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Diversification patterns of the grasshopper genus *Zoniopoda* Stål (Romaleidae, Acridoidea, Orthoptera) in open vegetation biomes of South America

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Abstract. The open vegetation biomes, within the limits of the Chacoan subregion, occur along a diagonal in eastern South America covering a large range of environmental conditions. In order to contribute to the knowledge on the biodiversity of these open biomes, we analysed the phylogenetic relationships of the grasshopper genus *Zoniopoda* to the remaining South American Romaleinae, and examined the biogeographical patterns of diversification of the genus. The study is based on morphological and molecular (*COI* and *H3*) evidence, including 12 species of *Zoniopoda* and 17 species of four tribes of South American Romaleinae. We describe a new species of *Zoniopoda*, and test its taxonomic placement within the group. Results of our phylogenetic analyses recovered *Zoniopoda* as a monophyletic group with high support values. According to the dispersion–vicariance analysis, the ancestor of *Zoniopoda* may have been distributed in an area corresponding to the Chacoan and Cerrado provinces. A vicariant event, that could be explained by the uplift of the Brazilian Plateau and the subsidence of the Chaco, is hypothesized to have occurred splitting the ancestral distribution of *Zoniopoda*, resulting in the independent evolution of the Tarsata group within the Cerrado and the Iheringi group in the Chacoan subregion.

This published work has been registered in ZooBank, http://zoobank.org/urn:lsid:zoobank.org:act:FCFB4C5D-1741-46F1-8E25-B37ED2B9D872.

Introduction

The open vegetation biomes of South America, within the limits of the Chacoan subregion, occur along a diagonal in eastern South America that covers a large range of environmental conditions. Three tropical/subtropical biomes are within these limits: the Seasonally Dry Tropical Forests [SDTF, extending disjunctly from the Caatinga in northeastern Brazil to the Uruguay River valley, with three nuclei regions known as the 'Caatingas Nucleus', the 'Misiones Nucleus', and the 'Subandean Piedmont Nucleus' (Prado & Gibbs, 1993; Prado, 2000)], the Cerrado savanna (central Brazil) (Kier *et al.*, 2005; Mendonça *et al.*, 2008) and the Chaco (southwestern South America) (Pennington *et al.*, 2006; Werneck, 2011). These biomes characterized by vegetation adjusted to drought stress, constitute unique biotas defined by composite mosaic-type distributions (Werneck, 2011). The SDTF, Chaco and Cerrado are at present considered as natural units sharing close biogeographical affinities (Werneck, 2011). The Chaco and Cerrado are characterized by strong seasonality, although the Chaco has more severe summers and winter frosts (Prado, 1993a; Pennington *et al.*, 2000; Werneck, 2011). Endemism in these South American open biomes is high, mostly in vascular plants (Oliveira & Marquis,

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2002; Simon *et al.*, 2009; Prado *et al.*, 2012; Werneck *et al.*, 2012b), amphibians, reptiles (Silva & Bates, 2002; Nogueira *et al.*, 2011; Gamble *et al.*, 2012; Guarnizo *et al.*, 2016) and insects (Lanteri & del Río, 2006; Amorim *et al.*, 2009; Ramos & Melo, 2010; del Río *et al.*, 2015; Lanteri & del Río, 2016) including grasshopper species (Ronderos, 1976; Ronderos & Sánchez, 1983; Cigliano, 2007). Even though it is currently considered that the biodiversity of these biomes is rich, they have received little research attention compared to other biomes of South America and thus are still poorly characterized in terms of biological and genetic diversity (Sarmiento, 1975; Pennington *et al.*, 2006; Werneck, 2011; Werneck *et al.*, 2012a).

Zoniopoda Stål is among the grasshopper genera that characterize these open biomes, inhabiting grasslands and arbustive vegetation. It is largely represented in the Chaco and Cerrado, as well as in the SDTF 'Misiones Nucleus' (Carbonell, 2007; Pocco *et al.*, 2011). *Zoniopoda* belongs to the Neotropical Romaleinae (lubber grasshoppers) which, with more than 250 species included in 69 genera (Cigliano *et al.*, 2017), constitutes a group of large and colourful grasshoppers, highly diversified in South America. All known species of *Zoniopoda* (11 valid species) occur east of the Andes, mostly represented in the south-central Chacoan subregion (Chacoan and Parana dominions) (Morrone, 2014). *Zoniopoda* also reaches the south of the Brazilian subregion (South Brazilian dominion) and one species extends into the South American Transition Zone, in Argentina (Monte province).

The genus *Zoniopoda* was revised by Carbonell (2007) who recognized two groups of species (five within the Iheringi group and five in the Tarsata group) based on body colour patterns and characters of the dorsal median carina of the pronotum. Recently, Pocco *et al.* (2011) described a new species from Argentina, *Zoniopoda serrana* Pocco, Rubio & Cigliano, within the Iheringi group. The major species richness within the Tarsata group is found in the north of the distribution range of the genus, whereas in the Iheringi group the species richness is distributed homogeneously (Fig. 1). *Zoniopoda tarsata* (Serville) is the only species of the genus considered to have some economic importance as a pest (Lange *et al.*, 2005; Cigliano *et al.*, 2014; Carbonell *et al.*, 2016), and is the most abundant and widely distributed species of *Zoniopoda* reaching the southernmost distribution range of the genus. In Argentina, *Zoniopoda* is represented by six species, two belonging to the Tarsata group and the remaining four to the Iheringi group. During recent field trips to the hills of San Luis and Córdoba provinces, in central Argentina, we found a new species of Romaleinae. Although some characters did not totally fit within the variation of *Zoniopoda*, we tentatively assigned this species to the genus because some features of the external morphology and the general structure of the phallic complex are shared with other species belonging to this genus.

In order to contribute to the knowledge of the biological and genetic diversity of these open biomes of South America, we analyse the phylogenetic relationships of *Zoniopoda* to the remaining Romaleinae distributed in the region, and the biogeographical patterns of diversification of the whole genus. We also describe a new species of *Zoniopoda*, and test its taxonomic placement based on morphological and molecular evidence.

Material and methods

Studied material

Material examined originates from surveys conducted in central and northern Argentina, and from museum collections (MLPA, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; FCMU, Facultad de Ciencias de la República del Uruguay, Uruguay; and ANSP, The Academy of Natural Sciences of Drexel University, United States).

Specimens of the new species described herein were collected in Cerro El Amago, San Luis province and in La Cumbre, Córdoba province, Argentina. In both localities, specimens were found on top of the hills, between 1405 and 1743 m a.s.l. Specimens examined were deposited at MLPA.

Hind legs of specimens were stored in absolute ethanol for DNA analysis. Specimens and DNA extracts were kept as vouchers in the entomological collection at the MLPA.

Morphological studies

Terminology for external morphology and male genitalia follows Carbonell (2007) and Amédégnato (1976), respectively.

In order to study the male genitalia, dry specimens were relaxed in a humid chamber and abdomen terminalia moistened with ammonia. Genitalia were then removed from the body using a finely hooked pin, cleared in potassium hydroxide and stored in glycerine.

Measurements are given in millimeters. Body length was measured from the fastigium verticis to the apex of tegmina at rest (F–T) and to the end of the abdomen (F–A). Head and pronotum and tegmina were measured along the midline from the front to hind margin. Length of hind femur was measured from the dorso-proximal lobe to the distal extremity. The specimens measured correspond to the material designated as holotype, allotype and paratypes.

Photographs in natural habitat were captured with a Nikon D60 digital camera and of the male habitus with a Canon EOS Rebel 60D digital camera. Images of the distal segments of the abdomen and phallic complex were captured with a Micrometrics digital camera attached to the microscope. The program Combine Z5.3 (Hadley, 2006) was used for focus stacking.

Phylogenetic analyses

Morphological characters

Data matrix

The phylogenetic analysis was conducted on a matrix consisting of 31 species (12 species of *Zoniopoda* and 17 species of Romaleinae; two species of Ommexechidae were included and

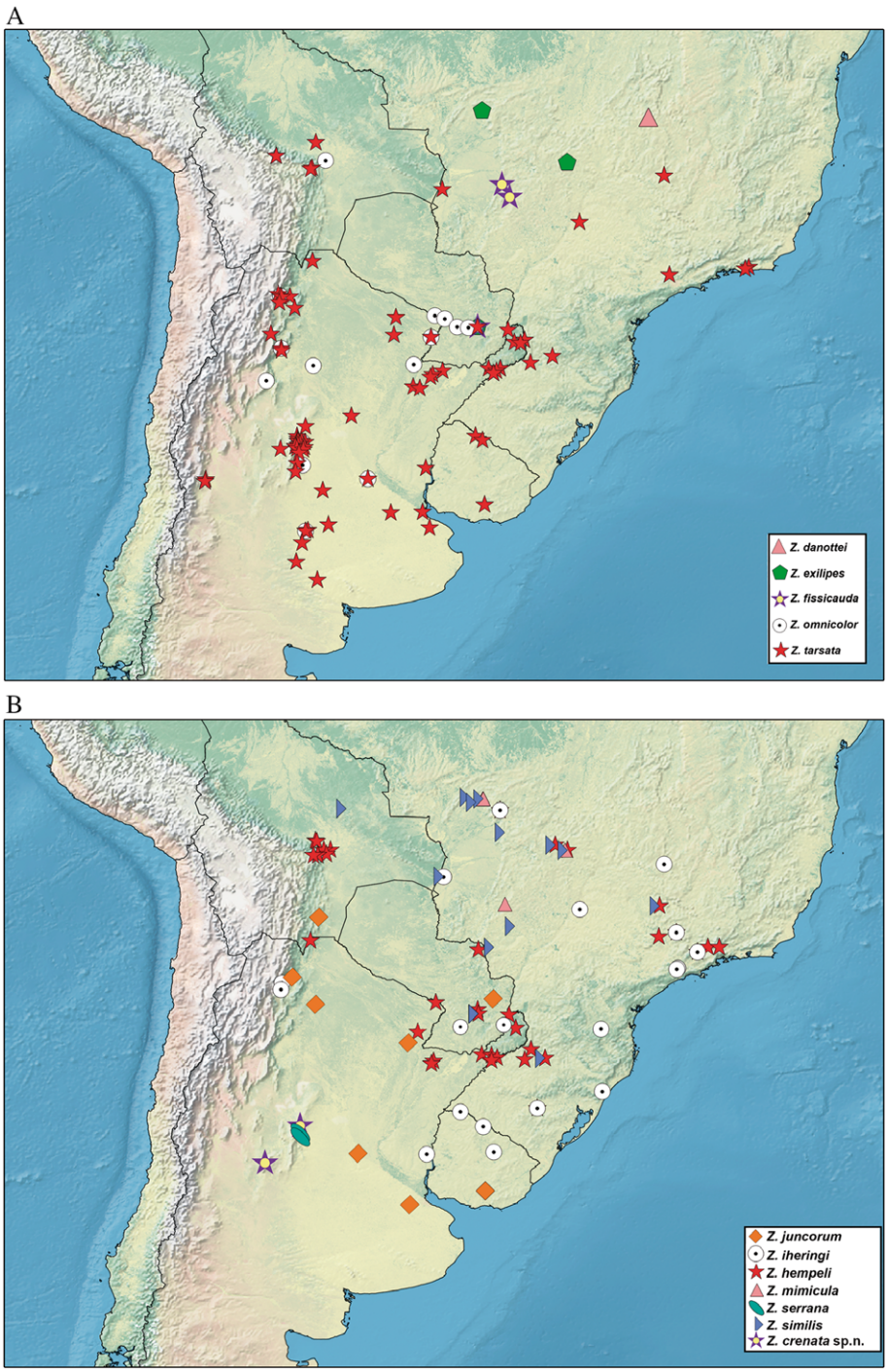

Fig. 1. Distribution records of *Zoniopoda* species. (A) Species of the Tarsata group. (B) Species of the Iheringi group and *Zoniopoda crenata* **sp.n.** [Colour figure can be viewed at wileyonlinelibrary.com].

selected as outgroups) and 43 morphological characters. All valid species of *Zoniopoda* were included in the analysis plus the new one described herein. The morphological matrix was constructed based on one published by Pocco *et al.* (2011), adding new characters and increasing the taxon sampling.

