

Patterns of diversification in the high Andean *Ponderacris* grasshoppers (Orthoptera: Acrididae: Melanoplinae)

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Abstract. The Andes, the world's longest mountain chain, harbours great taxonomic and ecological diversity. Despite their young age, the tropical Andes are highly diverse due to recent geological uplift. Speciation either followed the orogeny closely or occurred after the Andean uplift, as a result of subsequent climatic changes. Different scenarios have been proposed to explain the diversification of high Andean taxa. The Melanoplinae grasshopper *Ponderacris* Ronderos & Cigliano is endemic to the eastern slopes of the Andes of Peru and Bolivia, mostly distributed between 1000 and 4000 m above sea level. Diversification in several montane habitats of Bolivia and Peru allows tests via cladistic analysis of distinct possible geographic modes of speciation. Eight species are recognized, with three described here as new with revised diagnostic morphological characters provided: *Ponderacris carlcarbonelli* sp.n., *P. chulumaniensis* sp.n. and *P. amboroensis* sp.n. Cladistic analyses of 15 species (8 ingroup and 7 outgroup) and 38 morphological characters, under equal and implied weighting, confirm the monophyly of *Ponderacris*. Characters from the external morphology and colour pattern provided less phylogenetic information than did the male abdominal terminalia and phallic complex. Species distributed in the Peruvian Andes constituted a monophyletic group, whereas those from the Bolivian Andes formed a basal paraphyletic grade. Dispersal–vicariance analysis resulted in one ancestral distribution reconstruction indicating that the most recent common ancestor was distributed in the Lower Montane Yungas of Bolivia. Eleven dispersal and one vicariant events are postulated, with a South-to-North speciation pattern coincident with progressive Andean uplift. Vicariance could relate to fragmentation of montane forest during the dry intervals of the late Cenozoic. From the Bolivian area, ancestral Peruvian *Ponderacris* may have dispersed northward, coinciding with the rise of the Andes. Ten of 11 dispersal events occurred at terminal taxa and are likely to be recent. However, diversification of *Ponderacris* cannot be explained solely by the South-to-North speciation hypothesis, but may also include both vicariance and dispersal across barriers influenced by Pleistocene climatic cycles.

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Introduction

The Melanoplinae constitute one of the largest subfamilies of Acrididae, with about 137 genera and 970 species distributed throughout Eurasia and the Americas (Otte, 1995; Eades *et al.*, 2012). In the Americas it extends from Alaska to Patagonia, inhabiting a broad range of habitats. Members of the Melanoplinae usually dominate both in species and individuals in most temperate grasshopper communities of the Americas (Cigliano *et al.*, 2000) and are one of the main components of Acrididae fauna in the high Andes of South America (Rowell & Carbonell, 1977; Chintauan-Marquier *et al.*, 2010).

The Andes constitute the world's longest mountain chain, harbouring great taxonomic and ecological diversity (Luteyn & Churchill, 2000; Cigliano & Amédégnato, 2010; Särkinen *et al.*, 2011). The formation of the Andes, despite being relatively recent, has resulted in a most biologically diverse area, especially in the tropics, and a world biodiversity hotspot (Myers *et al.*, 2000; Morawetz & Raedig, 2007). Andean biodiversity has been explained through habitat diversity resulting from differences in orogeny, topography, soils, climate and elevation. Species have spread North and South along this mountain chain, and also up and down in elevation during colder times through repeated glaciations (Young *et al.*, 2002). The Andes provide altitudinally zoned habitats from rainforest to Paramo to glaciated peaks, an East–West differentiation into wetter and drier slopes through rain shadow effects, a discontinuous North–South migratory pathway for mid- and high-elevation biotas, and an even more discontinuous route for higher Andean and Paramo elements (Graham, 2009).

Speciation may have closely followed the orogeny of the Andes (Ribas *et al.*, 2007; Picard *et al.*, 2008; Elias *et al.*, 2009; Guarnizo *et al.*, 2009) or occurred after the Andean uplift resulting from subsequent climatic changes (Chesser, 2000; Willmott *et al.*, 2001; Koscinski *et al.*, 2008). Different scenarios have been proposed to explain the diversification of high Andean taxa. Doan (2003) proposed a South-to-North Speciation Hypothesis (SNSH) for species groups with speciation of high Andean taxa following a South-to-North pattern, generally coinciding with the progression of final uplift of the Andes. According to this scenario, a phylogenetic hypothesis of relationships of a taxonomic group occurring in the high Andes would show a branching pattern in which the southernmost species diverged first, followed by the more northern species, and so on in a northerly pattern. An alternative, based on the morphological diversification found in *Ponderacris* Ronderos & Cigliano of the Melanoplinae, posited a North-to-South progression of speciation for this Andean genus (Ronderos & Carbonell, 1971).

Given these alternatives, we test the history of diversification inferred from a cladistic analysis of *Ponderacris* species. The genus is endemic to the oriental slopes of the Andes of Peru and Bolivia, between latitudes 10° and 19°S. Excepting a species from 400 m above sea level (a.s.l.), the majority of the species are distributed between 1000 and 4000 m a.s.l., whereas regional species richness peaks from 2200 to

2500 m a.s.l. The genus comprises eight species, including three newly discovered members that inhabit montane Bolivia and Peru. The diversification of *Ponderacris* within the region thus allows testing of distinct possible geographical modes of speciation in montane habitats within a phylogenetic framework.

In order to assess the diversification hypotheses, first we describe the three newly discovered species of *Ponderacris* and analyse the characters useful in distinguishing them from the closest related species. We then reconstruct the phylogenetic relationships of *Ponderacris*, and finally examine the relationships and geographic ranges of the species to test the biogeographic hypotheses.

Material and methods

Specimen preparation

Most material examined originates from several collecting trips (surveys) conducted by Cigliano and Lange in the Andes of Bolivia and Peru during 2003, 2004, 2007 and 2008: all material examined is deposited at the Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina (MLPA).

Specimens were relaxed in a humid chamber and abdomen terminalia moistened with ammonia. Genitalia then were pulled off from the body using a finely hooked pin, cleared in potassium hydroxide and stored in glycerine. Photographs of the habitus were captured with a Canon EOS Rebel digital camera. Images of the distal segments of the abdomen and phallic complex were captured with a Micrometrics digital camera attached to a Nikon SMZ1000 stereomicroscope. The program Combine Z5.3 (Hadley, 2006) was used for focus stacking. Measurements are given in millimetres. Body length was measured from the fastigium verticis to the end of abdomen. Prozone and metazone of the pronotum and tegmina were measured along the midline from the front to hind margin. Length of hind femur was measured from the dorso-proximal lobe to the distal extremity.

Cladistic analysis

The phylogenetic analysis was conducted on a matrix consisting of 15 species (8 ingroup and 7 outgroup) and 38 morphological characters. All described species of *Ponderacris* were included in the analysis plus the three new ones described herein. Morphological characters comprised structures from head and thorax, male abdominal terminalia and internal genitalia, as well as colouration patterns. Although colour in Acrididae is known to be variable and is sometimes affected by local environmental conditions, the body colour characters used in this analysis were invariable at the intraspecific level and appear to be heritable. The morphological characters and their states are listed in Appendix 1 and are shown in Figs 1–9. The data matrix is presented in Table S1. The dataset was

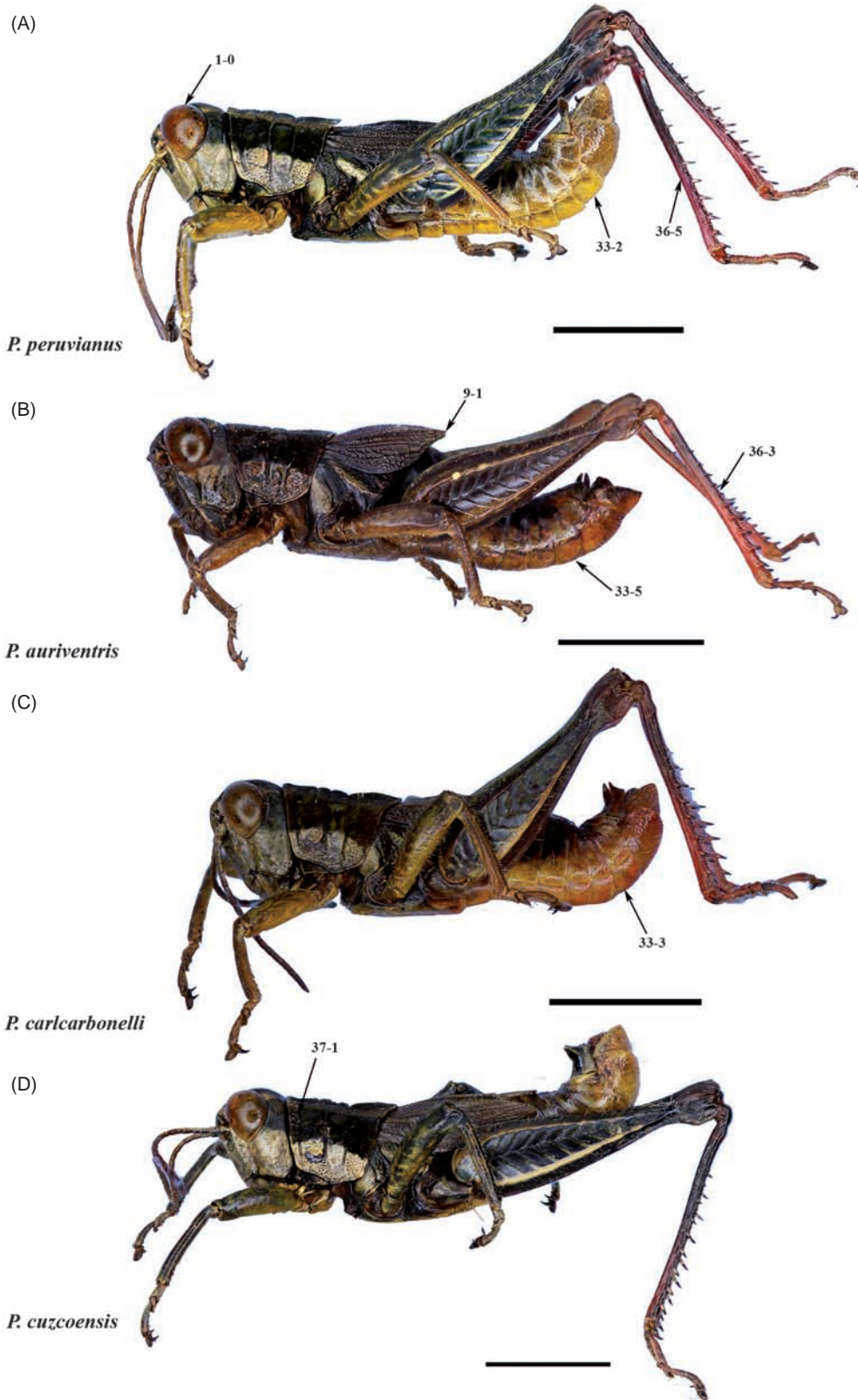


Fig. 1. *Ponderacris* males, species as indicated. (A–D) habitus. Scale bars: 5 mm. Numbers indicate characters and states used in the cladistic analysis.

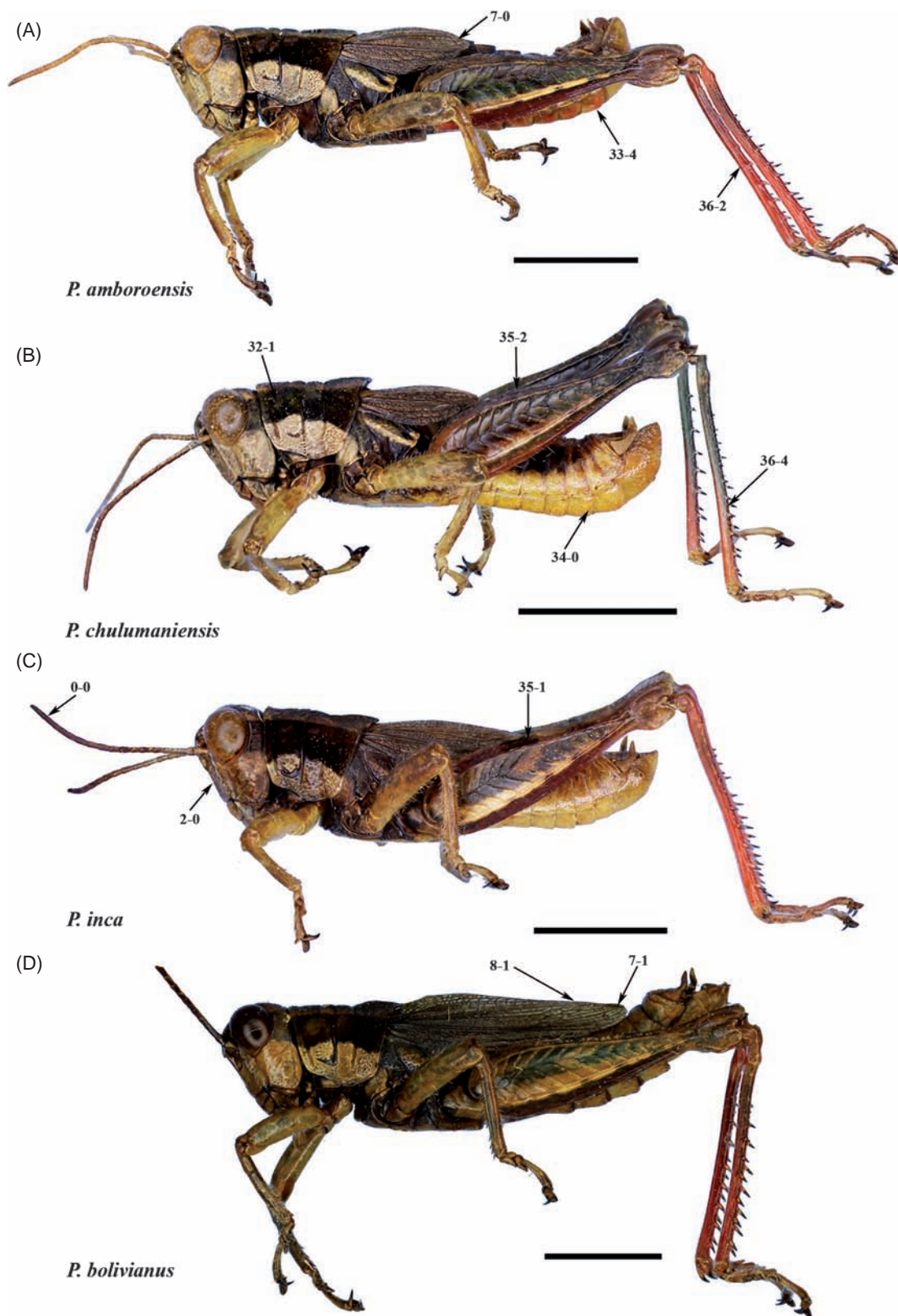


Fig. 2. *Ponderacris* males, species as indicated. (A–D) habitus. Scale bars: 5 mm. Numbers indicate characters and states used in the cladistic analysis.



Fig. 3. *Ponderacris* males, species as indicated. (A), (C), (E), (G), (I), (K), (M), (O), distal abdominal segments, lateral view; (B), (D), (F), (H), (J), (L), (N), (P), distal abdominal segments, dorsal view. Numbers indicate characters and states used in the cladistic analysis.

analysed using two procedures: (i) equally weighted character analysis and (ii) the implied weighting method (Goloboff, 1993). Under the implied weight criterion the existing character conflicts in the dataset are resolved in favour of the characters with lower homoplasy by searching trees with a maximum total fit. We repeated this analysis with concavity (K) values of 1–30. All tree searches were conducted in TNT (Goloboff *et al.*, 2003a) under the implicit enumeration option. Multistate characters were treated as unordered. Support for individual nodes was assessed by calculation of absolute Bremer support (Bremer, 1994) and bootstrap support (500 replicates) for the equally weighted analysis, and symmetric resampling (change probability = 33) which is not distorted by weights (Goloboff *et al.*, 2003b) was used for the implied weighting analysis, with 500 replicates (Goloboff *et al.*, 2003b).

