# The high-Andean *Jivarus* Giglio-Tos (Orthoptera, Acridoidea, Melanoplinae): systematics, phylogenetic and biogeographic considerations

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Abstract. The high-Andean genus Jivarus Giglio-Tos from Ecuador, Colombia and Peru is revised. Morphological cladistic analysis indicated that Jivarus montanus and the new species digiticercus sp.n. and rugosus sp.n. must be treated as a separate genus, Maylasacris gen.n. The remaining species included in the analysis are assigned to the genus Jivarus, for which the following six species groups are identified: americanus group, antisanae group, carbonelli group, cohni group, pictifrons group and *jagoi* group. Twenty-nine species are recognized for *Jivarus*, with ten described as new: J. rectus sp.n., J. megacercus sp.n., J. spatulus sp.n., J. auriculus sp.n., J. riveti **sp.n.**, J. sphaericus **sp.n.**, J. discoloris **sp.n.**, J. profundus **sp.n.**, J. ronderosi **sp.n.** and J. guarandaensis sp.n. The following new synonymies are proposed: Jivarus albolineatus Ronderos with J. antisanae (Bolivar) syn.n., J. cerdai Ronderos and J. osunai Ronderos with J. alienus (Walker) syn.n., and J. rubriventris Ronderos with J. ecuadorica (Hebard) syn.n.; the new combinations Jivarus ecuadorica (Ronderos) comb.n. and Maylasacris montanus (Ronderos) comb.n. are proposed. Keys to the species of the genera and a review of the morphological characters defining the taxa are provided. Patterns of distribution of the clades coincide with the geography of the northern Andes of Colombia and Ecuador. Areas of endemism of the Jivarus species groups and Maylasacris are delimited by both the high-altitude curves, including transverse zones, and the drier climates of the intra-Andean valleys, clearly indicating recent, post-glacial palaeogeography, as shown also in vegetation distributions. This paper has been formatted with many embedded links to images of type and paratype specimens, maps based on geo-referenced specimen data and species keys available on the Orthoptera Species file online (http://orthoptera.speciesfile.org).

## Introduction

Jivarini is a high-Andean tribe of grasshopper species, distributed from the Southern Andes in Argentina and Chile (*Hydnosternacris* Amedegnato & Descamps and *Nahuelia* Liebermann) to the Northern Andes in Venezuela (*Oreophilacris*)

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Roberts). Within the tribe, *Jivarus* Giglio-Tos is restricted to the Andes of Ecuador and Colombia, with only two species in the Peruvian Andes. A few species of *Jivarus* inhabit the lower-altitude Andean montane forest (cloud forest, Vuilleumier & Monasterio 1986) but most inhabit the 'páramos', distributed discontinuously between latitudes 11°N and 8°S, and concentrated in the northwest corner, mostly in Venezuela, Colombia and Ecuador (Cabrera & Willink, 1973; Balslev & Luteyn, 1992; Morrone, 2006). In South America, the Páramos occupy no more than 2% of the land area of the Northern Andes, but are highly biodiverse, containing especially many endemic plants (Luteyn, 1999). Páramo habitats underwent repeated expansion and contraction during the late Pliocene and Pleistocene (Clapperton, 1993).

Giglio-Tos (1898) erected *Jivarus* based on *J. americanus* Giglio-Tos and *Pezotettix antinsanae* Bolivar. Uvarov (1925) transferred *Caloptenus alienus* Walker to the genus, and Rehn (1963) described the species *J. camposi* for it. Amedegnato (1974), in her classification of Neotropical Acridoidea, assigned *Jivarus* to the subfamily Melanoplinae, and subsequently Ronderos (1979, 1981) described 19 out of 22 currently known valid species.

*Jivarus* is highly variable in body colour and external morphology; however, species can be separated from other genera of Jivarini based on male genitalic characters. Based on external morphology, Ronderos (1979, 1981) divided the genus into four species groups (i.e. antisanae, americanus, alienus and carbonelli species groups); however, no hypothesis of phylogenetic relationships has been postulated for *Jivarus*.

New collections from the Andes of Ecuador and Peru have resulted in the discovery of new species and have shown that some nominal species of *Jivarus* are difficult to identify. A primary objective was to revise *Jivarus* and describe new species and to give brief redescriptions of those species for which new diagnostic characters are provided after examination of large series of specimens. The other objectives were to conduct a cladistic analysis of the species of *Jivarus* to test the monophyly of the defined species groups and to analyse their distribution patterns.

#### Materials and methods

## Material

Most specimens were collected by Christiane Amedegnato and Simon Poulain between 1990 and 1997 and in 2001. Additional specimens were borrowed from or are deposited at the following Institutions (acronyms used throughout the text): Muséum national d'Histoire Naturelle, Paris, France (MNHN); The Academy of Natural Sciences, Philadelphia, U.S.A. (ANSP); The Natural History Museum, formerly British Museum (Natural History), London, U.K. (BMNH); Museo de La Plata, La Plata, Argentina (MLPA); Museo Regionale di Scienze Naturali de Torino, Italy (MRSNT); Pontifica Universidad Catolica del Ecuador (PUCE).

#### Specimen preparation

Museum specimens were relaxed in a humid chamber, and abdomen terminalia moistened with ammonia. Genitalia then were pulled from the body using a finely hooked pin, cleared in potassium hydroxide and stored in glycerine.

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

## Terms for structures

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

Redescriptions of species were included only if new diagnostic characters were observed in the larger series of examined specimens.

#### Cladistic analysis

Phylogenetic analyses were performed on a matrix comprising 33 species and 38 morphological characters (Tables S1 and S2 in Supporting Information). All described species of Jivarus were included in the analysis, plus 12 new un-described species that showed affinities to Jivarus. Morphological characters comprised structures from the head and thorax, male genitalia and coloration patterns. Although coloration 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. Tree searches were conducted in NONA (Goloboff, 1999) run within WinClada 1.00.08 (Nixon, 2002) and in TNT (Goloboff et al., 2003). Heuristic searches were performed by tree bisection-reconnection (TBR) branch swapping on 5000 series of random-addition sequence replicates, and tree search options of Hold 1000, Hold/1000, Mult\* 5000 were used in NONA. All characters were considered to be of equal weight, and multistate characters were treated as unordered. Support for individual nodes was assessed by calculation of absolute Bremer support values (Bremer, 1994) and bootstrap performed in TNT. The root was set as Argemiacris platicercis Ronderos (Jivarini).

#### Electronic content and hyperlinks

This publication includes 'hyperlinks' (embedded links that allow simple redirection to online resources via the internet). When the text is viewed using hyperlink-enabled software, clicking on the hyperlink text (blue) using the computer mouse pointer will redirect the reader to the hyperlinked location in the taxonomic database Orthoptera Species File Online (OSF, http://orthoptera.speciesfile.org) (Eades & Otte, 2010). Prior to the publication of this paper, a 'private' species file for the tribe Jivarini that contained all the relevant information from OSF was generated by David Eades, Principal Database Manager of OSF online at the Illinois Natural History Survey, U.S.A., allowing entry of data and information pertaining to the new species herein described, the images of type and paratype specimens, the geo-referenced specimen data,

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as well as the species keys. This new feature of OSF was implemented for the first time in Cigliano *et al.* (2010) and is described in Cigliano & Eades (2010). Links to species keys, images of type specimens, and maps in Orthoptera Species File Online are embedded throught the text and indicated in Table S3.

## Cladistic analysis

Parsimony analysis of the data matrix (Table S2) vielded three most-parsimonious trees of length 89 (consistency index, 0.74; retention index, 0.91) in TNT and NONA (Preferred tree, Fig. 1). Unambiguous optimizations were used to map the characters onto the tree. Analyses consistently recovered nine species groups; however, their relationships varied between trees, except for the major clade and the group constituted by M. montanus, M. digiticercus sp.n. and M. rugosus sp.n., which always appears as sister to the main clade. The tree supports the monophyly of nine species groups, all displaying bootstrap and Bremer support values. One of the clades with the highest branch support is constituted by M. montanus and the new species digiticercus sp.n. and rugosus sp.n. This clade is defined by the following characters: prominent fastigium, with lateral carinae evident and acute apex (7:5); male subgenital plate short not exceeding the level of epiproct, roundedshaped (17:2); male cerci, in lateral view, with the distal half portion thin, up-curved (18:4); male cerci, in caudal view, elbow-shaped (19:1); and zygoma of cinglulum highly elevated (36:1). The remaining species are grouped into a clade based on anchorae of epiphallus developed (21:1); apical valves of aedeagus highly developed ventrally into an axial portion (23:1); basal fold of ectophallic membrane with scleroltized shield (32:1); apical valves of aedeagus with lateral projections (33:1); cingulum normally developed (34:1); apodemes of cingulum straight (35:1). Within this main group the best supported component is constituted by the sister species J. pictifrons and J. discoloris, defined by the lophi of the epiphallus not too prominent, without dorsal projection in the internal border (22:4); lateral projection of apical valves of aedeagus without dorsal development (25:2); bridge of epiphallus long and straight (26:0); sheath of aedeagus with spines (27:1); and axial portion of apical valves of aedeagus thin (29:3). This group is related to the clade comprising J. hubbelli, J. guarandaensis, J. rentzi, J. ronderosi, and the sister species J. jagoi and J. profundus, supported by the male epiproct wide, with elevated sinuous margins (16:2). Another supported group comprises J. gurneyi, J. cohni and J. ecuadorica based on the shape of the lophi of the epiphallus (22:6); body hair abundant (5:1); pronotal disk with deeply impressed transverse sulci (8:0). Within this clade, J. cohni and J. ecuadorica are sister species based on the male cerci short, curved inwards (18:5). The clade comprising J. ochraceus, J. alienus, J. alticola, J. eumera, J. marginalis, J. carbonelli, J. rectus and J. brunneus shows one of the highest branch supports of the tree and is based on four synapomorphies and a parallelism: male subgenital plate high, exceeding the level of epiproct, with acute apex (17:1); male cerci short, conical, slightly curved inwards, acute apex (18:1); lateral plates of epiphallus convergent caudally (24:1); epiphallus with bridge short and concave (26:2); apical valves of endophallus very short, with reduced dorsal development (25:1). Within this clade, two groups show branch support, one constituted by J. alticola, J. ochraceus and J. alienus, and the other polytomy constituted by J. brunneus, J. rectus sp.n., J. carbonelli, J. marginalis and J. eumera. Another group delimited in the tree with boostrap and Bremer support values is constituted by J. pubescens, J. megacercus sp.n., and the polytomy: J. spatulus sp.n., J. laevis and J. americanus. This group is defined by tegmina with dorsal third portion horizontally placed (15:1); epiphallus with lophi narrow, extending only half along caudal edge of lateral plates, prominent (22:1); medio-longitudinal carina strongly indicated all throughout the pronotum (37:2). The remaining clade is supported by the characters ventral margin of hind femur dentate (14:1); male epiproct wide, with elevated sinuous margins (16:2); male furculae reduced or absent (38:1); and shape of the male cerci (18:2). Within this clade two species groups are delimited, one constituted by J. auriculus sp.n. – J. riveti sp.n. based on lateral projection of apical valves of aedeagus very short, with reduced dorsal development (25:1) and apical valves of aedeagus earshaped (28:1); and the polytomy: J. antisannae, J. viridis and J. sphaericus sp.n., defined by male cerci with a hook at the apex (20:1).

Based on the species relationships resulting from the tree, we consider that *Jivarus montanus* and the new species *digiticercus* and *rugosus* must be treated as a separate genus that we name *Maylasacris* gen.n. The remaining species constitute the genus *Jivarus*, for which the following six species groups can be identified: *americanus* group, *antisanae* group, *carbonelli* group, *cohni* group, *pictifrons* group and *jagoi* group.

## Taxonomy

## Jivarus Giglio-Tos, 1898

*Jivarus* Giglio-Tos, 1898: 54; Liebermann, 1942: 307; Liebermann, 1968: 32; Amedegnato, 1974:199; Ronderos, 1979: 196, 1982:151, 1983: 131; Otte, 1995: 364; Amedegnato *et al.* 2003: 116; Chapco, 2006: 62.

#### Type species

Jivarus americanus Giglio-Tos, by subsequent designation, authority: Ronderos 1979

*Diagnosis.* Male phallic complex with apical valves of aedeagus with lateral projections (Fig. 6M); internal face of axial portion of the apical valves concave (Fig. 6Z) or with an internal longitudinal furrow (6AO); basal fold of ectophallic membrane with numerous thickened lobes (Fig. 6P, Q); lateral sclerites of ectophallic membrane large (Fig. 6P).



**Fig. 1.** One of three most-parsimonious tree of the genus *Jivarus* (length 89, consistency index = 0.74, retention index = 0.91) resulting from the cladistic analysis of the unordered morphological character dataset. Black circles indicate unique changes, and white circles indicate homoplasies. The numbers below the nodes are bootstrap support, and those above are Bremer support.

Based on the tree, the following six groups of species are identified for the *Jivarus*.

Americanus species group: *americanus*, *laevis*, *megacercus* **sp.n.**, *spatulus* **sp.n.**, *pubescens* 

Small fragile insects; Body colour brownish green with dark post-ocular band on head and pronotal lobes (2:0); head conical with oblique face; Eyes ovate, not exceeding level of vertex in lateral view.

Pronotum trapezoidal with ridge along the transition zone between disk and lateral pronotal lobes; Medio-longitudinal carina on pronotum strongly indicated throughout (37:2); Pronotal disk with transverse sulci weakly impressed; Hind femora elongate, with entire lower margin; Tegmina with

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dorsal third portion horizontally placed (15:1); Male epiproct quadrangular, with sinuous distal margin slightly projected in the middle; Male cerci short, slightly curved inwards, distal third portion laterally compressed; Male subgenital plate short, with distal apex not surpassing level of epiproct; Lophi of epiphallus narrow, extending only half along caudal edge of lateral plates, prominent (22:1).

