1	1	0	0
Odontogryllus sp. nov. 1	0	1	2	1	0	1	1	0	0	0	0	1	1	0	0
Odontogryllus sp. nov. 2	0	1	2	1	0	1	1	0	0	0	1	0	1	0	0
Brasilodontus riodocensis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Brasilodontus mucuriensis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Brasilodontus itabunensis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Valchica rinconensis	1	1	2	1	0	1	1	0	1	-	-	-	-	-	-
Yarrubura nigricephala	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Xulavuna adenoptera	0	1	2	1	0	1	1	0	0	0	1	1	1	1	1
Odontogryllini gen. nov.	0	1	2	1	0	1	1	0	0	0	0	1	1	0	1
Ahldreva nondugli	0	1	1	1	0	1	1	1	0	0	1	1	1	1	0
Ahldreva andreevi	0	1	1	1	0	1	1	0	0	0	1	1	1	1	0
Ajorama balatucanis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Apiotarsoides semialatus	0	1	1	1	0	1	1	1	1	-	-	-	-	-	-
Avdrenia ajax	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Avdrenia fordi	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Duolandrevus bodemensis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Duolandrevus palawanensis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Ectodrelanva marginalis	0	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Ectodrelanva paramarginalis	0	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Endodrelanva peculiares	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Endodrelanva tomentosa	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Endodrelanva macrorachis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Endolandrevus halmahera	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Endolandrevus saussurei	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Endolandrevus biak	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Ginidra wauensis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Kotama maii	0	1	1	1	0	1	1	0	0	0	1	1	1	1	0
Kotama incisa	0	1	1	1	0	1	1	0	0	1	0	1	1	1	0
Landreva angustifrons	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Odontogryllodes angulatus	0	1	1	1	0	1	1	0	0	0	0	1	1	1	0
Odontogryllodes rotundatus	0	1	1	1	0	1	1	0	0	0	0	1	1	0	0
Papava aiyurae	0	1	1	1	0	1	1	0	0	0	0	0	0	-	0
Repapa sapagaya	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Repapa tenompokae	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Repapa trusmadi	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Sigeva gressitti	0	1	1	1	0	1	1	0	0	0	0	1	0	-	0
Sulawemina nítida	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Vasilia vietnamensis	1	1	1	1	0	1	1	0	1	-	-	-	-	-	-
Creolandreva aptera	0	0	0	1	1	0	0	0	0	0	0	0	0	-	0
Creolandreva chaloupensis	1	0	0	1	1	0	0	0	1	-	-	-	-	-	-
Microlandreva parvotibialis	1	0	0	1	1	0	0	1	1	-	-	-	-	-	-
Oreolandreva brevipennis	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0
Prolandreva mirabilis	0	0	0	1	1	0	0	0	0	0	2	1	0	-	0

Appendix 2 - Data matrix: terminals and characters (continuation).