Morphological characters comprised structures from head and thorax (characters 0–18), male abdominal terminalia (characters 19–27) and internal genitalia (characters 28–32), as well as body colouration patterns (characters 33–42). Although colour in Romaleidae is known to be variable and is sometimes affected

Table 1. Morphological data matrix used in the phylogenetic analysis of *Zoniopoda*.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Ommexecha virens	0	0	2	1	4	2	3	0	0	0	–	0	0	0	0	0	2	2	0	0	0	1	0	0	0	–	–	4	1	3	1	–	–	0	3	0	0	–	0	0	6	0	0
O. macropterum	0	0	3	1	4	3	3	0	0	0	–	0	0	0	0	0	2	2	0	0	0	1	0	0	0	–	–	4	1	3	1	–	–	0	3	0	0	–	0	0	6	0	0
Z. tarsata	0	0	1	1	1	1	1	0	1	1	2	1	2	0	0	0	2	2	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	5	1	3	1	0	0	0	0	1	1
Z. omnicolor	0	0	1	1	1	1	1	0	1	1	2	1	2	0	1	0	1	2	1	1	0	1	2	1	1	0	0	1	1	1	1	1	2	5	6	3	1	1	0	1	0	1	1
Z. exilipes	0	0	1	1	1	1	1	0	1	1	2	1	2	0	0	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	1	1	2	5	2	3	1	1	0	1	0	1	1
Z. fissicauda	0	0	1	1	1	1	1	0	1	1	2	1	2	0	0	0	1	2	1	1	1	1	1	1	1	0	0	1	1	1	1	1	2	5	2	3	1	0	0	1	0	1	1
Z. danottei	0	0	1	1	1	1	1	0	1	1	2	1	2	0	0	0	2	2	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	5	1	3	1	0	0	0	0	1	1
Z. iheringi	0	0	1	1	1	1	1	0	1	1	2	1	2	4	0	1	2	2	1	1	1	1	3	1	1	0	1	1	1	1	1	1	2	1	3	3	0	–	0	0	2	0	0
Z. juncorum	0	0	1	1	1	1	1	0	1	1	2	1	2	3	0	0	2	2	1	1	1	1	4	1	1	0	1	1	1	1	1	1	0	1	3	3	0	–	0	0	1	0	0
Z. similis	0	0	1	1	1	1	1	0	1	1	2	1	2	2	0	0	2	2	1	1	1	1	3	1	1	1	1	1	1	1	1	1	2	2	1	3	0	–	0	0	1	0	0
Z. mimicula	0	0	1	1	1	1	1	0	1	1	2	1	2	2	1	0	2	2	1	1	1	1	3	1	1	0	1	1	1	1	1	1	0	1	3	3	0	–	0	0	1	0	0
Z. hempeli	0	0	1	1	1	1	1	0	1	1	2	1	2	3	0	1	2	2	1	1	1	1	4	1	1	0	0	1	1	1	1	1	3	1	3	3	0	–	0	2	2	0	0
Z. serrana	0	0	1	1	1	1	1	0	1	1	2	1	2	2	0	0	2	2	1	1	1	1	3	1	1	1	0	1	1	1	1	1	2	2	1	3	0	–	0	2	1	0	1
Z. sp.n.	0	0	1	2	3	1	1	0	1	1	2	1	2	4	0	1	2	2	1	1	1	1	5	1	0	1	1	2	1	1	1	1	3	1	3	3	0	–	0	2	2	0	0
Diponthus argentinus	0	0	0	0	1	1	0	1	1	1	2	0	1	0	1	0	2	3	0	0	0	0	–	0	2	2	0	3	0	0	0	2	–	3	0	2	1	0	2	–	3	0	1
D. pycnostictus	0	0	0	0	1	1	0	1	1	1	2	0	1	0	1	0	2	3	0	0	0	0	–	0	2	2	0	3	0	0	0	2	–	3	0	2	1	0	2	–	3	0	1
D. paraguayensis	0	0	0	0	1	1	0	1	1	1	2	0	0	0	1	0	2	3	0	0	0	0	–	0	2	2	0	3	0	0	0	2	–	3	0	2	1	0	1	–	3	0	1
D. puelchus	0	0	0	1	1	1	0	1	1	1	2	0	1	0	1	0	2	3	0	0	0	0	–	0	2	2	0	3	0	0	0	2	–	3	0	2	1	0	2	–	3	0	1
D. crassus	0	0	0	1	1	1	0	1	1	1	2	0	2	0	2	0	2	3	0	0	0	0	–	0	2	2	0	3	0	0	0	2	–	3	0	2	0	–	3	–	3	0	1
Chromacris speciosa	0	0	0	2	0	0	1	0	1	1	2	0	2	0	1	1	1	1	2	0	0	1	0	0	3	0	0	1	1	2	1	3	–	5	5	1	1	1	0	0	0	1	1
Coryacris angustipennis	1	0	2	0	2	1	2	0	1	1	0	0	2	0	0	0	2	1	2	0	1	0	–	0	1	0	0	4	1	1	2	0	–	4	4	0	0	–	0	0	4	0	0
Prionolopha serrata	1	2	1	2	2	1	0	0	1	1	1	1	2	5	0	2	2	4	1	0	0	1	0	0	0	0	0	4	1	1	1	4	–	0	7	0	0	–	4	–	4	0	0
Gurneyacris nigrofasciata	0	0	0	1	1	1	0	1	1	1	2	2	2	0	1	0	2	2	2	0	0	0	–	0	1	2	0	5	0	1	0	2	–	5	1	0	0	–	0	–	0	0	1
Xyleus laevipes	1	1	1	2	3	1	2	0	1	1	1	0	2	0	0	2	2	4	0	0	1	1	0	0	0	0	0	4	1	1	1	4	–	0	3	1	0	–	5	–	4	0	0
X. d. discoideus	1	1	1	2	3	1	2	0	1	1	1	2	2	0	0	2	2	4	0	0	0	1	0	0	0	0	0	4	1	1	1	4	–	0	3	1	0	–	5	–	4	0	0
X. modestus	1	1	1	2	3	1	2	0	1	1	1	2	2	0	0	2	2	4	0	0	1	1	0	0	0	0	0	4	1	1	1	4	–	0	3	1	0	–	5	–	4	0	0
X. insignis	1	1	1	2	3	1	2	0	1	1	1	2	2	0	0	2	2	4	0	0	1	1	0	0	0	0	0	4	1	1	1	4	–	0	3	1	0	–	5	–	4	0	0
Tropidacris collaris	0	0	0	1	1	0	0	0	1	1	0	2	3	0	0	2	0	0	2	1	1	1	0	0	1	0	–	0	1	1	2	0	–	0	3	1	0	–	0	0	4	0	0
Staleochlora v. viridicata	1	2	2	2	3	1	2	0	1	1	2	1	2	1	0	1	2	2	2	0	1	0	–	0	2	1	1	4	1	1	1	4	–	0	7	0	0	–	4	–	5	0	1
S. ronderosi	1	2	2	2	3	1	2	0	1	1	2	1	2	1	0	1	2	2	2	0	1	0	–	0	2	1	1	4	1	1	1	4	–	0	7	0	0	–	4	–	5	0	1
S. a. iguazuensis	1	2	2	2	3	1	2	0	1	1	2	1	2	1	0	1	2	2	2	0	0	0	–	0	2	1	1	4	1	1	1	4	–	0	7	0	0	–	4	–	5	0	1

by local environmental conditions, the body colour characters used in this analysis were invariable at the intraspecific level and appear to be heritable. The morphological characters and their states are listed in Appendix and are shown in Figs 3–6. The data matrix is presented in Table 1.

Cladistic analysis

Tree searches were conducted in TNT (Goloboff *et al.*, 2003) under the heuristic procedure which consisted of 'TBR branch swapping' applied to a series of 100 random addition sequences, retaining ten cladograms per replicate. All characters were considered to be of equal weight, and multistate characters were treated as unordered. Nonapplicable data were recorded as '–'. Support for individual nodes was assessed by calculation of absolute Bremer support (Bremer, 1994). Winclada (Nixon, 2002) was used to map the characters and plot the tree. The root was set as *Ommexecha virens* Serville (Ommexechidae).

Molecular characters

Specimens included in the phylogenetic analyses

Ten specimens of six *Zoniopoda* species, representing both species groups (Tarsata and Iheringi) were included in the molecular analyses. We also included 23 specimens of 15 species from seven Romaleinae genera. Information on the sequenced specimens is provided in Table 2. *Ommexecha virens* Serville (Ommexechidae) [GenBank accession number (AN) JX913775.1; Leavitt *et al.*, 2013] was also included and selected to root the trees.

DNA extraction and sequencing

Genomic DNA was extracted from legs preserved in ethanol using REDExtract-Amp Tissue PCR Kit. We amplified one mitochondrial fragment of the *COI* gene (Cytochrome C Oxidase subunit I) and one nuclear fragment of the *H3* gene (Histone) using a standard PCR protocol. Primers for the amplification of both segments were obtained from Husemann *et al.* (2013).

PCR amplifications were carried out in 50-μL reaction volumes containing 33 μL H_2O, 5 μL of 10× buffer (reaction concentration 1×), 3 μL of Cl_2Mg, 5 μL of dNTP mixture (0.25 μM each), 1 μL of Invitrogen DNA Polymerase, 1 μL of each primer (0.5 μM) and 1 μL of DNA template. Amplification conditions were as follows: 94°C for 3 min, followed by 30 cycles of 94°C for 1 min, 48–57°C for 1 min (COI-H3 respectively) and 72°C for 2 min, with a final step at 72°C for 10 min.

PCR products were purified using EXO-FASAP enzymes under conditions specified by the manufacturer (Thermo-Fisher) and were sequenced at the 'Unidad de Secuenciación y Genotipificado' (FCEyN, UBA, Buenos Aires, Argentina). Sequences were deposited at GenBank (Table 2), and inspected, trimmed

Table 2. List of specimens analysed including ID, species name, geographical location and GenBank accession numbers for each gene.