Antisanae species group: *antisanae*, *auriculus* **sp.n.**, *riveti* **sp.n.**, *viridis*, *sphaericus* **sp.n.** 

Head conical with oblique face; eyes ovate, exceeding the level of vertex in lateral view;

Pronotum trapezoidal, slightly expanded in metazone, with the lateral ridges weakly indicated; Pronotal disk with transverse sulci well impressed; Hind femora elongate, with dentate lower margin (14:1); Male cerci with basal third portion robust, abruptly narrowing at the distal middle third, where they curve dorsally (18:2), in some species distal portion like a walkingstick shape, apex hook-shaped; Male epiproct widely triangular, with prominent lateral margins (16:2); Male furculae reduced or absent (38:1).

Carbonelli species group: carbonelli, rectus sp.n., marignalis, alienus, brunneus, ochraceus, alticola, eumera

Medio-longitudinal carina of pronotum weakly indicated throughout; Male subgenital plate conical with acute apex, highly exceeding level of epiproct (17:1); Male epiproct triangular, narrow, without elevated margins; Male cerci short conical, slightly curved inwards, tapering towards acute apex (18:1); Epiphallus with lophi largely developed horizontally, extending all along caudal edge of lateral plates; Bridge of aedeagus short and concave (26:2); Lateral plates of epiphallus convergent caudally (24:1); Lateral projections of apical valves of aedeagus short, with reduced dorsal development (25:1); Sheath of aedeagus gibous; Axial portion of apical valves of aedeagus with reduced vertical development.

There are two subgroups of species within the carbonelli group: one constituted by *carbonelli*, *brunneus* and *rectus* **sp.n.**, *eumera* and *marginallis* that can be identified as follows:

Fastigium triangular, horizontal, with its width at the base longer than its length, apex acute; Eyes not exceeding vertex in lateral view; Pronotum trapezoidal, with transverse sulci weakly impressed; medio-longitudinal carina weakly indicated (37:1).

The second subgroup is constituted by *alticola*, *ochraceous*, *alienus* and is defined by the following characters (mostly parallelisms):

Fastigium triangular, declivent, apex blunt, as wide at base as its length (7:3); Eyes prominent laterally; Pronotum with lateral edges parallel (10:0), with transverse sulci deeply impressed (8:0).

Pictifrons species group: pictifrons, discoloris sp.n.

Stocky insects; Body dark with patches of bright colours; Fastigium shorter than its width at base; Face perpendicular; Pronotum flat trapezoidal, with transverse sulci deeply impressed delimiting irregular lobes, hind margin only weakly emarginated; Male cerci gradually reducing its width to apex, distal third portion gently curved inwards; Subgenital plate short not exceeding epiproct, with rounded apex; Epiphallus with lophi not too prominent without dorsal projection in internal border (22:4); and bridge long and straight (26:0); Apical valves of aedeagus without dorsal development of lateral projections (25:2); Sheath of aedeagus with spines (27:1).

Jagoi species group: *jagoi*, *profundus* **sp.n.**, *rentzi*, *guarandaensis* **sp.n.**, *ronderosi* **sp.n.**, *hubbelli* 

Stocky insects; Head with perpendicular face; globe-shaped eyes; Fastigium triangular with lateral carinae evident; Pronotal disk flat, with transverse sulci deeply impressed delimiting irregular lobes, hind margin widely emarginate; Male epiproct widely triangular, with prominent margins (16:2); Male cerci with broad base, abruptly narrowing at distal middle third, where they curve dorsally, with distal two-thirds narrow, apex hook-shaped.

Cohni species group: cohni, ecuadorica, gurneyi

Small fragile insects; Body with abundant pubescens (5:1); Head with perpendicular face; globe-shaped eyes, exceeding level of vertex in lateral view; Fastigium declivent, with lateral carinae developed; Pronotum with lateral borders parallel, pronotal disk without lateral ridges; Pronotum with transverse sulci deeply impressed (8:0); Hind margin broadly emarginate.

Male epiproct subtriangular, apex acute; Male cerci curved inwards at middle, with distal portion thinner than basal portion; Lateral projection of apical valves of aedeagus short, axial portion of apical valves of aedeagus largely developed vertically, extending beyond lateral projections and with internal face highly convex; Epiphallus with lophi extending along twothirds of caudal edge of lateral plates, with dorsal projection in internal border (22:6).

# Key to males of Jivarus

<ol> <li>Male cerci reduced in width sharply in the apical two-thirds, dorsally curved, distal portion resembling walking stick, with (Fig. 3X) or without (Fig. 5H) hooked apex</li></ol>
2. Head conical, with oblique face (Fig. 3AC)    3      - Head globe-shaped, with perpendicular face (Fig. 4E)    5
3. Male cerci with apex hook-shaped
4. Body colour green; males with hind tibiae bluish green; male cerci shorter and slightly wider at end of distal half (Fig. 3AF) 
- Body colour brown; males with hind tibiae light purple; male cerci longer and narrower at end of distal half (Fig. 3AB) J.auriculus <b>sp.n</b> .

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5. Furculae absent (Fig. 4G)	<ul> <li>in lateral view (Fig. 4 sulci weakly impresse</li> <li>Fastigium declivent, (Fig. 4R); eyes promi lateral edges parallel,</li> <li>16. Phallic complex w long, with reduced w narrow with deep mid</li> <li>Phallic complex w ventral keel; aedeagus</li> <li>17. Male cerci sharply as its maximum width lateral edges subparall</li> <li>Male cerci gradual twice the length of triangular.</li> </ul>
<ul> <li>6. Male cerci without apical hook at apex (Fig. 5H)7</li> <li>– Male cerci with apical hook (Fig. 5C, D)</li></ul>	
<ul> <li>7. Pronotum with lobes delimited by transverse sulci irregular and high (Fig. 5E); hind margin of pronotal disk widely concave (Fig. 5F)</li></ul>	
8. Pronotum with transverse sulci more deeply impressed and mid-longitudinal carina vestigial (Fig. 5B); male cerci with basal portion slender and distal up-curved portion shorter than basal portion (Fig. 5D) <i>J. profundus</i> <b>sp.n.</b> – Pronotum with transverse sulci less impressed and with mid-longitudinal carina; male cerci with basal portion wider and distal up-curved portion longer than basal portion <i>J. jagoi</i>	
<ul> <li>9. Male cerci narrowing gradually towards apex, slightly curved dorsally (Fig. 4X, L); male epiproct triangular (Fig. 4O)</li> <li></li></ul>	<ul> <li>18. Male epiproct wirapex of subgenital platof the epiproct, without – Male epiproct trian, subgenital plate; male</li> <li>19. Male cerci narrow curved inwards, distal</li> <li>- Male cerci of other</li> <li>20. Pronotum with travit perpendicular fatof vertex in lateral vice – Pronotum with trans</li> <li>21. Body with metallit – Body colours opaque yellow; eyes red (salm abdominal tergite with first and second pair or green</li> </ul>
10. Males with dorsal half or whole tegmina cream (Fig. 2F); subgenital plate short, not exceeding the epiproct (Fig. 4AB); male cerci shorter (Fig. 4X, AB); sheath of aedeagus gibbous with multiple spines (Fig. 7Z, AE)	
<ul> <li>11. Body with brighter coloration; tegmina homogeneously cream (Fig. 2F)</li></ul>	
<ul> <li>12. Pronotum slightly convex in lateral view, with transverse sulci weakly impressed (Fig. 7M)</li></ul>	
13. Antennae short in both sexes, not longer than head and pronotum together; general body colour dark green	22. Male cerci with th insects 14 (13.7–14) 1 – Male cerci with di 12–12.7 mm (male)
14. Fastigium declivent; male cerci wider; general body colour brown; knees of caudal femur and proximal portion of caudal tibia red	<ul><li>23. Male cerci with d</li><li>base or much wider</li><li>Male cerci with dist</li></ul>
- Fastigium horizontal; male cerci slim; general body colour light green; knees of caudal femur and proximal portion of caudal tibia greenJ. carbonelli	<ul><li>24. Male cerci with a epiproct quadrangular</li><li>Male cerci bulkv.</li></ul>
15. Fastigium horizontal, with its width at base longer than its length, apex acute (Fig. 4J); eyes not exceeding vertex	curved upwards, with in middle, apex trunca

I); pronotum trapezoidal with transverse as wide at base as its length, apex blunt inent laterally (Fig. 4Q); pronotum with with transverse sulci deeply impressed. ith axial portion of apical valves straight, vertical development; aedeagus sheath l-longitudinal division (Figs. 7K,L,M)... .....J. rectus sp.n. vith axial portion of apical valves with sheath wide.....J. marginalis y narrowing towards apex, twice as long . Male epiproct with basal two-thirds of lel....J. alienus lly narrowing towards apex, more than its maximum width; male epiproct ith convergent lateral margins, reaching ate; male cerci parallel to lateral margin ut curving at middle.....J. eumera igular and shorter, not reaching apex of cerci slightly curved at middle..... .....J. ochraceus wing at the distal two-thirds, gradually third compressed laterally (Fig. 3G; 5S) ransverse sulci deeply impressed; head ce; globe-shaped eyes, exceeding level sverse sulci weakly indicated......23 ic colours in life.....22 e; males general colour olive brown, face non pink when alive) dorsally black; first h wide circular yellow or white macula; of legs green; hind femur and hind tibiae .....J. gurneyi ne distal one-third wider (Fig. 5S); larger mm (male) ..... J. ecuadorica istal one-third narrower; smaller insects .....J. cohni listal portion with the same diameter as tal portion narrower than base......25 dorso-apical projection (Fig. 3D); male with emarginate apex ... J. americanus

epiproct quadrangular with emarginate apex ... J. americanus – Male cerci bulky, highly surpassing the apex of epiproct curved upwards, with third distal portion slightly compressed in middle, apex truncate (Fig. 3L).....J. megacercus **sp.n**.

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**Fig. 2.** *Jivarus* males, species as indicated. Habitus. Scale bar = 1 cm.

J. laevis

27. Male cerci broad with the distal half portion compressed and upcurved in a right angle (Fig. 5L); general colour green, with white face and blue cheeks (in live specimens) yellow in preserved insects; pronotum with red margins; tegmina reddish brown; hind tibiae bluish green ...........J. ronderosi sp.n. Jivarus americanus Giglio-Tos (Figs 3A-D; 6A-E)

*Jivarus americanus* Giglio-Tos, 1898: 54; Hebard, 1924: 198; Liebermann, 1968: 32; Ronderos, 1979:198; Chapco, 2006: 59.

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**Fig. 4.** *Jivarus* males, species as indicated. A, E, I, M, Q, U, Y, head and pronotum, lateral view; B, F, J, N, R, V, Z, head and pronotum, dorsal view; C, G, K, O, S, W, AA, distal abdominal segments, dorsal view; D, H, L, P, T, X, AB, distal abdominal segments, lateral view.

*Diagnosis*. Closely related to *J. laevis*, from which it can be easily distinguished by the male cerci with distal third portion broad, laterally compressed with distal margin obcordate.

*Redescription.* Dark brown ferruginous insects; head with an ivory stripe extending from the back of eyes; dark brown post-ocular band on sides of head extending on sides of pronotum, ventral half of tegmina and sides of abdomen. Dorsal half of tegmina, lower half of lateral lobes of pronotum light brown.

Hind femur with outer medial area green, dorsal area dusky brown, ventral area light brown; hind tibiae dark green. Male cerci short and wide, slightly curved inwards, distal third portion broad, laterally compressed, distal margin obcordate. Phallic complex: epiphallus with lophi highly prominent, with reduced horizontal development, ancorae curved inwards; apical valves of aedeagus similar to *J. laevis* (Fig. 6A, B).

Females similar to males except for the pronotal disk light brown, fastigium wider, lateral margins of pronotal disk



**Fig. 5.** *Jivarus* and *Maylasacris* males, species as indicated. A, E, I, M, Q, U, Z, head and pronotum, lateral view; B, F, J, N, R, V, AA, head and pronotum, dorsal view; C, G, K, O, S, W, AB, distal abdominal segments, lateral view; D, H, L, P, T, X, AC, distal abdominal segments, lateral view; Y, AD, distal abdominal segments, caudal view.

diverging caudally. Cerci short, ovipositor valves curved, with entire margin and acute apex.

*Measurements (in mm).* Body length to end of femur III: 12 (male), 14 (female); femur III length: 7 (male), 9 (female).

*Material examined.* Ecuador: Allolectotype male and paralectotype male, Cañar, MRSNT; 17 males, 24 females, Cañar, El Tambo, 3200 m, 05/12/1997, (Amedegnato and Poulain), MNHN, MLPA; one male and female syntypes, Ecuador, Cañar, MRSNT; one female, Ecuador, Azuay, Cerro Tinajilla, 3100 m, 18–20/03/1965, (Peña), MLPA; one female, Azuay,



**Fig. 6.** *Jivarus* males. Phallic complex, species as indicated. A, F, K, S, X, AC, AH, AM, endophallic plates (basal and apical valves of aedeagus) and cingulum, lateral view; B, G, L, T, Y, AD, AI, AN, endophallic plates (basal and apical valves of aedeagus) and cingulum, dorsal view; C, H, M, U, Z, AE, AJ, AO, distal portion of aedeagal valves, ventral view; D, I, N, V, AA, AF, AK, AP, epiphallus, dorsal view; E, J, O, W, AB, AG, AL, AQ, epiphallus, lateral view; P, Q, phallic complex, lateral and dorsal view; R, endophallic plates, lateral view.

Cerro Tinajilla, 3100 m, (Peña), 18–20/03/1965, MLPA; one male, Tioloma, 4200 m, (Rivet), 1904, MNHN (Fig. 9(4)).

*Observations.* Based on the images of the specimens deposited at the MRSNT, it is evident that there is more than

one species among the original syntypes series of *americanus* Giglio-Tos. However, the male specimen from Cañar selected by Carbonell (1966 in litt.), bearing a red 'allolectotype' label, and designated by Ronderos (1979) as the male 'Allotype' coincides with the original description of Giglio-Tos (1898).

*Distribution.* Ecuador: Cañar, Azuay in open grassy areas, pastures resulting from deforestation of the *Polylepis* forest (see geographic distribution in OSF).