	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Anurogryllus toledopizai	3	1	0	1	1	0	-	1	1	1	0	0	1	1	0	-	1	0
Hemigryllus sp.	3	1	0	1	1	0	-	1	1	1	1	1	1	0	0	-	0	0
Titanogryllus oxente	2	1	0	1	1	0	-	1	0	0	0	0	0	-	0	-	0	0
Odontogryllus acutus	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	1
Odontogryllus bifidus	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	1
Odontogryllus sp. nov. 1	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	1
Odontogryllus sp. nov. 2	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	1
Brasilodontus riodocensis	1	1	0	?	1	0	-	0	0	1	1	0	0	-	0	-	0	1
Brasilodontus mucuriensis	1	1	0	1	1	0	-	0	0	1	1	0	0	-	0	-	0	1
Brasilodontus itabunensis	1	1	0	1	1	0	-	0	0	1	1	0	0	-	0	-	0	1
Valchica rinconensis	1	1	?	?	0	-	-	0	0	?	?	?	1	1	0	-	0	1
Yarrubura nigricephala	2	1	0	2	0	-	-	0	0	1	1	0	0	-	0	-	0	1
Xulavuna adenoptera	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	1
Odontogryllini gen. nov.	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	1
Ahldreva nondugli	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Ahldreva andreevi	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Ajorama balatucanis	2	1	1	1	1	1	?	1	0	1	1	1	1	1	0	-	0	0
Apiotarsoides semialatus	1	0	-	-	0	-	-	0	-	0	0	0	0	-	0	-	0	0
Avdrenia ajax	2	1	1	0	1	1	1	0	0	1	0	0	0	-	0	-	0	0
Avdrenia fordi	2	1	1	0	1	1	1	0	0	1	0	0	0	-	0	-	0	0
Duolandrevus bodemensis	2	1	1	1	1	1	1	1	0	1	1	0	0	-	0	-	0	0
Duolandrevus palawanensis	2	1	1	0	1	1	1	0	0	?	?	?	0	-	0	-	0	0
Ectodrelanva marginalis	2	1	1	1	1	1	1	0	0	1	0	1	1	1	0	-	0	0
Ectodrelanva paramarginalis	2	1	1	1	1	1	1	0	0	1	0	1	1	1	0	-	0	0
Endodrelanva peculiares	2	1	1	1	1	1	1	0	0	1	0	0	1	1	0	-	0	0
Endodrelanva tomentosa	2	1	1	1	1	1	1	0	0	0	0	0	1	1	0	-	0	0
Endodrelanva macrorachis	2	1	1	1	1	1	1	0	0	0	0	0	1	1	0	-	0	0
Endolandrevus halmahera	2	1	1	0	1	1	1	1	0	1	1	1	0	-	0	-	0	0
Endolandrevus saussurei	2	1	1	1	1	1	1	1	0	1	1	1	0	-	0	-	0	0
Endolandrevus biak	2	1	1	1	1	1	1	1	0	1	1	1	0	-	0	-	0	0
Ginidra wauensis	1	1	0	1	1	1	0	0	0	0	0	0	0	-	0	-	0	0
Kotama maii	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Kotama incisa	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Landreva angustifrons	2	1	1	1	1	0	-	0	0	1	1	0	0	-	0	-	0	0
Odontogryllodes angulatus	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Odontogryllodes rotundatus	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Papava aiyurae	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Repapa sapagaya	2	1	0	1	1	1	1	0	0	1	1	0	0	-	0	-	0	0
Repapa tenompokae	2	1	0	1	1	1	1	0	0	1	1	0	0	-	0	-	0	0
Repapa trusmadi	2	1	0	1	1	1	1	0	0	1	1	0	0	-	0	-	0	0
Sigeva gressitti	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	0
Sulawemina nítida	2	1	1	1	1	1	1	0	0	1	0	0	?	?	0	-	0	0
Vasilia vietnamensis	2	1	1	1	1	1	1	0	0	1	0	0	0	-	0	-	0	0
Creolandreva aptera	-	-	-	-	-	-	-	-	-	-	-	-	0	-	1	0	0	1
Creolandreva chaloupensis	3	0	-	2	0	-	-	0	?	0	0	0	1	0	1	0	0	1
Microlandreva parvotibialis	2	0	-	2	0	-	-	0	?	0	0	0	1	0	1	0	0	1
Oreolandreva brevipennis	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	0	1
Prolandreva mirabilis	-	-	-	-	-	-	-	-	-	-	-	-	0	-	1	1	0	0

Appendix 2 - Data matrix: terminals and characters (continuation).

