Molecular Phylogenetics and Evolution xxx (2013) xxx–xxx

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Inside the Melanoplinae: New molecular evidence for the evolutionary history of the Eurasian Podismini (Orthoptera: Acrididae)

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A R T I C L E I N F O

Article history:
Received 25 February 2013
Revised 30 August 2013
Accepted 9 September 2013
Available online xxxx

Keywords:
Grasshopper
Acrididae
Melanoplinae
Podismini
Combined phylogeny
Nuclear and mitochondrial DNA

A B S T R A C T

The Podismini are melanopline grasshoppers with a Holarctic distribution and well represented in the Eurasian fauna. To investigate their controversial taxonomy and evolutionary history, we studied 86%, 78% and 33% respectively of the Eurasian, European and Asian Palaearctic genera (Otte, 1995; Eades et al., 2013). We reconstructed parsimony, maximum likelihood and Bayesian phylogenies using fragments of four genes (ITS1, 16S, 12S, CO2). We applied a Bayesian molecular clock to estimate the times of species divergence, and the event-based parsimony method to depict the biogeographic framework of the diversification. Our results suggest that the selected Eurasian Podismini constitute a monophyletic group inside the Melanoplinae, provided it includes the North American genus *Phaulotettix*. The clades proposed by the present study inside the Podismini do not fit the older morphological or cytological classifications, but are in agreement with more recent proposals. Furthermore, our results can be explained by a plausible biogeographic history in which the present geographical distribution of the Eurasian Podismini resulted from known changes, to the Cenozoic climate and vegetation, induced by major geological events including the genesis of high mountain chains (e.g., Himalayas, Altay, Alps) and large deserts (e.g., Gobi, Karakoum, Taklamakan), and the opening of marginal seas (e.g., Bering, Japanese and Yellow Seas).

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1. Introduction

Podismini grasshoppers (Acrididae, Melanoplinae) are a major component of the alpine fauna in the Holarctic. They are particularly diversified in Eurasia and the western and eastern regions of the North America, in the grassland and scrub formations from 200 to about 2200 m above sea level (e.g., Bei-Bienko and Mishchenko, 1963; Galvagni, 1987; Harz, 1975; Kis, 1978; Sergeev et al., 1997; Uvarov, 1977). The podismines are strongly shaped in their biogeographical and evolutionary history by the climatic, floral and geographical complexity of the different European and Asian high mountains systems (e.g., Schmitt, 2009; Sergeev, 1992, 1993; Varga and Schmitt, 2008). Some Eurasian Podismini genera have restricted geographic areas, representing endemism hot spots, like *Chortopodisma* (southern Tirol and Dolomites), *Italopodisma* (central part of the Appenines) and *Pseudoprumna* (Monte Baldo) (e.g., Fontana and Pozzebon, 2007; La Greca, 1977; Kenyeres et al., 2009; Massa et al., 2012). Others are widespread in Europe and Asia Minor, such as *Miramella*, *Odontopodisma* and *Podisma* (e.g., Harz, 1975; Kis, 1978; Sergeev, 1992, 1998). Although the Podismini have a limited effect on agriculture, they have served well as model organisms. For example, Podismini were used as model to study the evolution of the auditory system in insects (e.g., Lehmann et al., 2010) and the alpine grasshopper, *Podisma pedestris*, has been used for investigating pattern of chromosomal and rDNA pseudogene evolution (Hewitt, 1979; Nichols and Hewitt, 1986; Keller et al., 2006). In particular, the Podismini have been used in genetic studies to reconstruct past geographical distribution and speciation (e.g., Keller et al., 2008; Veltsos et al., 2008). These studies require a firmer foundation of robust and comprehensive phylogenetic data, which is presently lacking (e.g., Litzenberger and Chapco, 2001, 2003).

The systematics of the Podismini is still controversial, with different authors recognizing different groups of genera (e.g., Rehn et al., 1963; Fontana and Vickery, 1976; Vickery, 1987) or ranks of the group (e.g., Otte, 1995; Eades et al., 2013), and their evolutionary history remains unclear. Three scenarios have been proposed to explain their early biogeographic history. One assumes an Asian (Angaran) origin (e.g., Rehn and Rehn, 1939; Vickery, 1987) followed by migrations to Europe and North America.