Jivarus laevis Ronderos (Figs 3E-H; 6F-J)

Jivarus laevis Ronderos 1979: 214.

*Diagnosis*. Similar to *J. americanus* differing mostly in the shape of male cerci slightly curved inwards with the distal third portion ovate and slender, laterally compressed.

Redescription. Highly variable in coloration, general body colour from mostly green to almost black. Body lateral, with a dark brown post-ocular band extending onto the lateral lobes of pronotum, ventral half of tegmina and sides of abdomen, limited dorsally by an ivory stripe on head and pronotal disk; dorsal half of tegmina cream (white when alive); abdomen ventrally vellow (in some specimens red when alive). Hind femur green with upper area dusky brown, knees and male distal abdomen reddish brown; hind tibiae green. Head with prominent fastigium, triangular, with lateral carinae evident, with shallow middle groove; fastigio-facial angle rounded. Eyes large, subcircular; not exceeding the level of vertex in lateral view. Pronotum trapezoidal, weakly constricted at the middle, with the division between the disk and the lateral lobes clearly indicated by ridges; mid-longitudinal carina well indicated throughout, cut by the principal transverse sulcus; posterior margin of pronotal disk emarginate, with the distal angle between the disk and the lobes rounded. Hind femur with entire lower margin. Tegmina narrowly ovate, with the dorsal third portion horizontally placed. Male subgenital plate short with acute apex; epiproct quadrangular, with sinuous distal margin slightly projected in the middle; furculae prominent and acute; male cerci short, weakly curved inwards; distal third portion ovate, slender laterally compressed. Phallic complex: epiphallus with prominent narrow lophi, ancorae curved inwards. Lateral projections of apical valves of aedeagus widely developed dorsal and ventrally, leaving uncovered only the tip of the sheath of aedeagus; axial portion of apical valves of aedeagus with ventral development, internally concave. Sheath of aedeagus with short mid-longitudinal division.

Females similar to males, except for the body coloration that it is highly variable from green or grey/pink (alive) to completely marmorated, clear/dark. Head with fastigium wider than in males, lateral margins of pronotal disk diverging caudally. Female cerci long, reaching distal margin of paraprocts. Ovipositor valves strongly curved, with entire margin and acute apex.

*Measurements (in mm).* Body length to end of femur III: 12.08 (11–13) (male), 14.75 (14–16) (female); femur III length: 6.5 (6–7) (male), 8.5 (8–9) (female). Specimens from Azuay, Cuenca: Cajas, Lag. Zurucucho, 3100 m, are larger

than all the other material examined, body length to end of femur III: 15 (male), 16 (female); femur III length: 9 (male), 9 (female).

Material examined. Ecuador: 12 males, 22 females, 8 nymphs, Azuay, Sigsig, 2500/2900 m, 02/12/1997, (Amedegnato & Poulain), MNHN, MLPA, PUCE; one male, one nymph, Azuay, Cuenca: Cajas, 3350 m, 14/04/1995, (Poulain), MNHN; 18 males, 17 females, Azuay, Gualaceo, 3100 m (Amedegnato & Poulain), 03/12/1997, MNHN, MLPA, PUCE; 5 males, 8 females, Azuay, Gualaceo, 2700 m, 03-04/12/1997, (Amedegnato & Poulain), MNHN; 2 males, 9 females, Cañar, Azogues, Taday-Guarainag, 3000 m, 09/02/1990, (Poulain), MNHN; 4 females, Cañar, Cañar, 3000 m, 18/02/1990, (Poulain), MNHN; 4 males, 6 females, Cañar, Azogues, 3000 m, 05/12/1997, (Amedegnato & Poulain), MNHN, MLPA; 7 males, 9 females, 5 nymphs, Azuay, Cuenca, Nabon, 3100 m, 25/07/1991, (Amedegnato & Poulain), MNHN, MLPA; 3 males, 4 females, Azuay, Cuenca, Shina, 2800 m, 10/02/1990, (Poulain); 13 males, 17 females, Azuay, Cuenca, Cajas, Lag. Zurucucho, 3100 m, (Amedegnato & Poulain), 06/08/1991, MNHN, MLPA, PUCE; 7 males, 10 females, Azuay, Cuenca: Cajas, Lag. Zurucucho, 3100 m (Poulain), 08/02/1990, MNHN, MLPA; one paratype male (see image in OSF), 2 females paratype, Azuay, Tarqui, 2800 m, (Peña), 3/03/1965, MLPA; one male, one female, Cañar, Biblian, 3400 m, 05/12/1997, (Amedegnato & Poulain), MNHN (Fig. 9(4)).

*Distribution.* Ecuador: Azuay, Cañar; in open areas with short relatively dry dense grasses, with few bushes (see geographic distribution in OSF).

Jivarus megacercus sp.n. (Figs 3I–L; 6K–R)

*Diagnosis.* Easily recognized by the unique shape and large size of its male cercus, as shown in Fig. 3K, L

Description. Body colour similar to J. americanus but with hind tibiae light green. Similar to J. americanus, but differing in the head with fastigium robust and more prominent; posterior margin of pronotal disk irregular; male cerci bulky, highly surpassing the apex of epiproct, curved upwards, with the third distal portion slightly compressed in the middle, apex truncate; epiproct narrower than in J. americanus, with the distal margin prominent in the middle; furculae stockier. Phallic complex similar to J. americanus, differing in the apical valves of the aedeagus with the lateral projection not covering the apex nor the mid-ventral part of the axial portion; axial portion of apical valves widely developed ventrally, and highly convex in its internal face.

Measurements (in mm). Body length to end of femur III: 12 (male), 13.5 (female); femur III length: 7 (male), 8 (female).

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*Material examined.* Ecuador: Holotype male and allotype female, Azuay, Gualaceo (Res. De Maylas), 3175 m, 03/12/1997 (Amedegnato & Poulain), MNHN; Paratypes: two males (see image in OSF), one female, two nymphs, Azuay, Gualaceo (Res. De Maylas), 3175 m, 03/12/1997 (Amedegnato & Poulain), MNHN, MLPA (Fig. 9(4)).

*Distribution.* Ecuador: Azuay; in open grassy areas surrounded by residual montane forest; sympatric with *Maylasacris digiticercus* **sp.n.** (see geographic distribution in OSF).

Jivarus spatulus **sp.n.** (Figs 2A; 3M–P; 6S–W)

*Diagnosis.* Similar to *J. laevis*, but differing in the male cerci short slightly curved inwards, with spatulate distal third portion; reduced male furculae; and differences in the phallic complex as indicated in Fig. 6S–W.

Description. Brown ferruginous insects, head with an ivory stripe extending from the back of eyes; dark brown postocular band on sides of head extending on sides of pronotum, ventral half of tegmina and sides of abdomen. Dorsal half of tegmina, lower half of lateral lobes of pronotum light brown. Hind femur with outer medial area green, upper area dusky brown, ventral area light brown, genicular lobes red; hind tibiae green, with proximal portion red. Male epiproct quadrangular with sinuous distal margin, weakly projected in the middle. Phallic complex: epiphallus with lateral plates widely developed; sheath of aedeagus with a hump and a deep mid-longitudinal division, apical valves of aedeagus with internal longitudinal open furrow, lateral projections of valves only covering the mid-dorsal part of the axial portion; arch of cingulum large, with valves definitely developed.

Females, ovipositor valves straight and slender, with the dorsal margin serrate.

*Measurements (in mm).* Body length to end of femur III: 14.3 (14–15) (male), 16 (female); femur III length: 7 (male), 9 (female).

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

*Material examined.* Ecuador: Holotype male and female allotype, Cotopaxi, San Miguel de Salcedo, Cashaloma, 3400 m, 26/12/1997, (Amedegnato & Poulain), MNHN; Paratypes: 3 males (see image in OSF), 7 females, Cotopaxi, San Miguel de Salcedo, Cashaloma, 3400 m, 26/12/1997, (Amedegnato & Poulain), MNHN, MLPA. Other material: one male, Tungurahua, Laguna Pisayambo, Pajonal, 3800 m, 30/11/85, one female, id,06/12/1985 (Moret), MNHN, MLPA; one female, one male, Danas, 3792 m, 1904, (Rivet), MNHN, MLPA (Fig. 9(4)).

*Distribution.* Ecuador: Cotopaxi, Chimborazo, Tungurahua; in open areas with short dry dense grasses (see geographic distribution in OSF).

*Jivarus pubescens* Ronderos (Figs 3Q-T; 6X-AB)

Jivarus pubescens Ronderos 1979:212.

*Diagnosis*. Similar to *J. laevis* but more robust, with the pronotum weakly constricted at the principal sulcus; hind margin crenate, slightly emarginate; mid-longitudinal carina well indicated on prozone, not so in metazone. Body colour brownish red, hind femur with internal and external face reddish, hind tibia brownish green. Male cerci as in *J. laevis*, but wider and with the distal half compressed laterally, third distal portion curving gradually. Phallic complex with the lateral projection of the apical valves of the aedeagus without covering the midventral part of the axial portion of the valves; axial portion of apical valves widely developed ventrally.

*Material examined.* Ecuador: one male, 2 females, Azuay, Cuenca, Nabon, 3100 m, (Amedegnato & Poulain), 25/07/1991, MNHN; one female, Azuay, Cuenca, Cumbe, 3100 m, (Amedegnato & Poulain) 25/07/1991; 3 males (see image in OSF), 3 females, Azuay, Cuenca, Nabon, 3000 m, (Poulain), 12/02/1990, MNHN, MLPA; one male, Ecuador, Azuay, Tarqui, 2800 m, 8/03/1965, (Peña), MLPA (Fig. 9(4)).

*Measurements (in mm).* Body length to end of femur III: 14 (13–14.4) (male), 17 (15–17) (female); femur III length: 8 (male), 9 (female) (see geographic distribution in OSF).

*Distribution*. Ecuador: Azuay; was found in distinctly drier and less grassy microhabitats than *J. laevis*, with which it seems to be parapatric.

Jivarus antisanae (Bolivar) (Figs 2B; 3U–X; 6AC–AG)

Pezotettix antisanae Bolivar, 1881:36

*Jivarus antisanae*: Giglio-Tos 1898:23; Ronderos 1979: 199; Liebermann 1942:306; Otte 1995:364; Chapco, 2006: 59–63

Melanoplus antisanae: Kirby, 1910:532

Jivarus camposi Rehn:2; Ronderos 1979:199 (= Jivarus antisanae)

Jivarus albolineatus Ronderos 1979:203, new synonymy

*Diagnosis.* Similar to *J. sphaericus*, differing mostly in the male cerci with a distal hook, fastigium more prominent, eyes subtriangular, pronotum narrower, with transverse sulci smoothly impressed and lateral ridges throughout the pronotum.

Redescription. Body colour green, ventrally yellowish, without traces of post-ocular band; some specimens with a light vellowish longitudinal band on the dorsum of abdomen; hind femur with the dorsal surface brownish, knees with the ventral area with tinges of red; hind tibiae green in males, red in females. Head retreating, with large ovoid eyes, fastigium prominent, wider than long, with traces of lateral carinae. Pronotum narrowly trapezoidal, finely rugose; pronotal disk flat, with weak lateral ridges; mid-longitudinal carina absent, posterior margin undulate, emarginate at the middle, transverse sulci well indicated. Tegmina widely ovate with rounded apex. Hind femur with dentate lower margin. Male cerci long, sharply narrowing at the middle third, with the distal two-thirds resembling a walking stick, dorsally curved, apex hook-shaped; epiproct triangular, wider than long with undulate elevated lateral margins; furculae not developed. Phallic complex: epiphallus with long acute ancorae; lophi highly elevated, bridge narrow, lateral plates widely developed; lateral projection of apical valves of aedeagus well developed covering the apex of the valves leaving the mid-ventral part of the axial portion of the valves uncovered, axial portion of apical valves widely developed ventrally, with the internal face highly convex, apices of apical valves truncate.

Observations. Bolivar (1881) describes this species as Pezotettix antisanae based on a female specimen from Antisana (Ecuador), and Giglio-Tos (1898) considers that it belongs to the genus Jivarus. Later, Ronderos (1979) redescribed the species and designated an 'allotype male' from Pichincha, Quito, (La Merced), 2600 m, VI-76, Ecuador. However, after a close examination of the 'allotype male' that was designated by Ronderos and deposited at the 'Museo de La Plata', and the holotype male specimen of Jivarus albolineatus Ronderos, we came to the conclusion that they belong to the same species. Furthermore, we also examined materials collected by one of the authors (Amedegnato) from the type localities and surrounding areas of J. antisanae and J. albolineatus and came to the conclusion that they belong to the same species, and thus J. albolineatus has to be listed as a synonym under J. antisanae.

*Measurements (in mm).* Body length to end of femur III: 16.3 (15.2-17.4) (male), 19.6 (18.9-20.3) (female); femur III length: 9 (male), 10.5 (10-11) (female).