	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
Anurogryllus toledopizai	0	-	2	1	0	1	0	0	1	0	1	0	0	-	-	-	0	0
Hemigryllus sp.	0	-	1	0	0	1	1	0	2	0	1	0	0	-	-	-	0	0
Titanogryllus oxente	0	-	2	0	0	0	1	0	2	0	1	0	1	0	0	-	0	0
Odontogryllus acutus	-	0	0	0	0	0	1	0	0	0	2	0	0	-	-	-	0	0
Odontogryllus bifidus	-	0	0	0	0	0	1	0	0	0	2	0	0	-	-	-	0	0
Odontogryllus sp. nov. 1	-	0	0	0	0	0	1	0	0	0	2	0	0	-	-	-	0	0
Odontogryllus sp. nov. 2	-	0	0	0	0	0	1	0	0	0	2	0	0	-	-	-	0	0
Brasilodontus riodocensis	-	0	0	0	0	0	1	0	0	0	1	0	0	-	-	-	0	2
Brasilodontus mucuriensis	-	0	0	0	0	0	1	0	0	0	1	0	0	-	-	-	0	2
Brasilodontus itabunensis	-	0	0	0	0	0	1	0	0	0	1	0	0	-	-	-	0	2
Valchica rinconensis	-	0	0	0	0	0	1	0	0	0	1	0	0	-	-	-	0	0
Yarrubura nigricephala	-	0	0	0	0	0	1	0	1	0	2	0	0	-	-	-	0	0
Xulavuna adenoptera	-	0	0	0	0	0	1	0	1	1	0	0	0	-	-	-	0	1
Odontogryllini gen. nov.	-	1	0	0	0	0	1	0	0	0	0	0	0	-	-	-	0	1
Ahldreva nondugli	1	-	1	0	1	0	1	0	0	0	2	0	0	-	-	-	0	0
Ahldreva andreevi	1	-	1	0	1	0	1	0	0	0	2	0	0	-	-	-	0	0
Ajorama balatucanis	0	-	2	1	1	0	1	0	0	0	2	0	1	1	1	0	0	2
Apiotarsoides semialatus	0	-	2	0	0	1	1	1	2	0	2	0	1	0	0	-	0	0
Avdrenia ajax	1	-	1	0	1	0	1	0	2	1	2	0	0	-	-	-	0	2
Avdrenia fordi	1	-	1	0	1	0	1	0	2	1	2	0	0	-	-	-	0	2
Duolandrevus bodemensis	0	-	2	0	1	1	1	0	2	0	2	0	1	0	0	-	0	0
Duolandrevus palawanensis	0	-	1	0	0	1	1	0	2	0	2	0	1	1	0	1	0	2
Ectodrelanva marginalis	1	-	1	0	1	0	1	0	0	0	1	0	0	-	-	-	0	0
Ectodrelanva paramarginalis	1	-	1	0	1	0	1	0	0	0	1	0	0	-	-	-	0	0
Endodrelanva peculiares	0	-	2	0	0	1	1	0	0	1	2	0	1	1	2	1	1	0
Endodrelanva tomentosa	0	-	2	0	0	1	1	0	0	1	2	0	1	1	2	1	0	0
Endodrelanva macrorachis	1	-	2	0	0	1	1	0	0	1	2	0	1	1	2	1	1	0
Endolandrevus halmahera	1	-	2	1	0	0	1	0	2	0	2	0	1	1	2	0	0	2
Endolandrevus saussurei	1	-	2	1	0	0	1	0	1	0	2	0	1	0	0	-	0	0
Endolandrevus biak	1	-	2	1	0	0	1	0	1	0	2	0	1	1	0	0	0	0
Ginidra wauensis	1	-	2	0	1	1	1	0	1	0	2	0	0	-	-	-	0	0
Kotama maii	1	-	1	0	1	0	1	0	2	1	2	0	1	1	0	0	1	0