Specimen ID		Species name	Geographical coordinates	Location	Accession number	
					COI	*H3*
MLP-OR4285	*Zoniopoda*	*tarsata*	25°41′31.71″S 54°28′39.09″W	Misiones (PN Iguazú), Argentina	MF682224	MF682210
MLP-OR3661	*Zoniopoda*	*tarsata*	31°00′5.25″S 64°26′24.04″W	Córdoba (7 km La Cumbre), Argentina	MF682225	MF682195
MLP-OR3662	*Zoniopoda*	*omnicolor*	32°09′54.7″S 64°45′28.6″W	Córdoba (El Durazno), Argentina	MF682226	MF682211
MLP-OR3663	*Zoniopoda*	*omnicolor*	32°21′43.45″S 64°56′56.85″W	San Luis (Merlo, Mirador del Sol), Argentina	MF682227	MF682198
MLP-OR3664	*Zoniopoda*	*hempeli*	25°40′45.20″S 54°26′57.20″W	Misiones (PN Iguazú), Argentina	MF682228	MF682203
MLP-OR3665	*Zoniopoda*	*serrana*	31°00′5.25″S 64°26′24.04″W	Córdoba (9 km La Cumbre), Argentina	MF682229	–
MLP-OR3666	*Zoniopoda*	*serrana*	31°00′5.25″S 64°26′24.04″W	Córdoba (9 km La Cumbre), Argentina	MF682230	MF682197
MLP-OR3667	*Zoniopoda*	*iheringi*	25°41′31.71″S 54°28′39.09″W	Misiones (PN Iguazú), Argentina	MF682231	–
MLP-OR3668	*Zoniopoda*	*iheringi*	25°41′31.71″S 54°28′39.09″W	Misiones (PN Iguazú), Argentina	MF682232	MF682199
MLP-OR3669	*Zoniopoda*	*crenata sp.n.*	31°00′5.25″S 64°26′24.04″W	Córdoba (9 km La Cumbre), Argentina	MF682233	MF682212
MLP-OR4301	*Prionolopha*	*serrata*	25°40′38.76″S 54°26′57.82″W	Misiones (PN Iguazú), Argentina	MF682223	MF682204
MLP-OR3670	*Xyleus*	*laevipes*	31°00′31.2″S 64°26′11.0″W	Córdoba (7 km La Cumbre to Candonga), Argentina	MF682234	MF682196
MLP-OR3671	*Xyleus*	*modestus*	25°33′57″S 59°16′52″W	Formosa (1 km Palo Santo), Argentina	MF682245	MF682194
MLP-OR3597	*Xyleus*	*modestus*	24°37′05.2″S 60°31′03.55″W	Formosa (RP28, 12 km Las Lomitas), Argentina	MF682251	MF682220
MLP-OR3622	*Xyleus*	*modestus*	30°17′45.5″S 61°13′57.4″W	Santa Fe (San Cristobal), Argentina	MF682247	MF682221
MLP-OR3672	*Xyleus*	*modestus*	32°1′04.7″S 65°02′19.7″W	Córdoba (RP14, 30 km La Paz), Argentina	MF682250	MF682193
MLP-OR3673	*Xyleus*	*discoideus discoideus*	25°40′45.20″S 54°26′57.20″W	Misiones (PN Iguazú), Argentina	MF682246	MF682201
MLP-OR3601	*Xyleus*	*insignis*	24°43′54.24″S 60°33′5.28″W	Formosa (5 km Las Lomitas), Argentina	MF682248	MF682216
MLP-OR3674	*Xyleus*	*insignis*	32°08′36.9″S 65°03′34.3″W	Córdoba (Luyaba), Argentina	MF682249	MF682192
MLP-OR3675	*Staleochlora*	*viridicata viridicata*	30°59′58.8″S 64°26′33.2″W	Córdoba (8 km La Cumbre to Agua de Oro), Argentina	MF682235	MF682213
MLP-OR3528	*Staleochlora*	*viridicata viridicata*	33°01′11.3″S 59°27′51.2″W	Entre Ríos (R11, 18 km NW Gualeguay), Argentina	MF682237	MF682217
MLP-OR3595	*Staleochlora*	*ronderosi*	24°37′05.2″S 60°31′03.55″W	Formosa (RP28, 12 km Las Lomitas), Argentina	MF682236	MF682219
MLP-OR3676	*Diponthus*	*pycnostictus*	30°59′58.8″S 64°26′33.2″W	Córdoba (8 km La Cumbre to Agua de Oro), Argentina	MF682238	MF682215
MLP-OR3677	*Diponthus*	*puelchus*	30°47′19.5″S 64°28′29.0″W	Córdoba (Los Terrones), Argentina	MF682239	MF682209
MLP-OR3678	*Diponthus*	*paraguayensis*	27°46′50.3″S 55°06′49.4″W	Misiones (RP2, San Javier), Argentina	MF682240	MF682214
MLP-OR3679	*Diponthus*	*crassus*	27°10′03.8″S 53°59′36.1″W	Misiones (R. Yaboti, 8 km Saltos de Moconá), Argentina	MF682241	MF682207
MLP-OR3680	*Diponthus*	*argentinus*	31°00′5.25″S 64°26′24.04″W	Córdoba (9 km La Cumbre), Argentina	MF682242	MF682202
MLP-OR3681	*Chromacris*	*speciosa*	25°42′3.34″S 54°20′46.58″W	Misiones (PN Iguazú), Argentina	MF682243	MF682200
MLP-OR3596	*Chromacris*	*speciosa*	24°37′05.2″S 60°31′03.55″W	Formosa (RP28, 12 km Las Lomitas), Argentina	MF682244	MF682218
MLP-OR3682	*Coryacris*	*angustipennis*	30°12′51.52″S 61°44′26.74″W	Santa Fe (Arrufo), Argentina	–	MF682208
MLP-OR3648	*Coryacris*	*angustipennis*	24°37′05.2″S 60°31′03.55″W	Formosa (RP28, 12 km Las Lomitas), Argentina	–	MF682222
MLP-OR3683	*Tropidacris*	*collaris*	25°42′13.29″S 59° 2′4.34″W	Formosa (Pirané), Argentina	–	MF682205
MLP-OR3606	*Tropidacris*	*collaris*	24°19′22.1″S 60°16′37.1″W	Formosa (RP28, 15 km Bañado La Estrella), Argentina	–	MF682206

and aligned using Geneious 7.0.6 (http://www.geneious.com, Kearse *et al.*, 2012).

In order to avoid the possibility of amplification of *COI* pseudogenes (Bensansson *et al.*, 2000), sequences were translated according to the invertebrate mitochondrial genetic code and examined, using as reference amino acid sequences obtained for several insect orders (Lunt *et al.*, 1996). A copy was assumed to be mitochondrial if it contained no frameshifts or stop codons (Sorenson & Fleischer, 1996; Zhang & Hewitt, 1996).

Phylogenetic analysis of molecular characters

Phylogenetic analyses of molecular characters were performed employing Bayesian analyses (BA) with the program BEAST 2.4.7 (Bouckaert *et al.*, 2014); a Markov chain Monte Carlo (MCMC) simulation was run for 10 million generations, sampling trees every 1000 generations. Both partitions were treated as unlinked for substitution models but as linked for clock models and trees. JModelTest (Posada, 2008) was used to infer the most appropriate model of molecular evolution for each molecular dataset based on the Akaike information criterion (AIC) (Akaike, 1973). The HKY model of sequence evolution was used for both *COI* and *H3* data partitions (HKY; Hasegawa *et al.*, 1985). Rates for both partitions were assumed to vary across sites according to a gamma distribution (G; Yang, 1994). TRACER v1.6 was used to evaluate correct 'mixing' of chains (ESS > 200). TREEANNOTATOR v1.7.5 (Drummond *et al.*, 2012) was used to choose the maximum clade credibility tree with the 'mean node heights' option from the output trees.

Phylogenetic analysis based on combined characters and divergence time estimation

Bayesian analyses of combined partitions (*COI*, *H3* and morphological characters) and divergence time estimation was performed with BEAST 2.4.7 (Bouckaert *et al.*, 2014). All partitions were treated as unlinked for substitution models but as linked for clock models and trees. Models of sequence evolution for molecular partitions are mentioned above; the model of morphological evolution was 'MK Lewis' (Lewis, 2001) as implemented in BEAST v.2.4.7 (Bouckaert *et al.*, 2014). The divergence time of Ommexechidae and Romaleidae (76,74 Ma; 95% HPD: 95–57 Ma) was used as calibration point [time to the Most Recent Common Ancestor (MRCA)]. This node age was inferred by Song *et al.* (2015), who calibrated the phylogeny of Orthoptera using nine fossil calibration points to scale the entire chronogram. We used Calibrated Yule process as a tree prior and logNormal distribution as a distribution prior for the time to MRCA. We placed monophyly constraints on this single node and applied age constraints as priors. We applied a strict molecular clock. The result of the analysis based on combined characters is shown in Fig. 2.

Biogeographical analysis

Information on specimen records (latitude and longitude) was downloaded from the database OSF (Cigliano *et al.*, 2017). For the analysis, a total of 852 specimen records were considered. Geographical distribution of species was mapped with the software QGIS 2.4 Chugiak, using the shapefile of the Neotropical Region provided by Löwenberg-Neto (2014) based on the biogeographical regionalization proposed by Morrone (2014). Dispersal–vicariance analysis (DIVA; Ronquist, 1997) was performed to evaluate different possible biogeographical scenarios explaining the distribution of *Zoniopoda* species in southern South America. As area units we used the biogeographical regionalization of provinces of the Neotropical Region following Morrone (2014): Atlantic (A), Cerrado (B), Chacoan (C), Guajira (D), Caatinga (E), Monte (F), Pampean (G); Parana Forest (H), Rondonia (I), Roraima (J), Venezuelan (K), Xingu-Tapajós (L), Yungas (M), *Araucaria* Forest (N), Guianan Lowlands (O).

The taxon area cladogram, with each terminal taxon replaced by the area/s it inhabits, was analysed using the program RASP (Reconstruct Ancestral State in Phylogenies) v2.0 Beta (Yu *et al.*, 2011), a tool for inferring ancestral state using Bayesian, Parsimony or SDIVA methods. RASP complements DIVA v1.2 (Ronquist, 1996) which applies an exact search according to the dispersal–vicariance optimization as proposed by Ronquist (1997).

The tree based on morphological evidence, where all the species of *Zoniopoda* are represented, was used in the DIVA analysis. We used a simplified topology and collapsed the nodes so that only one terminal taxon per genus was included, except for *Zoniopoda*.

Results

Cladistic analysis of Zoniopoda based on morphological characters

Parsimony analysis under equal weights of the morphological data matrix (Table 1) resulted in one most parsimonious tree (L, 161; CI, 0.68; RI, 0.86), (Figure S1).

Analysis recovered *Zoniopoda* as a monophyletic group with moderate support value, based on the following characters: hind femora thin (18-1) (Fig. 3D); subgenital plate bifurcated (19-1); male epiproct with median band light-coloured (23-1); colour pattern of hindwings (35-3). The last two characters were recovered as synapomorphies for the genus (Figure S1).