*Material examined.* Ecuador: 14 males (see image in OSF), 16 females, 3 nymphs, Imbabura, Otavalo, 2900 m, 11/09/1991, (Amedegnato & Poulain), MNHN, MLPA; 10 males, 14 females, 4 nymphs, Carchi, Paramo de El Angel, 32/3400 m, 14/12/1997, (Amedegnato & Poulain), MNHN, MLPA, PUCE; 3 males, 2 females, Imbabura, Pimampiro: Pan de Azucar, 2600 m, 15/04/1990, (Poulain), MNHN, MLPA; 33 males, 20 females, 2 nymphs, Pichincha, Cayambe: Olmedo, 2980 m, 13/12/1997, (Amedegnato & Poulain), MNHN, MPLA; 39 males, 23 females, Pichincha, Quito/Baeza, Pifo, 3300 m, 24/09/1991, (Amedegnato & Poulain), MNHN, MLPA, PUCE; 3 males, 5 females, Pichincha, Quito/Pifo,

3700 m, 27/12/1997, (Amedegnato & Poulain), MNHN; 3 females, Quito/Pifo, 28/2900 m, 17/12/1997, (Amedegnato & Poulain), MNHN; 19 males, 31 females, Pichincha, Quito: Lloa, 2800 m, 07/07/1991, (Amedegnato & Poulain), MNHN, MLPA; PUCE; 2 males, Azuay, Cuenca: Nabon, 3100 m, 25/07/1991, (Amedegnato & Poulain), MLPA; one female, Chimborazo, Guamote, 3300 m, 24/07/1991, (Amedegnato & Poulain), MLPA; one male, one female, 3 nymphs, Pichincha, Quito: Nono, 2200 m, (Amedegnato & Poulain), 13/07/1991, MNHN, MPLA; 2 males, one female, Pichincha, Quito: Nono, 3200 m, 13/09/1997, (Amedegnato & Poulain), MNHN, MLPA; one male, one female, Patichubamba at Pintac, 2950 m, 24 km SE Quito, 6/11/65 (Hemmingsen), MLPA; 2 male paratypes (see image in OSF) of J. albolineatus Ronderos, Ecuador, Carchi, El Angel, 2700 m, 24/06/1965, (Peña), MLPA; one male bearing an 'allotype' label of Jivarus antisanae designated by Ronderos (1977 in litt.) and one female, Ecuador, Pichincha, Quito, La Merced, 2600 m, VI/76, (Martinez), identified as J. antisanae by Ronderos, MLPA; 5 males, 3 females, Ecuador, Pichincha, San Rafael, 15 km SE of Quito, 2800 m, 3/04/1963, (Hubbell & Peña), MLPA (Fig. 9(2)).

*Distribution.* Ecuador: Carchi, Imbabura, Pichincha, Azuay; the most common species in the inter-Andean depression of northern Ecuador, and in its internal slopes, found in all open grassy humid places resulting from the deforestation of *Polylepis* forests (see geographic distribution in OSF).

*Jivarus auriculus* **sp.n.** (Figs 3Y–AB; 6AH–AL)

*Diagnosis.* Closely related to *J. antisanae*, from which it differs in the male cerci long, slender, bent inwards and with the distal half portion ovate and the the distinctive shape of the apical valves of aedeagus ear-shaped diverging caudally, with mid-longitudinal internal furrow.

Description. Body colour brown, ventrally yellow, without traces of post-ocular dark band, face yellow, tegmina brown, base of cerci reddish brown. Hind femur with ventral area yellow, dorsal area brown; hind knees red; hind tibiae light purple; hind tarsi red. Head retreating, with large ovoid eyes, fastigium prominent, wider than long, without lateral carinae. Pronotum narrowly trapezoidal, finely rugose on metazone; mid-longitudinal carina indicated throughout. Pronotal disk with posterior margin widely emarginate; with acute dorsodistal angle between the disk and the lobes in dorsal view. Tegmina ovate with rounded apex. Hind femur with lower margin irregular. Male cerci long, slender, slightly compressed at the two thirds, distal third portion ovate; epiproct with the margin sinuous with acute mid-projection, furculae reduced. Phallic complex: epiphallus with long and acute ancorae; lophi highly elevated. Lateral projection of apical valves of aedeagus reduced and embracing only the base of the axial portion of valves; axial portion of apical valves of aedeagus broad,

ear-shaped diverging caudally, with internal mid-longitudinal furrow; sheath of aedeagus with short mid-longitudinal division.

Females, differing from males in the body color, with dark brown or green post-ocular band extending from the back of eyes onto the pronotal lobes; epimeron with a light-coloured stripe; ovipositor valves straight and slender, with the dorsal margin serrate; female cerci long.

*Measurements (in mm).* Body length to end of femur III: 17.5 (17-18) (male), 18.5 (18-19) (female); femur III length: 9 (male), 10.5 (10-11) (female).

*Etymology.* Auricula (L.) means ear, referring to the shape of the apical valves of aedeagus.

*Material examined.* Ecuador: Holotype male, allotype female, Cañar, Azogues, Taday-Guarainag, 3000 m, 09/02/1990, (Poulain), MNHN; Paratypes: four males (see image in OSF), six females, Cañar, Azogues, Taday-Guarainag, 3000 m, 09/02/1990, (Poulain), MNHN, MLPA; one male, Cañar, Biblian, 3400 m, 05/12/1997, (Amedegnato & Poulain), MNHN (Fig. 9(2)).

*Distribution*. Ecuador: Cañar; same habitat as *J. antisanae*, in the southern part of the distribution of the group; sympatric with *J. laevis* (see geographic distribution in OSF).

Jivarus riveti **sp.n.** (Figs 2C; 3AC–AF; 6AM–AQ)

*Diagnosis.* Closely related to *J. auriculus* from which it differs in body colour green without traces of dark post-ocular band, the shape of the male cerci shorter and slightly wider at the distal half end and differences in the male genitalia as shown in Fig. 6AM–AQ.

Description. Body colour green, ventrally yellow, without traces of post-ocular band, face cream; tegmina, base of cerci, sides of epiproct, and hind knees reddish brown; abdomen laterally with tinges of red; hind tibiae bluish green; hind tarsi red. Hind femur light green with the upper area brown; ventral area yellow. Male cerci wider than in *J. auriculus*, bent inwards at the mid-portion and with the distal half portion compressed and wider than in *J. auriculus*. Phallic complex: epiphallus with long and acute ancorae; lophi highly elevated. Lateral projection of apical valves of aedeagus reduced and embracing only the base of the axial portion of valves; axial portion of apical valves of aedeagus longer than in *J. auriculus*, broad, ear-shaped diverging caudally, concave internally; sheath of aedeagus with short mid-longitudinal division.

*Etymology.* The name of this new species is dedicated to Paul Rivet (1876–1958), a French physician who studied the

biodiversity of the Ecuadorian Andes as well as the native Andean cultures. He joined the Museum National d' histoire Naturelle, Paris, and founded the Musee de l'Home, Paris, France.

*Material examined.* Ecuador: Hotype male, allotype female, Azuay, Cuenca, Cajas, Lag. Zurucucho, 3100 m, 06/08/1991, (Amedegnato & Poulain), MNHN; Paratypes 6 males (see image in OSF), 5 females, Azuay, Cuenca, Cajas, Lag. Zurucucho, 3100 m, 06/08/1991, (Amedegnato & Poulain), MNHN, MLPA. Other materials: 4 males, Azuay, Cuenca, Cajas, 3350 m, 14/04/1995, (Poulain), MNHN; 7 males, 7 females, Azuay, Cuenca, Cajas, Lag. Zurucucho, 3100 m, 08/02/1990, (Poulain), MNHN; 5 males, 5 females, Tioloma, 4100 m, (Rivet), 1904, MNHN; 5 males, 5 females, Tioloma, 4300 m, 1904, (Rivet), MNHN; 2 males, Laguna Zurucucho, 11 mi of Cuenca, 16/12/55, (Schlinger & Ross), MNHN (Fig. 9(2)).

*Measurements.* Body length to end of femur III: 17.5 (17–18) (male), 18.5 (18–19) (female); femur III length: 9 (male), 10.5 (10–11)(female).

*Distribution.* Ecuador: Azuay, Chimborazo; on open grassy páramos with scattered bushes, on dicotyledonous plants (see geographic distribution in OSF).

*Jivarus sphaericus* **sp.n.** (Figs 4A–D; 7A–E)

Jivarus alienus sensu Ronderos 1979:206.

*Diagnosis.* Similar to *J. antisanae*, differing mostly in the male cerci without the distal hook, fastigium less prominent, eyes globe-shaped and the pronotum stockier, with transverse sulci deeply impressed and lateral ridges only present in metazone.

Description. Body colour dark green, with the distal segments of abdomen reddish, hind tibia green, hind tarsi reddish, tegmina reddish brown (bright red when alive). Head with fastigium carinated, triangular, wider at the base than its length; fastigio-facial angle rounded in lateral view; eyes circular, globose, exceeding the level of the vertex. Pronotum short and slightly stocky, weakly expanded in metazone, transverse sulci deeply impressed, lateral ridges only present in metazone; pronotal disk sinuous in lateral view, with posterior margin widely emarginate, with obtuse dorso-distal angle between the disk and the lobes. Epiproct triangular, with prominent margins and distal projection rounded, furculae broad, widely separated; male cerci as in J. antisanae, but without the distal hook; subgenital plate with acute apex. Phallic complex: epiphallus with oblique highly prominent lophi, extending along the entire distal margin of the lateral plates, widely separated in the middle (in J. antisanae they are closer); apical valves of aedeagus similar to J. antisanae, tapering towards the apex, deeply concave



internally at the base; sheath of aedeagus with mid-dorsal lobe extending weakly beyond the apical valves, with short midlongitudinal division.

Female similar to male but with fastigium flat, fastigio-facial angle prominent; eyes smaller and not so globose; ovipositor valves straight with dentate margin. General body brown, with red hind tibiae.

*Measurements (in mm).* Body length to end of femur III: 15.5 (15-16) (male), 17.5 (17-18) (female); femur III length: 9 (male), 10.5 (10-11) (female).

Etymology. Sphaera (L.), referring to the globe-shaped eyes.

*Material examined.* Ecuador: Holotype male, allotype female Pichincha, Quito/Sto. Domingo, 2700 m, 06/07/1991, (Amedegnato & Poulain), MNHN; Paratypes: 5 males (see

**Fig. 7.** *Jivarus* males. Phallic complex, species as indicated. A, F, K, P, U, Z, AE, endophallic plates (basal and apical valves of aedeagus) and cingulum lateral view; B, G, L, Q, V, AA, AF, endophallic plates (basal and apical valves of aedeagus) and cingulum, dorsal view; C, H, M, R, W, AB, AG, distal portion of aedeagal valves, ventral view; D, I, N, S, X, AC, AH, epiphallus, dorsal view; E, J, O, T, Y, AD, AI, epiphallus, lateral view.

image in OSF), one females, 7 nymphs, Pichincha, Quito/Sto. Domingo, 2700 m, 06/07/1991, (Amedegnato & Poulain), MNHN, MLPA. Other materials: 2 males, 4 females, Pichincha, id., 3000 m, 14/07/1991, (Amedegnato & Poulain), MNHN (Fig. 9(2)).

*Observations*. Ronderos (1979) redescribed *J. alienus* (Walker) based on the female holotype from Ecuador, Pichincha, Quito deposited at the British Museum, and on a male (that he designated as an 'allotype' of *J. alienus*) and a female specimens from Ecuador, Pichincha, 48 km S Quito, 06/05/75, (Gurney and Spangler), USNM. However, we have examined the female holotype of Walker and it is the same common and widely distributed species that Ronderos (1979) described as *J. osunai*. Thus, we herein give the new name *Jivarus sphaericus* to the misapplied *J. alienus* of Ronderos (1979) (see geographical distribution in OSF).

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*Jivarus viridis* Ronderos (Figs 4E–H; 7F–J)

Jivarus viridis Ronderos 1989: 203.

*Diagnosis.* Similar to *J. antisanae*, differing mostly in the smaller size, pronotum flat, not gibbous in lateral view, male cerci with a hook at the tip and epiphallus larger with an extra acute projection close to the prosterior process of the lateral plates.

Redescription. Body colour green with bluish green hind tibiae, ventrally yellowish green, hind tarsi red; tegmina with the dorsal half light brown and the lower half dark brown. Head with prominent wide triangular fastigium; globe-shaped eyes, exceeding the level of vertex in lateral view; mid-longitudinal carina weakly indicated. Pronotum widely trapezoidal: pronotal disk emarginated posteriorly with crenulate margin; metazone rugose; mid-longitudinal carina present throughout; with posterior angle between the disk and the lobes rounded. Male cerci as in J. antisanae but with the distal third portion shorter. Phallic complex with epiphallus large, with an extra acute projection close to the posterior process of the lateral plates; lateral projections of apical valves of aedeagus short; apical valves diverging outwards, with the apices extending beyond the sheath; sheath foliar-shaped with mid-longitudinal division short.

Female, with the fastigium triangular; pronotum more rugose than in males; ovipositor valves straight and long with serrate dorsal margin; tegmina with mid-dorsal area lighter than in males.

*Measurements (in mm).* Body length to end of femur III: 15 (15–16.7) (male), 17 (16.8–18.5) (female); femur III length: 8 (male), 10 (female).

*Material examined.* Ecuador: 16 males (see image in OSF), 22 females, Cotopaxi, San Miguel de Salcedo: Cashaloma, 3400 m, 26/12/1997, (Amedegnato & Poulain), MNHN, MLPA, PUCE; one male, one female paratypes, Ecuador, S Guamote, 3400 m, 14/XII/1970, (Peña), MLPA (Fig. 9(2)).

*Distribution.* Ecuador: Cotopaxi; sympatric with *J. spatulus*, in the same grassy pastures, on bushes (see geographic distribution in OSF).

Jivarus hubbelli Ronderos

Jivarus hubbelli Ronderos 1979:217.

Material examined. 2 males (see image in OSF) paratypes of J. hubbelli Ronderos 1979, Ecuador, Pino, (N.Cañar), 3200 m, 10/12/1970, (Peña), MLPA (Fig. 9(2)). Jivarus rectus **sp.n.** (Figs 2D; 4I–L; 7K–O)

*Diagnosis.* Similar to *J. carbonelli*, differing mostly in the narrower fastigium; eyes more prominent; disk of pronotum flat delimited by lateral ridges; phallic complex with lateral projections of the apical valves of aedeagus short without dorsal development; axial portion of apical valves straight and long, with reduced vertical development; sheath of aedeagus narrow with deep mid-longitudinal division.

Description. Body colour green with red tinges on the antenna, at the bases of anterior and median femora, internal and inferior face of hind femora and on pronotum sides (in live specimens); hind tibiae bluish green. Head large, with globe-shaped eyes; fastigium wide, strongly triangular and flat, with lateral carinae evident; fastigio-facial angle straight, not declivent; face almost orthognatus. Pronotum finely rugose, trapezoidal with mid-longitudinal carina weakly indicated; pronotal disk flat, delimited by parallel lateral ridges, posterior margin slightly emarginate, with obtuse disto-dorsal angle between the disk and the lobes, transverse sulci shallowly impressed. Tegmina broad, with rounded apex, lateral in position. Hind femur with entire lower margin. Male cerci short, weakly curved inwards, tapering towards the acute apex; male epiproct triangular, with mid-distal projection acute; furculae evident, widely separated. Subgential plate conical, highly surpassing the epiproct. Phallic complex: epiphallus large, lophi widely developed horizontally, lateral plates converging caudally, ancorae long and parallel; lateral projections of the apical valves of aedeagus short without dorsal development; axial projection of apical valves long and slender; sheath of aedeagus narrow.