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1055-7903/$ - see front matter © 2013 Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.ympev.2013.09.009

Please cite this article in press as: Chintauan-Marquier, I.C., et al. Inside the Melanoplinae: New molecular evidence for the evolutionary history of the Eurasian Podismini (Orthoptera: Acrididae). Mol. Phylogenet. Evol. (2013), http://dx.doi.org/10.1016/j.ympev.2013.09.009

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Another posits a vicariant origin, with Asia and North America as independent centers of evolution, after the split of the Laurasian super-continent (Vickery, 1986). A third alternative, based on recent molecular work (e.g., Litzenberger and Chapco, 2001, 2003; Chintauan-Marquier et al., 2011), suggests a Nearctic origin followed by westward dispersions towards the Palaearctic.

Given these diverse proposals, we aimed to clarify the evolutionary history of the Eurasian Podismini, and to evaluate the concordance between the evolutionary relationships inferred from molecular data and the affinities suggested by current morpho-taxonomies (Rehn and Randell, 1963; Vickery, 1987) and compilations (Otte, 1995; Vickery, 1997; Eades et al., 2012). More specifically, (i) we evaluated the monophyly of the Podismini and of its groups of genera (subtribes) in relation to possible ancestors from Eurasia and/or Americas, (ii) we assessed the most probable biogeographic scenario, (iii) we dated the events inferred from the phylogenies, and (iv) we checked the coherence of the current classifications and proposed an affiliation for "unassigned" morphologically described taxa (Table 1).

To this end, we analyzed nuclear and mitochondrial DNA sequences, separately and combined, for nineteen out of 48 genera of Podismini representing 86%, 78% and 33% of the Eurasian, European and Asian genera recognized for the Palaearctic (Eades et al., 2013). From the selected taxa, seven have not been previously analyzed in molecular phylogenies and fifteen are analyzed for the first time using nuclear DNA. We also included six related outgroup genera from the Acrididae (Table 1).

2. Materials and methods

2.1. Taxon sampling

DNA sequences were obtained from dried and in alcohol samples of the Caelifera (Insecta, Orthoptera) collections of the Muséum national d'Histoire naturelle (MNHN) in Paris (France) and of the Museum of the Biology–Geology Faculty from Cluj-Napoca (Romania) (Table 1). To organize our sampling, we followed the morphological classification recognizing three main tribes of

Table 1
Origin of study material and references of sequence data. LECA: Laboratoire d'écologie alpine, UMR CNRS-UJF 5553 Grenoble, France; MNHN: MNHN Caelifera collection; TS: type species.