Two major groups were recovered within *Zoniopoda*. One of them comprised the species of the Tarsata group, based on the hind femora with transverse bands (36-1) (Fig. 3G) and presence of colour rings in hind tibiae (41-1) (Fig. 3H), with *Z. tarsata* and *Z. danottei* Carbonell as sister species and *Z. fissicauda* Bruner sister to the clade *Z. exilipes* Bruner and *Z. omnicolor* (Blanchard). The other clade comprised the species of the Iheringi group, including the new species, *Zoniopoda* **sp.n.**, based on the following synapomorphies: median dorsal carina of pronotum slightly granulate (13-2); hind tibiae bicolour with red tips (33-2) (Fig. 3D); integument of thorax rugose

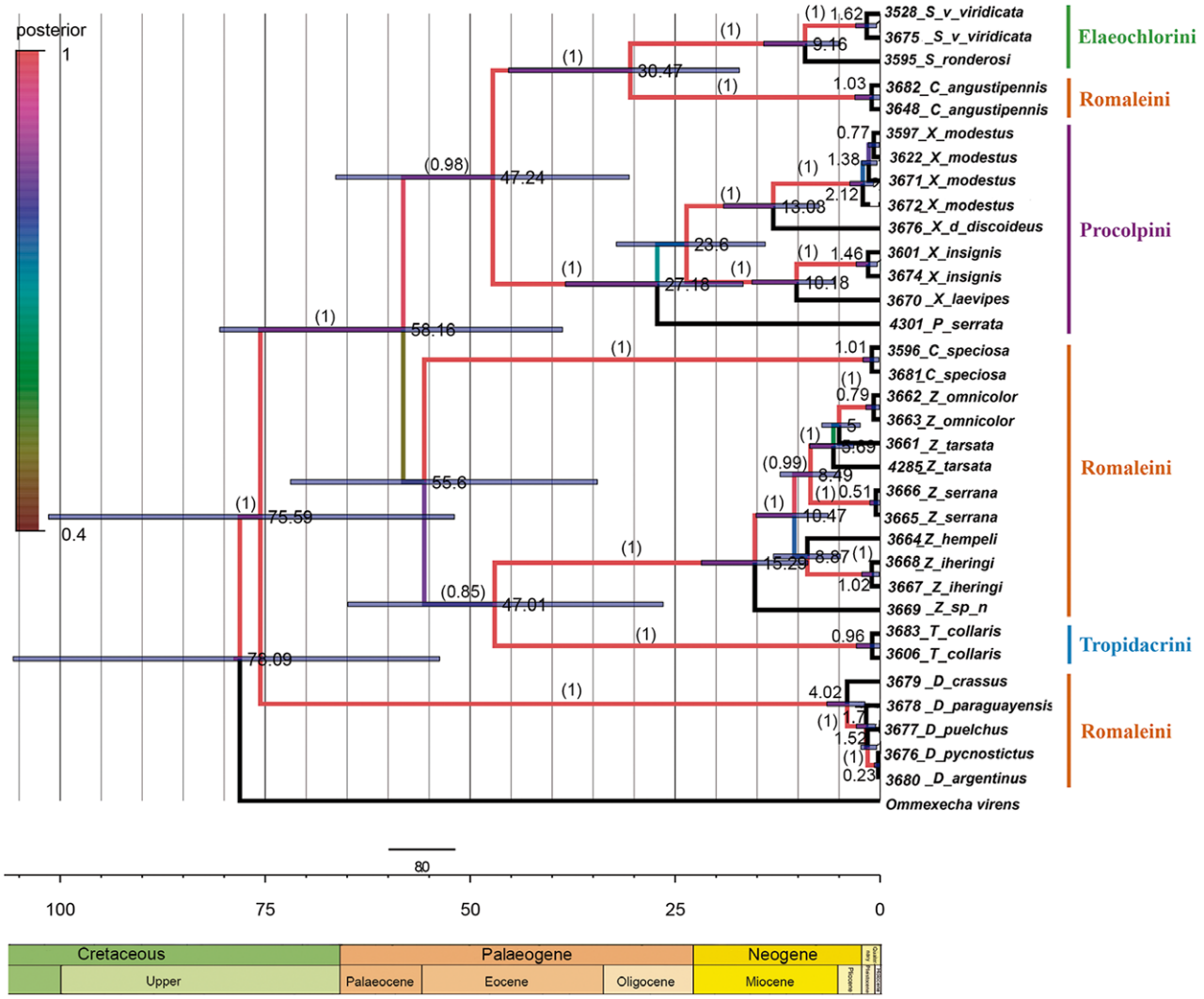

Fig. 2. Tree topology obtained from the Bayesian analysis of the total evidence dataset (*COI*, *H3* and morphology). Numbers on branches indicate node ages. Numbers between brackets correspond to PP values (>0.80). Acronyms of specimens according to Table 2. Node bars indicate 95% high confidence interval for node ages. [Colour figure can be viewed at wileyonlinelibrary.com].

(40-1); and by the parallelism subgenital plate elongate (20-1) (Fig. 5C). *Zoniopoda serrana* was recovered as the sister species to the remaining species of the Iheringi group. *Zoniopoda similis* Bruner was recovered as sister group to two clades, one of them constituted by the sister taxa *Z. mimicula* Rehn and *Z. juncorum* Berg, and the other one consisted of *Z. iheringi* Pictet & Saussure and the sister taxa *Z. hempeli* Bruner and *Zoniopoda* **sp.n.** The new species is characterized by several parallelisms (3-2, fastigium as long as the interocular distance, Fig. 4B; 4-3, fastigium apex angulate, Fig. 4B; 24-0, male epiproct and furculae uniformly light-coloured, Fig. 5I; 25-1, male furculae well-developed, Fig. 5I) and the autapomorphy male cerci with flattened distal portion (27-2) (Fig. 5C). It shares with *Z. hempeli* characters from male internal genitalia (lophi of epiphallus, 32-3) (Fig. 6G) and colour of tegminae veins (39-2) (Fig. 3D) and these two species share with *Z. iheringi* characters from median dorsal carina of pronotum (13-4, 15-1) and thorax integument (40-2).

The genus *Zoniopoda* was recovered as sister to the group *Chromacris speciosa* (Thunberg) (*Diponthus* Stål, *Gurneyacris nigrofasciata* Liebermann), based on five synapomorphies from head, male cerci, integument and colour patterns (6-1, 27-1, 33-5, 34-1, 40-0) and one parallelism (42-1).

The analysis recovered the tribes Elaeochlorini (represented by the genus *Staleochlora* Roberts & Carbonell) and Procolpini (*Xyleus* Gistel and *Prionolopha* Stål) as sister groups. The tribe Romaleini was not recovered because *Tropidacris collaris* (Stoll) (Tropidacrini) formed a clade with the Romaleini *Coryacris angustipennis* (Bruner). All the genera of Romaleinae were grouped based on seven synapomorphies from head (6-2, 8-1), thorax (9-1, 11-1, 12-2), endophallus (29-1) and integument (40-4).

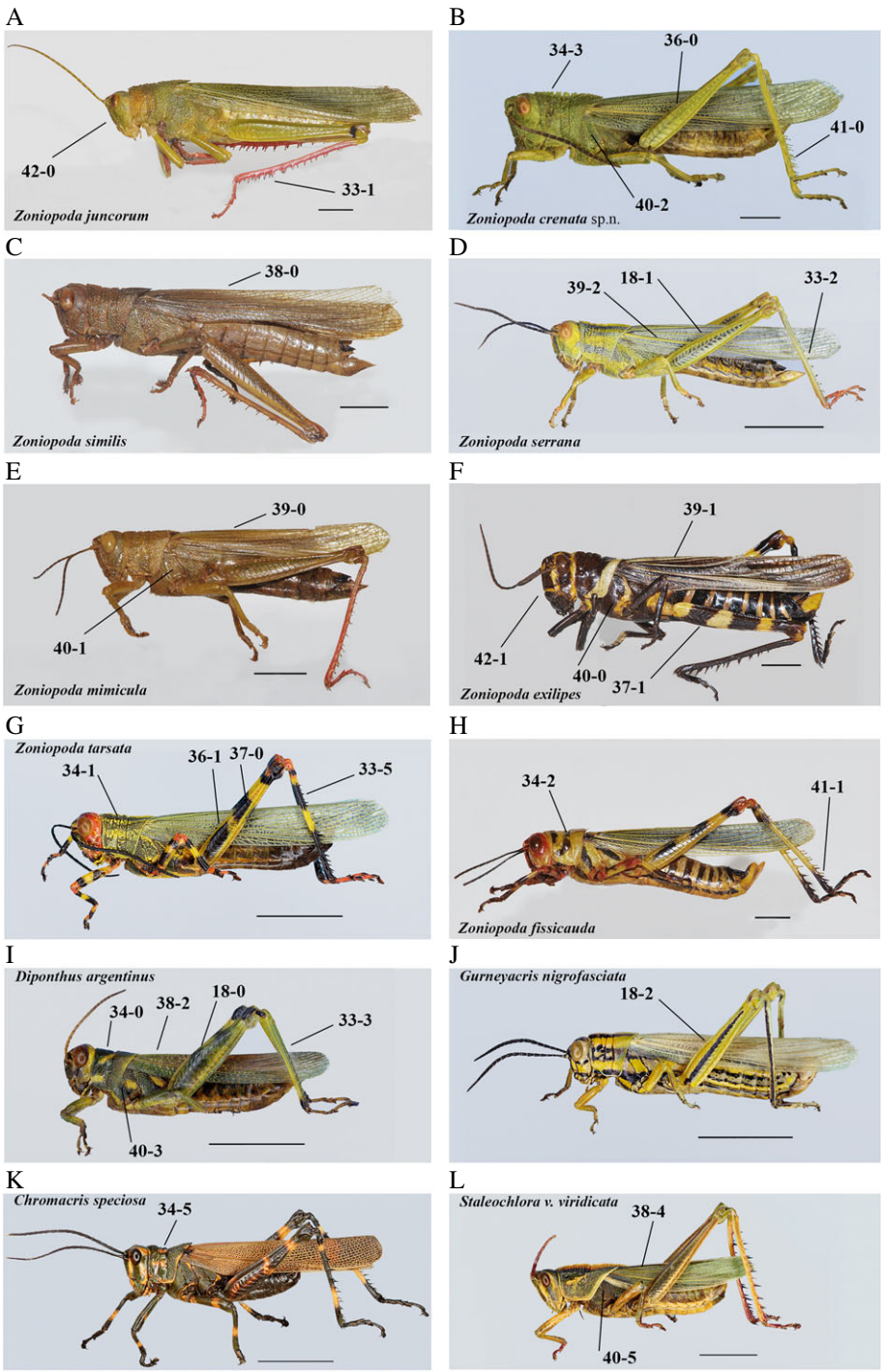

Fig. 3. (A–L) Habitus, males, lateral view. Numbers indicate characters and states used in the cladistics analysis, species as indicated. Scale bars: 5 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

Phylogenetic analyses based on molecular characters

The resulting alignments for *COI* and *H3* sequences consisted of 643 and 298 bp, respectively. Table 2 displays the number of sequenced individuals for each taxon and gene fragment and the corresponding GenBank accession numbers. The Bayesian analyses recovered *Zoniopoda* as a monophyletic group with the maximum posterior probability (PP) values, including *Zoniopoda* **sp.n.** that is the first diverging lineage within the genus *Zoniopoda* (Figure S2). Individuals of

Z. tarsata are not clustered together, because one of the specimens joins to the specimens of *Z. omnicolor* and the other one remains as the sister to the remaining species of *Zoniopoda*, except for *Zoniopoda* **sp.n.** (Figure S2). *Zoniopoda* resolved as sister to *Tropidacris* Scudder, and they constitute the sister clade to *Chromacris* Walker. This clade is sister to the other major clade of the tree that was constituted by the clade *Coryacris angustipennis* – *Staleochlora* as sister to the clade constituted by the well-supported group including the representatives of Procolpini [*Prionolopha serrata* (Linnaeus) and *Xyleus* species]. *Diponthus* is the sister genus to this major group.