*Measurements (in mm).* Body length to end of femur III: 16.5 (16–17) (male), 19.5 (19–20) (female); femur III length: 8.5 (8–9) (male), 10 (female).

*Etymology*. Rectus (L.), referring to the straight apical valves of aedeagus.

*Observations: Jivarus carbonelli* is found in páramos of *Espelettia* species, whereas *J. rectus* lives in open areas of montane forest.

*Material examined.* Ecuador: Holotype male, allotype female, Sucumbios, El Playon, 2800 m, 17/09/1991, (Amedgenato & Poulain), MNHN; Paratypes: 11 males (see image in OSF), 5 females, Sucumbios, El Playon, 2800 m, 17/09/1991, (Amedgenato & Poulain), MNHN, MLPA; one male, one female, Sucumbios, Santa Barbara, 25/2700 m, 15/12/1997, (Amedegnato & Poulain). Other materials: 15 males, 12 females, 3 nymphs, Sucumbios, El Playon/Sta. Barbara, 2600 m, (Amedegnato & Poulain), 17/09/1991, MNHN; 13 males, 7 females, Sucumbios, Santa Barbara, 25/2700 m, 15/12/1997, (Amedegnato & Poulain), MNHN, MLPA; MNHN; 13 males, 7 females, Sucumbios, Santa Barbara, 25/2700 m, 15/12/1997, (Amedegnato & Poulain), MNHN, MLPA; MARA, 25/2700 m, 15/12/1997, (Amedegnato & Poulain), MNHN, MLPA; MNHN, MLPA; MNHN, MLPA; MARA, 25/2700 m, 15/12/1997, (Amedegnato & Poulain), MNHN, MLPA; MNHN, MLPA; MARA, 25/2700 m, 15/12/1997, (Amedegnato & Poulain), MNHN, MLPA; MNHN, MLPA; MARA, 25/2700 m, 15/12/1997, (Amedegnato & Poulain), MNHN, MLPA; MNHN, MLPA; MNHN, MLPA; MARA, 25/2700 m, 15/12/1997, (Amedegnato & Poulain), MNHN, MLPA; MNHN, MLPA; MARA, 25/2700 m, 15/12/1997, MNHN; MARA, 25/2700 m, 15/12/1997, MARA, 25/2700 m, 15/12/1997, MNHN; MARA, 25/2700 m, 25/2700 m

PUCE; one male, Ecuador, (Bolivar), 1898, MNHN; 2 females, Sucumbios, Sta. Barbara, 2600 m, 16/09/1991, (Amedegnato & Poulain), MNHN (Fig. 9(1)).

*Distribution.* Ecuador: Sucumbios; in opening areas in montane forest (see geographic distribution in OSF).

*Jivarus carbonelli* Ronderos (Figs 4M–P; 7P–T)

Jivarus carbonelli Ronderos 1979: 206; Ronderos 1981: 145.

*Diagnosis.* Similar to *J. rectus* **sp.n.**, differing mostly in the wider fastigium, eyes less prominent, males with tegmina shorter, hardly reaching the second abdominal tergite; phallic complex with the lateral projections of the apical valves of aedeagus short without dorsal development; axial portion of apical valves of aedeagus with reduced vertical development, shorter and wider; sheath of aedeagus gibouse and wide, with deep mid-longitudinal division.

*Material examined.* Ecuador, 13 males, 7 females, Carchi, Paramo de El Angel, 32/3400 m, (Amedegnato & Poulain), 14/12/1997, MNHN, MLPA, PUCE; one male (see image in OSF), one female paratypes, Ecuador, Carchi, Troya, 5 mi S Tulcan, 0°44'N/77°41'W, (Peña), MLPA.

Colombia: 60 males, 105 females, Dept. Nariño, Tuqueres, 3100 m, 17/11/1968, (Descamps), MNHN; 4 males, 3 females, Dept. Nariño, 10 km de Pasto route, Puerto Asis, 2900 m, 06/11/1968, (Descamps), MHNH; 10 females, Dept. Nariño, El Pedregal, 1800 m, 17/11/1968, (Descamps), MNHN (Fig. 9(1)).

*Distribution.* Ecuador: Carchi; Colombia, Nariño; in páramos of *Espeletia* species (see geographic distribution in OSF).

*Jivarus alienus* (Walker) (Figs 2E; 4Q-T; 7U-Y)

> Caloptenus alienus Walker 1870:684 Paradichroplus alienus: Kirby 1910:492 Jivarus? alienus: Uvarov 1925:288

*Jivarus osunai* Ronderos 1981:146; Carbonell *et al.* 2007:50; new synonym

*Jivarus cerdai* Ronderos 1981:145; Carbonell *et al.* 2007:50; new synonym

*Diagnosis*. Closely related to *J. ochraceus*, differing mostly in the smaller size, males with pronotal disk with transverse sulci more deeply impressed; male cerci not curved.

*Redescription.* Body colour in males dorsally olive, ventrally yellowish, legs green, frons yellow; lateral lobes of pronotum with dark olive green post-ocular band and the mid-ventral area yellow; hind tibiae green with the proximal portion red; tegmina brown; hind femur with genicular lobes red, ventral margin yellow. Head with prominent horizontal fastigium, as long as the width of interocular distance; eyes prominent. Pronotal disk with lateral ridges sinuous, transverse sulci weakly impressed; mid-longitudinal carina weakly indicated; hind margin crenate. Tegmina broad, with rounded apex, lateral in position. Hind femur with entire lower margin. Male cerci short, almost straight, tapering towards the acute apex; male epiproct narrowly triangular, with mid-distal projection acute; furculae large, widely separated. Subgential plate conical, highly surpassing the epiproct. Phallic complex with epiphallus large, with widely horizontally developed lophi, bridge concave; lateral projections of apical valves of aedeagus short, without dorsal development; apical valves of aedeagus as long as the sheath; sheath of aedeagus gibouse and narrow, with deep mid-longitudinal division.

Females with frons not prominent between the antennae, body colour brownish red, darker on the outer face of hind femur; with dark post-ocular band on pronotal lobes; hind tibiae light green with the proximal portion red; hind femur with the internal face and genicular lobes red. Some specimens have a pair of yellow spots on the pronotal disk, and the mid-ventral area of pronotal lobes yellow, hind femur with internal face and ventral area light red to yellow, and dorsal surface with two light wide brown bands.

Observations. Walker (1870) described the species Caloptenus alienus based on a single female type from Ecuador, Pichincha. Later, Ronderos (1981) described the five new species for Jivarus, among them J. osunai based on material from Colombia, Nariño, El Ingenio, 2030 m, and J. cerdai from Colombia, Nariño, La Florida, Pasto, 2200 m. However, after examining the holotype males and allotype females of J. osunai and J. cerdai deposited at the MNHN, the female holotype of C. alienus Walker deposited at the British Museum, and a large series of specimens collected from the region, we came to the conclusion that they belong to the same common species, and thus J. osunai and J. cerdai must be listed as a synonym under J. alienus (Walker).

*Material examined.* Male holotype and female allotype of *J. osuani* Ronderos, Colombia, Nariño, El Ingenio, 2030 m, 24/11/1968, (Descamps), MNHN; one male (see image in OSF), one female paratypes of *J. osunai* Ronderos, Colombia, Nariño, El Ingenio, 2030 m, 24/11/1968, (Descamps), MLPA; female holotype of *C. alienus* Walker, Ecuador, Pichincha, BMNH; 100 males and females, Colombia, Dept. Nariño, Pasto, 15/07 to 15/08/1968, (Simon), MNHN, MLPA, PUCE; one male, one female, Depto. Nariño, El Ingenio, 2050 m, 24/11/1968, (Descamps), MNHN; male holotype and female allotype of *J. cerdai* Colombia, Dept. Nariño, La Florida, Pasto, 2200 m, 24/11/1968, (Descamps), MNHN; 5 males and 3 females paratypes of *J. cerdai* Ronderos, Colombia, Dept. Nariño, La Florida, Pasto, 2200 m, 24/11/1968, (Descamps), MNHN; 5 males and 3 females paratypes of *J. cerdai* Ronderos, Colombia, Dept. Nariño, La Florida, Pasto, 2200 m, 24/11/1968, (Descamps), MNHN; 5 males and 3 females paratypes of *J. cerdai* Ronderos, Colombia, Dept. Nariño, La Florida, Pasto, 2200 m, 24/11/1968, (Descamps), MNHN; 5 males and 3 females paratypes of *J. cerdai* Ronderos, Colombia, Dept. Nariño, La Florida, Pasto, 2200 m, 24/11/1968, (Descamps), MNHN; 5 males and 3 females paratypes of *J. cerdai* Ronderos, Colombia, Dept. Nariño, La Florida, Pasto, 2200 m, 24/11/1968, (Descamps), MNHN, MLPA (Fig. 9(1)).

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*Measurements (in mm).* Body length to end of femur III: 15.6 (15-16.5) (male), 19.5 (19-20) (female); femur III length: 8.1 (7-9) (male), 11 (female).

*Distribution.* Colombia: Nariño in páramos of *Espeletia* species (see geographic distribution).

#### Jivarus alticola Ronderos

Jivarus alticola Ronderos 1981:150; Carbonell et al. 2007:50.

*Material examined.* Male holotype and female allotype of *J. alticola*, Colombia, Dept. Putumayo, La Piscicultura, 3200 m, 06/11/1968, (Descamps), MNHN, MLPA; 9 males, 10 females, Dept. Putumayo, San Jose Pasto, Sibundoy, 2900 m, 6/11/1968, (Descamps), MNHN; 2 males, Dept. Nariño, Paramos de Tabano, 3200 m, 06/11/1968, (Descamps), MNHN (Fig. 9(1)).

*Observations*. Based on the material deposited for *J. alticola* Ronderos in the MNHN, there is an error in the type locality registered in Ronderos (1981). The male holotype and female allotype (see image in OSF) of *J. alticola* are from Colombia, Dept. Putumayo, La Piscicultura, 3200 m, 06/11/1968, (Descamps), MNHN, MLPA. The remaining material cited by Ronderos (1981) under *J. alticola* belongs to *J. ochraceus*.

*Distribution.* Colombia: Putumayo, Nariño; in páramos of *Espeletia* species (see geographic distribution in OSF). The collecting site Paramos de Tabano is situated between El Pasto and El Encano.

#### Jivarus ochraceus Ronderos

Jivarus ochraceus Ronderos 1981: 148; Carbonell et al. 2007: 50.

*Material examined.* Male holotype, female allotype, Colombia, Dept. Putumayo, San Francisco, 2300 m, 07/11/1968, (Descamps), MNHN; paratypes: 3 males (see image in OSF) and 3 females, idem, MNHN, MLPA; 23 males, 15 females, Dept. Putumayo, San Francisco, 2500 m, 07/11/1968, (Descamps), MNHN; 19 males, 13 females, Dept. 2300 m, 07/11/1968, (Descamps), MNHN; 18 males, 4 females, Dept. Putuymayo, San Francisco, Sibundoy, 2100 m, 31/12/1970, (Drachsler), MNHN (Fig. 9(1)).

*Distribution.* Colombia: Putumayo (see geographic distribution in OSF).

## Jivarus eumera (Hebard)

Dicaearchus eumera Hebard 1923: 240 Jivarus eumera: Ronderos 1983:135; Carbonell et al. 2007:50. *Material examined.* Colombia: male holotype, Cali, 03/1912, ANSP.

#### Jivarus brunneus Ronderos

Jivarus brunneus Ronderos 1981: 148; Carbonell et al. 2007:50.

*Material examined.* Colombia: Holotype male, allotype female, Depto. Cauca, Páramo de Purace (Popoyan), 3450 m, MNHN; 4 males (see image in OSF), 4 females, Depto. Cauca, Páramo de Purace, (Popoyan), 3450 m, MNHN, MLPA (Fig. 9(1)).

*Distribution.* Colombia: Cauca (see geographic distribution in OSF).

#### Jivarus marginalis Ronderos

Jivarus marginalis Ronderos 1979: 208; Carbonell et al. 2007:50.

*Material examined.* Colombia: two males, one female (see image in OSF) paratypes, Valle, Tenerife, paramo, 12 000 ft, (Dietz), 09/1970, MLPA (Fig. 9(1)).

*Distribution.* Colombia: Cauca (see geographic distribution in OSF).

Jivarus pictifrons Ronderos

(Figs 4U-X; 7Z-AD)

*Diagnosis.* Similar to *J. discoloris*, but differing mostly in body colour and in the phallic complex (Fig. 7Z–D).

Redescription. Males with hairy body; head and pronotum dark burgundy, face cream (white in live specimens); anterior and middle legs green; hind femur green with genicular lobe with dorsal half dark brownish red, ventral half bright red; hind tibia green with proximal portion red. Abdomen dark burgundy, with cream (white in live specimens) macula on each tergite; lateral surface of distal abdomen segments red; epiproct red, cerci with the basal portion red and distal portion green. Tegmina with the ventral two-thirds burgundy, and the dorsal third cream. Head with fastigium shorter than its basal width, with lateral carinae well indicated. Face perpendicular. Eyes globe-shaped. Pronotum flat, trapezoidal, with transverse sulci deeply impressed, hind margin only slightly emarginate. Male cerci gradually reducing its width to the apex, the distal third portion gently curved inwards, apex rounded; subgenital plate short, not exceeding the epiproct. Epiproct triangular; furculae thin and contiguous. Phallic complex: sheath of aedeagus gibbous with multiple spines, covering dorsally the tips of apical valves of aedeagus; lateral projections of apical valves of aedeagus short with multiple spines; axial part of the apical valves of aedeagus slender, with reduced vertical development, with sharp edges, diverging caudally with acute apices. Epiphallus with narrow bridge, lophi not too prominent; ancorae widely separated.