In order to test the effect on topology of different character sets of potentially varying homoplasy, we also partitioned the data into external and chromatic (0–9, 32–37), and male

abdominal terminalia and genitalia (10–31) character sets, and analysed each separately. Winclada (Nixon, 2002) was used to map the characters and plot the tree.

Characters were polarized by outgroup comparison with the Andean Dichroplini *Timotes malleatus* Ronderos & Cerda, *Chibchacris meridensis* Ronderos, *Keyopsis palidiventer* (Ronderos & Cigliano), *Bogatocris varicolor* (Stål), *Boliviocris jujuyensis* Ronderos & Cigliano, *Baeacris penianus* (Ronderos) and *Baeacris punctulatus* (Thunberg). The root was set as *T. malleatus*.

Biogeographic analysis

Dispersal–vicariance analysis (DIVA; Ronquist, 1997) was performed to evaluate different possible biogeographical scenarios explaining the distribution of *Ponderacris* in the Andes. DIVA, an event-based biogeographical method, allows

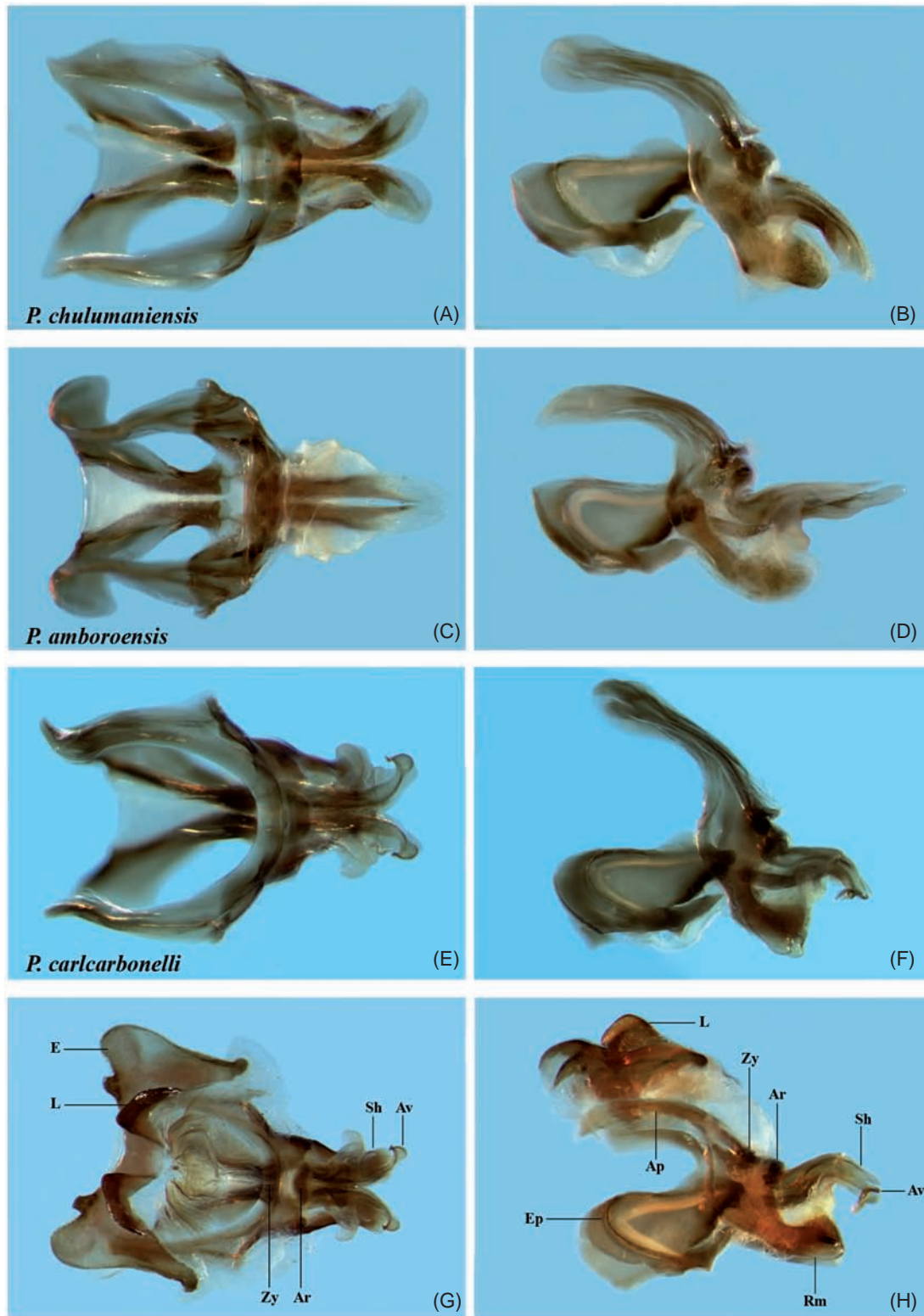


Fig. 4. *Ponderacris* males. Phallic complex, species as indicated. (A, C, E) endophallic plates (basal and apical valves of aedeagus) and cingulum, dorsal view; (B, D, F) endophallic plates (basal and apical valves of aedeagus) and cingulum, lateral view; (G, H) *P. carlcarbonelli*, phallic complex, dorsal (G) and lateral views (H). Abbreviations: Ap, apodemes of cingulum; Ar, arch of aedeagus; Av, aedeagal valves; Ep, endophallic plates; E, epiphallus; L, lophi of epiphallus; Rm, rami; Sh, sheath of aedeagus, Zy, zygoma.

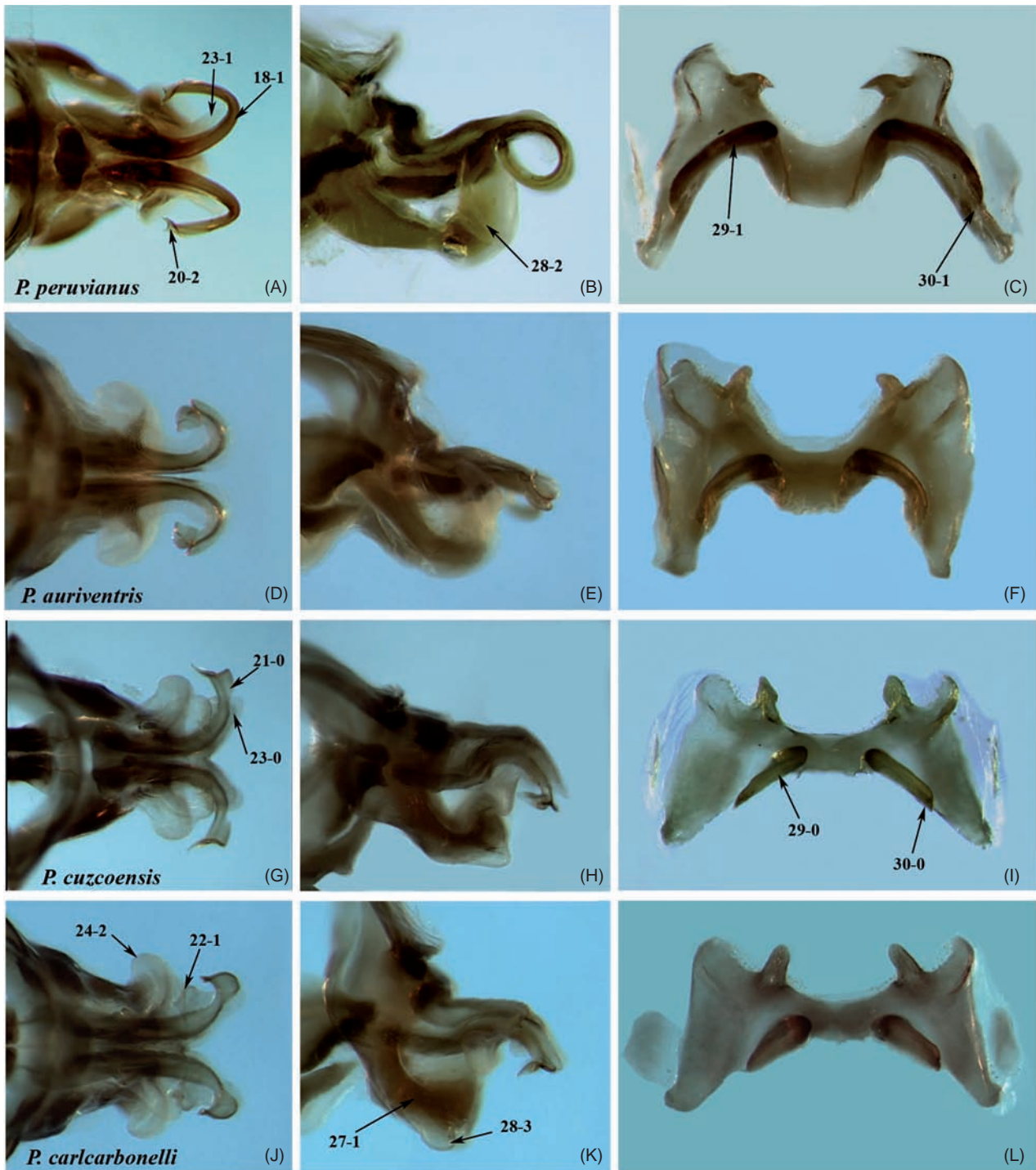


Fig. 5. *Ponderacris* males. Phallic complex, species as indicated. (A), (D), (G), (J) distal portion of aedeagal valves, dorsal view; (B), (E), (H), (K) distal portion of aedeagal valves, lateral view; (C), (F), (I), (L) epiphallus, dorsal view. Numbers indicate characters and states used in the cladistic analysis.

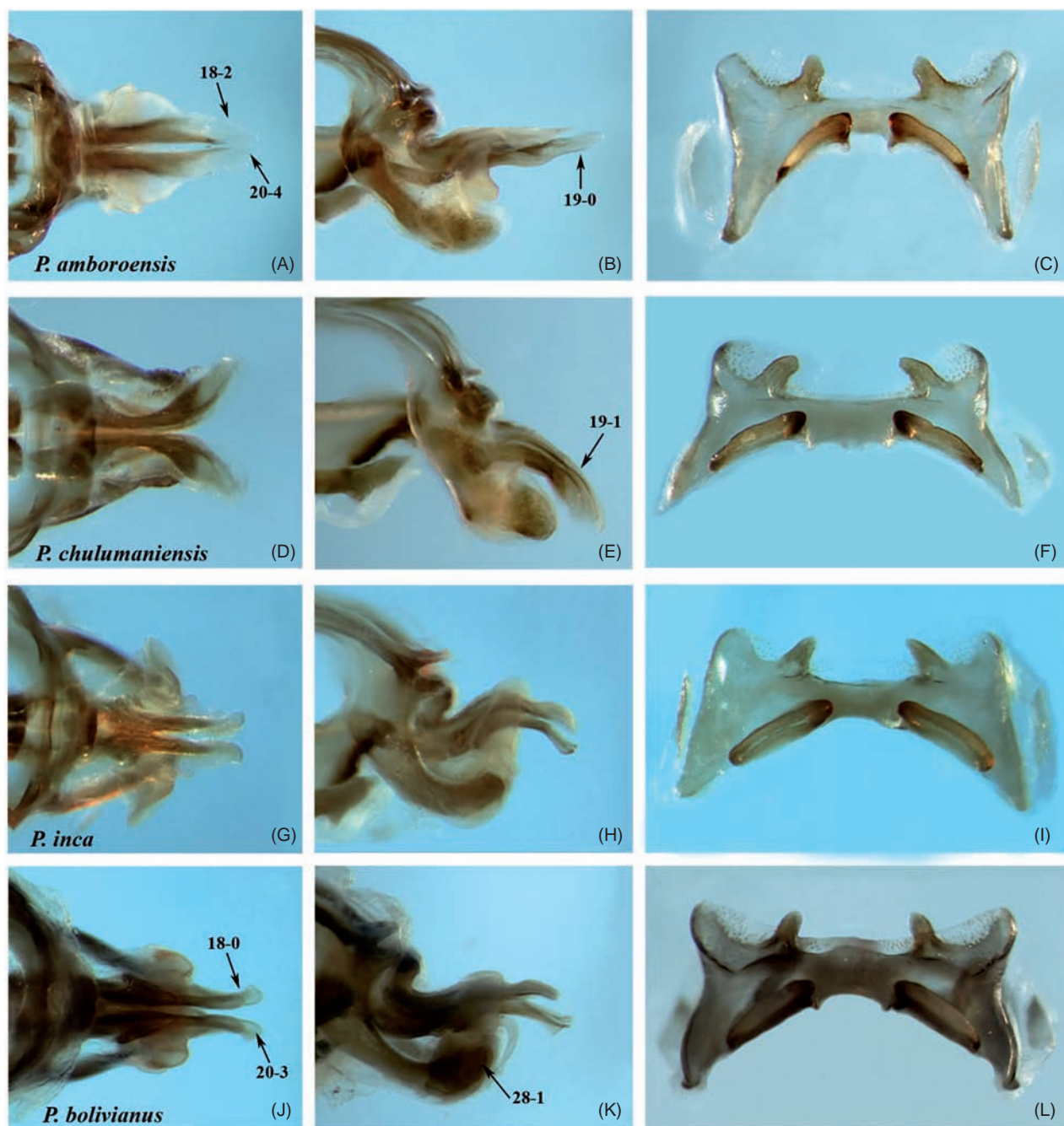


Fig. 6. *Ponderacris* males. Phallic complex, species as indicated. (A), (D), (G), (J) distal portion of aedeagal valves, dorsal view; (B), (E), (H), (K) distal portion of aedeagal valves, lateral view; (C), (F), (I), (L) epiphallus, dorsal view. Numbers indicate characters and states used in the cladistic analysis.

reconstruction of ancestral distributions, maximizing vicariant events and minimizing dispersal and extinction events, allowing nonhierarchical area relationships (Crisci *et al.*, 2003), assuming that distributions of taxa and ancestors may be described in a set of area units. It allows inference of the ancestral distribution of a taxon and thus allows the vicariance and dispersal events that account for the geographic history

of the taxon under consideration to be evaluated. To correlate the current habitat distribution with the biogeographic history of this group, we characterized the habitats in which each species occurs. Accordingly, as area units we used the biogeographical subdivisions of the Peruvian and Bolivian forests defined by Hueck (1978) (Fig. 12C): 'Ceja' Forest, Peru (from 2500 to 4000 m a.s.l.), Upper Montane Rainforest, Peru

