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Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis

Ioana C. Chintauan-Marquier^{a,†}, Frédéric Legendre^{a,†}, Sylvain Hugel^b,
Tony Robillard^a, Philippe Grandcolas^a, André Nel^a, Dario Zuccon^c and
Laure Desutter-Grandcolas^{a,*}

^aInstitut de Systématique, Evolution, Biodiversité, ISYEB - UMR 7205 CNRS, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, CP 50, 45, rue Buffon, Paris 75005, France; ^bINCI, UPR3212 CNRS, Université de Strasbourg, 21, rue René Descartes, Strasbourg F-67084, France; ^cService de Systématique Moléculaire, UMS2700 MNHN-CNRS, Département Systématique et Evolution, Muséum national d'Histoire naturelle, Paris Cedex 05, France

Abstract

Orthoptera have been used for decades for numerous evolutionary questions but several of its constituent groups, notably crickets, still suffer from a lack of a robust phylogenetic hypothesis. We propose the first phylogenetic hypothesis for the evolution of crickets *sensu lato*, based on analysis of 205 species, representing 88% of the subfamilies and 71% tribes currently listed in the database Orthoptera Species File (OSF). We reconstructed parsimony, maximum likelihood and Bayesian phylogenies using fragments of 18S, 28SA, 28SD, H3, 12S, 16S, and cytb (~3600 bp). Our results support the monophyly of the cricket clade, and its subdivision into two clades: mole crickets and ant-loving crickets on the one hand, and all the other crickets on the other (i.e. crickets *sensu stricto*). Crickets *sensu stricto* form seven monophyletic clades, which support part of the OSF families, “subfamily groups”, or subfamilies: the mole crickets (OSF Gryllotalpidae), the scaly crickets (OSF Mogoplistidae), and the true crickets (OSF Gryllidae) are recovered as monophyletic. Among the 22 sampled subfamilies, only six are monophyletic: Gryllotalpinae, Trigonidiinae, Pteroplistinae, Euscyrinae, Oecanthinae, and Phaloriinae. Most of the 37 tribes sampled are para- or polyphyletic. We propose the best-supported clades as backbones for future definitions of familial groups, validating some taxonomic hypotheses proposed in the past. These clades fit variously with the morphological characters used today to identify crickets. Our study emphasizes the utility of a classificatory system that accommodates diagnostic characters and monophyletic units of evolution. Moreover, the phylogenetic hypotheses proposed by the present study open new perspectives for further evolutionary research, especially on acoustic communication and biogeography.

Introduction

For more than 30 years now, phylogenetics has become the reference system in a tree-thinking perspective for evolutionary biology (Eldredge and Cracraft, 1980; Carpenter, 1989; Brooks and McLennan, 1991, 2002; O’Hara, 1992; Larsen and Losos, 1996). Phylogenetic trees are currently used to propose and test

evolutionary hypotheses in all domains where evolution may interplay with systems studied. As a consequence, phylogenies have also become the backbone of modern classifications. Both fields of application are important and require robust phylogenetic hypotheses based on relevant and broad taxonomic sampling.

Studies on orthopteran insects have investigated many important aspects of animal behaviour, from the neural basis of behaviour to the ecology of acoustic communication (Gwynne and Morris, 1983; Huber et al., 1989; Bailey and Rentz, 1990; Field, 2001; Gwynne, 2001). However, the lack of phylogenetic

*Corresponding author:

E-mail address: desutter@mnhn.fr

†Both authors contributed equally to this work.

foundation has made it difficult to interpret the results of these studies in an evolutionary or comparative framework. In the past, taxonomy has been used as a proxy for phylogeny, with hypotheses of “lower” (i.e. “primitive”) and “higher” taxa, and varied assumptions about “ancestral” character states and evolutionary series (Baccetti, 1987; Bailey, 1991; Otte, 1992; Field, 1993). This applies also to the numerous, and frequently well preserve, orthopteran fossils, which are currently not classified in a satisfactory, phylogenetic manner, resulting in a majority of fossil families and subfamilies not correctly defined on the basis of clear synapomorphies. Only one preliminary cladistic analysis was made on the basis of the forewing venation (Béthoux and Nel, 2002), but it would need significant improvement by the addition of the numerous fossil taxa more recently described and a better comparison with the recent taxa.

Earlier attempts to reconstruct the molecular phylogeny of Orthoptera and their suborders took into account too few taxa and markers to achieve any stability and robustness (Flook and Rowell, 1997a, 1998; Rowell and Flook, 1998; Flook et al., 1999; Jost and Shaw, 2006), as shown in Legendre et al. (2010) for Ensifera, and most published phylogenies have been performed at a limited taxonomic scale (Chapco et al., 2001; Litzenberger and Chapco, 2001; Bugrov et al., 2006; references in Heller, 2006; Allegrucci et al., 2009; Ullrich et al., 2010; Chintauan-Marquier et al., 2011, 2014; but see Nattier et al., 2011a; Song et al., 2015). Only recently, phylogenies relying on large taxonomic and/or character samples have been performed, which suggest that a comprehensive phylogeny for the Orthoptera could be achieved in the near future: Leavitt et al. (2013) explored large dataset partitions while studying the phylogeny of caeliferan Acridoidea, and Mugleston et al. (2013) studied the phylogeny of Tettigonoidea. However, crickets, a large group of Orthoptera (~5000 species), are missing in this global achievement of orthopteran phylogeny and this is the goal of our study.

As crickets have been used as a model system for studies on speciation and acoustic communication (Huber et al., 1989; Gerhardt and Huber, 2002), the first phylogenies of crickets focused on restricted groups based on model species. For example, hypotheses about speciation have been tested in the Hawaiian genus *Laupala* (Shaw, 2002), the Caribbean genus *Amphiacusta* (Oneal et al., 2010) and the New Caledonian genus *Agnotecous* (Nattier et al., 2011b, 2012). Acoustic signal evolution has been analysed in the North American species of *Gryllus* (Huang et al., 2000; Desutter-Grandcolas and Robillard, 2003), and the diversification of stridulatory structures and calling songs in the cricket subfamily Eneopterinae has been studied first in a phylogenetic perspective (Robillard and

Desutter-Grandcolas, 2004, 2006, 2011a), and later taking into account functional data (Robillard et al., 2007, 2013).

These studies did not aim to analyse evolutionary questions at the scale of the entire cricket clade, neither in terms of evolutionary origin nor in terms of diversification. Gwynne (1995, 1997) gathered all available information from local phylogenetic trees and classificatory hypotheses to derive hypotheses about cricket mating behaviour, acoustic communication, and habitat. The lack of a wide-scale phylogeny of crickets weakened, however, any evolutionary interpretation, not only because of the lack of a historical framework to follow character transformations, but also because of a deficient sampling of cricket diversity (Gerhardt and Huber, 2002; Desutter-Grandcolas and Robillard, 2004). For example, studies on cricket acoustic communication have been based mostly on just a few species of *Gryllus*, *Teleogryllus* and *Acheta*, which has given rise to a straightforward, narrow view of cricket acoustics (Nocke, 1972; Elliott and Koch, 1985; Otte, 1992; Bennet-Clark, 2003). However, original sound emission and apparatus, including non-resonant or high-frequency calls, and asymmetrical or complex sound apparatus were discovered in Phalangopsidae and Eneopterinae crickets (Desutter-Grandcolas, 1992, 1997, 1998; Robillard and Desutter-Grandcolas, 2004). Their actual diversity and the complexity of the stridulum functioning mechanism (Robillard et al., 2013) escaped the classic “cricket model”, and a possible explanation has emerged only when a sound phylogenetic reference became available (Robillard et al., 2007, 2013; Robillard and Desutter-Grandcolas, 2011a). Therefore, cricket phylogenetic relationships need to be investigated with state-of-the-art phylogenetic tools.