Most of the genera included in the analysis are recovered with high support, except for *Prionolopha* that is clustered within *Xyleus* clade.

Phylogenetic analysis based on combined dataset and divergence time

Bayesian analyses of combined partitions recovered *Zoniopoda* as a monophyletic clade with maximum support values, and *Zoniopoda* **sp.n.** as the first diverging lineage within the genus *Zoniopoda* (Fig. 2). The topology of the tree is highly congruent with that one based only on molecular evidence, except that in this hypothesis all the genera are recovered (including *Prionolopha* as sister to *Xyleus*) and with higher values of support.

Our molecular clock analysis suggested the split between *Ommexecha* Serville and the romaleinae genera occurred around 75 Ma. The diversification time between *Zoniopoda* and *Tropidacris* was estimated to be at *c*. 47.01 Ma and the diversification of *Zoniopoda* at around 15.29 Ma (Fig. 2).

Biogeography

The DIVA (Fig. 7) performed on the morphological tree, where all *Zoniopoda* species are represented, yielded a single possible ancestral distribution reconstruction for all ancestral nodes of *Zoniopoda*. The common ancestor of *Zoniopoda* (node 32) may have been distributed in the area represented by the Cerrado and Chacoan provinces (BC). A vicariant event is suggested to have occurred, separating the Cerrado province (B), where the lineage of the Tarsata species group (node 25) would have diversified, and the Chacoan province (C) in which the diversification of the Iheringi group would have occurred (node 31). In both species groups, the widest terminal distributions correspond to recent dispersal events of the terminal taxa.

According to DIVA analysis, the common ancestor of *Zoniopoda* and its sister group (*Chromacris* (*Gurneyacris*, *Diponthus*)) (node 35), may have been distributed in the Chacoan province. A dispersal event to Cerrado may have taken place in the lineage *Zoniopoda* previous to the vicariant event mentioned above (node 32).

The ancestral area for the Romaleinae represented in this study appeared to be the Chacoan province (node 40).

Taxonomy

Genus *Zoniopoda* Stål, 1873

Type species. Acridium tarsatum Serville, 1831

Zoniopoda crenata sp.n. Pocco, Lange & Cigliano

ZooBank LSID: http://zoobank.org/urn:lsid:zoobank.org:act:FCFB4C5D-1741-46F1-8E25-B37ED2B9D872
OSF LSID: http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:498125

Diagnosis. Fastigium prominent, triangular-shaped in dorsal view (Fig. 4B). Dorsal median carina of pronotum high, strongly crenulated in lateral view, cut by deep transverse sulci (Fig. 4F). Pronotal front margin projected over occiput (Fig. 4B). Male furculae well-developed, sub-triangular, placed close together; epiproct sub-rectangular with slightly oblique distal margins (Fig. 5I); male cerci long, surpassing the end of epiproct with a constriction before distal third; distal portion flattened and slightly down-curved (Fig. 5C, I); subgenital plate long and apically bifurcated, with up-curved and rounded apices (Fig. 5I). Epiphallus with prominent sub-triangular lophi (in frontal view) (Fig. 6G), placed perpendicular to the bridge; lateral plates with prominent anterior processes (dorsal view). Body uniformly light green; tegminae light green with yellow veins (Figs 3B, 8B).

Description. Integument rugose, tuberculate on pronotum, smooth on top of head and postocular area (Fig. 4B, F). Head and pronotum elevated. Fastigium prominent, triangular-shaped in dorsal view (Fig. 4B). Interocular distance wide (Fig. 4B). Dorsal median carina of pronotum high, strongly crenulated in lateral view, cut by three deep transverse sulci (Fig. 4F). Pronotal front margin projected over occiput (Fig. 4B). Male abdominal terminalia with furculae well-developed, sub-triangular, placed close together; epiproct sub-rectangular with oblique distal margins (Fig. 5I); male cerci long, surpassing the end of epiproct with a constriction before distal third; distal portion flattened and slightly down-curved (Fig. 5C, I); subgenital plate long and apically bifurcated, with up-curved and rounded apices (Fig. 5I). Male phallic complex (Fig. 6A, B, G) as in the remaining species of *Zoniopoda*, differing in the shape of epiphallus. Epiphallus with prominent sub-triangular lophi (in frontal view) (Fig. 6G), placed perpendicular to the bridge; lateral plates with prominent anterior processes (dorsal view).

Body colour: uniformly light green (Fig. 3B). Antennae brown with green scape; each antennal segment with light green distal end, in living specimens (Fig. 8B). Tegminae light green with yellow veins, especially the radius (Fig. 3B). Hindwings light blue.

Males. Terminalia: subgenital plate, furculae and cerci green; epiproct green with a median cream-coloured band (Fig. 5I).

Females (Fig. 8B). Similar to males, but more robust. Ovipositor valves of soil-laying type, green coloured, with the tips brown.

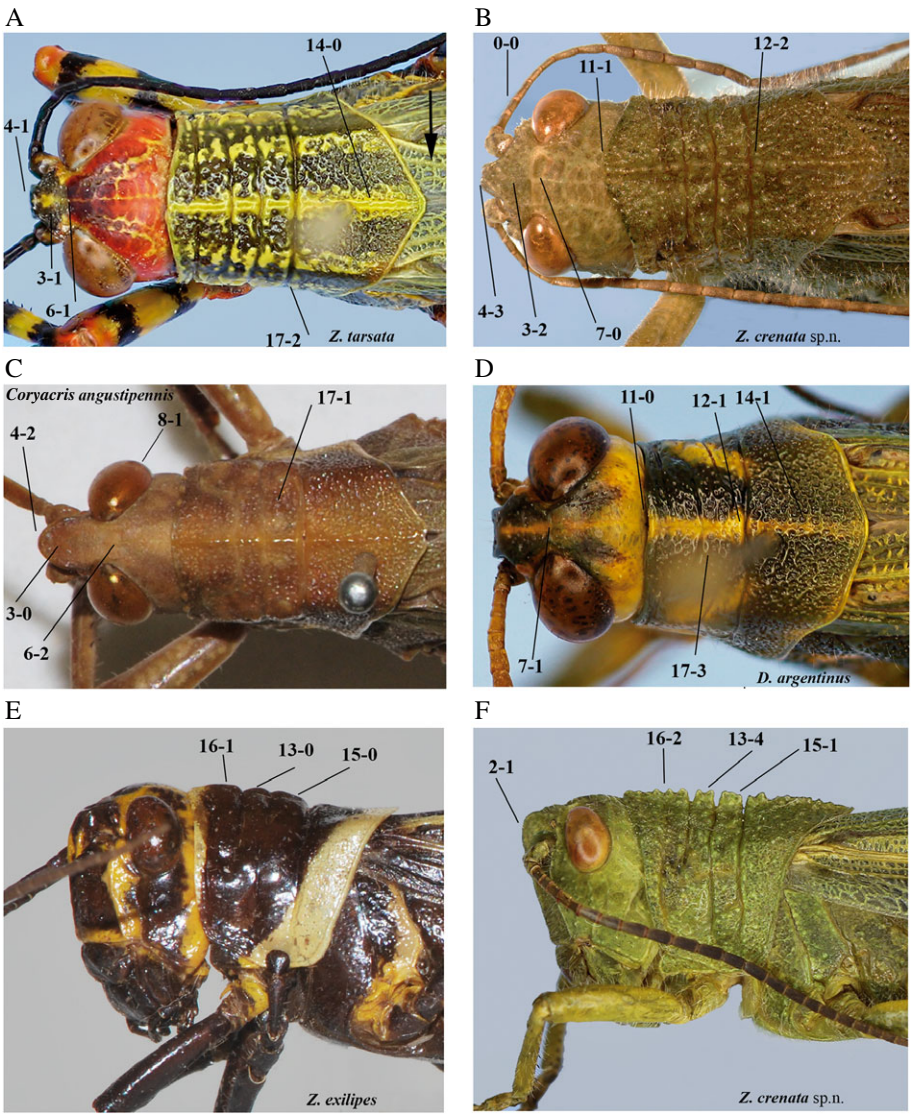

Fig. 4. Head and pronotum. (A–D) Dorsal view; (E, F) lateral view. Numbers indicate characters and states used in the cladistics analysis. Species as indicated. [Colour figure can be viewed at wileyonlinelibrary.com].

Measurements (in mm). Body length: F–T: males 41 (40–42), females 56.5 (56–57); F–A: males 35.5 (35–36), females 49.5 (49–50); hind femur: males 17, females 23.7 (23.5–24); head + pronotum: males 12, females 18.5; pronotum: males 8.2 (8–8.5), females 13.2 (13–13.5); tegmina: males 30 (29–31); females 41.5 (41–42).

Etymology. The name refers to the crenulated median carina of pronotum; *crena* (Latin): notch, rounded projection.

Type material. Holotype ♂, ARGENTINA, Córdoba, La Cumbre, 9 km La Cumbre, 31°00′5.25″S, 64°26′24.04″W, 1405 m a.s.l., 21.ii.2014, Cigliano & Lange, MLPA; *allotype* ♀, ARGENTINA, San Luis, Cerro El Amago, between La Carolina and San Francisco, 32°46′14.04″S, 66°06′26.4″W, 1743 m a.s.l., 14.iii.2012, Pocco & Plischuk, MLPA. *Paratypes*: 1 ♂, ARGENTINA, Córdoba, La Cumbre, 9 km La Cumbre, 31°00′5.25″S, 64°26′24.04″W, 1405 m a.s.l., 21.ii.2014, Cigliano & Lange, MLPA; 1 ♀, ARGENTINA, San Luis, Cerro El Amago, between La Carolina and San Francisco, 32°46′14.04″S, 66°06′26.4″W, 1743 m a.s.l., 14.iii.2012, Pocco & Plischuk, MLPA.