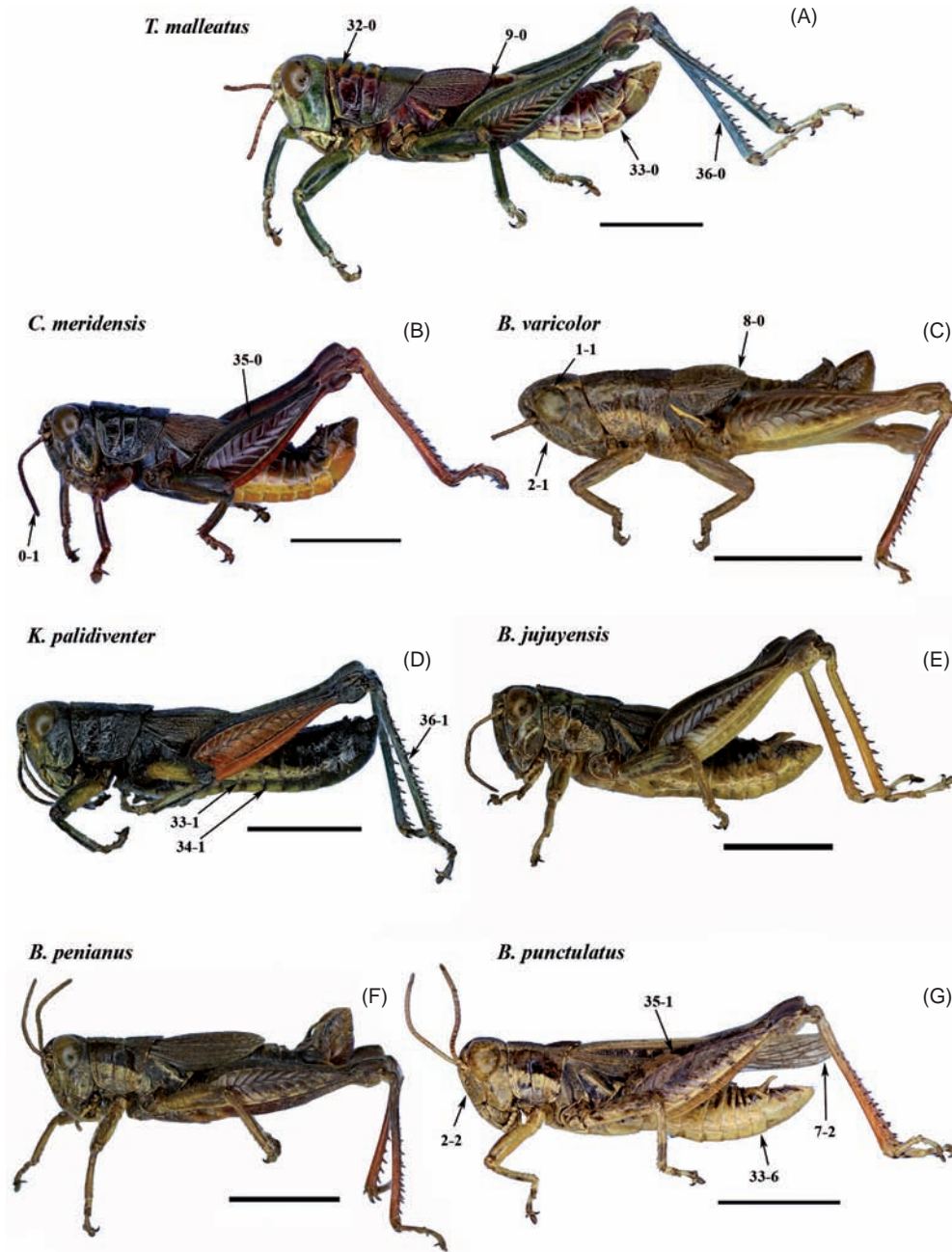


Fig. 7. Outgroup taxa used in the cladistic analysis, species as indicated. (A–G) male habitus. Scale bars: 5 mm. Numbers indicate characters and states used in the cladistic analysis.

(from 1500 to 2500 m a.s.l.), Lower Montane Rainforest, Peru (< 1500 m a.s.l.), 'Ceja' Forest, Bolivia (from 2800 to 3400 m a.s.l.), Upper Montane Yungas, Bolivia (from 2000 to 2800 m a.s.l.), Lower Montane Yungas, Bolivia (< 2000 m a.s.l.), and the biogeographic areas (provinces) defined by Morrone (2006) (Fig. 12B): Puna (eastern Bolivia, northern Argentina and Chile, and southern Peru), North Andean Paramo (high cordilleras of Venezuela, Colombia, Ecuador and Peru, at altitudes above 3000 m), Chaco (southern Bolivia, western

Paraguay, southern Brazil and north-central Argentina), Pampa (central western Argentina, Uruguay, and south of Rio Grande do Sul, Brazil), Monte (central Argentina between latitudes 24° and 43°S), Brazilian Atlantic Forest (narrow strip along the Brazilian coast, between latitudes 7° and 32°S), and Parana Forest (southeastern Brazil, northeastern Argentina and eastern Paraguay). The taxon area cladogram, with each terminal taxon replaced by the area/s it inhabits (see Fig. 12A) was analysed using the program RASP (Reconstruct Ancestral State in

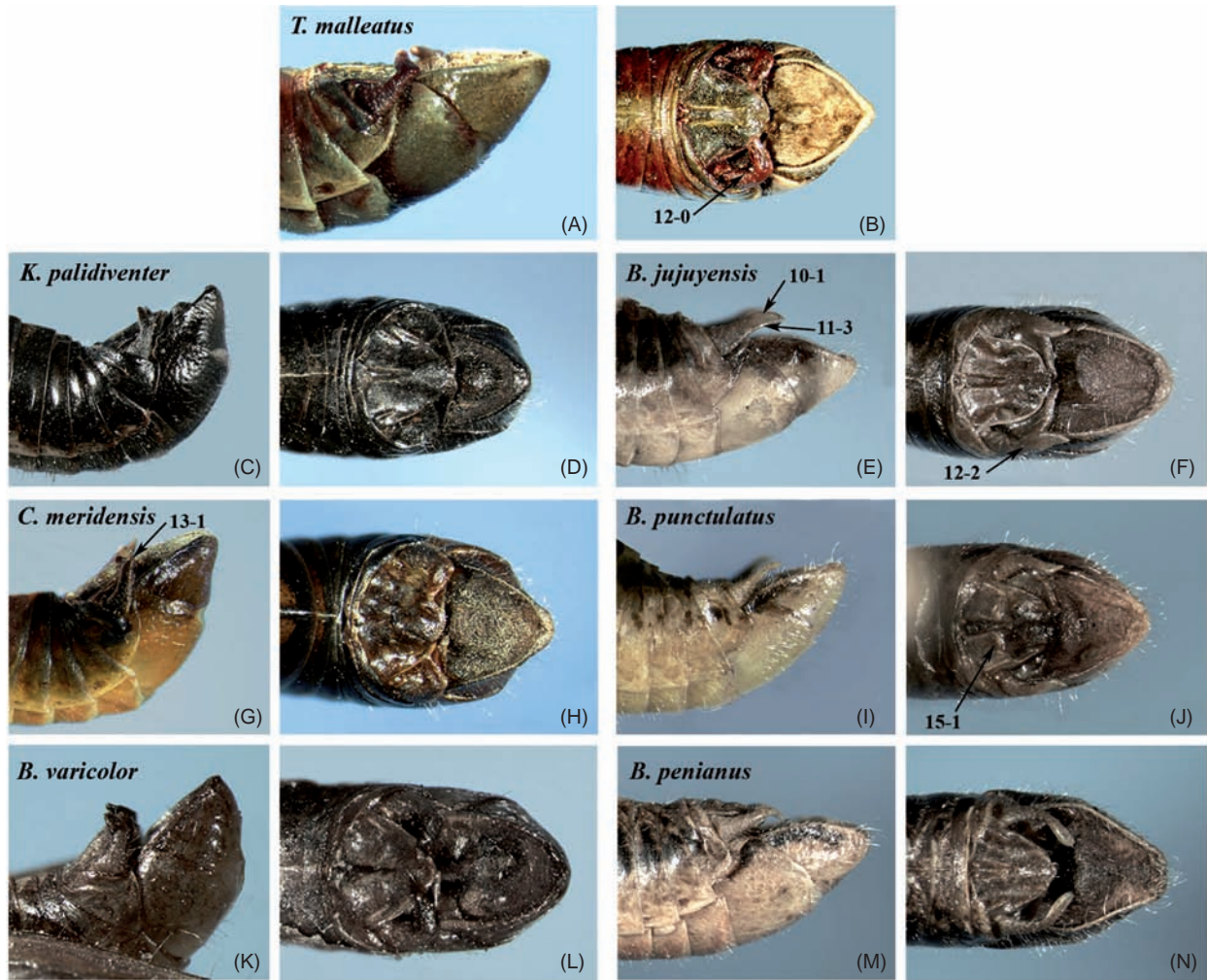


Fig. 8. Outgroup taxa used in the cladistic analysis, species as indicated. (A), (C), (E), (G), (I), (K), (M) male distal abdominal segments, lateral view; (B), (D), (F), (H), (J), (L), (N) male distal abdominal segments, dorsal view. Numbers indicate characters and states used in the cladistic analysis.

Phylogenies) v2.0 Beta (Yu *et al.*, 2011), a tool for inferring ancestral state using Bayesian, Parsimony, or SDIVA methods. RASP complements DIVA v1.2 (Ronquist, 1996) which applies an exact search according to the dispersal–vicariance optimization as proposed by Ronquist (1997). Because Kodandaramaiah (2010) has postulated that DIVA is sensitive towards the exclusion of outgroup taxa, resulting in a bias towards a widespread ancestral distribution at the root node, we avoid this by using seven terminal taxa as outgroups.

Electronic content and hyperlinks

This article includes ‘hyperlinks’ to the Orthoptera Species File (OSF) online (<http://orthoptera.speciesfile.org>) (Eades *et al.*, 2012) following procedures described in Cigliano & Eades (2010). Taxon LSIDs provided by the Orthoptera Species File are also included.

Results

Systematics

Ponderacris Ronderos & Cigliano, 1991

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:54944>

Ponderacris Ronderos & Cigliano, 1991: 176; Otte, 1995: 408; Cigliano, 1997 [1998]: 2; Eades *et al.*, 2012

Type species: *Pezotettix peruvianus* Stål, by original designation

Diagnosis. Brachypterous or half-winged (i.e. tegmina covering half of the abdomen), occasionally macropterous. Eyes exceeding the level of vertex; face perpendicular to slightly oblique. Prozone about one third longer than metazone (length ratio prozone/metazone approximately 1.33); pronotal disk with front margin slightly emarginate and hind margin obtusely angulated; lateral borders of metazone slightly divergent. Male

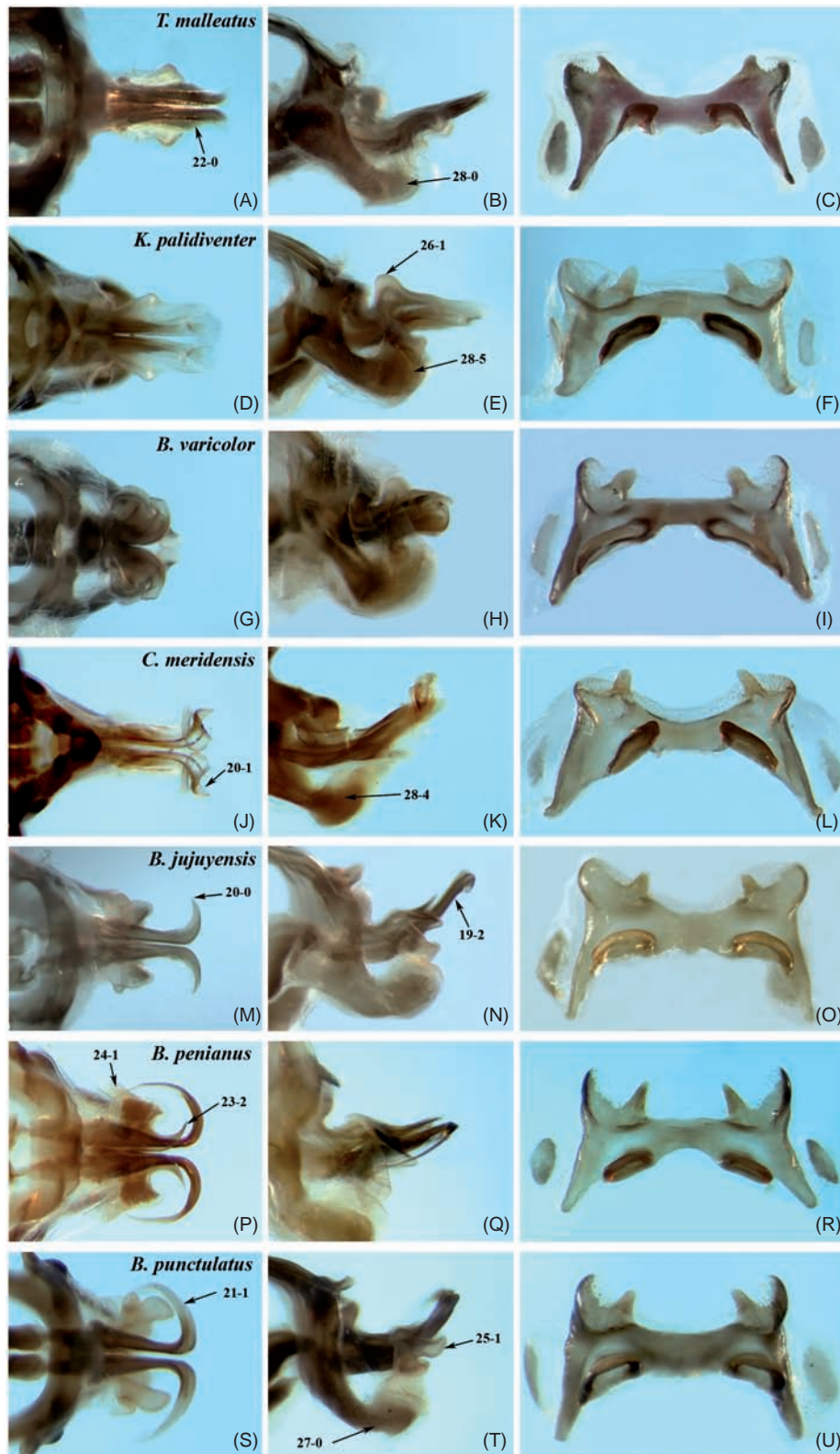


Fig. 9. Outgroup taxa used in the cladistic analysis, species as indicated. Phallic complex. (A), (D), (G), (J), (M), (P), (S) distal portion of aedeagal valves, dorsal view; (B), (E), (H), (K), (N), (Q), (T) distal portion of aedeagal valves, lateral view; (C), (F), (I), (L), (O), (R), (U) epiphallus, dorsal view. Numbers indicate characters and states used in the cladistic analysis.

cerci slightly bent inwards, distal half upcurved; furculae absent or present. Phallic complex: cingulum with rami expanded caudally; apical valves of aedeagus uniformly sclerotized with longitudinal internal furrow; sheath of aedeagus wide and highly lobulate; basal lobes of aedeagus sheath well developed. General body colour dull brown or dark green; laterally with dark brown post-ocular band, extending from behind the eyes along mid-dorsal portion of lateral lobes of pronotum; mid-ventral portion of lateral lobes of pronotum cream; hind femora with inner face and ventral area red.