Females with head, pronotum and abdomen homogeneously dark brown; hind femur red; hind tibiae green, with proximal portion red. Tegmina with the two ventral thirds burgundy, and the dorsal third cream.

*Measurements (in mm).* Body length to end of femur III: 16.5 (16–17) (male), 19.5 (19–20) (female); femur III length: 9 (male), 11 (female).

*Material examined.* Ecuador: 6 males, 5 females, Loja, Jimbura/Zumba: km 13, 3000 m, (Poulain), 20/04/1990, MNHN, MLPA; Perú: one male, 5 females, 8 nymphs, Piura, Canchaque/ Huancabamba, 3000 m, (Amedegnato & Poulain), 22/09/2001, MNHM, MLPA (Fig. 9(4)).

*Distribution*. Ecuador, Loja; Perú, Piura; on bushes, in dense shrubby páramos ('jalca' formations; van der Hammen & Cleef, 1986) (see geographic distribution in OSF).

Jivarus discoloris **sp.n.** (Figs 2F; 4Y–AB; 7AE–AI)

*Diagnosis.* Closely related to *J. pictifrons*, differing mostly in the shape of the pronotum, body with brighter coloration, and tegmina homogeneously cream; apical valves of aedeagus much shorter and stockier than in *J. pictifrons*.

Description. Body hairy, brightly coloured, with dark brown head, face cream; pronotum dark brown with yellow margins. Abdomen dorsally brown with tinges of red; anterior and median legs with dorsal surface red and ventral green; hind femora with dorsal surface red, outer and inner face bright green, genicular lobes with dorsal half brown and ventral half brightly orange red; hind tibiae bluish green with proximal portion brightly orange red. Tegmina homogeneously cream. Head orthogonal with globe-shaped eyes. Pronotum with deeply impressed transverse sulci, delimiting irregular lobes, hind margin slightly emarginate, with rounded posterior angle between the pronotal disk and the lateral lobes of pronotum. Subgenital plate not exceeding the level of epiproct; epiproct triangular, furculae slender and contiguous. Male cerci slender, tapering towards the apex, weakly curved inwards at the distal third portion. Phallic complex sheath of aedeagus gibbous with multiple spines, covering dorsally the tips of apical valves of aedeagus; lateral projections of apical valves of aedeagus short with multiple spines; axial part of apical valves of aedeagus slender, with reduced vertical development, with sharp edges, diverging caudally with acute apices. Epiphallus with narrow bridge, lophi not too prominent, ancorae widely separated.

Females with head with flat triangular fastigium; lobeshaped tegmina homogeneously cream. Pronotum broadly trapezoidal, with the transverse sulci not so deeply impressed. Body colour similar to male, but with pronotum and abdomen more homogeneously brown coloured. Hind femur green with the dorsal surface brownish red; ventral portion of genicular lobes brightly red; hind tibiae green with the proximal portion brightly red; tegmina homogeneously cream.

*Measurements (in mm).* Body length to end of femur III: 18 (male), 19.5 (19–20) (female); femur III length: 11 (male), 12 (female).

*Material examined.* Peru: Holotype male, allotype female, Piura, Huancabamba: Zapalache, Carmen de la Frontera, 2400 m, (Amedegnato & Poulain), 21/09/2001, MNHN; Paratypes: 3 males (see image in OSF), 4 females, 9 nymphs, Piura, Huancabamba: Zapalache, Carmen de la Frontera, 2400 m, (Amedegnato & Poulain), 21/09/2001, MNHN, MLPA, PUCE (Fig. 9(4)).

*Etymology.* Discolour (L.) meaning of different colours, referring to the general coloration, mostly of the males.

*Distribution.* Peru, Piura; on bushes in deforestation of montane forest areas (see geographic distribution in OSF).

Jivarus profundus **sp.n.** (Figs 5A–D; 8A–E)

*Diagnosis.* Closely related to *J. jagoi*, differing mostly in the shape of the pronotum with transverse sulci more deeply impressed and mid-longitudinal carina vestigial, fastigium more prominent; male cerci with basal portion slender and the distal portion up-curved shorter than the basal portion (in *J. jagoi* it is longer), and differences in male genitalia.

Description. Body colour highly variable. Males dark brown, with the lower part of pronotal lobes, face and cheeks cream; pronotum margins red; abdomen with a mid-dorsal longitudinal stripe; epiproct and cerci red; hind femur with ventral area red, ventral area of genicular lobes yellow; hind tibiae dark green; tarsi of hind legs yellow. Other specimens with body colour light brown, pronotum margins yellowish, with red tinges on hind femur and hind tibia light brown. Other specimens with body colour red dorsally and yellow ventrally; ventral area of pronotal lobes and face cream; abdomen with a cream mid-dorsal longitudinal stripe; hind femur and tibiae red; genicular lobes of hind femur ventrally cream.

Head with perpendicular face; globe-shaped eyes; fastigium triangular with lateral carinae evident; pronotal disk flat with deep transverse sulci; mid-longitudinal carina vestigial interrupted by the sulci. Pronotal disk flat, with transverse sulci deeply impressed delimiting irregular lobes, hind margin widely emarginate. Pronotum shorter and wider than

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**Fig. 8.** *Jivarus* and *Maylasacris* males. Phallic complex, species as indicated. A, F, K, P, U, Z, AE, endophallic plates (basal and apical valves of aedeagus) and cingulum, lateral view; B, G, L, Q, V, AA, AF, endophallic plates (basal and apical valves of aedeagus) and cingulum, dorsal view; C, H, M, R, W, AB, AG, distal portion of aedeagal valves, ventral view; D, I, N, S, X, AC, AH, epiphallus, dorsal view; E, J, O, T, Y, AD, AI, epiphallus, lateral view.

in *J. guarandaensis*. Tegmina with rounded apex, reaching the second abdominal tergite. Distal abdominal segments bulky and up-curved. Male epiproct widely triangular, with prominent margins. Male cerci broad, abruptly narrowing at the distal middle third, where they curve dorsally, with the distal two-thirds narrow, apex hook-shaped. Phallic complex: epiphallus with lophi widely developed horizontally, with the internal protuberance prominent directed anteriorly; ancorae prominent, parallel; lateral projection of apical valves of aedeagus partially

covering the axial portion of valves in lateral view; axial portion of apical valves of aedeagus widely developed vertically, highly convex; sheath of aedeagus covering dorsally the apices of valves.

Female body colour highly variable reddish brown, with the lower half of pronotal lobes, face, hind femur yellow; hind tibiae red; other specimens dark brown with the margins of pronotum red, hind femur with ventral surface and genicular lobe red, hind tibiae dark purple with red tarsi; other specimens



Fig. 9. Geographic distribution of the species of Jivarus and Maylasacris. Symbols indicate localities of collection of specimens examined.

brown with ventral body and legs light green; hind tibiae green and hind tarsi red.

*Measurements (in mm).* Body length to end of femur III: 18.75 (18-19.5) (male), 21 (19-23) (female); femur III length: 10 (male), 13 (11-15) (female).

*Etymology.* Profundus (L.), meaning deep, referring to the deep transverse sulcus of the pronotum.

*Material examined.* Ecuador: Holotype male, and allotype female, Chimborazo, Sisambe/Huigra, 2000 m, 06/12/1997, (Amedegnato & Poulain), MNHN; paratypes: 10 males (see image in OSF), 9 females, Chimborazo, Sisambe/Huigra, 2000 m, 06/12/1997, (Amedegnato & Poulain), MNHN, MLPA; one male, one female, Chimborazo, El Triunfo/Huigra, 1500 m, (Amedegnato & Poulain), 05/09/1997, MLPA. Other materials: 3 males, 3 females, 4 nymphs, Cañar, El Triunfo/Huigra, 1600 m, (Amedegnato & Poulain), 06/09/1997, MNHN; 4 males, 2 females, 7 nymphs, Chimborazo, El Triunfo/Huigra, 1500 m, (Amedegnato & Poulain), 05/09/1997, MNHN, MLPA; 29 males, 29 females, 9 nymphs, Chimborazo, Sisambe/Huigra, 2000 m, (Amedegnato & Poulain), 07/09/1997, MNHN, MLPA (Fig. 9(3)).

*Distribution*. Ecuador, Chimborazo; in openings of relatively dense and humid montane forest of the Andean western slopes (see geographic distribution in OSF).

## Jivarus jagoi Ronderos 1979

Jiarus jagoi Ronderos 1979: 206.

*Diagnosis.* Males with body colour dorsally green with yellow bright areas, body laterally and ventrally yellow (bright yellow in live specimens); abdomen with a series of light spots on dorsum; tegmina, antenna, epiproct and cerci red; front and middle legs green with tarsi brightly red; hind femur green with genicular lobes dorsally red and ventrally yellow; hind tibiae green, hind tarsi bright red.

Females with body colour brownish red (dark red with yellow tinges on face and sides of body in live specimens); antennae red; hind femur with the external face yellow, dorsal area dark red, ventral area red; hind tibiae and tarsi red.

*Material examined.* Ecuador: one male, one female, Tungurahua, Baños, 1800 m, (Poulain), 05/05/1990, MNHN; one nymph, Tungurahua, Rio Verde, 1500 m, (Poulain), 11/05/1990, MNHN; 16 males (see image in OSF), 15 females, 8 nymphs, Tungurahua, Baños, 19/2300 m, (Amedegnato & Poulain), 09/09/1997, MNHN,MLPA; one male, Chimborazo, 30 mi SW Alausi, 2500 m, (Schlinger & Ross), 14/02/1955, CAF.; 2 males, 6–12 mi SW Baños, N slope of Tungurahua, 2500–3000 m, (Schlinger & Ross), 13/02/1955, CAF; one male, Bolivar, Totoras, (T. Devries & L. Coloma), 01/1987, PUCE; one male id. (M. Llerena, 12/1977, PUCE; one female, Chimborazo, Totoras-Ozogachi, Pajonal, 3900 m, (Moret), 25/07/1985, MNHN.). (Fig. 9(3)).

*Distribution.* Ecuador: Tungurahua, Chimborazo (see geographic distribution in OSF).

Jivarus guarandaensis **sp.n.** (Figs 2G; 5E–H; 8F–J)

*Diagnosis.* Similar to *J. profundus*, but differing in the smaller size, interocular distance narrower; the shape of pronotum with the transverse sulci not so deeply impressed; male cerci with basal third narrower; abdomen with a series of cream spots, one on each tergite; and differences in the male genitalia, mostly the epiphalus with lophi not so widely developed and oblique, axial portion of apical valves of aedeagus with less vertical development, covered by the lateral projection in lateral view.

Description. General body colour green, with the lower third area of pronotal lobes yellow; tegmina green or brownish red; epiproct and cerci reddish brown; legs green with tarsi red; hind tibiae green; hind tarsi brightly red. Males, head with fastigium triangular with lateral carinae weakly developed; fastigiumfacial angle rounded; eyes globose, subcircular. Pronotum with transverse sulci deeply impressed delimiting irregular lobes; mid-longitudinal carinae vestigial; posterior margin widely concave; with obtuse angle between the disk and the lobes. Tegmina narrow, reaching the third abdominal segment. Hind femur with ventral margin serrate. Male cerci broad at the base, abruptly narrowing at the distal middle third where they curve dorsally in a right angle, distal third portion slender, apex acute; epiproct narrower than in J. jagoi; furculae reduced. Phallic complex, with epiphallus with lophi oblique, ancorae curved inwards; lateral plates with divergent posterior processes; lateral projection of apical valves of aedeagus covering the axial portion of the valves in lateral view; axial portion of apical valves of aedeagus widely developed vertically and convex; sheath of aedeagus covering dorsally the apices of valves.

Females, general body colour reddish brown, hind tibiae red, ovipositor valves straight with serrate margins.

*Measurements (in mm).* Body length to end of femur III: 17 (16–18) (male), 19.5 (19–20) (female); femur III length: 9 (9–10) (male), 10.50 (10–11) (female).

*Material examined.* Ecuador, Holotype male, allotype female, Bolivar, Guaranda, 2900 m, (Amedegnato & Poulain), 25/12/1997, MNHN; Paratypes: 6 males (see image in OSF), 6 females, Bolivar, Guaranda, 2900 m, (Amedegnato & Poulain), 25/12/1997, MNHN, MLPA (Fig. 9(3)).

*Distribution.* Ecuador, Bolivar (see geographic distribution in OSF).

Jivarus ronderosi **sp.n.** (Figs 5I–L; 8K–O)

*Diagnosis.* Similar to *J. jagoi*, but differing in body colour, the smaller size, the shape of the male cerci and differences in the shape of the sheath of aedeagus and apical valves of aedeagus.

Description. Body hirsute, general colour green, with white face and blue cheeks (in live specimens), yellow in collection insects; pronotum with red margins; tegmina reddish brown; hind femur bluish green, with distal end close to the knees red; hind knees with the upper half brown, lower half red; hind tibiae bluish green; abdomen ventrally yellow; distal abdominal segments with tinges of red. Some specimens with body colour brownish red, hind femur reddish brown, and hind tibiae dark purple. Head with triangular fastigium with prominent lateral carinae, globe-shape eyes exceeding the vertex in lateral view; face orthogonal in lateral view. Pronotum with disk flat; with transverse sulci deeply impressed; medio-longitudinal carina weakly indicated and cut by the transverse sulci; hind margin widely emarginate. Metazone rugose. Male cerci broad with the distal half portion compressed and upcurved in a right angle; epiproct with sinuous margin, furculae broad and well separated. Phallic complex with the sheath gibbous in lateral view; lateral projections of apical valves short, axial portion of apical valves robust with basal protuberance in ventral view; epiphallus with convergent ancorae, narrow short bridge, and prominent robust lophi.

Female with general body colour brown, with dark brown post-ocular band, ventral half of the pronotal lobes cream; hind femur variable in colour, in some specimens green, in others red, except for the dorsal surface brown and the knees with tinges of red; hind tibiae greenish blue. Face with eyes not so globe-shaped and less prominent than in males; fastigium with lateral carinae less prominent; pronotum widely trapezoidal with the transverse sulci less impressed than in males; ovipositor valves straight and slender, with serrate dorsal margin.