The lack of a phylogeny for crickets goes along with the lack of a stable and well-supported classification for this group. Defined on various morpho-anatomical datasets, different classifications have been proposed (Brunner von Wattenwy, 1873; de Saussure, 1874, 1877; Scudder, 1897; Bruner, 1916; Blatchley, 1920; Chopard, 1949, 1969; Vickery, 1977; Gorochoy, 1986, 1995; emended in Storozhenko, 1997; Desutter, 1987, 1988). These classifications had various internal structures and were a mix of stable groups, well characterized by their morphology and used by a majority of authors, and of artificial, vaguely defined groups. This situation resulted in much confusion about cricket taxonomy, increased by the assignment of newly described taxa to higher taxonomic categories according to ambiguous diagnoses. Today, the most widely used classification system for crickets is the internet reference Orthoptera Species File (OSF; <http://orthoptera.speciesfile.org>), but this classification system has not been subject to recent and thorough phylogenetic

hypotheses. It is now an important challenge to build a robust phylogeny of crickets, not only to understand their evolution and that of Orthoptera in general, but also to establish a stable classification for this diverse clade.

Here we present the first attempt to reconstruct a phylogeny of crickets using a wide taxonomic and character sample (i.e. 205 species representative of cricket diversity; four nuclear and three mitochondrial markers), analysed with parsimony, maximum likelihood, and Bayesian inference. Our aims are: (i) to test the monophyly of a putative cricket clade comprising true crickets, mole crickets, ant-loving crickets, and scaly crickets; (ii) to determine the phylogenetic relationships between these groups, (iii) to determine their main phylogenetic subdivisions and compare them with the OSF; and (iv) to draw from this phylogenetic hypothesis the backbone of a phylogenetic classification of crickets and the framework for future evolutionary studies. We discuss some general outcomes about acoustic communication and biogeography in crickets, which may help guide future evolutionary studies.

Material and methods

Taxon sampling

Taxon sampling was designed to lay the foundation of a phylogenetic classification of crickets *sensu lato*, that is, true crickets, mole crickets, ant-loving crickets, and scaly crickets. As no clear hypothesis of cricket classification exists today, we referred to the Internet database OSF. We included species belonging to as many suprageneric groups as possible among those listed in the OSF on 1 September 2014. To improve the phylogenetic diversity of the ingroup, and to avoid sampling biases, we also sampled genera that are not currently classified in a suprageneric category in the OSF, and we took into account the genera that were previously classified in tribal or subfamilial groups no longer in use in the OSF.

According to the OSF (Table 1), crickets *sensu lato* are classified into one superfamily, the Grylloidea, comprising four families, the Mogoplistidae (Mogoplistinae – or scaly crickets – and the Malgasiinae with the Malagasy genus *Malgasia* Uvarov, 1940), the Gryllotalpidae (Gryllotalpinae and Scapteriscinae – mole crickets), the Myrmecophilidae (Myrmecophilinae – ant-loving crickets) and the Gryllidae (true crickets). Gryllidae include three “subfamily groups” (the Gryllinae, Phalangopsinae, and Podoscirtinae “subfamily groups”, comprising 16 subfamilies) and four unclassified subfamilies (Nemobiinae, Trigonidiinae, Oecanthinae, Eneopterinae).

Table 1
Taxonomic sampling used in this study, with taxonomic assignment according to the internet database Orthoptera Species File

Families/Subfamilies	Tribes	Sampled genera	Sampled species
GRYLLIDAE			
“Gryllinae subfamily group”			
Gryllinae	6 of 7	28	31
Gryllomiminae	No tribe	–	–
Gryllomorphinae	2 of 2	3	4
Itarinae	No tribe	–	–
Landrevinae	1 of 2	5	6
Sclerogryllinae	0 of 1	1	1
“Phalangopsinae subfamily group”			
Cachoplistinae	1 of 2	3	4
Luzarinae	No tribe	15	17
Paragryllinae	1 of 1	12	15
Phalangopsinae	2 of 3	7	11
Phaloriinae	1 of 2	3	9
Pteroplistinae	1 of 1	2	2
No subfamily	1 of 2	3	7
No subfamily	No tribe	2	2
“Podoscirtinae subfamily group”			
Euscyrinae	No tribe	2	3
Hapithinae	2 of 2	5	5
Podoscirtinae	3 of 3	14	17
Pentacentrinae	1 of 5	2	2
No hypothesized “subfamily group”			
Eneopterinae	5 of 5	15	19
Nemobiinae	4 of 6	13	18
Oecanthinae	1 of 2	1	3
Trigonidiinae	2 of 2	8	13
GRYLLOTALPIDAE			
Gryllotalpinae	No tribe	1	4
Scapteriscinae	No tribe	–	–
MOGOPLISTIDAE			
Malgasiinae	No tribe	1	1
Mogoplistinae	2 of 2	5	9
MYRMECOPHILIDAE			
Myrmecophilinae	1 of 2	1	2
4 of 4 families		37 of 52	152
22 of 25 subfamilies			205

–, not sampled.

Our ingroup includes a total of 205 species (Tables 1 and 2), belonging to 152 genera (~23% of all known genera). These samples represent 22 of the 25 subfamilies (~88%) and 37 of the 52 tribes (~71%) listed in the OSF. All OSF families and “subfamily groups” are represented.

In addition, two species of Schizodactylidae were included: *Schizodactylus monstrosus* Drury, 1770 and *Comicus campestris* Irish, 1986. Sand crickets have been considered potentially close to crickets, on a morphological (Gwynne, 1995) or molecular (Jost and Shaw, 2006; Legendre et al., 2010) basis (see also Blanchard (1845) for *S. monstrosus*). They are classified as a distinct superfamily in the OSF, that is the Schizodactyloidea, but constitute the sister group of the leaf-roller crickets (Stenopelmatoidea, Gryllacridinae) in Gorochov (1995, 2001).