Key to the species of *Ponderacris*

1. Half-winged or macropterous insects (Figs 1A, C, D, 2C, D) 2
 - Brachypterous insects (Figs 1B, 2A, B) 6
2. Male cerci with distal portion compressed and posterior-distal margin semicircular (Fig. 3A); rami of cingulum constricted at the middle and with expanded distal third (Fig. 5B); apical valves of aedeagus long, caudally divergent, conspicuously curved down and outwards, spiral-shaped (Fig. 5A, B); lophi of epiphallus prominent and rectangular (frontal view), expanded towards the posterior process of lateral plates (dorsal view) (Fig. 5C) *P. peruvianus*
 - Male cerci and rami of cingulum shaped differently; apical valves of aedeagus shorter, with the distal third portion slightly curved outwards (Fig. 5G, H); lophi of epiphallus low (frontal view) and dorsally narrow (Fig. 5I) 3
3. Male cerci with distal third flat and upper margin oblique (Fig. 3I, M); subgenital plate with blunt apex (Fig. 3I, M); apical valves of aedeagus with a wide longitudinal groove, distal third diverging caudally, slightly curved and directed downwards, with the apices moderately expanded (Fig. 5G, H, J, K) 4
 - Male cerci with distal third cone-shaped and lower margin elbow-shaped, (Fig. 3K, O); subgenital plate with apex pointed or slightly rounded (Fig. 3K, O); apical valves of aedeagus short, directed downwards (Fig. 6H, K), with sub-triangular and slightly divergent apex (Fig. 6G, J) 5
4. Apical valves of aedeagus shorter, basal lobes of aedeagus sheath globose (Figs 4E, G, 5J); abdomen ventrally orange-red; hind tibiae red; smaller body size (males 14–15 mm, females 17–20.5 mm) *P. carlcarbonelli* **sp.n.**
 - Apical valves of aedeagus longer, basal lobes not globose (Fig. 5G); abdomen ventrally yellow; hind tibiae with proximal half burgundy and distal half red; larger body size (males 14–21 mm, females 20–21.5 mm) *P. cuzcoensis*
5. Smaller body size (males 16.5–19.5 mm, females 19–28 mm); basal lobes of aedeagus sheath ear-shaped (Fig. 6G), surpassing the level of the sheath in lateral view (Fig. 6H) *P. inca*
 - Larger body size (males 20–22 mm, females 27.5–28 mm); basal lobes of aedeagus sheath not ear-shaped (Fig. 6J), barely

reaching the level of the sheath of aedeagus in lateral view (Fig. 6K) *P. bolivianus*

6. Furculae absent (Fig. 3F); distal portion of apical valves of aedeagus spiral-shaped (Fig. 5E); from Peru *P. auriventris*

– Furculae present (Fig. 3D, H); distal portion of apical valves of aedeagus not spiral-shaped (Fig. 6B, E); from Bolivia 7

7. Male cerci with upper margin oblique (Fig. 3C); apical valves of aedeagus with distal third not divergent caudally (Figs 4C, 6A), directed straight forward (Figs 4D, 6B); upper face of hind femur with black spots; abdomen ventrally orange with tinges of yellow; hind tibiae red *P. amboroensis* **sp.n.**

– Male cerci with pointed apex and posterior-distal margin rounded (Fig. 3G); apical valves of aedeagus divergent caudally (Figs 4A, 6D) and conspicuously directed downwards (Figs 4B, 6E); upper face of hind femur without black spots; abdomen ventrally yellow; hind tibiae with proximal half dark green, distal half orange-red *P. chulumaniensis* **sp.n.**

Ponderacris peruvianus (Stål)

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:54945> (Figs 1A, 3A, B, 5A–C, 13)

Pezotettix peruvianus Stål, 1878: 7

Dichroplis peruvianus: Scudder 1897: 406; Ronderos & Carbonell 1971:16

Trigonophymus peruvianus: Kirby, W.F. 1910: 490

Dichroplis peruvianus peruvianus: Liebermann 1968: 30

Ponderacris peruvianus: Ronderos & Cigliano 1991:176; Eades *et al.*, 2012

Diagnosis. Male cerci with distal portion compressed, posterior-distal margin semicircular, anterior margin slightly concave and posterior-proximal margin straight (Fig. 3A). Furculae not developed (Fig. 3B). Apical valves of aedeagus long, with distal third diverging caudally (Fig. 5A), conspicuously curved down and outwards, spiral-shaped (Fig. 5B). Rami of cingulum constricted in the middle and with expanded distal third (Fig. 5B). Basal lobes of aedeagus sheath ear-shaped (Fig. 5A). Lophi of epiphallus prominent and rectangular (frontal view), placed perpendicular to bridge, widely expanded towards the posterior process of the lateral plates (dorsal view) (Fig. 5C). Half-winged insects (Fig. 1A). Abdomen ventrally yellow; hind tibiae with proximal half burgundy and distal half red.

Material examined. PERU: 9 ♂, 7 ♀, one nymph, Junín, 2 km from San Ramón to Tarma, Pan de Azúcar bridge (11°10'09.9"S, 75°27'08.9"W), 1343 m, 26.iv.2008 (Cigliano, M.M. & Lange, C.E.) (MLPA); 1 ♂, Junín, Huacapistana, 1800 m, 27–30.vii.1965 (Wygodzinsky P. & B.) (MLPA); 1 ♂, Pasco, Oxapampa, 1200 m, 15.iii.1940 (Weyrauch) (MLPA); 1 ♂, Junín, San Nicolás to km 71 Pichis Trail, 4–6000 feet, ii.1930 (Carriker, M.A.) (MLPA); 1 ♂, Junín, Pichita Caluga,

hoya del río Chanchamayo, 2200 m, 27.viii.1959 (*Weyrauch*) (MLPA); 1 ♀, Junín, Pichita Caluga, 1300 m, 14.v.1955 (*Weyrauch*) (MLPA); 3 ♂, 2 ♀, Junín, San Ramón, Chanchamayo, 850 m, 29.xi.1974 (*Martínez A.*) (MLPA).

Measurements (in mm). Body length: males 18.8 (16–21), females 22.8 (21–24.5); femur III: males 11.08 (10.5–11.7), females 14.8 (14.5–15); ratio pronotum length/tegmina length: males 0.72 (0.67–0.77), females 0.74 (0.73–0.76).

Distribution. Peru, Junín (San Ramón, Huacapistana, San Nicolás, Chanchamayo, Pichita Caluga, Carpapata), Pasco (Oxapampa), Huánuco (Conchamarca) (Fig. 13) (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=42374>)

***Ponderacris auriventris* (Bruner)**

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:54955>
(Figs 1B, 3E, F, 5D–F, 13)

Dichroplus peruvianus auriventris Bruner, 1913: 184; Liebermann 1968:30

Dichroplus auriventris: Ronderos & Carbonell 1971:20

Ponderacris auriventris: Ronderos & Cigliano 1991:176; Eades *et al.*, 2012

Diagnosis. Male cerci thin, digitiform, with rounded posterior-distal margin (Fig. 3E). Furculae not developed (Fig. 3F). Apical valves of aedeagus similar to *P. peruvianus* but shorter and slightly wider (Fig. 5D). Rami of cingulum not constricted, with apex less broad (Fig. 5E). Basal lobes of aedeagus sheath globose, laterally prominent (Fig. 5D). Lophi of epiphallus less expanded along the posterior process of lateral plates (Fig. 5F). Brachypterous insects (Fig. 1B). Abdomen ventrally yellow with tinges of orange-red; hind tibiae orange-red.

Material examined. PERU: 1 ♂, 3 ♀, Cusco, Machu Picchu, 06.xii.1964 (*Silveira A.*) (MLPA); 1 ♂, 1 ♀, Cusco, Machu Picchu, above Ruins C., 2600 m, 08.i.1963 (*Hubbell T.H.H.*) (MLPA); 2 ♂, 4 ♀, Cusco, Machu Picchu, 26.xii.1965 (*Carrasco F.*) (MLPA); 1 ♀, Cusco, Convención, 01.iv.1969 (*Carrasco F.*) (MLPA); 1 ♂, Cusco, Machu Picchu, 2300 m., 21–24.x.1972 (*Wygodzinsky P.*) (MLPA).

Measurements (in mm). Body length: males 16.6 (15–17.5), females 20.5 (18–22); femur III: males 9.2 (9–10), females 11.7 (11.5–12); ratio pronotum length/tegmina length: males 0.95 (0.87–1.09), females 0.98 (0.8–1.11).

Distribution. Peru, Cusco (Machu Picchu, Convención, Tincochaca, Huadquiña). (Fig. 13). (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=42370>)

***Ponderacris cuzcoensis* (Ronderos & Carbonell)**

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:54951>
(Figs 1D, 3I, J, 5G–I, 13)

Dichroplus cuzcoensis Ronderos & Carbonell, 1971: 22

Ponderacris cuzcoensis: Ronderos & Cigliano 1991:176; Eades *et al.*, 2012

Diagnosis. Male cerci with the upper margin oblique, anterior margin concave and posterior margin straight (Fig. 3I). Male subgenital plate with blunt apex (Fig. 3I). Furculae absent (Fig. 3J). Apical valves of aedeagus with a wide longitudinal groove, distal third diverging caudally (Fig. 5G), slightly curved and directed downwards (Fig. 5H), with the apices moderately expanded (Fig. 5G). Rami with a distinct apical notch (Fig. 5H). Sheath of aedeagus with a pair of latero-distal lobes covering dorso-laterally the valves of the aedeagus (Fig. 5G). Basal lobes well developed (Fig. 5G). Epiphallus with lophi low, placed parallel to bridge, dorsally narrow (Fig. 5I). Half-winged insects (Fig. 1D), occasionally long-winged. Abdomen ventrally yellow; hind tibiae with proximal half burgundy and distal half red.

Material examined. PERU: 1 ♂, paratype (MLPA); 2 ♂, 4 ♀, Cusco, Santa Isabel, between Paucartambo and Pillahuata (13°06'23.0"S, 71°34'12.2"W), 1996 m, 21.v.2008 (*Cigliano M.M. & Lange C.E.*) (MLPA); 2 ♂, Cusco, between Paucartambo and Pillahuata (13°3'31.49"S, 71°32'25.75"W), 1500 m, 21.v.2008 (*Cigliano M.M. & Lange C.E.*) (MLPA).

Measurements (in mm). Body length: males 16.9 (14–21), females 20.6 (20–21.5); femur III: males 10.7 (10–11.5), females 13.1 (12.7–14); ratio pronotum length/tegmina length: males 0.75 (0.72–0.80) (half-winged specimens), 0.34 (long-winged specimen), females 0.79 (0.74–0.86).

Distribution. Peru, Cusco (Cuzco, Callanga, Lauramarca, Santa Isabel) (Fig. 13). (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=42372>)

***Ponderacris carlcarbonelli* sp.n. Pocco, Lange & Cigliano**

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:74242>
(Figs 1C, 3M, N, 4E–H, 5J–L, 13)

Diagnosis. Closely related to *P. cuzcoensis*, from which it can be distinguished by the following characteristics: apical valves of aedeagus shorter (Figs 4E,G, 5J), basal lobes of aedeagus sheath globose (Figs 4E, G, 5J), abdomen ventrally orange-red, hind tibiae red, smaller body size (Fig. 1C).

Description. Males. Half-winged insects (Fig. 1C). Tegmina about one third longer than the pronotum. Tegmina elongate. Cerci with distal third flat and pointed dorso-distal apex, upper

margin oblique, anterior margin concave and posterior margin straight (Fig. 3M). Subgenital plate with blunt apex (Fig. 3M). Furculae absent (Fig. 3N). Phallic complex (Figs 4E–H): apical valves of aedeagus with wide longitudinal internal groove, distal third diverging caudally (Figs 4E, G, 5J), directed downwards and slightly curved (Figs 4F, H, 5K), with the apices moderately expanded (Figs 4E, G, 5J). Rami with a distinct lateral apical notch (Figs 4F, H, 5K). Sheath of aedeagus with a pair of latero-distal lobes covering dorso-laterally the valves of the aedeagus (Figs 4E, G, 5J); mid-dorsal apical lobes long, covering most of the apical valves; basal lobes globose (Figs 4E, G, 5J). Lophi of epiphallus low, placed parallel to bridge, dorsally narrow (Fig. 5L). Body colour dark greenish; abdomen ventrally orange-red; upper face of hind femur darkly mottled; hind tibiae red.

Females: similar to males but more robust.

Measurements (in mm). Body length: males 14.5 (14–15), females 19 (17–20.5); femur III: males 8.7 (8–9), females 11.25 (11–11.5); ratio pronotum length/tegmina length: males 0.77 (0.71–0.85), females 0.84 (0.78–0.88).

Etymology. The name of this new species is dedicated to Prof. Carlos S. Carbonell for his outstanding contributions to the knowledge of Neotropical Acridomorpha.

Material examined. PERU: holotype ♂, allotype ♀, Ayacucho, to San Francisco 42 km from Tambo (12°46'35.4''S, 73°59'52.2''W), 2809 m, 21.xi.2007 (Cigliano M.M. & Lange C.E.) (MLPA). Paratypes: 4 ♂, 2 ♀, Ayacucho, to San Francisco 42 km from Tambo (12°46'35.4''S, 73°59'52.2''W), 2809 m, 21.xi.2007 (Cigliano M.M. & Lange C.E.) (MLPA).

Distribution. Peru, Ayacucho (between San Francisco and Tambo). (Fig. 13) (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=78521>)

Ponderacris inca (Ronderos & Carbonell)

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:54949>
(Figs 2C, 3O, P, 6G–I, 13)

Dichroplus inca Ronderos & Carbonell, 1971: 25

Ponderacris inca: Ronderos & Cigliano 1991:176; Eades et al., 2012

Diagnosis. Male cerci with distal third cone-shaped, lower margin elbow-shaped, anterior margin concave (Fig. 3O). Apical valves of aedeagus short, directed downwards (Fig. 6H), with sub-triangular and slightly divergent apex (Fig. 6G). Rami of cingulum with apex crescent-shaped (Fig. 6H). Basal lobes of aedeagus sheath ear-shaped (Fig. 6G), surpassing the level of the sheath in lateral view (Fig. 6H). Lophi of epiphallus low, placed parallel to bridge, dorsally narrow (Fig. 6I). Half or long-winged insects (Fig. 2C). Abdomen ventrally yellow; hind tibiae red.

Material examined. PERU: 4 ♂, 4 ♀, Cusco, Atalaya, confluence of Alto Madre de Dios and Carbón rivers, 700 m, vi.1976 (Carbonell & Descamps) (MLPA). BOLIVIA: 1 ♂, La Paz, Chulumani, Sur Yungas, i.1948 (Williner) (MLPA); 13 ♂, 10 ♀, Cochabamba, road from Cochabamba to Va. Tunari, 81 km E Cochabamba, Río Ronco, (17°11'16.8''S, 65°45'15.51''W), 23.ii.2003 (Cigliano M.M. & Lange C.E.) (MLPA); 1 ♂, Cochabamba, Chapare, Cristal Mayu, 03.ii.1971 (Martinez) (MLPA); 3 ♂, 4 ♀, La Paz, Coroico, 10 km from Coroico, road to Chulumani, (16°16'26.70''S, 67°41'28.69''W), 1750 m, 25.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA); 2 ♂, La Paz, Chulumani, 4 km from Irupana (16°27'3.71''S, 67°28'59.20''W), 26.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA); 1 ♂, La Paz, Chulumani, (16°24'33.24''S, 67°32'11.77''W), 1825 m, 27.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA); 1 ♂, 1 ♀, La Paz, Chulumani, (16°24'11.27''S, 67°32'43.34''W), 2040 m, 27.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA); 1 ♂, Santa Cruz, Samaipata, Parque Nacional Amboró, 9 km Achiras Camping, Los Paredones (18°07'06.27''S, 63°48'03.24''W), 2040 m, 16.iv.2004 (Cigliano M.M. & Lange C.E.) (MLPA).

Measurements (in mm). Body length: males 17.4 (16.5–19.5), females 23.1 (19–28); femur III: males 10.4 (10–11.5), females 13.2 (12–14.5); ratio pronotum length/tegmina length: males 0.55 (0.29–0.66), females 0.54 (0.28–0.68).

Distribution. Peru, Cusco (Atalaya, Marcapata, Urubamba, Lauramarca), Junín (Chanchamayo); Bolivia, La Paz (Chulumani, Coroico, Incachaca), Cochabamba (Va. Tunari), Santa Cruz (Samaipata), Chapare (Cristal Mayu) (Fig. 13). (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=42373>)

Ponderacris bolivianus (Ronderos & Carbonell)

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:54953>
(Figs 2D, 3K, L, 6J–L, 13).

Dichroplus bolivianus Ronderos & Carbonell, 1971:25

Ponderacris bolivianus: Ronderos & Cigliano 1991: 176; Eades et al., 2012

Diagnosis. Closely related to *P. inca*, from which it can be distinguished by the basal lobes of aedeagus sheath which are not ear-shaped (Fig. 6J), barely reach the level of the sheath of aedeagus in lateral view (Fig. 6K) and by the larger body size (Fig. 2D).

Material examined. BOLIVIA: holotype ♂, allotype ♀, Santa Cruz de la Sierra, El Espejo, ii.1962 (Martinez A.) (MLPA). Paratypes: 1 ♂, 1 ♀, Santa Cruz de la Sierra, El Espejo, ii.1962 (Martinez A.) (MLPA).