Kotama incisa	1	-	1	0	1	0	1	0	2	1	2	0	1	1	1	1	1	0
Landreva angustifrons	0	-	1	0	1	0	1	0	2	0	2	0	0	-	-	-	0	0
Odontogryllodes angulatus	0	-	1	0	1	0	0	1	1	1	2	0	1	0	0	-	0	0
Odontogryllodes rotundatus	0	-	1	0	1	0	0	1	1	1	2	0	1	0	0	-	0	0
Papava aiyurae	1	-	1	0	1	0	1	0	2	0	2	0	1	0	1	-	0	2
Repapa sapagaya	0	-	1	0	1	1	1	1	2	1	2	1	1	0	0	-	0	2
Repapa tenompokae	0	-	1	0	1	1	1	1	2	1	2	1	1	1	0	0	0	2
Repapa trusmadi	0	-	1	0	1	1	1	1	2	1	2	1	1	0	0	-	0	2
Sigeva gressitti	1	-	2	0	0	1	1	0	2	0	2	0	0	-	-	-	0	0
Sulawemina nítida	0	-	1	0	0	1	1	0	2	0	2	1	1	0	0	-	0	2
Vasilia vietnamensis	0	-	2	0	0	0	0	0	1	1	2	1	0	-	-	-	0	2
Creolandreva aptera	-	0	0	0	0	0	1	0	0	0	2	0	0	-	-	-	0	0
Creolandreva chaloupensis	-	0	0	0	0	0	1	0	0	0	2	0	0	-	-	-	0	0
Microlandreva parvotibialis	-	0	0	0	0	0	1	0	0	1	2	0	0	-	-	-	1	0
Oreolandreva brevipennis	-	0	0	0	0	0	1	0	1	1	2	0	0	-	-	-	-	-
Prolandreva mirabilis	0	-	1	0	0	0	1	0	1	0	2	0	0	-	-	-	0	0

Appendix 2 - Data matrix: terminals and characters (continuation).

	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Anurogryllus toledopizai	-	0	0	-	1	1	0	1	1	0	0	0	2	0	0	0	1	1
Hemigryllus sp.	-	0	1	1	1	1	1	0	0	0	?	1	2	0	1	0	0	-
Titanogryllus oxente	-	0	0	-	1	1	1	1	1	0	1	0	2	0	1	0	1	0
Odontogryllus acutus	-	1	0	-	1	0	1	1	0	0	1	0	0	2	0	0	1	0
Odontogryllus bifidus	-	1	0	-	1	0	1	1	0	0	1	0	0	2	0	0	1	0
Odontogryllus sp. nov. 1	-	1	0	-	1	0	1	1	0	0	1	0	0	2	0	0	1	0
Odontogryllus sp. nov. 2	-	1	0	-	1	0	1	1	0	0	1	0	0	2	0	0	1	0
Brasilodontus riodocensis	-	0	1	0	0	-	-	-	-	-	-	-	-	0	1	0	0	-
Brasilodontus mucuriensis	-	0	1	0	0	-	-	-	-	-	-	-	-	0	1	0	0	-
Brasilodontus itabunensis	-	0	1	0	0	-	-	-	-	-	-	-	-	0	1	0	0	-
Valchica rinconensis	-	0	-	-	1	1	1	0	1	0	1	1	0	1	0	0	0	-
Yarrubura nigricephala	-	0	-	-	1	0	1	1	1	?	0	1	0	1	0	0	0	-
Xulavuna adenoptera	-	0	1	1	1	0	0	1	1	0	1	0	0	2	0	0	1	1
Odontogryllini gen. nov.	-	0	0	-	1	0	0	1	1	0	1	1	0	2	0	1	0	-
Ahldreva nondugli	-	1	1	0	1	1	0	1	1	1	1	0	2	2	1	0	1	0
Ahldreva andreevi	-	1	1	0	1	0	0	1	1	1	1	1	2	2	1	0	1	0