Table 2
Specimens use for molecular analysis, with voucher data and GenBank accession numbers (sequences generated for this study are in bold)

Genus	Species	Subfam/tribe	Molecular codes	Voucher/repository	Locality	12S	16S	cyt b	18S	28SA	28SD	H3
<i>Absonemobius</i>	<i>guyanensis</i> Desutter-Grandcolas, 1993	NEMO-Ple	LDG 047	ENSIF3252	French Guiana, Arataye	KR903868	ND	KR903363	KR904058	KR903497	KR902996	KR903183
<i>Acantholaciarida</i>	<i>nigra</i> Desutter-Grandcolas, 1992	LUZA	LDG 221	ENSIF3277	French Guiana, Arataye	KR903995	KR903804	KR903467	KR904178	KR903644	KR903122	KR903301
<i>Acheta</i>	<i>domesticus</i> (Linnaeus, 1758)	GRYL-Gry	Adom	ENSIF3523	Breeding strain	KR903831	KR903672	KR903330	KR904025	KR903498	KR902997	KR903150
<i>Acheta</i>	<i>rafanictus</i> Uvarov, 1957	GRYL-Gry	LDG 178	RF-2010-10	Yemen, Soocra	KR903964	KR903786	KR903446	KR904150	KR903623	KR903101	KR903272
<i>Acicella</i>	<i>nova</i> Desutter-Grandcolas, 2014	PARA-Par	LDG 065	INBio 05/TH/06/016	Costa Rica	KR903883	ND	ND	KR904074	KR903548	ND	KR903199
<i>Adenopterus</i> (<i>Archenopterus</i>)	<i>sp1_NC</i>	PODO	LDG 200	ENSIF3297	New Caledonia	KR903979	KR903795	KR903454	KR904163	ND	KR902993	KR903286
<i>Adenopterus</i> (<i>Archenopterus</i>)	<i>sp2_NC</i>	PODO	LDG 218	ENSIF3271	New Caledonia	KR903992	KR903802	KR903464	KR904175	ND	KR903119	KR903299
<i>Afrophalarida</i>	<i>amant</i> Desutter-Grandcolas, 2015	PHOR	LDG 037	ENSIF3341	Tanzania	KR903858	KR903696	KR903353	KR904049	KR903524	KR903023	KR903173
<i>Agnateocus</i>	<i>tapinopus</i> Saussure, 1878	ENEQ-Leb	ATaMo	ENSIF2769	New Caledonia	JX897379	JX897345	JX897326	JX897580	KR903499	ND	JX897557
<i>Allonemobius</i>	<i>fasciatus</i> (De Geer, 1773)	NEMO-Pe	LDG 141	SH-2005-002	Quebec	KR903934	ND	KR903422	ND	KR903595	KR903081	KR903244
<i>Anaphiacusta</i>	<i>carabica</i> Saussure, 1897	LUZA	LDG 020	ENSIF3045	West Indies, Guadeloupe	KR903848	KR903687	KR903344	KR904039	KR903515	KR903014	KR903165
<i>Anusodes</i>	<i>sp affinis estrellae</i> Hebard, 1928	LUZA	LDG 242	MEUV	Colombia	KR904003	KR903812	KR903475	KR904185	KR903651	KR903128	KR903309
<i>Anusargus</i>	<i>sp_Van</i>	TRIG-Tri	LDG 167	ENSIF3368	Vanuatu, Espiritu Santo	KR903957	KR903779	KR903439	ND	KR903617	ND	KR903265
<i>Anaxipha</i>	<i>sp affinis nitida</i> (Chopard, 1912)	TRIG-Tri	LDG 101	ENSIF3260	French Guiana, Arataye	KR903906	KR903735	KR903396	KR904094	KR903570	KR903058	KR903220
<i>Anaxipha</i>	<i>sp_GDE</i>	TRIG-Tri	LDG 151	SH-2010-038	West Indies, Guadeloupe	KR903943	KR903768	KR903429	KR904130	KR903604	ND	KR903253
<i>Anaxipha</i>	<i>sp affinis fuscocinctum</i> (Chopard, 1925)	TRIG-Tri	LDG 168	ENSIF3371	Vanuatu, Espiritu Santo	KR903958	KR903780	KR903440	KR904144	KR903618	KR903096	KR903266
<i>Antiltharis</i>	<i>maximius</i> (Desutter-Grandcolas, 2003)	ENEQ	LDG 194	ENSIF3269	West Indies, Guadeloupe	KR903975	KR903794	ND	KR904159	ND	KR903108	KR903282
<i>Anurogryllus</i>	<i>muticus</i> (De Geer, 1773)	GRYL-Gry	Amu	ENSIF3172	Nicaragua	KR903832	AY905322	ND	AY905346	ND	ND	ND
<i>Anurogryllus</i> (<i>Urogryllus</i>)	<i>sp_FGu</i>	GRYL-Gry	LDG 103	ENSIF3262	French Guiana, Arataye	KR903908	KR903737	KR903398	KR904096	KR903572	KR903060	KR903222
<i>Aphononorphus</i>	<i>sp_FGu</i>	PODO-Pod	LDG 210	ENSIF3299	French Guiana	KR903986	ND	KR903460	ND	ND	ND	ND
<i>Aphononorphus</i> (<i>Euphonus</i>)	<i>sp_FGu</i>	PODO-Pod	LDG 179	ENSIF3245	French Guiana	KR903965	KR903787	ND	ND	KR903624	ND	KR903273
<i>Apterogryllus</i>	<i>nsp_Van</i>	GRYL-Cep	LDG 165	ENSIF3367	Vanuatu, Espiritu Santo	KR903955	KR903778	KR903438	KR904142	KR903615	ND	KR903263
<i>Aracamby</i>	<i>nsp_Bra</i>	LUZA	LDG 039	ENSIF3305	Brazil, Sao Paulo	KR903860	KR903698	KR903355	KR904051	KR903526	ND	KR903175
<i>Arachnocephalus</i>	<i>vestitus</i> Costa, 1855	MOGO-Ara	LDG 215	SH-2007-001	France, Corse	KR903990	ND	ND	KR904173	KR903640	ND	ND
<i>Arilpa</i>	<i>gibba</i> Ote & Alexander, 1983	ENEQ-Eur	Agi	ANIC	Western Australia	AY905268	AY905297	AY905351	AY905327	ND	ND	ND
<i>Brachytrapes</i>	<i>membranaceus</i> (Drury, 1770)	GRYL	LDG 125	ENSIF3385	Mozambique	KR903922	KR903749	KR903410	KR904109	KR903583	KR903071	KR903232
<i>Brasilodontus</i>	<i>riodocensis</i> de Mello, 1992	LAND-Lan	LDG 227	ENSIF3338	Brazil, Espiritu Santo	KR903999	KR903807	KR903470	ND	ND	ND	ND
<i>Brevizuela</i>	<i>molisae</i> Desutter-Grandcolas, 2009	PARA-Par	LDG 010	ENSIF2832	Vanuatu, Espiritu Santo	KR903842	KR903681	KR903338	KR904033	KR903510	KR903008	KR903159
<i>Bullia</i>	<i>sp_NC</i>	NEMO-Nem	LDG 235	ENSIF3393	New Caledonia	KR904001	KR903810	KR903473	KR904183	KR903649	KR903126	KR903307
<i>Calacirius</i>	<i>amaoa</i> Ote, 1987	PODO-Pod	LDG 219	ENSIF3110	New Caledonia	KR903993	ND	KR903465	KR904176	KR903642	KR903120	KR903300
<i>Callithra</i>	<i>sp_NC</i>	PARA-Par	LDG 006	ENSIF3326	New Caledonia	KR903841	KR903680	KR903337	KR904032	KR903509	KR903007	KR903158

Table 2
(Continued)