Measurements (in mm). Body length: males 21 (20–22), females 27.7 (27.5–28); femur III: males 12, females 14.5 (14–15); ratio pronotum length/tegmina length: males 0.54 (0.48–0.60), females 0.43 (0.34–0.51).

Distribution. Bolivia, Santa Cruz de la Sierra (El Espejo), Cochabamba (Carrasco, Palmar río San Mateo) (Fig. 13) (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=42371>)

***Ponderacris chulumaniensis* sp.n. Pocco, Lange & Cigliano**

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:74240>
(Figs 2B, 3G, H, 4A, B, 6D–F, 13)

Diagnosis. *Ponderacris chulumaniensis* differs from the remaining species of the genus by male cerci with pointed apex, concave anterior margin and rounded posterior margin (Fig. 3G). Furculae developed (Fig. 3H). Apical valves of aedeagus directed downwards (Figs 4B, 6E), constricted in the middle, widening towards the apex (Figs 4A, 6D); caudally divergent, with broad and rounded apices (Figs 4A, 6D). Rami of cingulum wide with expanded apex (Figs 4B, 6E). Lophi of epiphallus low, placed parallel to bridge, dorsally narrow (Fig. 6F). Abdomen ventrally yellow; hind tibiae with proximal half dark green and distal half orange-red.

Description. Males. Brachypterous insects (Fig. 2B). Tegmina approximately as long as pronotum and lobiform. Cerci with pointed apex, concave anterior margin and rounded posterior margin (Fig. 3G). Subgenital plate with pointed or slightly rounded apex (Fig. 3G). Furculae very short (Fig. 3H). Apical valves of aedeagus directed downwards (Figs 4B, 6E), constricted in the middle, widening towards the apex (Figs 4A, 6D); caudally divergent, with broad and rounded apices (Figs 4A, 6D). Rami of cingulum wide with expanded apex (Figs 4B, 6E). Mid-dorsal apical lobes of sheath of aedeagus long, covering wholly or most of the apical valves. Lophi of epiphallus low, placed parallel to bridge, dorsally narrow (Fig. 6F). Body colour dull brown, abdomen ventrally yellow, upper face of hind femur darkly mottled, hind tibiae with proximal half dark green and distal half orange-red.

Females. Similar to males, but more robust.

Measurements (in mm). Body length: males 14.8 (13.9–16), females 21.3 (20–23); femur III: males 9.03 (8.5–9.7), females 11.75 (11–12); ratio pronotum length/tegmina length: males 1.05 (0.89–1.16), females 0.93 (0.80–1.03).

Etymology. The name refers to the distribution of the species in and around Chulumani, La Paz, Bolivia.

Material examined. BOLIVIA: holotype ♂, allotype ♀, La Paz, Chulumani, (16°24'33.24"S, 67°32'11.77"W), 1825 m, 27.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA). Paratypes: 13 ♂, 11 ♀, La Paz, Chulumani, (16°24'41.39"S, 67°32'12.57"W), 1729 m, 26.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA); 10 ♂, 9 ♀, La Paz Chulumani, (16°24'33.24"S, 67°32'11.77"W), 1825 m, 27.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA); 1 ♂, 1 nymph, La Paz, Chulumani, 4 km from Irupana (16°27'3.71"S, 67°28'59.20"W), 26.iii.2003 (Cigliano M.M. & Lange C.E.) (MLPA).

Distribution. Bolivia (Fig. 13) La Paz (Chulumani). (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=78518>)

***Ponderacris amoroensis* sp.n. Pocco, Lange & Cigliano**

<http://lsid.speciesfile.org/urn:lsid:orthoptera.speciesfile.org:TaxonName:74241>
(Figs 2A, 3C, D, 4C, D, 6A–C, 13)

Diagnosis. Similar to *P. chulumaniensis* differing mostly in the shape of male cerci and characteristics of the phallic complex. Male cerci wide, with upper margin oblique, anterior margin concave and posterior margin slightly rounded (Fig. 3C). Furculae present (Fig. 3D). Apical valves of aedeagus wide, with distal third straight (Figs 4D, 6B), apex rounded (Figs 4C, 6A). Rami of cingulum with expanded apex (Figs 4D, 6B). Basal lobes of aedeagus sheath well developed (Figs 4C, 6A). Abdomen ventrally orange with tinges of yellow; hind tibiae red.

Description. Males. Brachypterous insects (Fig. 2A). Tegmina approximately as long as pronotum and lobiform. Cerci wide, with upper margin oblique, anterior margin concave and posterior margin slightly rounded (Fig. 3C). Subgenital plate with apex pointed or slightly rounded (Fig. 3C). Furculae very short (Fig. 3D). Apical valves of aedeagus wide, with distal third straight (Figs 4D, 6B), apex rounded (Figs 4C, 6A). Rami of cingulum with apex broad and expanded (Figs 4D, 6B). Mid-dorsal apical lobes of sheath of aedeagus long, covering wholly or most of the apical valves; basal lobes of aedeagus sheath well developed (Figs 4C, 6A). Lophi of epiphallus low, parallel to bridge, dorsally narrow (Fig. 6C). Body colour dull brown, abdomen ventrally orange with tinges of yellow, upper face of hind femur with black spots, hind tibiae red.

Females: similar to males, but more robust.

Measurements (in mm). Body length: males 16.9 (15–20), females 22.1 (18.5–24); femur III: males 10.6 (10–11), females 13.2 (12–15); ratio pronotum length/tegmina length: males 0.95 (0.90–0.99), females 0.99 (0.93–1.11).

Etymology. The name refers to the distribution of the species around the Amboró National Park, Santa Cruz, Bolivia.

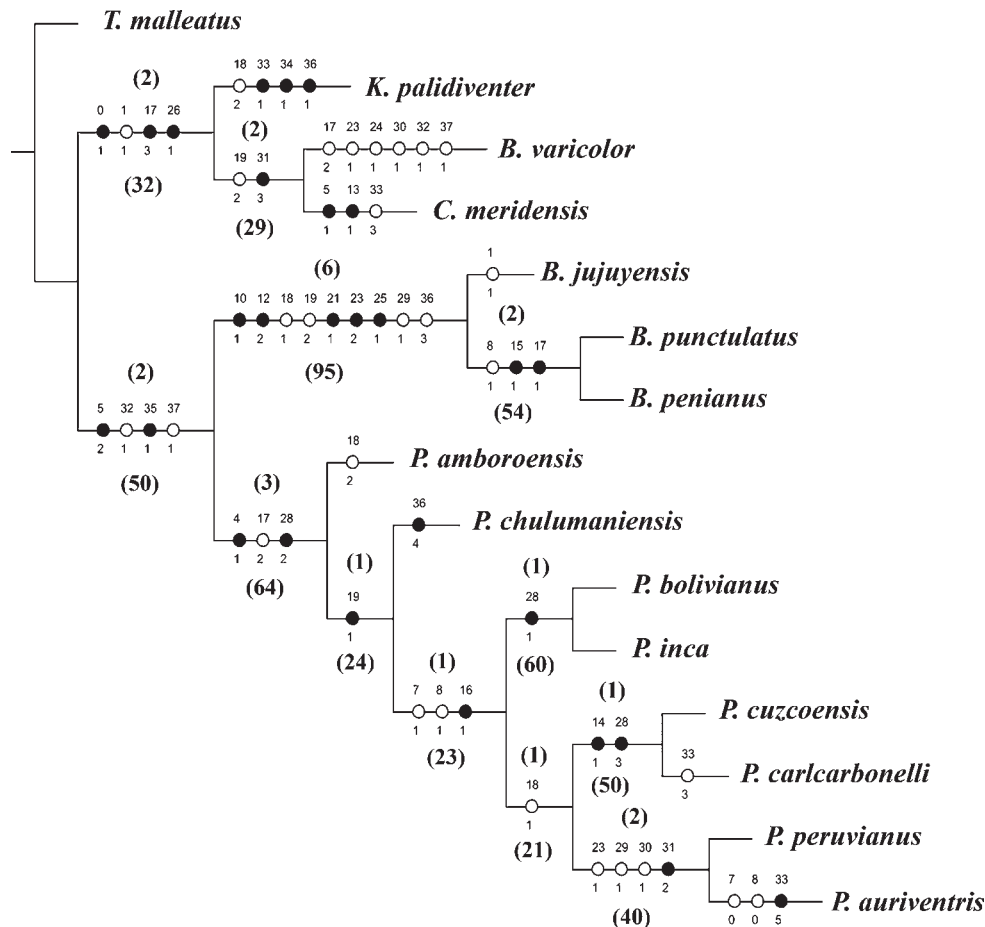


Fig. 10. Most parsimonious tree of the genus *Ponderacris* (length 105, consistency index = 0.705, retention index = 0.765) resulting from the cladistic analysis of the morphological character dataset, under equal weights. Black circles indicate unique changes and white circles indicate homoplasies. The numbers between brackets below the nodes are bootstrap support values, and those above are Bremer support values.

Material examined. BOLIVIA: *holotype* ♂, *allotype* ♀, Santa Cruz, Samaipata, Parque Nacional Amboró, Los Paredones, 13 km from Achiras Camping (18°6'47.19"S, 63°52'30.93"W), 25.ii.2003 (Cigliano M.M. & Lange C.E.) (MLPA). *Paratypes* (all collected Cigliano M.M. & Lange C.E., deposited MLPA): 2 ♂, 5 ♀, Santa Cruz, Samaipata, Parque Nacional Amboró, Las Yungas (Mairana) (18°3'31.07"S, 63°54'35.59"W), 2323 m, 16.iv.2004; 16 ♂, 10 ♀, Santa Cruz, Samaipata, Parque Nacional Amboró, Los Paredones, 9 km from Achiras Camping (18°7'6.27"S, 63°48'3.24"W), 2040 m, 16.iv.2004; 1 ♂, 2 ♀, Santa Cruz, Samaipata, Parque Nacional Amboró, Los Paredones, 6 km from Achiras Camping (18°7'46.12"S, 63°48'28.14"W), 1714 m, 16.iv.2004; 18 ♂, 26 ♀, Santa Cruz, Samaipata, Parque Nacional Amboró, Los Paredones, 13 km from Achiras Camping (18°6'47.19"S, 63°52'30.93"W), 25.ii.2003; 1 ♂, 1 ♀, Santa Cruz, Samaipata, Achiras Camping 7 km on road to Parque Nacional Amboró, (18°6'51.59"S, 63°48'2.23"W), 25.ii.2003; 1 ♂, Santa Cruz, Samaipata, Achiras Camping on road to Parque Nacional Amboró (18°7'49.60"S, 63°48'32.12"W), 25.ii.2003.

Distribution. Bolivia (Fig. 13) Santa Cruz (Samaipata) (See geographic distribution in OSF, <http://orthoptera.speciesfile.org/Common/editTaxon/Distribution/SpecimensMap.aspx?TaxonNameID=78519>).

Tree topology and support

Parsimony analysis under equal weights of the data matrix (Table S1) resulted in one most parsimonious tree (Fig. 10) of length 105 (CI, 0.705; RI, 0.765): the same topology was obtained under implied weighting (on trees with $K = 1-30$) with increase of K from 1 to 30 yielding no change in topology.

Support values for most clades in the equal weight analysis were low. However, implied weighting analysis from $K = 1$ to 30 resulted in the same topology obtained under equal weights, implying a conservative topology and allowing to postulation of a solid biogeographical hypothesis.

Analysis recovered *Ponderacris* as a monophyletic group with moderate bootstrap support (64%), based on the following

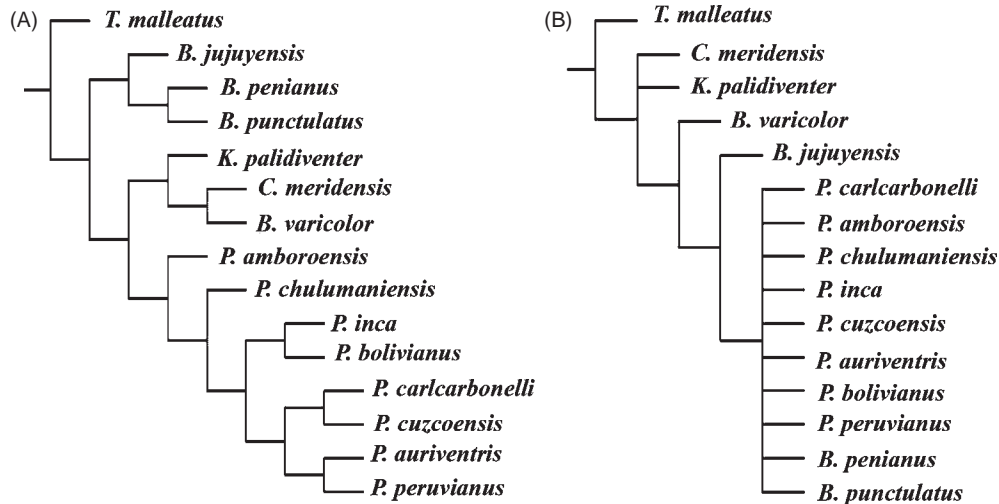


Fig. 11. (A) One of the three most parsimonious tree of the genus *Ponderacris* (length 53, CI = 0.792, RI = 0.849) resulting from the cladistic analysis of the abdominal terminalia and genitalia character set. (B) Strict consensus of 19 MPTs (length 43, CI = 0.744, RI = 0.814) obtained from the cladistic analysis based on the character set of the external morphology and colouration.

synapomorphies: pronotal front margin slightly emarginate (4:1) and rami with distal third broad and rounded (28:2) (Fig. 5B). *Ponderacris amboroensis* arises from the basal node and the remaining species group in a clade based on the synapomorphy: apical valves of aedeagus directed downwards (19:1) (Fig. 6E). Within this clade, *P. chulumaniensis* is sister to the remaining species that constitute a monophyletic group based on absent furculae (16:1) and two parallelisms: half-winged (7:1) (Fig. 2D); tegmina elongate (8:1) (Fig. 2D). Within this group the best supported clade (bootstrap values: 60%) is constituted by the sister species *P. inca* and *P. bolivianus*, defined by the rami with crescent-shaped distal third (28:1) (Fig. 6K). Another group is defined by the apical valves of the aedeagus being long and divergent (18:1) (Fig. 5A). Within this clade, two groups are recovered: one group (bootstrap values: 50%) comprising the sister species *P. cuzcoensis* and *P. carlcarbonelli*, supported by the blunt subgenital plate (14:1) (Fig. 3M) and apex of rami with a notch at inferior margin (28:3) (Fig. 5K). The other group (bootstrap values: 40%) includes the sister species *P. auriventris* and *P. peruvianus*, based on epiphallus with prominent and rectangular lophi (31:2), mid-dorsal apical lobes of sheath of aedeagus long, covering two thirds of the apical valves (23:1) (Fig. 5A), lophi of epiphallus perpendicular to disk (29:1) (Fig. 5C) and widely expanded towards the posterior process of lateral plates (30:1) (Fig. 5C). The analysis resolves *Ponderacris* as the sister group to the well supported clade (bootstrap values: 95%) comprised by *Boliviocris jujuyensis* and *Baeacris* species based on the following synapomorphies: hind margin of pronotal disk angulate (5:2) and hind femur with black spots (35:1) (Fig. 2C) and the homoplasies: body with dull tegument (32:1) (Fig. 2B) and postocular band present (37:1) (Fig. 1D). The remaining outgroup species (*K. palidiventer*, *B. varicolor* and *C. meridensis*) are grouped into a clade with low bootstrap support.

Three most parsimonious trees of 53 steps long (CI, 0.792; RI, 0.849) were obtained based on the analysis of the character set from male abdominal terminalia and genitalia. The topologies of the trees are highly congruent to that obtained with all characters. Only minor changes are found compared to the original tree and mostly located in the relationships within outgroup species. The chosen tree (Fig. 11A) shows that the clade consisting of *Boliviocris jujuyensis* and *Baeacris* species is branches off at the root.