Ajorama balatucanis	-	0	1	0	1	0	0	1	2	1	0	1	2	1	1	0	1	0
Apiotarsoides semialatus	-	0	1	0	1	1	1	1	1	0	1	0	2	0	1	0	1	0
Avdrenia ajax	-	1	1	0	1	0	0	1	2	1	1	2	2	0	1	0	1	0
Avdrenia fordi	-	1	1	0	1	0	0	1	2	1	1	2	2	0	1	0	1	0
Duolandrevus bodemensis	-	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	1	0
Duolandrevus palawanensis	-	0	1	0	1	0	1	1	1	1	1	1	0	0	1	0	1	0
Ectodrelanva marginalis	-	0	0	-	1	0	1	0	0	0	1	1	2	2	1	0	0	-
Ectodrelanva paramarginalis	-	0	0	-	1	0	1	0	0	0	1	1	2	2	1	0	0	-
Endodrelanva peculiares	1	0	0	-	1	0	1	1	1	1	0	2	0	0	1	0	1	1
Endodrelanva tomentosa	-	0	0	-	1	0	1	1	1	1	0	2	0	0	1	0	1	1
Endodrelanva macrorachis	1	0	0	-	1	0	1	1	1	1	0	2	0	0	1	0	1	1
Endolandrevus halmahera	-	0	0	-	1	0	1	0	2	1	1	1	0	0	1	0	1	0
Endolandrevus saussurei	-	0	0	-	1	0	1	1	2	1	0	1	0	0	1	0	1	0
Endolandrevus biak	-	0	0	-	1	0	1	1	2	1	0	0	0	0	1	0	1	1
Ginidra wauensis	-	1	1	2	1	1	0	1	2	0	0	0	2	0	1	0	1	0
Kotama maii	1	1	1	1	1	0	1	1	2	1	0	2	0	1	1	0	1	0
Kotama incisa	1	1	1	1	1	0	1	1	2	1	0	2	0	1	1	0	1	0
Landreva angustifrons	-	0	0	-	1	1	1	1	1	0	?	1	2	0	1	0	1	1
Odontogryllodes angulatus	-	0	0	-	1	0	1	1	2	1	0	1	0	0	1	0	1	0
Odontogryllodes rotundatus	-	0	0	-	1	0	1	1	2	1	0	1	0	0	1	0	1	0
Papava aiyurae	-	1	1	0	1	0	1	1	2	1	0	2	0	0	1	0	1	0
Repapa sapagaya	-	0	0	-	1	0	1	1	2	1	0	2	0	0	1	0	1	1
Repapa tenompokae	-	0	0	-	1	0	1	1	2	1	0	2	0	0	1	0	1	1
Repapa trusmadi	-	0	0	-	1	0	1	1	2	1	0	2	0	0	1	0	1	1
Sigeva gressitti	-	1	?	0	1	1	0	1	2	0	0	0	2	0	1	0	1	0
Sulawemina nítida	-	0	1	0	1	0	1	1	2	1	0	1	0	0	1	0	1	0
Vasilia vietnamensis	-	0	0	-	1	1	1	1	2	1	0	2	1	0	1	0	1	0
Creolandreva aptera	0	0	0	-	1	2	1	1	1	0	0	1	0	2	0	0	1	0
Creolandreva chaloupensis	0	0	0	-	1	2	1	1	1	0	0	1	0	2	0	0	1	0
Microlandreva parvotibialis	0	0	0	-	1	2	1	1	1	0	0	2	2	2	0	0	1	1
Oreolandreva brevipennis	-	0	0	-	1	1	1	1	1	0	0	2	1	1	0	0	0	-
Prolandreva mirabilis	0	0	0	-	1	1	1	1	1	0	1	1	2	0	1	0	1	1

Appendix 2 - Data matrix: terminals and characters (continuation).