Genus	Species	Subfam./tribe	Molecular codes	Voucher/repository	Locality	12S	16S	cyt b	18S	28S-A	28S-D	H3
<i>Caltatbra</i>	<i>sp. affinis doensis</i> Desutter-Grandcolas, 2006	PARA-Par	LDG 134	ENSIF3087	New Caledonia	KR903929	KR903756	KR903417	KR904116	KR903590	KR903078	KR903239
<i>Cardiodactylus</i>	<i>novaequeanae</i> (Haan, 1842)	ENE0-Leb	CnoPe	ENSIF2030	Vanuatu, Espiritu Santo	JF972506	JF972521	JF972490	JF972537	KR903500	KR902998	KR903151
<i>Cardiodactylus</i>	<i>kondo</i> 1 Ote, 2007	ENE0-Leb	Cphh2	ENSIF3154	Philippines, Luçon	KR903833	KR903673	ND	KR904027	KR903501	KR902999	KR903152
<i>Cearacsa</i>	<i>nsp. Bra</i>	HAPI-Cea	LDG 209	ENSIF3270	Brazil, Pernambuco	KR903985	KR903798	KR903459	KR904170	KR903638	ND	KR903294
<i>Cearacsa</i>	<i>sp. Bra</i>	HAPI-Cea	LDG 166	ENSIF3318	Brazil	KR903956	ND	ND	KR904143	KR903616	ND	KR903264
<i>Coblenemus</i>	<i>sp. India</i>	GRYL	LDG 072	ENSIF3410	India	KR903888	KR903720	KR903380	KR904079	KR903553	ND	KR903204
<i>Cophogryllus</i>	<i>sp. India</i>	GRYL-Cop	LDG 080	ENSIF3412	India, Karnataka	KR903892	KR903724	KR903383	KR904083	KR903557	KR903048	KR903208
<i>Cophonemobius</i>	<i>faustini</i> Desutter-Grandcolas, 2009	NEMO	LDG 162	ENSIF2144	Vanuatu, Espiritu Santo	KR903952	KR903776	KR903435	KR904139	KR903612	KR903093	KR903260
<i>Cranisus</i>	<i>sp. Mex</i>	TRIG-Phy	LDG 114	ENSIF3376	Mexico, Jalisco	KR903917	ND	KR903405	ND	ND	ND	KR903228
<i>Creolandra</i>	<i>crepitans</i> Hugel, 2009	LAND	LDG 138	SH-2009-197	Mauritius	KR903931	KR903758	KR903419	KR904118	KR903592	KR903079	KR903241
<i>Cycloptiloides</i>	<i>orientalis</i> Chopard, 1925	MOGO-Mog	LDG 188	SH-2009-195	La Réunion	KR903970	ND	ND	ND	KR903630	KR903104	ND
<i>Derecctotus</i>	<i>sp. Com</i>	MOGO-Mog	LDG 097	ENSIF3374	Comoros, Moheli	KR903902	KR903731	KR903392	KR904090	KR903567	ND	KR903217
<i>Derecctotus</i>	<i>sp. May</i>	MOGO-Mog	LDG 098	ENSIF3375	Mayotte	KR903903	KR903732	KR903393	KR904091	KR903568	ND	KR903218
<i>Diatripa</i>	<i>sp. FGu</i>	PODO-Aph	LDG 092	ENSIF3261	French Guiana, Arataye	KR903899	KR903728	KR903389	KR904087	KR903564	KR903054	KR903214
<i>Ectatoderus</i>	<i>brevipalpis</i> Chopard, 1957	MOGO-Mog	LDG 146	SH-2009-106	La Réunion	KR903938	KR903763	KR903425	KR904125	KR903599	KR903083	KR903248
<i>Ectatoderus</i>	<i>sp. Mar</i>	MOGO-Mog	LDG 193	SH-2008-040	West Indies, Martinique	KR903974	ND	KR903451	KR904158	ND	ND	KR903281
<i>Ectatoderus</i>	<i>sp. FGu</i>	MOGO-Mog	LDG 105	ENSIF3275	French Guiana, Arataye	ND	KR903739	ND	KR904085	ND	KR902989	ND
<i>Ectococcus</i>	<i>sp. FGu</i>	PARA-Par	LDG 090	ENSIF3384	French Guiana	KR903897	KR903726	KR903387	KR904085	KR903562	KR903052	KR903212
<i>Eneoptera</i>	<i>guyanensis</i> Chopard, 1931	ENE0-Ene	Egu	ENSIF2741	French Guiana	AY905272	AY905301	AY905355	AY905331	KR903502	KR903000	JX897547
<i>Eugryllodes</i>	<i>pipiens</i> (Dufour, 1820)	GRMP-Grm	LDG 189	ES	France	KR903971	KR903792	ND	ND	ND	KR903105	KR903278
<i>Eumemobius</i>	<i>carolinus</i> (Seudder, 1877)	NEMO-Pte	LDG 149	SH-2005-01	Quebec	KR903941	KR903766	ND	KR904128	KR903602	KR903086	KR903251
<i>Eurepa</i>	<i>margitipennis</i> (White, 1841)	ENE0-Eur	Ema	ANIC	South Australia	AY905274	AY905303	AY905357	JF972540	ND	ND	ND
<i>Eurepella</i>	<i>mojeria</i> Ote & Alexander, 1983	ENE0-Eur	Emo	ANIC	Australia, Queensland	AY905277	AY905307	AY905361	ND	ND	ND	ND
<i>Eurepini</i>	<i>sp. Aus</i>	ENE0-Eur	Eursp	ENSIF3155	Australia, Northern Territory	KR903834	KR903674	KR903331	KR904028	KR903503	KR903001	KR903153
<i>Euscyrus</i>	<i>sp. affinis bipunctatus</i> Chopard, 1958	EUSC	LDG 161	ENSIF3310	Vanuatu, Espiritu Santo	KR903951	KR903775	ND	KR904138	KR903492	KR902988	KR903259
<i>Euscyrus</i>	<i>bivittatus</i> Guérin-Méneville, 1844	EUSC	LDG 187	SH-2008-071	Mauritius	KR903969	KR903791	ND	KR904155	KR903629	ND	KR903277
<i>Fraxinus</i>	<i>sp. Com</i>	PODO-Pod	LDG 096	ENSIF3378	Comoros, Moheli	KR903901	KR903730	KR903391	KR904089	KR903566	KR903056	KR903216
<i>Gaenoblemmus</i>	<i>rasilis</i> Karsch, 1893	GRYL-Gry	LDG 158	ENSIF3387	Gabon, La Makande	KR903948	ND	KR903433	KR904135	KR903609	KR903091	KR903257
<i>Gaialta</i>	<i>strasbergi</i> Hugel, 2014	GRYL-Gry	LDG 148	SH-2009-173	Mauritius	KR903940	KR903765	KR903427	KR904127	KR903601	KR903085	KR903250
<i>Gryllinae</i>	<i>sp. Moz</i>	GRYL	LDG 121	ENSIF3602	Mozambique	KR903920	KR903747	KR903408	KR904107	KR903581	KR903069	KR903230
<i>Gryllodes</i>	<i>sigillatus</i> (Walker, 1869)	GRYL-Mod	LDG 042	ENSIF3249	Comoros, Anjouan	KR903863	KR903701	KR903358	KR904053	KR903529	KR903027	KR903178
<i>Gryllomorpha</i>	<i>dalmatina</i> (Oeskay, 1832)	GRMP-Grm	LDG 185	ENSIF3332	France	KR903968	KR903790	KR903449	KR904153	KR903627	KR903103	KR903276
<i>Gryllotalpa</i>	<i>sp. Moz</i>	GRTL-Gtl	LDG 171	ENSIF3315	Mozambique	KR903961	KR903783	KR903443	KR904147	KR903621	KR903099	KR903269
<i>Gryllotalpa</i>	<i>africana</i> Pulisot de Beauvois, 1805	GRTL-Gtl	LDG 175	RF-2009-312	Yemen, Socotra	KR903963	ND	KR903445	ND	ND	ND	ND
<i>Gryllotalpa</i>	<i>sp. PNG</i>	GRTL-Gtl	LDG 253	ENSIF3317	PNG, Mt Wilhelm	KR904013	KR903821	KR903484	KR904195	KR903661	ND	KR903317