Relationships. Based on characters from median dorsal carina of pronotum, colour pattern of hind tibiae, integument of thorax, and male subgenital plate, *Zoniopoda crenata* is included in the Iheringi species group, that was shown to be monophyletic in the morphological hypothesis presented herein (Figure S1). The most closely related species, in the morphological tree (Figure S1), is *Z. hempeli*, based on characters from

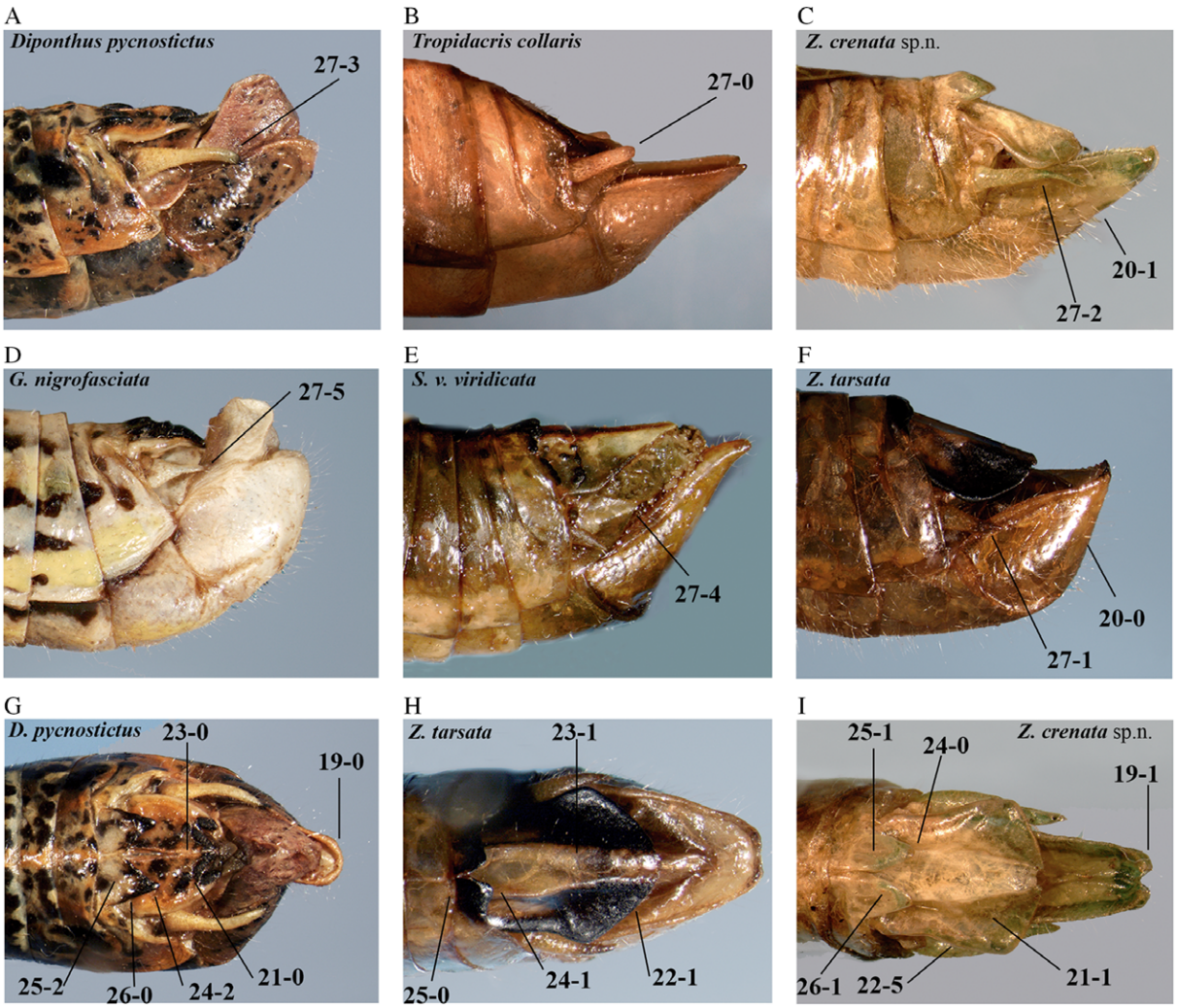

Fig. 5. Male abdominal terminalia. (A–F) Lateral view; (G–I), dorsal view. Numbers indicate characters and states used in the cladistics analysis. Species as indicated. [Colour figure can be viewed at wileyonlinelibrary.com].

male internal genitalia (lophi of epiphallus) and colour of tegminae veins. Both species are related to *Z. iheringi* by characters from median dorsal carina of pronotum and integument.

It can be distinguished from the remaining *Zoniopoda* species by the strongly crenulated median dorsal carina of pronotum, the acute apex and more prominent fastigium, the male cerci long, with a flattened and slightly down-curved distal portion, the light-coloured male epiproct and furculae and by the body uniformly light green coloured, including the hind tibiae.

Distribution and habitat. The species is known from Cerro El Amago, between San Francisco and La Carolina, San Luis Province, Argentina (Fig. 8C), and from La Cumbre, Córdoba province, Argentina (Fig. 8D), where individuals were found between 1400 and 1743 m a.s.l.. The vegetation consisted of tall grasses and herbaceous dicots.

Comments: nomenclatural change

Chariacris basalis (Bruner) **n.comb.**

Zoniopoda basalis Bruner, 1913; Carbonell, 2007; Cigliano *et al.*, 2017.

OSF LSID: http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:498126

Zoniopoda basalis was described by Bruner (1913) based on only one female from Santa Cruz de La Sierra, Bolivia. In the revision of the genus *Zoniopoda*, Carbonell (2007) proposed that this species belongs to the Romaleinae genus *Chariacris* Walker 1870. However, he did not establish the new combination. We agree with his taxonomic decision, and therefore we establish the new combination *Chariacris basalis* (Bruner).

Images of the holotype female of *Chariacris basalis* (Bruner) are available in the Orthoptera Species File, OSF (http://orthoptera.speciesfile.org).

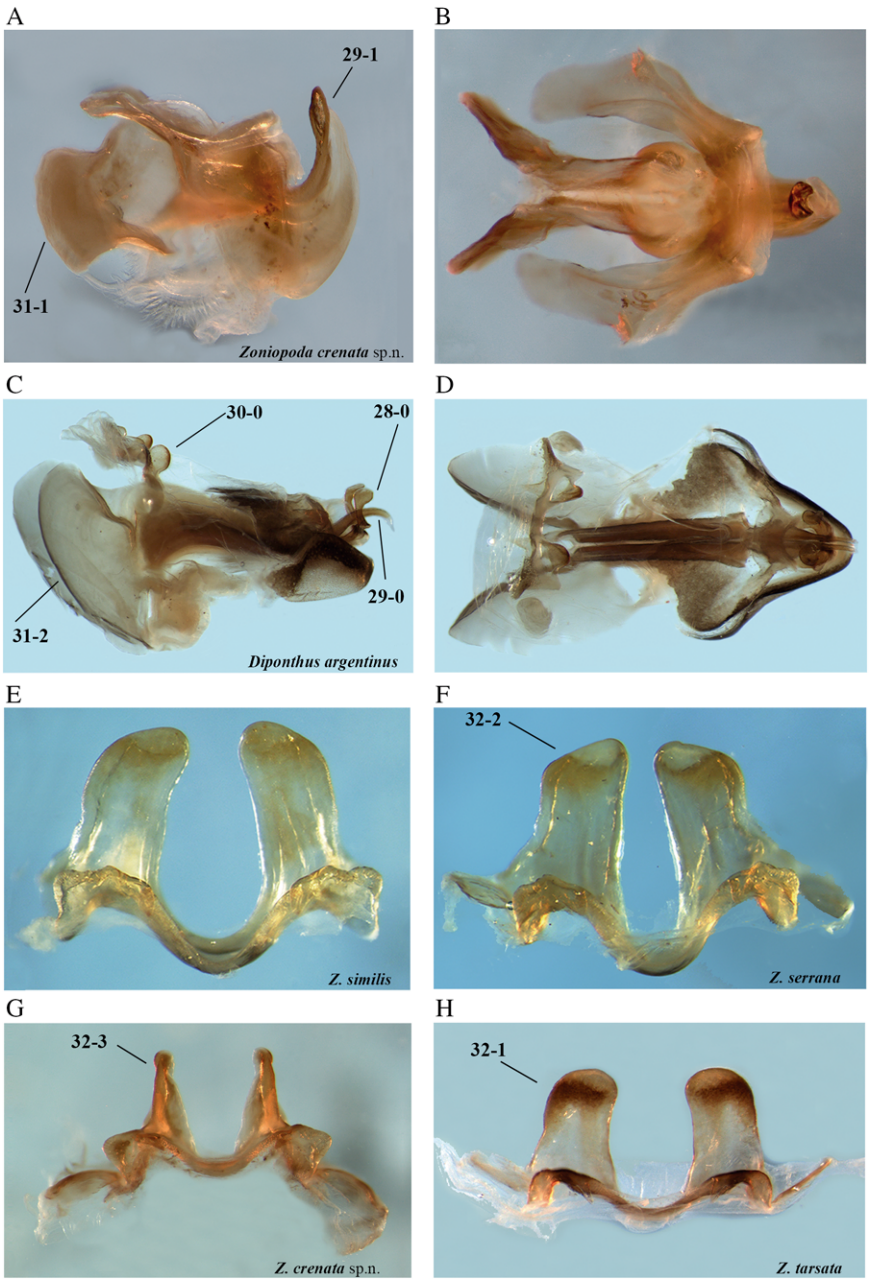

Fig. 6. Male genitalia. (A–D) Phallic complex, lateral (A, C), and dorsal (B, D) views. (A, B) *Zoniopoda crenata* **sp.n**. (C, D) *Diponthus argentinus* Pictet & Saussure. (E–H) Epiphallus, frontal view. (E) *Z. similis*. (F) *Z. serrana*. (G) *Z. crenata* **sp.n.** (H) *Z. tarsata*. [Colour figure can be viewed at wileyonlinelibrary.com].

Discussion

Biogeography

According to the DIVA based on the tree topology that included all the species of the genus, the ancestral area for the Romaleinae represented in this study appeared to be the Chacoan province. Considering that the split of the Romaleinae was estimated to have occurred during Late Cretaceous–early Palaeogene, the diversification of this group in the Chacoan coincided with a period of multiple geodynamic events, including the multiphased uplift of the Andes and the formation of Amazonian lowlands (Sempere *et al.*, 2008; Hoorn *et al.*, 2010). The ancestor of *Zoniopoda* may have been distributed in an area corresponding to the Chacoan and Cerrado provinces, within the Chacoan subregion (Morrone, 2014). The vicariant event that split the ancestral distribution of *Zoniopoda* resulted in the independent evolution of the clade constituted by the species