Nineteen most parsimonious trees of 43 steps long (CI, 0.744; RI, 0.814) were obtained through cladistic analysis based on the character set of external morphology and colouration. The strict consensus tree (Fig. 11B) shows low resolution compared to the tree obtained with all the characters. The species of *Ponderacris* are grouped with the species of *Baeacris* with high bootstrap values (76%), and *B. jujuyensis* subtends this major, completely unresolved clade with the highest bootstrap values (86%) of the tree.

Biogeography

The results of DIVA are presented in Fig. 12A. All ancestral nodes of *Ponderacris* yielded a single possible ancestral distribution reconstruction. Only two nodes (17 and 28 in Fig. 12A) resulted in two possible ancestral distributions, but they correspond to the outgroup taxa. According to DIVA analysis the common ancestor of *Ponderacris* species was distributed in the Lower Montane Yungas (Bolivia) (node 26). Subsequent dispersal from Bolivia to the 'Ceja' Forest (Peru) would have taken place before the cladogenetic event represented by node 24, which separates these areas (Fig. 12A). Therefore, the ancestor of the clade constituted by *P. bolivianus* and *P. inca* (node 20) inhabited the Lower Montane Yungas (Bolivia), and the ancestor of the clade

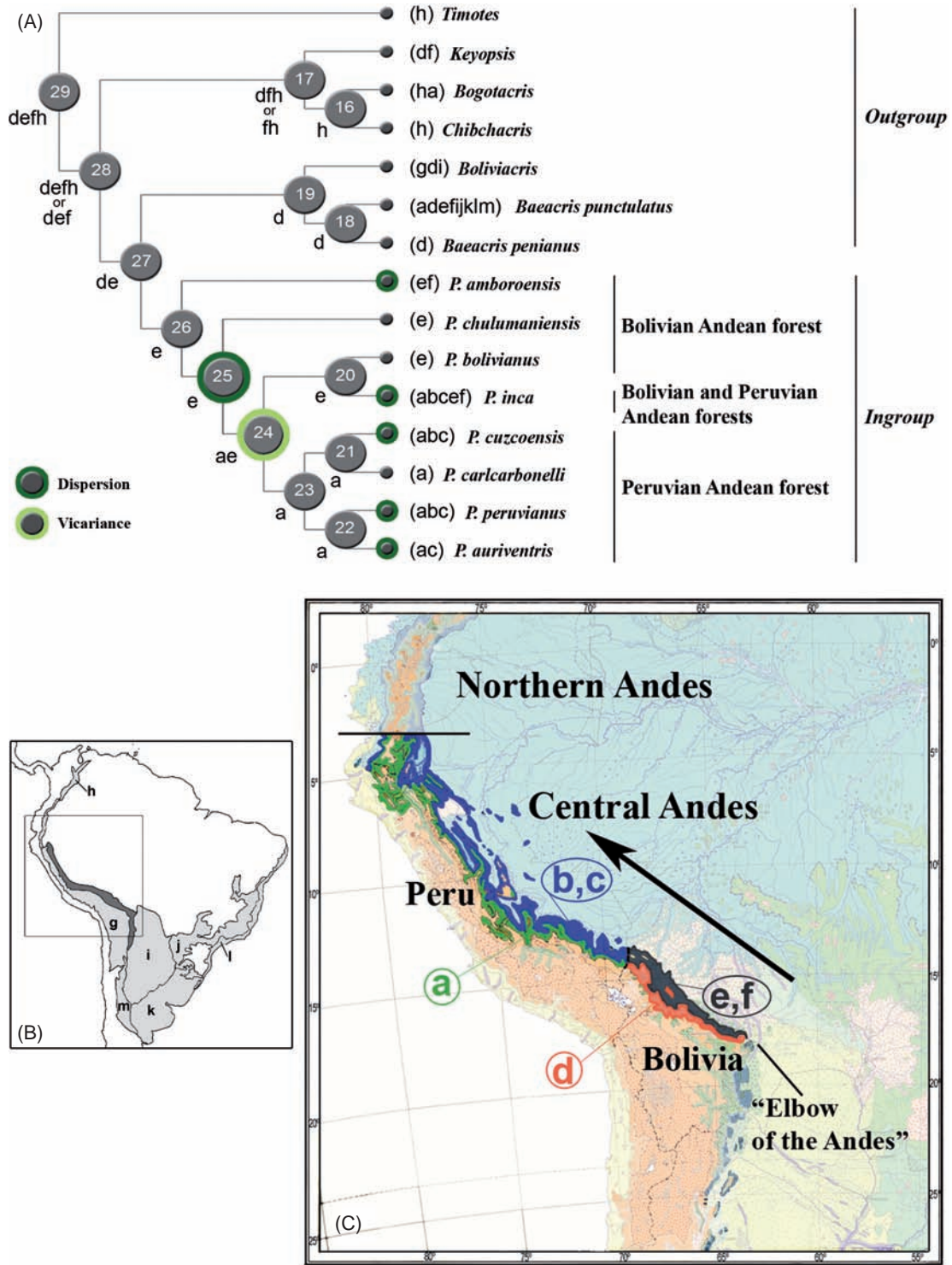


Fig. 12. (A) Taxon area cladogram showing the results of DIVA. Numbers indicate nodes and letters indicate resulting ancestral distribution at each node. (a) 'Ceja' Forest Peru (2500 to 4000 m a.s.l.), (b) Lower Montane Rainforest (Peru) (<1500 m a.s.l.), (c) Upper Montane Rainforest (Peru) (1500 to 2500 m a.s.l.), (d) 'Ceja' Forest (Bolivia) (2800 to 3400 m a.s.l.), (e) Lower Montane Yungas (Bolivia) (<2000 m a.s.l.), (f) Upper Montane Yungas (Bolivia) (2000 to 2800 m a.s.l.), (g) Puna, (h) North Andean Paramo, (i) Chaco, (j): Parana Forest, (k): Pampa, (l): Brazilian Atlantic Forest, (m): Monte. (B) biogeographic areas (provinces) defined by Morrone (2006), used in the DIVA analysis. Map modified from Morrone (2006). (C) Biogeographical subdivisions of the Peruvian and Bolivian forests defined by Hueck (1978) used in the DIVA analysis. Map modified from Hueck (1978). The arrow indicates the direction of diversification of *Ponderacris*.

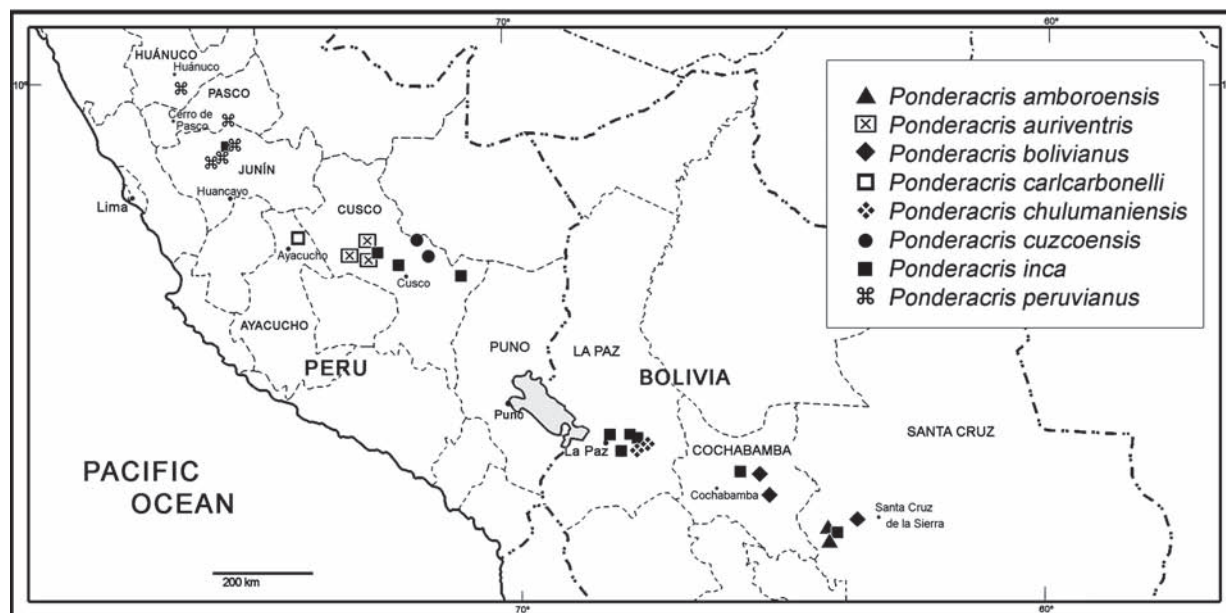


Fig. 13. Geographic distribution of *Ponderacris* species.

comprising *P. cuzcoensis*, *P. peruvianus*, *P. auriventris* and *P. carlcarbonelli* (node 23) inhabited the 'Ceja' Forest (Peru). Independent evolution is suggested here to have occurred in both groups matching the widest terminal distributions (e.g. *P. inca* at the 'Ceja' Forest, Upper and Lower Montane Rainforest, Lower and Upper Montane Yungas) with recent dispersal events of the terminal taxa.

Discussion

Diversity patterns in Ponderacris

The accelerating degradation of Andean habitats adds a special urgency to taxonomic research at the specific level in montane groups (Churchill *et al.*, 1995; Dinerstein *et al.*, 1995; Aldrich *et al.*, 1997; Cigliano *et al.*, 2011). Human activities severely reduce biodiversity in these habitats and threaten the survival of many as yet undescribed species. Describing them provides not only a record of their existence, but also is the basis for an understanding of spatial variation in species richness and endemism, as a path leading to conservation strategies. The discovery of three species of *Ponderacris* described herein parallels the situation of other Andean grasshopper groups in which recent studies have illustrated discrepancies between perceived and actual species diversity (Cigliano & Lange, 2007; Cigliano & Amédégnato, 2010; Cigliano *et al.*, 2010).

As evidenced from the results of the cladistic analysis *Baeacris* and *Boliviacris* form the sister group to *Ponderacris*, which is hypothesized to be monophyletic with species grouped according to their geographic location. The species distributed in the Peruvian Andes constitute a monophyletic clade, and

those from the Bolivian Andes form a paraphyletic grade basal to that group.

The different character sets (external morphology – chromatic characters and male abdominal terminalia – genitalia) showed different phylogenetic values. As in other genera of Dichroplini (i.e. *Baeacris*, *Chibchacris*, *Bogotacris*) characters from the external morphology and colour pattern provide less phylogenetic information than do the male abdominal terminalia and phallic complex. If characters only from the external morphology and chromatic characters were considered, the consensus tree showed less resolution than when the set of characters from the male abdominal terminalia and genitalia was analysed. Furthermore, when the analysis was based on the latter set of characters, the trees obtained were completely resolved and highly congruent with the analysis based on all characters. If only external characters were analysed, the species of *Ponderacris* were grouped with the species of *Baeacris*. Interestingly, all the species included in this latter group (except for the new ones) were described originally in the genus *Dichroplus* Stål. In the past, only characters from the external morphology were used to group species in the genus *Dichroplus* Stål s.l. Although this set of characters was not shown to be more homoplasious in the analysis of all the characters, it provided less phylogenetic information than did the male abdominal terminalia and genitalia.

The taxonomic diversity within *Ponderacris* as in the remaining Dichroplini is accompanied by great morphological uniformity, except in the divergent male genitalia. The genital divergence in the Dichroplini and Melanoplinae as a whole appears to be associated with the mode of courtship – or rather the almost complete lack of pre-contact courtship as females are unaware of males until they have

been jumped on (Otte, 1970). At this point tactile stimuli appear to assume great importance. In Dichroplini there is an apparent absence of corresponding female genitalic specificity; certainly females appear to be much more similar to one another than males (Cigliano & Lange, 2007). It is highly probable that genitalic differences evolved outside the context of reproductive isolation and that diversity of male genitalia is shaped by cryptic female choice (Eberhard, 1996). Females of different species of *Ponderacris* are almost undistinguishable from each other and thus there are fewer characters to differentiate species and to include in the data matrix. We are dealing with a group of grasshoppers whose external morphology is very homogeneous, and differences in female genitalia are almost nonexistent; thus the number of informative characters is reduced. The relatively low support value of several clades may be explained by the few characters included in the analysis. However, the stability of the obtained topology, which is the same using equal weights and implied weights ($K = 1-30$) analysis, justifies the robustness of the proposed cladogram.

Species differentiation and historical biogeography

Ponderacris and the outgroups, *Timotes*, *Chibchacris*, *Bogotacris*, *Boliviacris*, *Keyopsis* and *Baeacris* are Dichroplini genera confined to the highlands, except for *Baeacris* that includes two species (*B. punctulatus* and *B. pseudopunctulatus*) extending into the lowlands. In fact, *B. punctulatus* is the species with the widest distribution of the tribe Dichroplini being tolerant of varied ecological and climatic conditions (Rowell & Carbonell, 1977; Carbonell *et al.*, 2006). Interestingly, our results suggest that the origin of this species is in the Andes, in the Ceja Forest (Bolivia). From there, *B. punctulatus* dispersed following different routes and colonizing new areas and habitats. A dispersion route to north allows the colonization of Ceja Forest (Peru), and changes in altitudinal range enlarge the distribution of this species to Upper and Lower Yungas of Bolivia and far east to Chaco, Pampa, Parana and Atlantic Rain forest areas. Molecular phylogeographic studies of this species would bring clearest explanation of the time and processes which led to this biogeographic expansion.

The above-mentioned genera have been considered to constitute a natural group within the Dichroplini based on characters from the phallic complex (Ronderos & Cigliano, 1991). The Dichroplini is the largest tribe of South American Melanoplineae, including 24 genera and 130 valid species, and for the most part has given rise to temperate and subtropical forms, living in grasslands and other open plant formations.

Species belonging to *Ponderacris* are adapted to a wide altitudinal range and occur at high altitudes. Some of the specimens were collected at altitudes of up to 4000 m a.s.l. but modern distributions indicate that high altitudes do not necessarily represent important physical barriers to these taxa. However, no *Ponderacris* species was found in Paramo or Puna habitats, indicating that the genus is restricted to montane forest environments.

According to Amédégno *et al.* (2003) and Chintauan-Marquier *et al.* (2010) the diversification of the subfamily Melanoplineae in South America probably followed the uplift of the Andes. These studies, based on molecular evidence, have shown that the differentiation of the Melanoplineae clades coincided with the timing of the Andean orogenesis.

Presently three subdivisions have been recognized for the Andes (Gansser, 1973): southern Andes of Argentina and Chile, central Andes of Bolivia and Peru and northern Andes of Ecuador, Colombia and Venezuela. The Central Andes form the largest and most mountainous segment of the Cordillera. This 4000-km-long segment is divided into the northern Central Andes (5°30'S to 13°S; entirely located in Peru), Bolivian Orocline (13–28°S; over southern Peru, Bolivia, northern Chile, northwestern Argentina), and southern Central Andes (28–37°S; over central Chile and west-central Argentina).

Most studies favour the hypothesis that Andean uplift started in the Eocene or Oligocene, but many do recognize a subsequent resumption of uplift starting in the late Miocene (Garzzone *et al.*, 2008; Sempere *et al.*, 2008; Hoorn *et al.*, 2010). Thus, it is mostly considered that mountain building was attained in two steps, the first slowly developing from the mid-Eocene to the late Oligocene and early Miocene (including the uplift of the proto-Cordillera Oriental of Bolivia called the Yungas), and a later, apparently vigorous step starting at ~10 to 9 Ma and possibly lingering into the Pliocene and/or Present (Garzzone *et al.*, 2008; Sempere *et al.*, 2008). Although, as already pointed out by Mulch *et al.* (2010), additional studies integrating evidence from a larger spatial and temporal sampling size are required to resolve whether the paleogeographic data indicate a rapid or rather a gradual uplift of the Andes toward the late Miocene. Regardless of the exact timing of the uplift, all authors concur that the Andes reached their present elevation around the Mio-Pliocene (Luebert *et al.*, 2011).