Species	Authority	Collecting data	Collection nos.	GenBank nos.			
				ITS1	CO2	16S	12S
Acridoidea							
Acrididae							
Catantopinae							
Oxycatantops spissus	(Walker, 1870)	Guinea, Nimba, 1984	MNHN Gu8401	GQ354701	–	–	GQ354753
Pezotettix giornae **TS**	(Rossi, 1794)	France, Dordogne, 2000	MNHN Fr0001	GQ354702	–	xxx	GQ354755
Melanoplinae							
Dactylotini							
Dactylotum bicolor bicolor **TS**	(Charpentier, 1843)	Mexico, Hidalgo, 1986	MNHN Me8604	GQ354688	–	–	GQ354740
Hesperotettix viridis viridis	(Thomas, 1872)	Mexico, San Luis Potosi, 1986	MNHN Me8605	GQ354692	–	–	GQ354744
Melanoplini							
Melanoplus frigidus	(Boheman, 1846)	France, Lautaret, 1999	LECA MFFL0199	GQ354697	xxx	xxx	GQ354749
Phaulotettix compressus **TS**	Scudder, 1897	Mexico, Hidalgo, 1986	MNHN Me8602	GQ354703	–	–	GQ354756
Podismini							
Miramella group							
Anapodisma miramae **TS**	(Dovnar-Zapolskij, 1932)	Russia, 2000	LECA ANMI0100	xxx	xxx	xxx	xxx
Capraiuscola ebneri ebneri **TS**	(Galvani, 1953)	Romania, Sinaia, 1966	LECA MEE22021	xxx	xxx	xxx	–
Chortopodisma cobellii **TS**	(Krauss, 1883)	Italy, Abruzzo, 2001	LECA CC8011	xxx	xxx	xxx	xxx
Cophopodisma pyrenaea **TS**	(Fischer, 1853)	France, Pyrenées, 1997	LECA CP9021	xxx	xxx	xxx	xxx
Epipodisma pedemontana pedemontana **TS**	(Brunner von Wattenwyl, 1882)	Russia, 1997	LECA EP14011	xxx	xxx	xxx	xxx
Italopodisma costae **TS**	(Targioni-Tozzetti, 1881)	Italy , Abruzzo, 2000	LECA IC0100	xxx	xxx	–	xxx
Italopodisma fiscellana	(La Greca, 1954)	Italy , Abruzzo, 2000	LECA IF19061	xxx	xxx	xxx	xxx
Nadigella formosanta **TS**	(Fruhstorfer, 1921)	Italy, 1999	LECAMF22082	xxx	–	–	xxx
Parapodisma dairisama	(Scudder, 1897)	Japan, 1998	LECA CD28011	–	xxx	xxx	–
Parapodisma mikado	(Bolivar, 1890)	Japan, Sapporo, 1997	LECA PARMIK2	xxx	xxx	xxx	xxx
Parapodisma subastris	(Huang, 1983)	Japan, Sakurai, 1998	LECA PS28071	xxx	xxx	xxx	xxx
Pseudoprumna baldensis **TS**	(Krauss, 1883)	Italy, Monte Baldo, 1999	LECA PB37012	xxx	xxx	–	xxx
Sinopodisma punctata	(Mishchenko, 1954)	Japan, Tatsugou, 1998	LECA SPJT0198	GQ354708	xxx	xxx	GQ354760
Podisma group							
Micropodisma salamandra	(Fischer, 1853)	Austria, 1995	LECA MS21032	xxx	xxx	xxx	xxx
Odontopodisma carpathica	(Kis, 1961)	Romania, Ghinda, 2000	LECA OC24031	xxx	–	xxx	–
Odontopodisma rubripes	(Ramme, 1931)	Romania, Calimani, 2001	LECA OR24101	xxx	xxx	xxx	xxx
Ognevia longipennis	(Shiraki, 1910)	Japan, Sapporo, 1998	LECA OL25011	xxx	xxx	xxx	xxx
Podisma kanoi	(Storozhenko, 1994)	Japan, 1998	LECA PK31201	xxx	–	xxx	xxx
Podisma pedestris **TS**	(Linné, 1758)	France, Belledonne, 2000	LECA PPFB0100	GQ354704	xxx	xxx	GQ354757
Pseudopodisma transilvanica	(Galvani-Fontana, 1993)	Romania, 2001	LECA PT36031	xxx	–	xxx	–
Zubovskya koeppeni parvula **TS**	(Ikonnikov, 1911)	Japan, M. Ashibetsu, 1997	LECA ZKP43051	xxx	xxx	xxx	xxx
Unassigned subtribe							
Fruhstorferiola okinawaensis	(Shiraki, 1930)	Japan, Okinawa, 1998	LECA FO15041	xxx	xxx	xxx	xxx
Peripodisma tymphii **TS**	(Willemse, 1972)	Greece, Epiros, 1999	LECA PT30011	xxx	xxx	xxx	xxx
Tonkinacris sp.	(Carl, 1916)	Japan, Ouno, 1997	LECA T4101	xxx	xxx	xxx	xxx
Prumnini							
Prumna primnoa **TS**	(Motschulsky, 1846)	Mongolia, Selonge, 1997	LECA PP34191	xxx	xxx	xxx	xxx

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