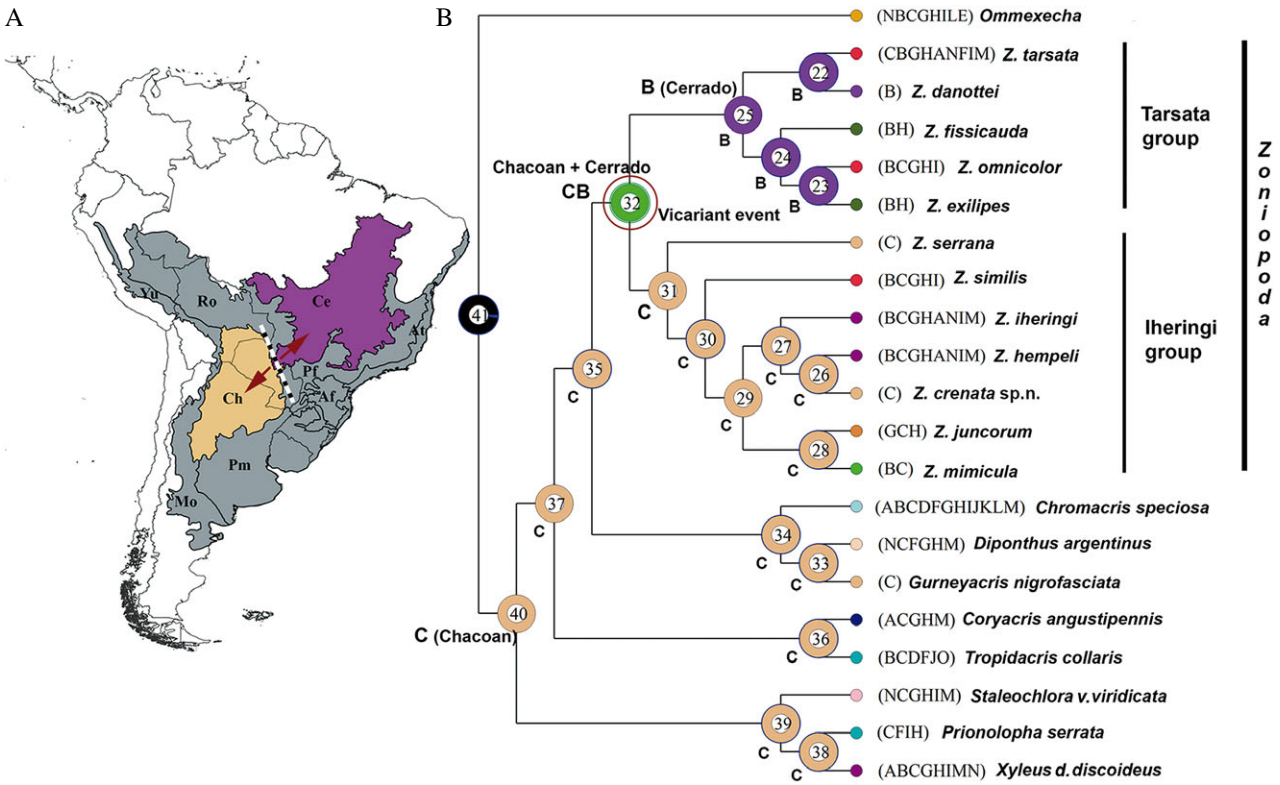

Fig. 7. (A) Biogeographical areas (provinces) following Morrone (2014), used in the DIVA analysis, in which *Zoniopoda* occurs: Af, *Araucaria* Forest; At, Atlantic; Ce, Cerrado; Ch, Chacoan; Mo, Monte; Pf, Parana Forest; Pm, Pampean; Ro, Rondonia; Yu, Yungas. White dotted line indicates the vicariant event that is supposed to have occurred splitting the ancestral distribution (Chacoan + Cerrado), resulting in the independent evolution of the clade constituted by the species of the Tarsata group in Cerrado and the clade comprising the species of the Iheringi group and *Z. crenata*, in Chacoan (indicated with arrows). (B) Taxon area cladogram showing the results of DIVA. Numbers indicate nodes and letters indicate resulting ancestral distribution at each node. [Colour figure can be viewed at wileyonlinelibrary.com].

of the Tarsata group in Cerrado and the clade comprising the species of the Iheringi group in Chacoan. The plateau of Cerrado surfaces are composed of rocks that were moulded during cycles of erosion in the Late Cretaceous, and in the early Palaeogene (Silva, 1997; Colli, 2005). From the late Palaeogene to the early Neogene, these plateaus were uplifted to their present-day elevations (500–1700 m a.s.l.; Silva, 1997; Nores, 2004; Rossetti *et al.*, 2005) causing the formation of depressions between plateaus and fragmenting the landscape (Prado *et al.*, 2012). Thus, we hypothesize that the vicariant event in *Zoniopoda* could be explained by the uplift of the Brazilian Plateau and the correlated subsidence of the Chaco and Pantanal due to an intense phase of uplift of the Andes (Silva, 1995; Colli, 2005; Porzecanski & Cracraft, 2005). The subsequent diversification of the Tarsata clade may have taken place within the Cerrado province, whereas the Iheringi clade would have diversified within the Chacoan province. Only one species within the Tarsata group is currently distributed exclusively in the Cerrado, and two species of the Iheringi group remain restricted to the Chacoan biogeographic area. The current wide distribution of the remaining species of both clades may be explained by recent dispersal events to other biogeographical provinces within the Chacoan subregion, and in some cases colonizing adjacent subregions to the west and south (*Z. tarsata*, *Z. omnicolor*, *Z. hempeli*, *Z. iheringi* and *Z. similis*), probably due to ecological adaptation to changes in humidity conditions within the open vegetation biomes that extend diagonally across central–eastern South America (Pennington *et al.*, 2000; Werneck, 2011).

The major representativeness of the genus *Zoniopoda* is found in the centre and south of these open vegetation biomes. The Cerrado and Chaco harbour the highest number of species of this genus, followed by the 'Misiones Nucleus' of the SDTF. The Chaco is an open vegetation biome of lowland alluvial plains that extends through northern Argentina, western Paraguay, southeastern Bolivia and the extreme western edge of Mato Grosso do Sul state in Brazil, covering about 840 000 km^2 (Prado, 1993b; Pennington *et al.*, 2000; Werneck, 2011). The Cerrado is a savanna biome that covers nearly 2 million km^2 of central Brazil, distributed across wide latitudinal and altitudinal gradients (Werneck, 2011). The climate of these biomes is characterized by strong seasonality although the Chaco has more severe summers and winter frosts (Prado, 1993a; Pennington *et al.*, 2000; Werneck, 2011). Within these biomes, species diversity and endemism are high for some animal (Ronderos, 1976; Ronderos & Sánchez, 1983; Silva & Bates, 2002; Lanteri

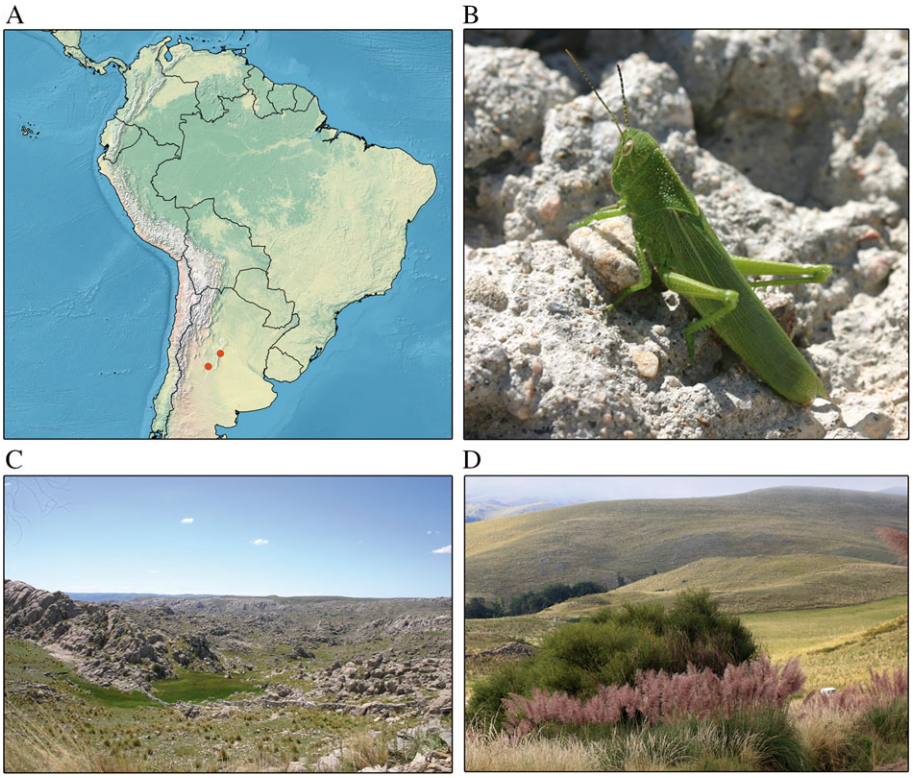

Fig. 8. *Zoniopoda crenata* **sp.n.** (A) Distribution records, (B) female, (C) habitat, Cerro El Amago, San Luis, Argentina. D, habitat, La Cumbre, Córdoba, Argentina. [Colour figure can be viewed at wileyonlinelibrary.com].

& del Río, 2006; Cigliano, 2007; Amorim *et al.*, 2009; Ramos & Melo, 2010; Nogueira *et al.*, 2011; Gamble *et al.*, 2012; del Río *et al.* 2015; Guarnizo *et al.*, 2016; Lanteri & del Río, 2016) and plant taxa (Oliveira & Marquis, 2002; Simon *et al.*, 2009; Prado *et al.*, 2012; Werneck *et al.*, 2012b). This high species diversity is suggested to have been produced and maintained by a combination of geological processes during the Late Cretaceous through the Palaeogene, and fluctuations in climate and vegetation that characterized the Neogene subperiod (Werneck, 2011).

Taxonomic and phylogenetic considerations

Results of the phylogenetic analyses conducted herein, based on morphological and molecular evidence, confirm the inclusion of the new species within the genus *Zoniopoda*, which was always recovered as a monophyletic group with moderate to maximum support depending on the datasets analysed. Even though the results of both, morphological and molecular (*COI* + *HIS*), analyses agreed in the placement of the new species within *Zoniopoda*, different relationships were recovered between *Zoniopoda crenata* **sp.n.** and the remaining species of the genus. Although in the morphological analyses *Zoniopoda crenata* was recovered as sister to *Z. hempeli*, in the molecular and total evidence analyses it resolved as the first diverging lineage within the genus *Zoniopoda*. This latter result is congruent with our preliminary uncertainty regarding the affinities of the new species.

Incongruences among the different analyses were also found within the relationships of *Zoniopoda* species. The two groups of species (Tarsata and Iheringi) proposed by Carbonell (2007) based on characters from median dorsal carina of pronotum and body colouration were recovered in the morphological analysis that included all of the valid species of the genus. In contrast, results of the analyses based on the molecular data and total evidence did not recover these two groupings. Because the molecular and total evidence analyses did not include all of the species of the genus, and thus the results might not be conclusive, we decide to maintain the classification proposed by Carbonell (2007) regarding the grouping of species. In addition, we also consider that the new species found certainly belongs to the genus *Zoniopoda* and we tentatively assign it to the Iheringi species group based on the morphological results.

Results also showed that the specimens of *Z. tarsata*, representing distant localities, did not cluster together. Although these specimens cannot be separated based on morphological grounds, the molecular evidence suggests that they may constitute separate species. Further studies based on a larger sample of the species covering the whole distribution area of *Z. tarsata* might shed light on the status of this taxon.

Aside from the generic characters mentioned by Carbonell (2007) and based on our morphological tree (Figure S1),

Zoniopoda can be additionally defined by the presence of a thin hind femur, the male subgenital plate bifurcated, a median wide longitudinal light-coloured band in male epiproct and the colour range (light blue, lilac to pink) of the hindwings.

According to Carbonell (2007), the Romaleinae genera most closely related to *Zoniopoda* are *Chariacris* Walker and *Diponthus*. This author also considers that the genus *Chromacris* may be also related to *Zoniopoda*. In our morphological analysis, the sister group of *Zoniopoda* was *Chromacris* (*Diponthus*, *Gurneyacris*), supported by a considerable number of synapomorphies. This relationship is lost in the molecular and total evidence analyses, because *Zoniopoda* appeared to be related to *Tropidacris* (Fig. 2, Figure S2).