In the central Andes, uplift progressively propagated northwards along the Andean backbone, rising new areas above altitude thresholds and thus making them available for colonization by highland, southern biota (Picard *et al.*, 2008).

Based on DIVA results *Ponderacris* seemingly arose in the Cordillera Oriental of Bolivia (the Yungas) (Fig. 12A, C) in a scenario consistent with the earlier uplift of the proto-Cordillera Oriental of Bolivia (Sempere *et al.*, 2008). The two earliest nodes show species (*P. amboroensis* and *P. chulumaniensis*) endemic (restricted) to the Bolivian Yungas inhabiting the Lower Montane Yungas (up to c.2000 m a.s.l.) and Upper Montane Yungas (between 2000 and 2800 m a.s.l.). The single dispersal event detected in an internal node of the area cladogram occurred between the nodes 25 and 24, and led to a range expansion from Bolivia to Peru (Fig. 12A). This event resulted in the incorporation of the 'Ceja' Forest of Peru to the ancestral distribution, originally represented by a single area (Lower Montane Yungas, Bolivia).

The vicariant event at node 24 splits the ancestral distribution (Lower Montane Yungas + 'Ceja' Forest from Peru) resulting in the independent evolution of the clade constituted

by *P. inca* and *P. bolivianus* from the clade constituted by the Peruvian species (see Fig. 12A). This event could relate to fragmentation of mountain forest that occurred during the dry intervals of the late Cenozoic. These forest fragments may have served as refugia especially in the most humid areas located around 18°S in the Bolivian territory. At this latitude the eastern chain of the Andes abruptly changes orientation turning northwest in a curving arc – the Bolivian orocline. This area, also known as the ‘elbow of the Andes’ (Fig. 12C), is an important geographical feature relevant to the biology of the region (Graham, 2009). This arc at right angle to winds from the Amazon Basin increases rainfall and may have perpetuated humid conditions during dry intervals of the late Cenozoic and served as refugia for rainforest taxa (Killeen *et al.*, 2007; Graham, 2009).

Ten out of the eleven dispersal events detected in our results occurred at terminal taxa and are considered as recent dispersal of the individual species, indicating that high altitudes do not necessarily represent important physical barriers for *Ponderacris*. One of the remaining species inhabiting Bolivia, *P. bolivianus*, is restricted to the Lower Montane Yungas and the sister species *P. inca* has the widest distribution of *Ponderacris*, inhabiting the entire range of the genus.

From the Bolivian orocline, it is likely that the Peruvian *Ponderacris* ancestors dispersed northward, colonizing the expanding montane habitats as they became available, coinciding with the rise of the Andes.

Peru is home to four species of *Ponderacris*, besides *P. inca*. *Ponderacris carlcarbonelli* that has quite small geographic range restricted to the ‘Ceja’ Forest is closely related to *P. cuzcoensis*, which occurs in the ‘Ceja’ as well as in the Lower and Upper Montane Rainforests. The remaining species from Peru are closely related, *P. auriventris* occurs in ‘Ceja’ Forest and Upper Montane Forest, whereas *P. peruvianus* is widely distributed in all the Peruvian areas delimited in the study.

In Peru, uplifts produced a profound modification of surface conditions which triggered a variety of radiations of cold-adapted highland biota (Picard *et al.*, 2008). Dispersal could have occurred along the Andean chain unless ice caps covered it. The early Pleistocene (2.6–0.8 Ma) was characterized by climatic fluctuations during which substantial ice sheets developed. But it was not until about 1.2 Ma that the glacial periods were long enough to allow for significant ice sheet development on a continental scale outside the Polar Regions (Ehlers & Gibbard, 2007). The Pleistocene glaciations indisputably had a major impact on many taxa as species distribution shifted repeatedly and frequently in response to climatic fluctuations (Hewitt, 1996). In South America, glaciations increased in intensity throughout the Andean mountain chain from 800 ka until the last glacial maximum about 20 ka (Rabassa *et al.*, 2011). The climatic oscillations of the Pleistocene caused cyclic vertical shifts of the vegetation belts, while at the same time causing the expansion of some of these belts during glacial periods. This allowed for dispersion and increased gene flow, that was interrupted during the interglacials, in which widespread

populations were broken and isolated, sometimes causing their diversification.

Speciation in *Ponderacris* appears linked to the uplift of the Andes. The branching order of the phylogenetic tree is consistent with the SNSH hypothesis (Doan, 2003). The earliest nodes are associated with Bolivia, the southernmost extent of the genus and nodes connecting more derived species having more northern geographic ranges in Peru. Recent studies on the processes that promoted diversification of several taxa in the Andes have suggested also that, at least in some groups, divergence was coupled to the Andean orogeny (Ribas *et al.*, 2007; Picard *et al.*, 2008; Soejima *et al.*, 2008; Chaves *et al.*, 2011; Luebert *et al.*, 2011; Husemann *et al.*, 2012).

However, the diversification patterns of *Ponderacris* cannot be solely explained by the SNSH hypothesis, but appears to be a more complex phenomenon that included both vicariance and dispersal across barriers heavily influenced by Pleistocene climatic cycles.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12001

Table S1. Data matrix used in the cladistic analysis of *Ponderacris*.

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References

- Aldrich, M., Billington, C., Edwards, M. & Laidlaw, R. (1997) *Tropical Montane Cloud Forests: An Urgent Priority for Conservation*, WCMC Biodiversity Bulletin 2. WCMC, Cambridge, U.K.
- Amédégno, C., Chapco, W. & Litzberger, G. (2003) Out of South America? Additional evidence for a southern origin of melanopline grasshoppers. *Molecular Phylogenetics and Evolution*, **29**, 115–119.
- Bremer, K. (1994) Branch support and tree stability. *Cladistics*, **10**, 235–304.
- Bruner, L. (1913) Results of the Yale Peruvian expedition of 1911. Orth. (Acridiidae-short horned locusts). *Proceedings of the United States National Museum*, **44**, 177–187.
- Carbonell, C.S., Cigliano, M.M. & Lange, C.E. (2006) *Especies de acridomorfos (Orthoptera) de Argentina y Uruguay [Acridomorpha (Orthoptera) species of Argentina and Uruguay]*. [CD ROM.] Publications on Orthopteran Diversity. The Orthopterists’ Society at the Museo de la Plata, La Plata.
- Chesser, R.T. (2000) Evolution in the high Andes: the phylogenetics of *Muscisaxicola* ground-tyrants. *Molecular Phylogenetics and Evolution*, **15**, 369–380.

- Cigliano, M.M. (1997 [1998]) *Ronderosia*, a new genus of South American Melanoplinae (Orthoptera: Acrididae). *Journal of Orthoptera Research*, **6**, 1–19.
- Cigliano, M.M. & Amédégnato, C. (2010) The high-andean *Jivarus* Giglio-Tos (Orthoptera, Acridoidea, Melanoplinae): systematics, phylogenetic and biogeographic considerations. *Systematic Entomology*, **35**, 692–721.
- Cigliano, M.M. & Eades, D. (2010) New technologies challenge the future of Taxonomy in Orthoptera. *Journal of Orthoptera Research*, **19**, 15–18.
- Cigliano, M.M. & Lange, C.E. (2007) Systematic revision and phylogenetic analysis of the South American genus *Chlorus* (Orthoptera, Acridoidea, Melanoplinae). *Zoologica Scripta*, **36**, 241–254.
- Cigliano, M.M., de Wysiecki, M.L. & Lange, C.E. (2000) Grasshopper (Orthoptera: Acridoidea) species diversity in the Pampas, Argentina. *Diversity and Distributions*, **6**, 81–91.
- Cigliano, M.M., Amédégnato, C., Pocco, M.E. & Lange, C.E. (2010) Revisionary study of *Pediella* Roberts (Orthoptera: Acrididae: Melanoplinae) from the Andes Highlands. *Zootaxa*, **2431**, 51–61.
- Cigliano, M.M., Pocco, M.E. & Lange, C.E. (2011) Grasshoppers of the Andes: new Melanoplinae and Gomphocerinae taxa (Orthoptera: Acridoidea: Acrididae) from Huascarán National Park and Callejón de Huaylas, Ancash, Perú. *Zoosystema*, **33**, 523–544.
- Chaves, J., Weir, J.T. & Smith, T.B. (2011) Diversification in *Aedolomyia* hummingbirds follows Andean uplift. *Molecular Ecology*, **20**, 4564–4576.
- Chintauan-Marquier, I., Jordan, S., Berthier, P., Amédégnato, C. & Pompanon, F. (2010) Multiple origins of a short-horned grasshopper subfamily: the Melanoplinae (Orthoptera: Acrididae). *Molecular Phylogenetics and Evolution*, **58**, 22–32.
- Churchill, S.P., Balslev, H., Forero, E. & Luteyn, J.L. (eds) (1995) *Biodiversity and Conservation of Neotropical Montane Forests*. The New York Botanical Garden, New York, NY.
- Crisci, J.V., Katinas, L. & Posadas, P. (2003) *Historical Biogeography: An Introduction*. Harvard University Press, Cambridge, MA.
- Dinerstein, E., Olson, D.M., Graham, D.J., Webster, A.L., Pimm, S.A., Bookbinder, M.P. & Ledec, G. (1995) *A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean*. The World Bank, Washington, DC.
- Doan, T.M. (2003) A south-to-north biogeographic hypothesis for Andean speciation: evidence from the lizard genus *Proctoporus* (Reptilia, Gymnophthalmidae). *Journal of Biogeography*, **30**, 361–374.
- Eades, D.C., Otte, D., Cigliano, M.M. & Braun, H. (2012) *Orthoptera Species File Online. Version 2.0/4.0* [WWW document]. URL <http://Orthoptera.SpeciesFile.org>. [accessed on 10 October 2012].
- Eberhard, W.G. (1996) *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton, NJ.
- Ehlers, J. & Gibbard, P.L. (2007) Glaciation: overview. *Encyclopedia of Quaternary Science* (ed. by S.A. Elias), pp. 1023–1031. Elsevier, Amsterdam.
- Elias, M., Joron, M., Willmott, K. et al. (2009) Out of the Andes: patterns of diversification in clearwing Butterflies. *Molecular Ecology*, **18**, 1716–1729.
- Gansser, A. (1973) Facts and theories on the Andes. *Journal Geological Society*, **129**, 93–131.
- Garzone, C.N., Hoke, G.D., Libarkin, J.C. et al. (2008) Rise of the Andes. *Science*, **320**, 1304–1307.
- Goloboff, P. (1993) Estimating character weights during tree search. *Cladistics*, **9**, 83–91.
- Goloboff, P.A., Farris, S. & Nixon, K. (2003a) *Tree Analysis using New Technology*. Published by the authors, Tucumán [WWW document]. URL <http://www.cladistics.com/aboutTNT.html>. [accessed on 10 March 2009].
- Goloboff, P.A., Farris, S., Källersjö, M., Oxelman, B., Ramírez, M.J. & Szumik, C.A. (2003b) Improvements to resampling measures of group support. *Cladistics*, **19**, 324–332.
- Graham, A. (2009) The Andes: a geological overview from a biological perspective. *Annals of the Missouri Botanical Garden*, **96**, 371–385.
- Guarnizo, C.E., Amézquita, A. & Eldredge, B. (2009) The relative roles of vicariance versus elevational gradients in the genetic differentiation of the high Andean tree frog, *Dendropsophus labialis*. *Molecular Phylogenetics and Evolution*, **50**, 84–92.
- Hadley, A. (2006) *CombineZ5*. Published by the author, London [WWW document]. URL <http://www.hadleyweb.pwp.blueyonder.co.uk>. [accessed on 10 April 2010].
- Hewitt, G. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, **58**, 247–276.
- Hoorn, C., Wesselink, F.P., ter Steege, H. et al. (2010) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, **330**, 927–931.
- Hueck, K. (1978) *Los bosques de Sudamérica. Ecología, composición e importancia económica*. Sociedad Alemana de Cooperación Técnica, Eschborn.
- Husemann, M., Guzman, N.V., Danley, P.D., Cigliano, M.M. & Con-falonieri, V.A. (2012) Biogeography of *Trimerotropis pallidipennis* (Acrididae: Oedipodinae): deep divergence across the Americas. *Journal of Biogeography*, doi:10.1111/jbi.12007.
- Killeen, T.J., Douglas, M., Consiglio, T., Jørgensen, P.M. & Mejia, J. (2007) Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography*, **34**, 1357–1373.
- Kirby, W.F. (1910) *A Synonymic Catalogue of Orthoptera (Orthoptera Saltatoria, Locustidae vel Acridiidae)*. British Museum, London.
- Kodandaramaiah, U. (2010) Use of dispersal–vicariance analysis in biogeography – a critique. *Journal of Biogeography*, **37**, 3–11.
- Koscinski, D., Handford, P., Tubaro, P.L., Sharp, S. & Lougheed, S.C. (2008) Pleistocene climatic cycling and diversification of the Andean treefrog, *Hypsiboas andinus*. *Molecular Ecology*, **17**, 2012–2025.
- Liebermann, J. (1968) Lista alfabética preliminar de las tucuras de la tribu Dichroplini de la región neotropical (Orthoptera Acrididae). *Revista de la Sociedad Entomológica Argentina*, **30**, 27–36.
- Luebert, F., Hilger, H.H. & Weigend, M. (2011) Diversification in the Andes: age and origins of South American *Heliotropium* lineages (Heliotropiaceae, Boraginales). *Molecular Phylogenetics and Evolution*, **61**, 90–102.
- Luteyn, J.L. & Churchill, S.P. (2000) Vegetation of the tropical Andes: an overview. *Imperfect Balance: Landscape Transformations in the Precolumbian Americas* (ed. by D.L. Lentz), pp. 281–310. Columbia University Press, New York, NY.
- Morawetz, W. & Raedig, C. (2007) Angiosperm biodiversity, endemism and conservation in the Neotropics. *Taxon*, **56**, 1245–1254.
- Morrone, J.J. (2006) Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Reviews of Entomology*, **51**, 467–494.
- Mulch, A., Uba, C.E., Strecker, M.R., Schoenberg, R. & Chamberlain, C.P. (2010) Late Miocene climate variability and surface elevation in the central Andes. *Earth and Planetary Science Letters*, **290**, 173–182.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