Table 2
(Continued)

Genus	Species	Subfam/tribe	Molecular codes	Voucher/repository	Locality	12S	16S	cyt b	18S	28SA	28SD	H3
<i>Gryllotalpa</i>	sp2_PNG	GRTL-Gil	LDG 254	ENSIF3339	PNG, Mt Wilhelm	KR904014	KR903822	KR903485	KR904196	KR903662	KR903138	KR903318
<i>Gryllus</i>	<i>binaculatus</i> De Geer, 1773	GRYL-Gry	Gbi2/LDG 075	ENSIF3324/3404	Breeding strain / India, Karnataka	KR903835	KR903675	KR903332	KR904029	KR903504	KR903002	KR903154
<i>Gymnogyllus</i>	sp_PNG	GRYL-Gry	LDG 249	ENSIF3320	PNG, Mt Wilhelm	KR904009	KR903817	KR903480	KR904191	KR903657	KR903134	KR903314
<i>Hapithinae</i> n. gen. n.	sp_Ven	PODO	LDG 226	ENSIF3377	Venezuela, Aragua	KR903998	ND	ND	ND	KR903647	ND	KR903304
<i>Hapithus</i>	sp_Mex	HAPL-Hap	LDG 204	ENSIF3316	Mexico, Chiapas	KR903982	ND	KR903456	KR904166	KR903635	KR903114	KR903289
<i>Hemigyllus</i>	sp_FCu	NEMO-Hem	LDG 089	ENSIF3383	French Guiana	KR903896	ND	KR903386	KR904084	KR903561	KR903051	ND
<i>Homocoryllus</i>	<i>gabonensis</i> Desutter, 1985	CACH-Hom	LDG 033	ENSIF3400	Dem Rep Congo	KR903856	ND	KR903351	KR904047	KR903523	KR903021	ND
<i>Homocoryllus</i>	<i>orientalis</i> Desutter, 1985	CACH-Hom	LDG 129	ENSIF3603	Mozambique, Cabo Delgado	KR903925	KR903752	KR903413	KR904112	KR903586	KR903074	KR903235
<i>Homocoxipha</i>	<i>cf lycoides</i> (Walker, 1869)	TRIG-Tri	LDG 140	SH-2010-135	Seychelles	KR903933	KR903760	KR903421	KR904120	KR903594	ND	KR903243
<i>Hygromemobius</i>	<i>amoenus</i> Chopard, 1912	NEMO-Pie	LDG 048	ENSIF3250	French Guiana, Arataye	KR903869	KR903706	ND	KR904059	KR903534	ND	KR903184
<i>Iaropsis</i>	<i>tenella</i> (Walker, 1869)	GRYL	l094	ENSIF3406	India, Karnataka	KR903836	KR903676	JN411891	ND	KR903496	KR902995	KR903155
<i>Kempia</i>	<i>flavipunctatus</i> Desutter-Grandcolas, 2012	CACH-Hom	LDG 013	ENSIF3054	India, Karnataka	KR903844	KR903683	KR903340	KR904035	KR903512	KR903010	KR903161
<i>Kevanacla</i>	<i>orientalis</i> Desutter-Grandcolas, 1992	PARA-Par	LDG 110	ENSIF3272	French Guiana, Arataye	KR903914	KR903743	KR903403	KR904103	KR903577	KR903066	KR903226
<i>Koghella</i>	sp_NC	NEMO-Nem	LDG 236	ENSIF3395	New Caledonia	KR904002	KR903811	KR903474	KR904184	KR903650	KR903127	KR903308
<i>Landreva</i>	nsp_India	LAND-Lan	LDG 032	ENSIF3292	India, Karnataka	KR903855	KR903694	KR903350	KR904046	KR903522	KR903020	KR903171
<i>Landrevini</i>	sp_PNG	LAND-Lan	LDG 255	ENSIF3298	PNG, Mt Wilhelm	KR904015	KR903823	KR903486	KR904197	KR903663	KR903139	KR903319
<i>Laurepa</i>	sp_GDE	HAPL-Hap	LDG 191	ENSIF3268	West Indies, Guadeloupe	KR903972	KR903793	KR903450	KR904156	ND	KR903106	KR903279
<i>(= Orochirus)</i>												
<i>Lebithus</i>	<i>santoensis</i> Robillard, 2009	ENE0-Leb	LsaV	ENSIF2437	Vanuatu, Espiritu Santo	JF972511	JF972527	JF972495	JF972542	JX897467	ND	JX897548
<i>Lebithus</i>	<i>laue</i> Robillard & Tan, 2013	ENE0-Leb	LbsS	ENSIF2740	Singapore	KR904017	JF972524	JF972493	KR904199	KR903665	KR903141	KR903321
<i>Lepidogyllus</i>	<i>comparatus</i> (Walker, 1869)	GRYL-Mod	LDG 202	ENSIF3243	New Caledonia	KR903980	KR903796	KR903455	KR904164	ND	KR903112	KR903287
<i>Lepidopedetes</i>	<i>idalimos</i> Otte, 2006	LUZA	LDG 011	ENSIF3398	Costa Rica	KR903843	KR903682	KR903339	KR904034	KR903511	KR903009	KR903160
<i>Lerneca</i>	<i>fuscipennis</i> (Saussure, 1874)	LUZA	LDG 067	ENSIF3528	French Guiana, Arataye	KR903884	KR903717	KR903376	KR904075	KR903549	KR903042	KR903200
<i>Lernecella</i>	nsp_GDE	LUZA	LDG 021	ENSIF3301	West Indies, Guadeloupe	KR903849	KR903688	KR903345	KR904040	KR903516	KR903015	KR903166
<i>Lernecella</i>	<i>minuta</i> Desutter-Grandcolas, 1992	LUZA	LDG 053	ENSIF3255	French Guiana, Guadeloupe	KR903874	KR903711	ND	KR904064	KR903539	KR903035	KR903189
<i>Ligypterus</i>	<i>fuscus</i> Chopard, 1920	ENE0-Ene	LfuN02	ENSIF3156	French Guiana, Arataye	KR904018	KR903825	KR903487	KR904200	KR903666	KR903142	KR903322
<i>Loxoblemmus</i>	sp_Indo	GRYL-Gry	LDG 130	ENSIF3331	Indonesia, Lombok	KR903926	KR903753	KR903414	KR904113	KR903587	KR903075	KR903236
<i>Luzara</i>	<i>brevipennis</i> Desutter-Grandcolas, 2014	LUZA	LDG 015	ENSIF3399	Costa Rica	KR903846	KR903685	KR903342	KR904037	ND	KR903012	KR903163
<i>Luzarida</i>	<i>grandis</i> Desutter-Grandcolas, 1992	LUZA	LDG 055	ENSIF3258	French Guiana, Arataye	KR903876	KR903713	KR903369	KR904066	KR903541	KR903037	KR903191
<i>Luzaridella</i>	<i>obscura</i> Desutter-Grandcolas, 1992	LUZA	LDG 050	ENSIF3253	French Guiana, Arataye	KR903871	KR903708	KR903365	KR904061	KR903536	KR903033	KR903186
<i>Luzaridella</i>	<i>clara</i> Desutter-Grandcolas, 1992	LUZA	LDG 054	ENSIF3254	French Guiana, Arataye	KR903875	KR903712	KR903368	KR904065	KR903540	KR903036	KR903190
<i>Malgasia</i>	sp_Com	MALG	LDG 026	ENSIF3382	Comoros, Grande Comore	KR903852	KR903691	ND	KR904043	KR903519	KR903017	KR903168
<i>Manianus</i>	<i>calcanicus</i> (Saussure, 1878)	PODO-Pod	Msp_Po	IAC	New Caledonia	KR904019	KR903826	KR903488	ND	ND	KR903143	KR903323
<i>Megacris</i>	<i>lpsae</i> Desutter-Grandcolas, 2009	no	LDG 084	ENSIF2901	Vanuatu, Espiritu Santo	KR903895	KR903725	ND	ND	KR903560	KR903050	ND