	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106
Anurogryllus toledopizai	0	2	?	1	0	1	0	?	1	0	?	1	-	0	1	0	0
Hemigryllus sp.	-	-	-	0	-	-	-	?	1	?	2	1	-	0	0	-	-
Titanogryllus oxente	0	1	1	1	1	0	?	0	1	0	?	1	-	?	1	0	0
Odontogryllus acutus	0	1	0	1	0	0	0	2	2	0	1	1	-	0	1	1	1
Odontogryllus bifidus	0	1	0	1	0	0	0	2	2	0	1	1	-	0	1	1	1
Odontogryllus sp. nov. 1	0	1	0	1	0	0	0	2	2	0	1	1	-	0	1	1	1
Odontogryllus sp. nov. 2	0	1	0	1	0	0	0	2	2	0	1	1	-	0	1	1	1
Brasilodontus riodocensis	-	-	-	0	-	-	-	3	1	1	?	0	0	0	0	-	-
Brasilodontus mucuriensis	-	-	-	0	-	-	-	3	1	1	?	0	0	0	0	-	-
Brasilodontus itabunensis	-	-	-	0	-	-	-	3	1	1	?	0	0	0	0	-	-
Valchica rinconensis	-	-	-	0	-	-	-	3	2	1	?	0	0	1	1	0	0
Yarrubura nigricephala	-	-	-	0	-	-	-	3	1	1	?	?	?	?	0	-	-
Xulavuna adenoptera	0	2	1	1	1	0	1	2	2	0	0	1	-	1	1	0	0
Odontogryllini gen. nov.	-	-	-	0	-	-	-	2	2	0	1	1	-	1	1	1	1
Ahldreva nondugli	0	0	1	1	0	0	1	0	2	0	2	0	1	0	1	0	0
Ahldreva andreevi	0	0	1	1	0	0	1	0	2	0	0	0	1	0	1	0	0
Ajorama balatucanis	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0
Apiotarsoides semialatus	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0
Avdrenia ajax	0	2	1	1	0	0	1	0	2	1	1	0	0	2	1	0	0
Avdrenia fordi	0	2	1	1	0	0	1	0	2	1	1	0	0	2	1	0	0
Duolandrevus bodemensis	0	1	1	1	0	1	0	0	1	0	2	0	1	0	1	0	0
Duolandrevus palawanensis	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	0	0
Ectodrelanva marginalis	-	-	1	0	-	-	-	0	1	0	2	0	1	0	1	0	0
Ectodrelanva paramarginalis	-	-	1	0	-	-	-	0	1	0	2	0	1	0	1	0	0
Endodrelanva peculiares	0	1	1	1	0	1	0	1	0	0	0	0	0	2	1	0	0
Endodrelanva tomentosa	0	1	1	1	0	1	0	1	0	0	0	0	0	2	1	0	0
Endodrelanva macrorachis	0	1	1	1	0	1	0	1	0	0	0	0	0	2	1	0	0
Endolandrevus halmahera	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0
Endolandrevus saussurei	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Endolandrevus biak	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0
Ginidra wauensis	0	1	1	1	1	0	1	0	2	0	2	0	1	1	1	0	0
Kotama maii	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0
Kotama incisa	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0
Landreva angustifrons	0	0	1	1	1	0	1	1	0	0	0	0	1	0	1	0	0
Odontogryllodes angulatus	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0
Odontogryllodes rotundatus	1	1	1	1	1	1	0	0	2	0	0	0	0	0	1	0	0
Papava aiyurae	0	1	1	1	1	0	1	0	1	0	0	0	1	0	1	0	0
Repapa sapagaya	0	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0
Repapa tenompokae	0	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0
Repapa trusmadi	0	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0
Sigeva gressitti	0	1	1	1	1	0	1	0	1	0	2	0	1	1	1	0	0
Sulawemina nítida	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	0
Vasilia vietnamensis	0	1	1	1	1	0	0	1	0	0	0	0	0	1	1	0	0
Creolandreva aptera	0	1	1	1	1	0	0	3	2	0	0	1	-	0	1	1	1
Creolandreva chaloupensis	0	1	1	1	1	0	0	3	2	0	0	1	-	0	1	1	1
Microlandreva parvotibialis	0	1	1	1	0	0	0	3	2	0	1	1	-	0	1	1	1
Oreolandreva brevipennis	-	-	-	0	-	-	-	3	2	1	0	1	-	0	1	1	1
Prolandreva mirabilis	0	0	1	1	0	1	1	3	2	0	0	0	0	0	1	0	0