- Nixon, K.C. (2002) *Winclada*, Version 1.00.08. Published by the author, Ithaca, NY.
- Otte, D. (1970) A Comparative Study of Communicative Behaviour in Grasshoppers. *Miscellaneous Publications, University of Michigan Museum of Zoology*, **141**, 1–168.
- Otte, D. (1995) *Grasshoppers [Acridomorpha] C. Orthoptera Species File*, 4. The Orthopterists' Society and The Academy of Natural Sciences of Philadelphia, Philadelphia, PA.
- Picard, D., Sempere, T. & Olivier, P. (2008) Direction and timing of uplift propagation in the Peruvian Andes deduced from molecular phylogenetics of highland biotaxa. *Earth and Planetary Science Letters*, **271**, 326–336.
- Rabassa, J., Coronato, A. & Martínez, O. (2011) Late Cenozoic glaciations in Patagonia and Tierra del Fuego: an updated review. *Biological Journal of the Linnean Society*, **103**, 316–335.
- Ribas, C.C., Moyle, R.G., Miyaki, C.Y. & Cracraft, J. (2007) The assembly of montane biotas: linking Andes tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proceedings of The Royal Society*, **274**, 2399–2408.
- Ronderos, R. & Carbonell, C. (1971) Revisión de las especies del grupo Peruvianus del género *Dichroplus* Stal (Orthoptera: Acrididae, Cantantopinae). *Revista de la Sociedad Entomológica Argentina*, **33**, 13–31.
- Ronderos, R. & Cigliano, M.M. (1991) The Andean Dichroplini: cladistic analysis with description of *Keyacris* n. gen. and *Ponderacris* n. gen. (Orthoptera: Acrididae: Melanoplinae). *Transactions of the American Entomological Society*, **117**, 167–191.
- Ronquist, F. (1996) *DIVA Version 1.1*. Computer Program and Manual Available by Anonimous FTP from Uppsala University [WWW document]. URL <http://diva.sourceforge.net/>. [accessed on 3 October 2012].
- Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195–203.
- Rowell, C.H.F. & Carbonell, C.S. (1977) *Baeacris talamancensis* gen. and sp. nov. (Acrididae, Melanoplinae), a neotropical montane grasshopper; its implications for the origin of the Dichroplini and the Costa Rican páramo. *Acrida*, **6**, 55–74.
- Särkinen, T., Pennington, R.T., Lavin, M., Simon, M.F. & Hughes, C.E. (2011) Evolutionary islands in the Andes: persistence and isolation explain high endemism in Andean dry tropical forests. *Journal of Biogeography*, **39**, 884–900.
- Scudder, S.H. (1897) Revision of the Orthopteran group Melanopli (Acrididae) with special reference to North American forms. *Proceedings of the United States National Museum*, **20**, 1–421.
- Sempere, T., Folguera, A. & Gerbault, M. (2008) New insights into Andean evolution: an introduction to contributions from the 6th ISAG symposium (Barcelona, 2005). *Tectonophysics*, **459**, 1–13.
- Soejima, A., Wen, J., Zapata, M. & Dillon, M.O. (2008) Phylogeny and putative hybridization in the subtribe Paranepheleinae (Liabeae, Asteraceae), implications for classification, biogeography, and Andean orogeny. *Journal of Systematics and Evolution*, **46**, 375–390.
- Stål, C. (1878) Observaciones orthoptérológicas 3. De genere Pezotettigis et nonnullis generibus affinis. *Bihang till Kungliga Svenska Vetenskaps-Akademiens Handlingar*, **5**, 1–20.
- Young, K., Ulloa Ulloa, C., Luteyn, J.L. & Knapp, S. (2002) Plant evolution and endemism in Andean South America: an introduction. *Botanical Review*, **68**, 4–21.
- Yu, Y., Harris, A.J. & He, X.J. (2011) *RASP (Reconstruct Ancestral State in Phylogenies) 2.0b* [WWW document]. URL http://rasp.googlecode.com/files/RASP_Win_20120310.zip [accessed on 3 October 2012].
- Willmott, K.R., Hall, J.P.W. & Lamas, G. (2001) Systematics of *Hypanartia* (Lepidoptera: Nymphalidae: Nymphalinae), with a test for geographical speciation mechanisms in the Andes. *Systematic Entomology*, **26**, 369–399.

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Appendix 1

List of characters and states used in the cladistic analysis of *Ponderacris*

Head and thorax

0. Antennae length: as long as or longer than head and pronotum together (0) (Fig. 2C); shorter than head and pronotum together (1) (Fig. 7B). In *Ponderacris* the antennae are longer than head + pronotum, and this condition is found in *Timotes*. In the remaining outgroup species the antennae may be either longer or shorter than head and pronotum together.
1. Eyes in males: exceeding the level of vertex (0) (Fig. 1A); not exceeding the level of vertex (1) (Fig. 7C). In males of *Ponderacris*, *Timotes* and *Baeacris* the eyes exceed the level of vertex in lateral view; in the other outgroup species the eyes do not exceed it.
2. Face in lateral view: straight to slightly oblique (0) (Fig. 2C); oblique (1) (Fig. 7C); convex (2) (Fig. 7G). In *Ponderacris* the face is straight or slightly oblique. This condition is found in *Timotes*, *Keyopsis* and *B. penianus*. *Bogotacris* is the only with sharply oblique face.
3. Pronotum–tegmina length ratio (mm): Tegmina about 1/3 shorter than the pronotum ($P/T = 1.21–1.5$) (0); tegmina approximately as long as pronotum ($P/T = 0.91–1.2$), (1); tegmina about 1/3 longer than the pronotum ($P/T = 0.71–0.9$) (2); tegmina about 2× the length of pronotum ($P/T = 0.5–0.7$) (3); tegmina about 3× the length of pronotum ($P/T = 0.2–0.4$) (4). In *Ponderacris* the tegmina are approximately as long as the pronotum, about 1/3 longer than the pronotum or about 2× the length of the pronotum. In *Timotes* the tegmina are about 1/3 shorter than the pronotum. In the other Andean Dichroplini the tegmina may vary from about 1/3 shorter than the pronotum to about 3× the length of pronotum.
4. Pronotal front margin: straight (0); slightly emarginate (1). In all *Ponderacris* species the front margin of the pronotum is slightly emarginate. In *T. malleatus* and in the remaining outgroup species the pronotal front margin is straight.
5. Hind margin of pronotal disk: rounded or almost straight (0); straight (1); angulate (2). In *Ponderacris* the posterior margin of the pronotum is angulate, as well as in *Baeacris* and *Boliviacris*. In *Timotes*, *Keyopsis* and *Bogotacris* the hind margin of pronotum is rounded or almost straight; in *Chibchacris* is straight.

6. Lateral borders of metazone: parallel (0); divergent (1). In *Ponderacris* the lateral borders of metazone are divergent, as well as in *Baeacris*. In the remaining outgroup species the borders of the metazone are parallel.
7. Tegmina length: brachypterous (0) (Fig. 2A); half-winged (1) (Fig. 2D); macropterous (2) (Fig. 7G); polymorphic (1, 2). *Ponderacris* species may be brachypterous or half-winged and occasionally macropterous. *Timotes* and the outgroup species are brachypterous, except for *B. punctulatus* and *B. penianus* that are macropterous and half-winged, respectively.
8. Shape of tegmina: lobiform (0) (Fig. 7C); elongate (1) (Fig. 2D). In *Ponderacris*, the shape of tegmina is either lobiform or elongate. In *Timotes* and the remaining outgroup species the tegmina is lobiform, except in *Baeacris* species.
9. Shape of apex of tegmina: rounded (0) (Fig. 7A); acute (1) (Fig. 1B). In *Ponderacris* and in *Baeacris* the apex of tegmina is acute. In *Timotes* and in the remaining outgroup species the apex of tegmina is rounded.

Male abdominal terminalia

10. Male cerci, distal half: upcurved (0) (Fig. 3O); down-curved (1) (Fig. 8E). In all *Ponderacris* species the distal half of male cerci is up-curved, as well as in *Timotes* and in the remaining outgroup species, except in *Baeacris* and *Boliviocris*.
11. Male cerci, margins: posterior lower margin elbow-shaped (0) (Fig. 3O); posterior margin straight and upper margin oblique (1) (Fig. 3I); posterior margin rounded (2) (Fig. 3E); posterior margin concave (3) (Fig. 8E); posterior proximal margin straight and posterior distal margin semicircular (4) (Fig. 3A). In *Timotes* the posterior margin of male cerci is elbow-shaped.
12. Male cerci, in dorsal view: strongly curved inwards (0) (Fig. 8B); slightly curved inwards (1) (Fig. 3B); not incurved (2) (Fig. 8F). Within Dichroplini the position of male cerci with respect to the epiproct is variable; in all *Ponderacris* species the male cerci are slightly curved inwards; in *Timotes* are strongly curved inwards.
13. Apical projection of male cerci: absent (0); present (1) (Fig. 8G). Within Dichroplini, male cerci with an apical projection are only found in *Chibchacris*. In *Timotes* and in the other Dichroplini the male cerci do not show an apical projection.
14. Male subgenital plate, apex: pointed or slightly rounded (0) (Fig. 3E); blunt (1) (Fig. 3M). Male subgenital plate with apex blunt is only found in *P. cuzcoensis* and *P. carlcarbonelli*. In the remaining *Ponderacris* species and in Andean Dichroplini the apex of male subgenital plate is pointed or slightly rounded.
15. Male epiproct: without transverse ridge (0); with transverse ridge (1) (Fig. 8J). In the tribe Dichroplini an epiproct with a transverse ridge is only found in *Baeacris*.
16. Furculae: developed (0) (Fig. 3D); not developed (1). In *Ponderacris* the furculae are not developed, except in two species (*P. amboroensis* and *P. chulumaniensis*). In the remaining outgroup species the furculae are developed.

Male genitalia

17. Apical valves of aedeagus, in cross section: cylindrical (0); with narrow furrow (1); with wide furrow (2); concave (3). In *Ponderacris*, the apical valves show a wide mid-longitudinal furrow. In *Timotes* and in *Boliviocris* the apical valves are cylindrical in cross section, without a furrow; the remaining Andean Dichroplini has concave apical valves or shows a mid-longitudinal furrow.
18. Apical valves of aedeagus: relatively short, caudally divergent (0) (Fig. 6J); long, caudally divergent (1) (Fig. 5A); not caudally divergent (2) (Fig. 6A). Within *Ponderacris* the apical valves of aedeagus may be relatively short with distal third portion diverging caudally, long and caudally divergent or not divergent caudally. In *T. malleatus* the apical valves are relatively short and caudally divergent.
19. Apical valves of aedeagus, orientation: straight (0) (Fig. 6B); downwards (1) (Fig. 6E); upwards (2) (Fig. 9N). In *Ponderacris* species the apical valves are directed downwards except in *P. amboroensis*, where they are straight. In *T. malleatus* and *K. palidiventer* the apical valves are straight. In the remaining outgroup species are directed upwards.
20. Apex of apical valves of aedeagus: acute (0) (Fig. 9M); wide (1) (Fig. 9J); curled (2) (Fig. 5A); sub-triangular (3) (Fig. 6J); broad and rounded (4) (Fig. 6A). Within *Ponderacris* the apex of the apical valves may be curled, sub-triangular or broad and rounded. In *Timotes* the apex of apical valves is acute.
21. Sclerotization of the apical valves: homogeneously sclerotized (0) (Fig. 5G); basal two thirds sclerotized (1) (Fig. 9S). In *Ponderacris*, the apical valves are homogeneously sclerotized; this condition is also found in *Timotes* and in the remaining Andean Dichroplini except in *Boliviocris* and *Baeacris* species.
22. Sheath of aedeagus: narrow (0) (Fig. 9A); wide and highly lobulate (1) (Fig. 5J). In *Timotes* the sheath of aedeagus is narrow. The Andean group of Dichroplini is characterized by the presence of a wide and highly lobulate sheath of the aedeagus.
23. Mid-dorsal apical lobes of sheath of aedeagus: long, covering wholly or most of apical valves (0) (Fig. 5G); long, covering 2/3 of the apical valves (1) (Fig. 5A); short (2) (Fig. 9P). In *Ponderacris* the sheath of aedeagus has long mid-dorsal apical lobes that may cover most of the apical valves or only 2/3 of the valves. In *T. malleatus* the mid-dorsal apical lobes cover most of the apical valves.

24. Basal lobes of sheath of aedeagus: reduced (0); moderately developed (1) (Fig. 9P); largely developed (2) (Fig. 5J). In *Ponderacris* the basal lobes of the aedeagus sheath are largely developed. In *Timotes* the basal lobes are reduced; in the other Andean Dichroplini the basal lobes may be reduced or moderately developed.
25. Vento-lateral lobes of sheath of aedeagus: reduced (0); largely developed (1) (Fig. 9T). In all *Ponderacris* species the ventro-lateral lobes are reduced, and this condition is also found in *Timotes* and in the outgroup species, except in *Baeacris* and *Boliviacris*.
26. Proximal hump of sheath of aedeagus: without proximal hump (0); with proximal hump (1) (Fig. 9E). Within Dichroplini, a proximal hump in the sheath of aedeagus is only found in *Keyopsis* and *Chibchacris*. *Bogotacris* shows both the apomorphic and plesiomorphic conditions.
27. Rami: normally developed (0) (Fig. 9T); highly developed (1) (Fig. 5K). In all Dichroplini the rami are normally developed, barely reaching 1/2 the length of the apical valves of aedeagus, but in *Ponderacris*, *Keyopsis*, *Chibchacris* and *Bogotacris* they are highly developed surpassing 1/2 the length of apical valves of aedeagus.
28. Rami: distal third: rounded (0) (Fig. 9B); crescent-shaped (1) (6K); broad and rounded (2) (Fig. 5B); with a notch at inferior margin (3) (Fig. 5K); constricted before apex, broad and expanded apex (4) (Fig. 9K); wide with truncate distal margin (5) (Fig. 9E). In *Ponderacris* species the distal 1/3 of rami may be crescent-shape, broad and rounded or with a notch at inferior margin. In *T. malleatus* the distal 1/3 of the rami is rounded.
29. Epiphallus: lophi: parallel to disk (0) (Fig. 5I); perpendicular to disk (1) (Fig. 5C). In *Ponderacris*, the lophi of epiphallus are placed parallel to disk except in *P. peruvianus* and *P. auriventris* in which the lophi are placed perpendicular to disk. In *T. malleatus* the lophi are placed parallel to disk. In the remaining Andean Dichroplini the lophi may be placed parallel or perpendicular to disk.
30. Epiphallus: lophi: dorsal view: narrow, far from the posterior process of lateral plates (0) (Fig. 5I); widely expanded towards the posterior process of lateral plates (1) (Fig. 5C). Within *Ponderacris*, an epiphallus with lophi widely expanded towards the posterior process of lateral plates is the condition found in *P. peruvianus* and *P. auriventris*. In *T. malleatus* and in the remaining outgroup species, except in *Bogotacris varicolor*, the lophi are narrow and placed far from the posterior process of lateral plates.
31. Epiphallus: shape of lophi: frontal view: low and rectangular (0); oblong (1); prominent and rectangular (2); rounded edges (3); low, columnar (4). In *Ponderacris*, the shape of lophi may be either low and columnar or prominent and rectangular; the last is found in *P. peruvianus* and *P. auriventris*. In *T. malleatus* the shape of the lophi is low and rectangular.

Chromatic characters

32. Body colour: bright tegument (0) (Fig. 7A), dull tegument (1) (Fig. 2B). All *Ponderacris* species have dull tegument. In *Timotes*, *Keyopsis* and *Chibchacris* the body tegument is bright.
33. Ventral abdomen: cream with tinges of burgundy (0) (Fig. 7A); yellow tinged with dark olive laterally (1) (Fig. 7D); yellow (2) (Fig. 1A); orange-red (3) (Fig. 1C); orange with tinges of yellow (4) (Fig. 2A); yellow with tinges of orange-red (5) (Fig. 1B), cream (6) (Fig. 7G). In *Ponderacris*, the colour of ventral abdomen may be yellow, orange-red, orange with tinges of yellow or yellow with tinges of orange-red. In *T. malleatus* the ventral abdomen is cream coloured with tinges of burgundy.
34. Integument of ventral abdomen: not striped (0) (Fig. 2B); brightly striped (1) (Fig. 7D). *Keyopsis* is the only genus within Dichroplini with a striped abdomen.
35. Hind femur: upper face: homogeneously coloured (0) (Fig. 7B); with black spots (1) (Fig. 2C); dark mottled (2) (Fig. 2B). In *Ponderacris*, the upper face of hind femur may be either dark mottled or coloured with black spots. In *T. malleatus* the upper face of hind femur is homogeneously coloured.
36. Hind tibia: bluish-green (0) (Fig. 7A); dark blue (1) (Fig. 7D); red (2) (Fig. 2A); orange-red (3) (Fig. 1B); proximal half dark green, distal half orange-red (4) (Fig. 2B); proximal half burgundy, distal half red (5) (Fig. 1A).
37. Postocular band: absent (0); present (1) (Fig. 1D). In all *Ponderacris* species the postocular band is present. In *Timotes*, *Chibchacris* and *Keyopsis* the postocular band is absent.