Table 2
(Continued)

Genus	Species	Subfam/tribe	Molecular codes	Voucher/repository	Locality	12S	16S	cyt b	18S	28SA	28SD	H3
<i>Meloinorpha</i>	<i>japonica yunnanensis</i> (Yin, 1998)	CACH-Hom	LDG 233	ENSIF3308	China, Padang	KR904000	KR903808	KR903471	KR904181	KR903648	KR903125	KR903305
<i>Microlandrewa</i> (?)	nsp_May	LAND-Lan	LDG 170	ENSIF3307	Mayotte	KR903960	KR903782	KR903442	KR904146	KR903620	KR903098	KR903268
<i>Micromerica</i>	<i>leiticia</i> de Mello, 1995	LUZA	LDG 040	ENSIF3072	Brazil	KR903861	KR903699	KR903356	ND	KR903527	KR903025	KR903176
<i>Miklathomaklathia</i>	sp_PNG	PARA-Par	LDG 252	ENSIF3294	PNG, Mt Wilhelm	KR904012	KR903820	KR903483	KR904194	KR903660	KR903137	KR903316
<i>Miogrillodes</i>	<i>hebardii</i> Desutter-Grandcolas, 2014	LUZA	LDG 059	ENSIF3397	Costa Rica	KR903879	ND	KR903371	KR904069	KR903544	KR903038	KR903194
<i>Miogrillus</i>	<i>verticalis</i> (Serville, 1839)	GRYL-Mod	LDG 102	ENSIF3248	French Guiana, Arataye	KR903907	KR903736	KR903397	KR904095	KR903571	KR903059	KR903221
<i>Misshenkenoana</i>	sp_Van	PODO-Aph	LDG 160	ENSIF3311	Vanuatu, Espiritu Santo	KR903950	KR903774	KR903434	KR904137	KR903611	KR903092	KR903258
<i>Modicogryllus</i>	<i>stannensis</i> Chopard, 1961	GRYL-Mod	LDG 081	ENSIF3413	India	KR903893	ND	KR903384	ND	KR903558	ND	KR903209
<i>Modicogryllus</i> (<i>Eumodicogryllus</i>)	<i>boridagensis</i> (Latreille, 1804)	GRYL-Mod	LDG 174	RF-2010	The Netherlands	KR903962	KR903785	KR903444	KR904149	KR903622	KR903100	KR903271
<i>Munda</i>	<i>sp affinis asyrinx</i> (Saussure, 1878)	PODO-Aph	LDG 131	ENSIF3373	Indonesia, Java	KR903927	KR903754	KR903415	KR904114	KR903588	KR903076	KR903237
<i>Myara</i>	<i>sordida</i> (Walker, 1869)	ENE0-Eur	Mso	ANIC	Australia, Queensland	AY905282	AY905312	AY905367	AY905339	ND	ND	ND
<i>Myrmecophilus</i> (<i>Myrmecophilus</i>)	<i>quadrifidus</i> Perkins, 1899	MYRM-Myr	LDG 186	SH-2003-001	La Réunion	ND	ND	ND	KR904154	KR903628	ND	ND
<i>Myrmecophilus</i> (<i>Myrmophilina</i>)	<i>americanus</i> Saussure, 1877	MYRM-Myr	LDG 156	SH-Antigua317	Antigua	KR903947	KR903772	KR903432	KR904134	KR903608	ND	ND
<i>Nattula</i>	<i>longipennis</i> (Serville, 1839)	TRIG-Tri	LDG 139	SH-2008-080	Mauritius	KR903932	KR903759	KR903420	KR904119	KR903593	KR903080	KR903242
<i>Nemobinae</i>	<i>ngen_NC</i>	NEMO	LDG 246	ENSIF3394	New Caledonia	KR904006	KR903814	KR903477	KR904188	KR903654	KR903131	KR903312
<i>Nemobinae</i>	sp_Com	NEMO	LDG 049	ENSIF3314	Comoros, Anjouan	KR903870	KR903707	KR903364	KR904060	KR903535	KR903032	KR903185
<i>Nemobius</i>	<i>sybextris</i> (Bosc, 1792)	NEMO-Nem	LDG 206	ENSIF3244	France	KR903983	ND	KR903458	KR904168	KR903636	KR903115	KR903291
<i>Neomegrypus</i>	sp_FGn	PODO-Pod	LDG 224	ENSIF3264	French Guiana, Arataye	KR903997	KR903806	KR903469	KR904180	KR903646	KR903124	KR903303
<i>Nigritana</i>	<i>physelis</i> (Otte, 2006)	LUZA	LDG 060	ENSIF3692	Costa Rica	KR903880	KR903715	KR903372	KR904070	KR903545	KR903039	KR903195
<i>Nisitrus</i>	<i>vittatus</i> (Haan, 1842)	ENE0-Nis	NvS	ENSIF2742	Singapur	AY905284	AY905314	AY905369	KR904021	KR903667	KR903144	KR903324
<i>Noctivox</i>	nsp_Mex	LUZA	LDG 208	ENSIF3340	Mexico, Tamaulipas	ND	ND	ND	KR904169	KR903637	ND	KR903293
<i>Noxosciobia</i>	nsp_NC	GRYL-Cep	LDG 164	ENSIF3325	New Caledonia	KR903954	KR903777	KR903437	KR904141	KR903614	KR903095	KR903262
<i>Odonotogryllus</i>	<i>setosus</i> Saussure, 1877	LAND-Lan	LDG 100	ENSIF3263	French Guiana, Arataye	KR903905	KR903734	KR903395	KR904093	KR903495	KR902994	ND
<i>Oecanthus</i>	sp_Com	OECA	LDG 045	ENSIF3293	Comoros, Grande Comore	KR903866	KR903704	KR903361	KR904056	KR903532	KR903030	KR903181
<i>Oecanthus</i>	sp_FGu	OECA	LDG 211	ENSIF3300	French Guiana	KR903987	KR903799	KR903461	ND	ND	ND	ND
<i>Oecanthus</i>	<i>chopardi</i> Uvarov, 1957	OECA	LDG 173	RF-2010-18	Yemen, Socotra	ND	KR903784	ND	KR904148	KR903493	KR902990	KR903270
<i>Opilostina</i>	<i>meridionalis</i> Desutter-Grandcolas, 2012	PHAL	LDG 014	ENSIF2946	India, Karnataka	KR903845	KR903684	KR903341	KR904036	KR903513	KR903011	KR903162
<i>Ornebius</i>	<i>xanthopterus</i> Guérin-Méneville, 1844	MOGO-Mog	LDG 153	SH-2011-016	Mauritius	KR903944	KR903769	KR903430	KR904131	KR903605	KR903088	KR903254
<i>Ornebius</i>	sp_GDE	MOGO-Mog	LDG 184	SH-2011-085	West Indies, Guadeloupe	KR903967	KR903789	KR903448	KR904152	KR903626	ND	KR903275
<i>Orocharis</i>	<i>sp affinis lividus</i> Chopard, 1912	HAP1-Hap	LDG 222	ENSIF3274	French Guiana, Arataye	KR903996	KR903805	KR903468	KR904179	KR903645	KR903123	KR903302
<i>Orthoxiphus</i>	sp_Com	PENT	LDG 220	ENSIF3379	Comoros, Anjouan	KR903994	KR903803	KR903466	KR904177	KR903643	KR903121	ND
<i>Poana</i>	sp_NC	NEMO-Tle	LDG 244	ENSIF3312	New Caledonia	KR904005	ND	ND	KR904187	KR903653	KR903130	KR903311
<i>Paragryllodes</i>	sp_Com	no-End	LDG 024	ENSIF3380	Comoros, Moheli	KR903851	KR903690	KR903347	KR904042	KR903518	KR903016	ND
<i>Paragryllodes</i>	sp_Mad	no-End	LDG 137	ENSIF3526	Madagascar	KR903930	KR903757	KR903418	KR904117	KR903591	ND	KR903240
<i>Paragryllodes</i>	<i>maritimi</i> Guérin-Méneville, 1844	PARA-Par	LDG 003	ENSIF3327	West Indies, Guadeloupe	KR903838	ND	KR903334	ND	KR903506	KR903004	ND
<i>Paranisitra</i>	<i>longipes</i> Chopard, 1925	ENE0-Nis	Pl02	ENSIF3157	Philippines, Luzon	KR904020	KR903827	ND	KR904202	KR903668	KR903145	KR903325
<i>Parentacastes</i>	<i>makassar</i> Gorochov, 2006	PHAL-Pta	LDG 001	ENSIF3330	Indonesia, Sulawesi	KR903837	KR903677	KR903333	KR904030	KR903505	KR903003	KR903156
<i>Parentacastes</i>	nsp_Indo	PHAL-Pta	LDG 016	ENSIF3372	Indonesia, Sumba	KR903847	KR903686	KR903343	KR904038	KR903514	KR903013	KR903164
<i>Parentacastes</i>	<i>liffoensis</i> Desutter-Grandcolas, 2002	PHAL-Pta	LDG 112	ENSIF2940	New Caledonia, Lifou	KR903915	ND	KR903404	ND	ND	ND	ND