*Measurements (in mm).* Body length to end of femur III: 17.6 (17–19) (male); femur III length: 9 (8–10) (male).

*Etymology*. The species name is dedicated to the memory of Ricardo Ronderos, an Argentine entomologist who has devoted his life to the study of the South American Acridoidea.

*Material examined.* Ecuador: Holotype male and allotype female, Loja, Loja, Pq. Podocarpus, 2550 m, (Amedegnato & Poulain), 30/07/1991, MNHN; Paratypes, 38 males (see image in OSF), 36 females, 10 nymphs, Loja, Loja, Pq. Podocarpus, 2550 m, (Amedegnato & Poulain), 30/07/1991,

MNHN, MLPA, PUCE; 2 males, 2 females, Loja, Loja, Saraguro: San Lucas, 2800 m, (Amedegnato & Poulain), 01/ 12/1997, MLPA. Other materials: 21 males, 11 females, Loja, Loja, Saraguro: San Lucas, 2800 m, (Amedegnato & Poulain), 01/12/1997, MNHN, MLPA; 3 males, one female, Loja, Loja, Zamora, 2600 m, (Amedegnato & Poulain), 01/08/1991, MNHN; one male, one female, Loja, Yangana, 22/2500 m, (Amedegnato & Poulain), 26/11/1997, MNHN; 2 males, 4 females, Zamora, Chinchipe, Loja/Zamora, 2600 m, (Poulain), 06/04/1995, MNHN; 2 males, one female, Loja, Loja: Parque Nacional Podocarpus, 25/2800 m, (Amedegnato & Poulain), 30/11/1997, MNHN (Fig. 9(3)).

*Distribution*. Ecuador: Loja; in open montane forest areas and in dense shrubby páramos (see geographic distribution in OSF).

Jivarus rentzi Ronderos

Jivarus rentzi Ronderos 1979: 217.

*Material examined*. Ecuador: 4 males, one female, 40 mi S Alausi, Chimborazo, 20/02/1955, (Schlinger & Ross), MNHN, MLPA (Fig. 9(3)).

*Distribution.* Ecuador: Chimborazo (see geographic distribution in OSF).

Jivarus gurneyi Ronderos (Figs 5M-P; 8P-T)

Jivarus gurneyi Ronderos 1979: 219.

*Diagnosis.* Similar to *J. cohni* and *J. ecuadorica*, but differing in body colour opaque, male cerci and characters of the male genitalia.

Redescription. Body highly hirsute, males general colour olive brown; head with face yellow and eyes laterally red (salmon pink when alive) and dorsally black; first abdominal tergite with a wide circular yellow or white macula; first and second pair of legs green; hind femur and hind tibiae green. Head with fastigium with lateral carinae prominent, shorter than the interocular distance; eyes globe-shaped, extending well beyond the level of vertex in lateral view. Pronotum without medio-longitudinal carina, pronotal disk without lateral ridges; with transverse sulci deeply impressed. Pronotum surface highly rugose. Tegmina short and narrow. Male subgenital plate short with blunt apex, epiproct triangular; furculae acute, widely separated; cerci curved inwards at the middle in right angle, with distal portion thinner than basal portion. Phallic complex: epiphallus with lophi largely expanded horizontally without internal protuberance; bridge narrow; lateral

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projection of apical valves of aedeagus short, axial portion of apical valves of aedeagus largely developed vertically, extending beyond the lateral projections and with the internal face highly convex. Abdomen ventrally yellow/orange.

Females general colour similar to males, with the yellow macula covering almost all the first abdominal tergite, and with a yellow ring on the hind margin of the remaining abdominal segments; legs reddish brown.

*Material examined.* Ecuador, 14 males, 14 females, 13 nymphs, Loja, Loja/Zamora, (Amedegnato & Poulain), 2600 m, 31/07–01/08/1991, MNHN, MLPA; one male (see image in OSF), one female paratype, Loja, km 30 between Loja and Zamora, 05/05/1965, (Peña), MLPA; 9 males, 9 females, Zamora-Chinchipe, Loja/Zamora, 2600 m, 06/04/1995, (Poulain), MNHN; 9 males, 9 females, Zamora-Chinchipe, Sabanilla, 1900 m, 31/07–01/08/19991, (Amedegnato & Poulain), MNHN (Fig. 9(5)).

*Measurements (in mm).* Body length to end of femur III: 16.5 (15.5–17.5) mm (male); 19.7 (18–21.2) (female); femur III length: 9 (male).

*Distribution*. Ecuador: Loja, Zamora Chinchipe; in open areas in dense montane forest (see geographic distribution in OSF).

*Jivarus ecuadorica* (Hebard) **comb.n.** (Figs 2I; 5Q–T; 8U–Y)

*Urubamba ecuadorica* Hebard, 1924:185; Ronderos, 1978: 211; Chapco, 2006:59–63

Jivarus rubriventris Ronderos, 1979:210, syn.n.

*Diagnosis.* Body with metal-like coloration in live specimens; similar to *J. cohni*, differing mostly in the shape of male cerci, wider at distal two-thirds; and body size larger.

Redescription. Males with body colour dark oil green with tinges of yellow (in live specimens body colour golden with red, other specimens golden with black tinges); antennae, coxas, distal portion of anterior and middle femora, knees of hind femora and distal abdominal segments red; hind tibia dark green or purple; hind tarsi red; tegmina with mid-superior portion cream and mid-inferior dark red. Hind femora dark green with ventral area yellow. Head with fastigium with the anterior edge declivent, with lateral carinae prominent, shorter than the interocular distance; eyes globe-shaped, extending well beyond the level of vertex in lateral view. Pronotum without mediolongitudinal carina, pronotal disk without lateral ridges; with transverse sulci deeply impressed. Pronotum surface highly rugose. Tegmina slightly wider than in J. gurneyi. Male subgenital plate short with blunt apex, epiproct subtriangular with the lateral borders curved and acute apex; furculae reduced, widely separated; cerci smoothly curved inwards, with the distal portion thinner than basal portion, apex compressed.

Phallic complex: epiphallus with lophi oblique with internal protuberance developed; lateral projections of apical valves of aedeagus short, sheath of aedeagus covering dorsally the apical valves; axial portion of apical valves large, well developed ventrally, highly convex in its internal face.

Females head and pronotum dark oil green with carinae and margins yellow.

*Measurements (in mm).* Body length to end of femur III: 14 (13.7–14) mm (male); 16.5 (14–17.3) (female); femur III length: 8 (male); femur III length: 9 (female).

Material examined. Holotype female of Urubamba ecuadorica Hebard, Ecuador, Azogues, C. Campos R., ANSP; one female, Ecuador, Azuay, Cerro Tinajillas, 3100 m, 18-20/ 03/1965, (Peña), identified by Ronderos as U. ecuadorica, MNHN; one male paratype (see image in OSF) of J. rubriventris Ronderos, Azuay, Cerro Tinajillas, 3100 m, 18/03/1965, (Peña), MLPA; Ecuador: 10 males (see image in OSF), 13 females, one nymph, Cuenca/ Cajas: Lag. Zurucucho, 3100 m, (Amedegnato & Poulain), 06/08/1991, MNHN, MLPA, PUCE; one male, Azuay, Cuenca,/Loja: Shina, 3200 m, (Poulain), 03/04/1995, MNHN; one male, one female, 4 nymphs, Azuay, Gualaceo, 3100 m, (Amedegnato & Poulain), 03/12/1997, MNHN; one nymph, Azuay, Gualaceo (Res. de Maylas), 3175 m, (Amedegnato & Poulain), 03/12/1997, MNHN; one female, Cañar, Azogues, 3000 m, 05/12/1097, (Amedegnato & Poulain), MNHN; one female, one nymph, Cañar, Azogues, Taday-Guarainag, 3000 m, (Poulain), 09/02/1990, MNHN; one male, one female, Azuay, Cuenca, Cajas, Laguna Zurucucho, 3100 m, (Poulain), 08/02/1990, MNHN; one male, 2 females, one nymph, Azuay, Cuenca, Nabon, 3000 m, (Poulain), 12/02/1990, MNHN; 8 males, 2 females, Laguna Zurucucho, 11 mi from Cuenca, 16/02/1955, (Schlinger & Ross), MNHN; one male, Cañar, Paute, 7/12/1989, (Onore), MNHN; 3 males, 6 females, Azuay, SW of Paute, 17/02/1955, (Schlinger & Ross), MNHN (Fig. 9(5)).

Observations. Hebard (1924) describes Urubamba ecuadorica based on a single female from Ecuador, Azogues. Ronderos (1979) describes the new species J. rubriventris based on a male holotype and a female allotype from Ecuador, Azuay, Cerro Tinajillas, 3100 m, 18-20/03/1965, (Peña), MRSNT, and a male paratype (see image in OSF) from the same locality and data as the type, MLPA. Later, Ronderos (1978) redescribed the genus Urubamba, and in the examined material section of U. ecuadorica, only known at that time from female specimens, he included two females that he identified as U. ecuadorica from Ecuador, Azuay, Cerro Tinajillas, 3100 m, 18–20/03/1965, (Peña), MNHN, and from Azuay, Cuenca, 10/03/1965, (Peña), MNHN. After revising the type material of U.ecuadorica Hebard and the male paratype of J. rubriventris deposited at MLPA, plus the two females identified by Ronderos as U. ecuadorica deposited at MNHN, as well as a good series of specimens collected at the type localities and surrounding areas of the nominal species we came to the

conclusion that *J. rubriventris* and *U. ecuadorica* are the same species and thus we consider *J. rubriventris* a synonym of *U. ecuadorica* Hebard. Furthermore, based on the characteristics of the male, *U. ecuadorica* is considered a species more related to some of the species within *Jivarus* than to the remaining species of *Urubamba*, and thus the new combination *Jivarus ecuadorica* (Hebard) is established herein.

*Distribution.* Ecuador, Azuay; sympatric with *J. laevis* and *J. riveti*, on bushes at edges of grassy areas (see geographic distribution in OSF).

## Jivarus cohni Ronderos

Jivarus cohni Ronderos 1979: 212.

*Material examined.* Ecuador: 7 males, 7 females, Loja, MalacatosYangana, 2000 m, (Poulain), 13/02/1990, MNHN, MLPA; one female, Loja, Gonzanama/Quilanga, 2000 m, 28/11/1997, (Amedegnato & Poulain), MNHN; one male, one female, Loja, Vilcabamba, 1650 m, 26/07/1991, (Amedegnato & Poulain), MNHN; 26 males, 23 females, Loja, Yangana, 22/2500 m, 26/11/1997, (Amedegnato & Poulain), MNHN, MLPA; 5 males, 2 females, 3 nymphs, Yangana, Valladolid, 2100 m, 26/07/1991, (Amedegnato & Poulain), MNHN; 26 males, 23 females, 3 nymphs, Loja, Parque Nacional Podocarpus, 25/2800 m, (Amedegnato & Poulain), MNHN, MLPA; 2 males, 4 females, Loja, Parque Nacional Podocarpus, 2550 m, 30/07/1991, (Amedegnato & Poulain), MNHN (Fig. 9(5)).

*Distribution.* Ecuador: Loja; on bushes in regeneration areas of montane forest (see geographic distribution in OSF).

#### Maylasacris gen.n.

Type species: Maylasacris rugosus sp.n.

*Etymology.* The genus name refers to the distribution area of the species in or around the Reservation of Maylas, Gualaceo. List of species: *Mayalsacris rugosus* **sp.n.**, *Maylasacris* 

digiticercus sp.n., Maylasacris montanus (Ronderos) comb.n.

*Diagnosis.* Male cerci with basal half portion wide; distal half up-curved finger-like, with acute apex, curved inwards in caudal view with an internal protuberance; phallic complex: epiphallus with ancorae not developed; cinglulum capsule-like with prominent zygoma.

Description. Body hirsute and rugose. Head with perpendicular face, and subcircular or globe-shaped eyes; fastigium triangular, horizontal. Pronotum with lateral ridges and tranverse sulci shallowly impressed with hind margin broadly emarginate. Male cerci with basal half portion wide; distal half up-curved finger-like, with acute apex, curved inwards in caudal view with an internal process. Epiproct with triangular acute apex. Male genitalia: cingulum large, capsule-like with wide rami and prominent zygoma. Epiphallus with ancorae not developed; bridge long and narrow. Sheath of aedeagus gibbous with an extra short dorsal lobe, extending beyond the apices of aedeagus. Apical valves of aedeagus slightly curved downwards, spoon-shaped in ventral view; without lateral projections

# Key to males of Maylasacris

2. Male cerci with the basal half portion broader (Fig. 5X) and distal half portion arched shape in caudal view (Fig. 5Y); eyes more prominent and globe-shaped (Fig. 5U); fastigium with rounded apex in dorsal view (Fig. 5V) ..... *M. rugosus* **sp.n.** – Male cerci slender, with the distal portion longer and less curved inwards (Fig. 5 AC); narrower fastigium with acute apex (Fig. 5 AA), body less rugose; eyes subcircular not exceeding the level of vertex in lateral view (Fig. 5Z) ...... *M. digiticercus* **sp.n.** 

Maylasacris rugosus **sp.n.** (Figs 2H; 5U-Y; 8Z-AD)

*Diagnosis.* Closely related to *J. digiticercus*, differing in the male cerci with the basal half portion broader and the distal half portion arched shape in caudal view; eyes more prominent and globe-shaped; fastigium with rounded apex in dorsal view.