Considering the relationships among the genera representing the South American tribes of Romaleinae included in our morphological analysis, the tribes Elaeochlorini and Procolpini were recovered as sister groups; the tribe Romaleini, which is the largest within the subfamily, resolved as paraphyletic because the representative of Tropidacrini (*Tropidacris collaris*) formed a clade with the Romaleini *Coryacris angustipennis*. The molecular and total evidence analyses also showed incongruent relationships with the actual classification of the Romaleini tribe shown in the Orthoptera Species File (Cigliano *et al.*, 2017). However, we avoid discussing in depth the affinities among the Romaleinae genera because in all of the analyses performed in this study their relationships were recovered with low support values. Further studies including a wider taxon sampling and additional molecular markers will allow us to elucidate the relationships among the tribes and genera of this subfamily of grasshoppers (Pocco *et al.*, in preparation).

As mentioned above, the new species described herein occurs in an open vegetation biome in the south of the Chacoan province where another recently discovered species of *Zoniopoda* is also present (Pocco *et al.*, 2011). In this area these two species included in the Iheringi group are sympatric with two other *Zoniopoda* species (*Z. tarsata* and *Z. omnicolor*), that belong to the Tarsata group. Even though the Chaco biome has been surveyed by outstanding acridiologists (Liebermann J., Carbonell C.S., Ronderos R.A., among others) rendering a significant knowledge of its acridiofauna, at least for some groups such as romaleids, it seems that there are still undiscovered species in the region. We emphasize the importance of systematic surveys of this highly diversified biome of South America that may not only render the discovery of new species, but also contribute to a better knowledge of species richness and endemism, as a path leading to improved conservation strategies (Pocco *et al.*, 2013).

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12277

Figure S1. Most parsimonious tree (L, 161; CI, 0.68; RI, 0.86) resulting from the cladistic analysis of the morphological character dataset, under equal weights. Black circles indicate unique changes and white circles indicate homoplasies. The numbers below the branches are Bremer support values.

Figure S2. Tree topology obtained from the Bayesian analysis of the COI and H3 datasets. Numbers on branches between brackets indicate posterior probabilities. Acronyms of specimens according to Table 2.

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Appendix

List of morphological characters

CI and RI are indicated for each character.

0 Antennae: shape: filiform (0) (Fig. 4B); slightly ensiform (1). CI: 0.5, RI: 0.87.

1 Antennae: longer than head and pronotum (0); shorter than head and pronotum (1); equal (2). CI: 1, RI: 1.

2 Union frons-fastigium in lateral view: quite rounded (0); angulated (1) (Fig. 4F); rounded (2); strongly angulated (3). CI: 0.6, RI: 0.81.

3 Fastigium: prominent, longer than the interocular distance (0) (Fig. 4C); shorter than the interocular distance (1) (Fig. 4A); equal (2) (Fig. 4B). CI: 0.5, RI: 0.77.

4 Fastigium: apex: concave (0); straight (1) (Fig. 4A); rounded (2) (Fig. 4C); angulate (3) (Fig. 4B); notched (4). CI: 0.66, RI: 0.77.

5 Frontal carina: absent below the median ocellus (0); narrow, extending below the median ocellus, reaching the epistomal suture (1); wide (2); absent, replaced by sulcus (3). CI: 0.75, RI: 0.

6 Transverse furrow on interocular space: unnoticeable marked (0); well-marked (1) (Fig. 4A); slightly marked (2) (Fig. 4C); strongly marked and wide (3). CI: 0.6, RI: 0.86.

7 Interocular distance: wider than apex of fastigium (0) (Fig. 4B); equal (1) (Fig. 4D). CI: 1, RI: 1.

8 Eyes: protruding, parallel to the mid-line of head (0); not protruding, oblique to the mid-line of head (1) (Fig. 4C). CI: 1, RI: 1.

9 Prosternal process: collar-like (0); tubercle (1). CI: 1, RI: 1.

10 Prosternal tubercle: slightly directed backwards (0); directed backwards (1), straight (2). CI: 1, RI: 1.

11 Pronotal front margin: not projected over occiput (0) (Fig. 4D); projected over occiput (1) (Fig. 4B); strongly projected over occiput (2). CI: 0.5, RI: 0.84.

12 Median dorsal carina of pronotum: number of transverse sulci cutting the median dorsal carina: one (0); two (1) (Fig. 4D); three (2) (Fig. 4B); four (3). CI: 0.75, RI: 0.75.

13 Median dorsal carina of pronotum, lateral view: smooth (0) (Fig. 4E); tuberculate (1); slightly granulate (2); granulate (3); crenulated (4) (Fig. 4F); serrate (5). CI: 0.83, RI: 0.83.

14 Median dorsal carina of pronotum: marked all throughout (0) (Fig. 4A); marked on metazona (1) (Fig. 4D); obsolete (2). CI: 0.5, RI: 0.71.

15 Median dorsal carina of pronotum: low (0) (Fig. 4E); elevated (1) (Fig. 4F); high (crest) (2). CI: 0.4, RI: 0.72.

16 Prozona: strongly lobed (0); lobed (1) (Fig. 4E); not lobed (2) (Fig. 4F). CI: 0.66, RI: 0.66.

17 Prozona and metazona length: prozona longer than metazona (0); prozona slightly longer than metazona (1) (Fig. 4C); subequal (2) (Fig. 4A); prozona slightly shorter than metazona (3) (Fig. 4D); prozona shorter than metazona (4). CI: 0.8, RI: 0.88.

18 Hind femora: robust (0) (Fig. 3I); thin (1) (Fig. 3D); intermediate (2) (Fig. 3J). CI: 0.4, RI: 0.81.

19 Male subgenital plate: apex: not bifurcated (0) (Fig. 5G); bifurcated (1) (Fig. 5I). CI: 0.5, RI: 0.91.

20 Male subgenital plate: short (0) (Fig. 5F); elongate (1) (Fig. 5C). CI: 0.2, RI: 0.71.

21 Male epiproct: with tubercles (0) (Fig. 5G); without tubercles (1) (Fig. 5I). CI: 0.33, RI: 0.77.

22 Male epiproct without tubercles: shape: triangular (0); rhomboidal with rounded distal edges (1) (Fig. 5H); rhomboidal with angulated distal edges (2); oval (3); rectangular (4); sub-rectangular with oblique distal edges (5) (Fig. 5I). CI: 0.83, RI: 0.85.

23 Male epiproct: colour pattern: with a wide, light median longitudinal band: absent (0) (Fig. 5G); present (1) (Fig. 5H). CI: 1, RI: 1.

24 Colouration of male epiproct and furculae: uniformly light-coloured (0) (Fig. 5I); furculae and edges of epiproct black (1) (Fig. 5H); epiproct uniformly coloured, tips of furculae and tubercles black (2) (Fig. 5G); uniformly black (3). CI: 0.6, RI: 0.85.

25 Male furculae: reduced (0) (Fig. 5H); well-developed (1) (Fig. 5I); prominent (2) (Fig. 5G). CI: 0.4, RI: 0.7.

26 Male furculae: placed far apart (0) (Fig. 5G); placed close together (1) (Fig. 5I). CI: 0.25, RI: 0.62.

27 Male cerci: shape: finger-like (0) (Fig. 5B); conical (1) (Fig. 5F); distal portion flattened (2) (Fig. 5C); tapering towards the down-curved apex (3) (Fig. 5A); subtriangular (4) (Fig. 5E); very wide basally with distal 1/3 very narrow (5) (Fig. 5D). CI: 1, RI: 1.

28 Ectophallus: expansion of rami extending into the ventral valves of aedeagus: present (0) (Fig. 6C); absent (1). CI: 1, RI: 1.

29 Endophallus: apical valves: dorsal valves of aedeagus: down-curved (0) (Fig. 6C); up curved (1) (Fig. 6A); reduced (2); not differentiated (3). CI: 1, RI: 1.

30 Epiphallus size relative to endophallus: small (0) (Fig. 6C); large (1); very large (2). CI: 1, RI: 1.

31 Endophallus: endophallic apodemes: shape: rectangular (0); sub-quadrangular (1) (Fig. 6A); ear-shaped (2) (Fig. 6C); quadrangular (3); oval (4). CI: 1, RI: 1.

32 Epiphallus: shape of lophi in frontal view: divergent, rounded apical margins (0); slightly convergent, rounded apical margins (1) (Fig. 6H); convergent, slightly oblique apical margins (2) (Fig. 6F); not convergent, sub-conical apical margins (3) (Fig. 6G). CI: 1, RI: 1.

33 Colour pattern of hind tibiae: homogeneously dull brownish (0); homogeneously bright, not brownish (1) (Fig. 3A); bicoloured with red tips (2) (Fig. 3D); bicoloured with brownish tips (3) (Fig. 3I); bicoloured with spots (4); bicoloured with bands (5) (Fig. 3G). CI: 1, RI: 1.

34 Colour pattern of pronotum: with longitudinal and oblique bands (0) (Fig. 3I); with longitudinal bands (1) (Fig. 3G); with transverse bands (2) (Fig. 3H); homogeneously coloured (3) (Fig. 3B); with lateral bands (4); with spots (5) (Fig. 3K); with longitudinal and transverse bands (6); with longitudinal band and lateral bands (7). CI: 0.77, RI: 0.83.

35 Colour pattern of hindwings: light-coloured, hyaline (0); orange with black in characteristic patterns (1); uniformly coloured, orange (2); uniformly coloured, light blue, lilac to pink (3). CI: 0.6, RI: 0.87.

36 Colour pattern of hind femora: without transverse bands (0) (Fig. 3B); with transverse bands (1) (Fig. 3G). CI: 0.33, RI: 0.77.

37 Transverse bands on hind femora: with incomplete transverse bands (0) (Fig. 3G); with complete transverse bands or rings (1) (Fig. 3F). CI: 0.5; RI: 0.5.

38 Colour pattern of tegminae: uniformly coloured (0) (Fig. 3C); with irregular light cells (1); with light blotches (2) (Fig. 3I); with regular light cells (3); with light band (4) (Fig. 3L); with dark irregular patches (5). CI: 1; RI: 1.

39 Colour of main longitudinal veins in uniformly coloured tegminae: not distinctively coloured (0) (Fig. 3E); all distinctively coloured (1) (Fig. 3F); only costal and radial vein distinctively coloured (2) (Fig. 3D); CI: 0.66; RI: 0.75.

40 Integument of thorax: mostly smooth and shiny (0) (Fig. 3F); rugose and dull (1) (Fig. 3E); strongly rugose and dull (2) (Fig. 3B); rugose and shiny (3) (Fig. 3I); with small tubercles (4); with conspicuous tubercles (5) (Fig. 3L). CI: 1, RI: 1.

41 Colour rings on hind tibiae: without rings (0) (Fig. 3B); with rings (1) (Fig. 3H). CI: 0.5, RI: 0.8.

42 Colour of head: without bands (0) (Fig. 3A); with bands (1) (Fig. 3F). CI: 0.33, RI: 0.85.

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