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(Continued)

Genus	Species	Subfam./tribe	Molecular codes	Voucher/repository	Locality	12S	16S	cyt b	18S	28SA	28SD	H3
<i>Parocentritus</i>	<i>sp.</i> FGcu	PODO-Pac	LDG 091	ENSIF3525	French Guiana, Arataye	KR903898	KR903727	KR903388	KR904086	KR903563	KR903053	KR903213
<i>Pentacentrus</i>	<i>cf. biroi</i> Chopard, 1927	PENT	LDG 159	ENSIF3370	Vanuatu, Espiritu Santo	KR903949	KR903773	ND	KR904136	KR903610	ND	ND
<i>Petalopilla</i>	<i>aliena</i> (Brunner von Wattenwyl, 1882)	GRMP-Pet	LDG 183	ESI	France	KR903966	KR903788	KR903447	KR904151	KR903625	KR903102	KR903274
<i>Petalopilla</i>	<i>andreni</i> Capra, 1937	GRMP-Pet	LDG 192	ES2	France	KR903973	ND	ND	KR904157	ND	KR903107	KR903280
<i>Phaeogryllus</i>	<i>fuscus</i> Bolivar, 1912	PHAL-Het	LDG 142	SH-2010-192	Seychelles	KR903935	KR903761	KR903423	KR904122	KR903596	KR903082	KR903245
<i>Phaeophylacris</i>	<i>nsp.</i> Com	no-End	LDG 022	ENSIF3381	Comoros, Anjouan	KR903850	KR903689	KR903346	KR904041	KR903517	ND	KR903167
<i>Phaeophylacris</i>	<i>nsp.</i> Gha	no-End	LDG 035/066	ENSIF3337	Ghana	KR903857	KR903695	KR903352	KR904048	KR903022	KR903022	KR903172
<i>Phaeophylacris</i>	<i>sp.</i> CAR	no-End	LDG 038	ENSIF3527	CAR	KR903859	KR903697	KR903354	KR904050	KR903525	KR903024	KR903174
<i>Phaeophylacris</i>	<i>spectrum</i> Saussure, 1878	no-End	LDG 124	ENSIF3336	Mozambique, Cabo Delgado	KR903921	KR903748	KR903409	KR904108	KR903582	KR903070	KR903231
<i>Phalangopsis</i>	<i>flavilongipes</i> Desutter-Grandcolas, 1992	PHAL-Pha	LDG 052	ENSIF3256	French Guiana, Arataye	KR903873	KR903710	KR903367	KR904063	KR903538	KR903034	KR903188
<i>Phaloria</i>	<i>chopardi</i> (Willemsse, 1925)	PHOR-Pho	LDG 203	ENSIF2108	Vanuatu, Espiritu Santo	KR903981	ND	ND	KR904165	KR903634	KR903113	KR903288
<i>Phalorinae</i>	<i>sp.</i> Indo	PHOR-Pho	LDG 132	ENSIF3324	Indonesia, Sumba	KR903928	KR903755	KR903416	KR904115	KR903589	KR903077	KR903238
<i>Phalorinae</i>	<i>sp.</i> Phi	PHOR-Pho	LDG 243	ENSIF3604	Philippines, Luçon	KR904008	KR903813	KR903476	KR904186	KR903652	KR903129	KR903310
<i>Phalorinae</i>	<i>sp.</i> PNG	PHOR-Pho	LDG 248	ENSIF3321	PNG, Mt Wilhelm	KR904008	KR903816	KR903479	KR904190	KR903656	KR903133	ND
<i>Phalorinae</i>	<i>sp.</i> PNG	PHOR-Pho	LDG 250	ENSIF3322	PNG, Mt Wilhelm	KR904010	KR903818	KR903481	KR904192	KR903658	KR903135	KR903315
<i>Phalorinae</i>	<i>sp.</i> PNG	PHOR-Pho	LDG 256	ENSIF3296	PNG, Mt Wilhelm	KR904016	KR903824	ND	KR904198	KR903664	KR903140	KR903320
<i>Philippopsis</i>	<i>guianae</i> Desutter-Grandcolas, 1992	PHAL-Pha	LDG 051	ENSIF3257	French Guiana, Arataye	KR903872	KR903709	KR903366	KR904062	KR903537	ND	KR903187
<i>Phonarellus</i>	<i>minor</i> (Chopard, 1959)	GRYL-Gry	LDG 078	ENSIF3414	India, Kerala	KR903891	KR903723	KR903382	KR904082	KR903556	KR903047	KR903207
<i>Phyllogryllus</i>	<i>nsp.</i> GDE	PODO-Pod	LDG 043	ENSIF3303	West Indies, Guadeloupe	KR903864	KR903702	KR903359	KR904054	KR903530	KR903028	KR903179
<i>Plebeiogryllus</i>	<i>guttiventris</i> (Walker, 1871)	GRYL-Gry	LDG 076	ENSIF3411	India	KR903889	KR903721	KR903381	KR904080	KR903554	KR903046	KR903205
<i>Poilonemobius</i>	<i>sp. affinis raprobanensis</i> (Walker, 1869)	NEMO-Pie	LDG 057	ENSIF3396	India, Karnataka	KR903877	KR903714	KR903370	KR904067	KR903542	ND	KR903192
<i>Ponca</i>	<i>venosa</i> Hebard, 1928	ENEO-Ene	Pve	ENSIF3158	Costa Rica	KR904021	KR903828	KR903489	KR904203	KR903669	KR903146	KR903326