Description. Body hirsute and highly rugose; males with body colour dark olive green, head dark green with cream face, mouthparts porcelain blue to white; antennae black; pronotum dark red; femora of first and second pairs of legs bright red except dorsal area dark green; hind femur dorsal area brownish green or yellow gold, external face and ventral area bright red; fore and middle femora dorsal area yellow gold; hind tibia blue, except proximal portion red; hind tarsi blue; epiproct and cerci brightly red; thorax ventrally blue; abdomen ventrally yellow gold. Tegmina red brown with golden yellow nervations. Head with prominent, broad triangular horizontal fastigium; with mid-longitudinal carina; eves globe-shaped, exceeding the level of vertex in lateral view. Pronotum with lateral ridges evident, weakly diverging backwards; transverse sulci shallowly impressed; hind margin crenate. Tegmina reaching the third abdominal segment. Male cerci with the basal half portion broad, distal half portion arched shape in caudal view, apex acute. Epiproct with triangular acute apex; furculae acute; subgenital plate short with rounded apex. Male genitalia:

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ectophallic membrane without dorsal sclerotized shield; cingulum large, capsule-like, with wide rami, zygoma prominent; apodemas of cingulum broad, down-curved in lateral view. Epiphallus with ancorae reduced, almost not developed. Sheath of aedeagus gibbous, with an extra short dorsal lobe, extending beyond the apices of aedeagus; apical valves of aedeagus slightly curved downwards, spoon-shaped in ventral view.

Female, similar to males with ovipositor valves slender and long, with serrate upper margins.

*Measurements (in mm).* Body length to end of femur III: 16 (15–17) mm (male); 18 (17–19) (female); femur III length: 9 (male); femur III length: 10 (female).

Etymology. Rugosus (L.) referring to the body tegument.

*Material examined.* Ecuador: Holotype male, allotype female, Morona, Santiago, Limon/Indanza:Plan de Milagro, 2500 m, (Amedegnato & Poulain), 04/12/1997, MNHN; Paratypes 26 males (see image in OSF), 19 females, Morona, Santiago, Limon/Indanza:Plan de Milagro, 2500 m, (Amedegnato & Poulain), 04/12/1997, MNHN, MLPA (Fig. 9(3)).

*Distribution.* Ecuador: Loja; on bushes in regeneration areas of montane forest (see geographic distribution in OSF).

Maylasacris digiticercus sp.n. (Figs 5Z–AD; 8AE–AI)

*Diagnosis.* Closely related to *J. rugosus*, differing in the narrower fastigium with acute apex, body less rugose; eyes subcircular not exceeding the level of vertex in lateral view; male cerci slender, with the distal portion longer and less curved inwards in caudal view; and characters from the male genitalia.

*Description.* Body hirsute and rugose; body colour dark brown, with the margins of pronotum red; hind femur reddish brown with dorsal surface dark brown, hind tibiae red; abdomen ventrally yellow.

Head with perpendicular face; fastigium triangular, with acute apex in dorsal view, with mid-longitudinal carina; eyes subcircular, not exceeding the level of vertex in lateral view. Pronotum weakly gibbous in lateral view, with lateral ridges evident, transverse sulci shallowly impressed. Tegmina narrow, not reaching the second abdominal segment. Male cerci with the basal half portion tapering towards the middle, distal half portion finger-like, directed forwards with acute apex, slightly curved inwards in caudal view. Epiproct with triangular acute apex; furculae acute; subgenital plate short with rounded apex. Male genitalia: ectophallic membrane without dorsal sclerotized shield; cingulum large, capsule-like, with wide rami, zygoma prominent; apodemas of cingulum broad, down-curved in lateral view. Epiphallus with ancorae reduced, almost not developed. Sheath of aedeagus gibbous, with an extra short dorsal lobe, extending beyond the apices of aedeagus; apical valves of aedeagus weakly curved downwards, spoon-shaped in ventral view.

Female, similar to males, with ovipositor valves slender with serrate upper margins.

*Measurements (in mm).* Body length to end of femur III: 16 (15–17) mm (male); 17 (17–18) (female); femur III length: 9 (male); femur III length: 10 (female).

*Etymology*. Digitus (L.) means finger, referring to the shape of the distal portion of the male cercus.

*Material examined.* Ecuador: Holotype male, female allotype, Azuay, Gualaceo (Res. de Maylas), 3175 m, 03/12/1997, MNHN; Paratypes: 3 males (see image in OSF), 2 females, Azuay, Gualaceo (Res. de Maylas), 3175 m, 03/12/1997, (Amedegnato & Poulain), MNHN, MLPA (Fig. 9(3)).

*Distribution.* Ecuador: Azuay; on bushes in xerophytic shrub páramo areas intermixed with montane forest (see geographic distribution in OSF).

Maylasacris montanus (Ronderos) comb.n.

Jivarus montanus Ronderos 1979: 215.

*Material examined.* Ecuador: one male (see image in OSF) and 2 females paratypes of *J. montanus* Ronderos, Azuay, Cerro Tinajillas, 3100 m, 18–20/03/1965, (Peña), MLPA (Fig. 9(3)).

*Distribution.* Ecuador: Azuay (see geographic distribution in OSF).

*Observations*. Based on the relationships shown on the tree (Fig. 1) we consider that *J. montanus* is closely related to the new species *digiticercus* and *rugosus* based on the synapomorphies: male subgenital plate short not exceeding the level of epiproct, rounded shape (17:2), male cerci elbow-shaped in caudal view (19:1) and zygoma of cinglulum highly elevated (36:1), and must be treated under a new genus that we name *Maylasacris* gen.n. The new combination *Maylasacris* montanus (Ronderos) comb.n. is established herein.

# Distribution patterns

In Ecuador, the Andes mountain range is divided into the Cordilleras Oriental and Occidental and it broadens towards the north. At the Nudo de Pasto, in Colombia, it splits into three separate cordilleras (Clapperton, 1993). Precipitation in the high Andes generally decreases from north to south, with

the high-Andean grass-dominated vegetation falling into three major types correlated with the precipitation level. The wettest northern high-Andean formation, called 'páramo', typically has the distinctive thick-stemmed Compositae genus Espeletia as a co-dominant with grasses. Páramo with Espeletia reaches south only to northernmost Ecuador. The intermediateprecipitation area, with formations called 'jalca' in northern Perú and páramo in Ecuador, is similar floristically to the northern Andean páramos except for a lack of the characteristically dominant Espeletia (Vuilleumier & Monasterio, 1986: Balslev & Luteyn, 1992; Luteyn et al., 1992; Luteyn, 1999). Patchy remnants of Andean forest may occur as ecological islands in the páramo, and are dominated by small slow-growing Polylepis reticulata, the only regional tree that can grow up to 4100 m. Stunted forest 10 m high known as the Ceja Andina is found below the páramo, occurring from 3800 to 3200 m. The forested Andean slopes ('ceja andina' in Ecuador, 'selva nublada' in Colombia, 'ceja de la montaña' in Peru) form a continuous band along the eastern Andean slopes. The Andean forest (cloud forest) occurs with local variations from 3200 to 2800 m. On the western slopes of the Andes, similar cloudforest formations occur south to central Ecuador, although their zonation is much less obvious in the super-saturated conditions of the Chocó region, where some cloud-forest features and elements extend down to sea level (Gentry, 1986). In southern Ecuador and northernmost Peru, inland from the Humboldt Current and thus drier, the cloud-forest band becomes more altitudinally restricted (Gentry, 1988).

The main vegetation types associated with the distribution of the various species of *Jivarus* are: the Colombian páramo type with *Espeletia* species, in the north; the herbaceous páramos, wet in the north, dry in the south; and the bush-like páramos, mainly in the south (Vuilleumier & Monasterio, 1986). *Maylasacris* and few species of *Jivarus* live in the open areas of Andean forest.

The Carbonelli species group (eight species) is distributed mainly in the Colombian páramos. Its known distribution (Pasto node and central Colombian cordillera, Fig. 9(1)) is isolated from the main distribution area of the Antisanae species group by the dry depression of the Rio Mir/Chota and the Hoya of Ibarra. However, the two groups are sympatric in the southern area of the Carbonelli distribution (in the páramo El Angel). Only one species of the group, *J. rectus*, inhabits the high-Andean montane forest.

The Antisanae species group (five species) is distributed along both the Oriental and Occidental cordilleras of Ecuador (Fig. 9(2)), mainly north of the Azuay node, where it is abundant in the páramo and subpáramo zones (van der Hammen & Cleef, 1986). The species are found mostly in grassland habitats resulting from the deforestation of high-altitude *Polylepis* forests (Laegaard, 1992; Kessler, 1995, 2002; Coblentz & Keating, 2008), or in open areas among *Polylepis* forests. Two species, *J. riveti* and *J. auriculus*, occur north of the Azuay node, in the páramos around the Hoya of Cuenca.

The Jagoi species group (six species), although apparently sympatric with the former group, actually is distributed north of the Azuay node and south of the Illiniza-Cotopaxi transverse axis (Fig. 9(3)). It seems to occupy a variety of habitats. The species are found mostly in montane forest areas, at lower elevations, on the eastern and western slopes of the Andes at the Hoya of Riobamba. Only one species, *J. ronderosi*, is found south of the last highest transverse axis.

The Americanus species group (five species) is characteristic of dry open grassland páramos around the Hoya of Cuenca, south of the Azuay node. *Jivarus spatulus* is the only known species of the group that has a northern distribution in sympatry with the Antisanae and Jagoi species groups (Fig. 9(4)).

The Pictifrons species group (two species) is the southernmost *Jivarus* species group. It is confined to the bushlike páramos biogeographic unit of southern Ecuador/northern Peru that constitutes the extreme end of the northern Andes (Fig. 9(4)). This group is isolated from all the former ones by a large low and dry Andean region.

The Cohni species group and *Maylasacris* are clearly characteristic of the south. The Cohni species group (three species) inhabits the highlands of southern Ecuador, associated with small bushes, around the Hoya of Cuenca (Fig. 9(5)). The genus *Maylasacris* (three species) is known only from the south oriental shrubby páramos south of the Azuay node. Apparently, its distribution is restricted to the western Andes by the dry valley of the Paute River (Fig. 9(3)).

## Discussion

Based on the phylogenetic analysis, *J. montanus* and the new species *digiticercus* and *rugosus* must be treated as a separate genus, *Maylasacris* gen.n. The remaining species included in the analysis constitute a clade that we assign to the genus *Jivarus* for which the following six species groups can be identified: *americanus* group, *antisanae* group, *carbonelli* group, *ecuadorica* group, *pictifrons* group and *jagoi* group. Although the diversity observed within the species groups of *Jivarus* could merit generic status, we await a phylogenetic analysis of the whole tribe before making a decision.

According to Chintauan-Marquier *et al.* (2010), the tribe Jivarini could represent the first group of South American Melanoplinae linked to the uplift of the Andes. In South America, the diversification of this subfamily probably followed the uplift of the Andes, as shown in recent molecular studies in which the splitting of the Melanoplinae clades is coincident with the timing of the Andean orogenesis (Amedegnato *et al.*, 2003; Chintauan-Marquier *et al.*, 2010).

Within the tribe, *Jivarus* is the most diversified genus. It is restricted mostly to the Andes of Ecuador and Colombia, with only two species in the Peruvian Andes. Species within *Jivarus* and *Maylasacris* have a low dispersion capacity owing to their lack of wings. The patterns of distribution of the clades depicted in the cladistic analysis coincide with the geography of the northern Andes of Colombia and Ecuador (Fig. 9). During the Andean Mountain uplift, the distribution of the biota may have been affected by geographic separation of the monophyletic groups, and by environmental changes that led to division of the groups (Vuilleumier & Simberloff, 1980). Palaeoecological studies indicate that Páramo habitats underwent

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repeated expansion and contraction in concert with glaciations of the late Pliocene and Pleistocene (Clapperton, 1993). Moulau (1988) and Jorgensen *et al.* (1995) suggested that dry valleys could have acted as barriers in warm interglacial periods and, by contrast, glaciers acted as barriers in the cold glacial periods. Furthermore, if we apply this view to a topographic map of the high Andes of Ecuador and Colombia combined with knowledge of the maximum extension of the Pleistocene glaciers, several possible barriers can be inferred. Distribution patterns in the páramos similar to those found here and congruent scenarios have been proposed for insects (Morrone, 1994a, b; Hines, 2008), vertebrates (Doan, 2003) and plants (Sklenar *et al.*, 1999; Quijano-Abril *et al.*, 2006; Alzate *et al.*, 2008).

The configurations of areas of endemism of the *Jivarus* species groups and *Maylasacris* are delimited by both the high-altitude curves, including transverse zones, and the drier climates of the intra-Andean valleys that clearly indicate a post-glacial recent palaeogeography, as shown in the vegetation distributional patterns (Jorgensen *et al.*, 1995). During the Last Glacial Maximum, areas above 3000/3500 m were occupied by large ice caps (Clapperton *et al.*, 1997; Smith *et al.*, 2005) and may have acted as geographical barriers.

The absence of *Jivarus* species on lower slopes (except for the Jagoi species group) indicates an exclusive highland recent origin of the genus, whose distribution corresponds with the Polylepis forests.

## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/j.1365-3113.2010.00538.x

**Table S1.** List of characters and states used in the phylogenetic analysis of *Jivarus*.

**Table S2.** Data matrix used in the phylogenetic analysis of *Jivarus*. Numbers of characters according to character list of S1. Missing values indicated as ?

**Table S3.** Links to images and maps based on latitude/ longitude specimen data, and species keys in Orthoptera Species File Online.

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# Acknowledgements

We are especially grateful to Professor Giovanni Onoré and the 'Pontifica Universidad Catolica' of Ecuador (PUCE). Thanks also go to Simon Poulain for his valuable collaboration during our field trips in Ecuador. We wish to thank Dr Luca Picciau and the Museo Regionale di Scienze Naturali de Torino for helping us to clarify the status of Giglio-Tos material. Field surveys in Ecuador were supported by the French Institute for Andean Studies (IFEA) and by the SOFT Program of the French Ministry of Environment. Field surveys in Peru were made with the help of SENASA. We especially thank David Eades (Illinois Natural History Survey, University of Illinois) for implementing the new feature in the Orthoptera Species File Online related to 'private' species files, which allowed us to include the many embedded links in this paper. Special thanks to Hernán Pereira, who helped to edit the embedded hyperlinks. We thank Nelida Caligaris, M. Estivariz and Bruno Pianzola for their valuable technical/professional assistance.

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Accepted 30 April 2010 First published online 4 August 2010

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