<i>Proshama</i>	<i>tessellata</i> Hebard, 1928	LUZA	LDG 062	ENSIF3694	Costa Rica	KR903881	ND	KR903374	KR904072	KR903546	KR903040	KR903197
<i>Protathra</i>	<i>centralis</i> Desutter-Grandcolas, 2014	no-End	LDG 005	ENSIF3124	New Caledonia	KR903840	KR903679	KR903336	KR904031	KR903508	KR903006	ND
<i>Proturana</i>	<i>subapertus</i> (Chopard, 1970)	EUSC	LDG 163	ENSIF3076	New Caledonia	KR903953	ND	KR903436	KR904140	KR903613	KR903094	KR903261
<i>Prozevella</i>	<i>bangalorensis</i> Desutter-Grandcolas, 2003	PODO-Pod	LDG 216	ENSIF3329	India, Karnataka	KR903991	ND	KR903463	KR904174	KR903641	KR903118	KR903298
<i>Pseudotrignidium</i>	<i>noctifolia</i> (Desutter-Grandcolas, 1997)	PHOR-Pho	LDG 213	ENSIF3111	New Caledonia	KR903988	KR903800	ND	KR904171	ND	KR903116	KR903296
<i>Pteronemobius</i>	<i>sp.</i> Moz	NEMO-Pie	LDG 127	ENSIF3391	Mozambique, Cabo Delgado	KR903924	KR903751	KR903412	KR904111	KR903585	KR903073	KR903234
<i>Pteronemobius</i>	<i>obscurior</i> Chopard, 1957	NEMO-Pie	LDG 155	SH-2009-192	La Réunion	KR903946	KR903771	KR903431	KR904133	KR903607	KR903090	KR903256
<i>Pteronemobius</i>	<i>heydeni</i> (Fischer, 1853)	NEMO-Pie	LDG 207	ENSIF3246	France	KR903984	ND	ND	ND	ND	ND	KR903292
<i>Pteroplistes</i>	<i>masingaudi</i> Jaiswara, 2014	PTER-Pir	LDG 031	BNHS	India, Tamil Nadu	KR903854	KR903693	KR903349	KR904045	KR903521	KR903019	KR903170
<i>Rhacogryllus</i>	<i>vietet</i> Chopard, 1957	TRIG-Tri	LDG 144	SH-2004-010	La Réunion	KR903936	KR903762	KR903424	KR904123	KR903597	ND	KR903246
<i>Rumea</i>	<i>guyanensis</i> Desutter-Grandcolas, 1992	PARA-Par	LDG 104	ENSIF3273	French Guiana, Arataye	KR903909	KR903738	ND	KR904097	KR903573	KR903061	ND
<i>Sciobia</i>	<i>fnazi</i> (Brunner von Wattenwyl, 1882)	GRYL-Sci	LDG 082	ENSIF3386	Algeria, Tizi Ouzou	KR903894	ND	KR903385	ND	KR903559	KR903049	KR903210
<i>Sclerogryllus</i>	<i>sp.</i> India	SCL-Sci	LDG 214	ENSIF3291	India, Tamil Nadu	KR903989	KR903801	KR903462	KR904172	KR903639	KR903117	KR903297
<i>Silvastella</i>	<i>gradanae</i> Desutter-Grandcolas, 1992	PARA-Par	LDG 106	ENSIF3265	French Guiana, Arataye	KR903910	KR903740	KR903399	KR904099	KR903574	KR903062	ND
<i>Silvastella</i>	<i>fuscofasciata</i> Desutter-Grandcolas, 1992	PARA-Par	LDG 107	ENSIF3259	French Guiana, Arataye	KR903911	KR903741	KR903400	KR904100	KR903575	KR903063	KR903223

Table 2
(Continued)

Genus	Species	Subfam./tribe	Molecular codes	Voucher/repository	Locality	12S	16S	cyt b	18S	28SA	28SD	H3
<i>Singapuricola</i>	<i>separata</i> Gorochov & Tan, 2012	PTER	LDG 120	ENSIF3091	Singapour	KR903919	KR903746	KR903407	KR904106	KR903580	ND	KR903229
<i>Socotraris</i>	<i>kleukeri</i> Felix & Desutter-Grandcolas, 2012	PHAL	LDG 041	ENSIF2933	Yemen, Socotra	KR903862	KR903700	KR903357	KR904052	KR903528	KR903026	KR903177
<i>Stalacris</i>	nsp. Swa	no	LDG 247	ENSIF3084	Swaziland	KR904007	KR903815	KR903478	KR904189	KR903655	KR903132	KR903313
<i>Strogilomorphini</i>	sp. CR	PARA-Par	LDG 061	ENSIF3333	Costa Rica	ND	KR903716	KR903373	KR904071	ND	ND	KR903196
<i>Supercala</i>	<i>choreutes</i> Ote, 2006	PARA-Par	LDG 064	ENSIF3335	Costa Rica	KR903882	ND	KR903375	KR904073	KR903547	KR903041	KR903198
<i>Svercus</i>	<i>palmetorum</i> (Krauss, 1902)	GRYL-Gry	LDG 044	ENSIF3247	Comoros, Anjouan	KR903865	KR903703	KR903360	KR904055	KR903531	KR903029	KR903180
<i>Svistella</i>	<i>cheikjawa</i> Tan & Robillard, 2012	TRIG	LDG 113	ENSIF3085	Singapour	KR903916	KR903744	ND	KR904104	KR903578	KR903067	KR903227
<i>Szewilderia</i>	sp. Fid	ENEO	Ssp	ENSIF2737	Fidji, Viti Levu	JF972514	JF972529	JF972498	JF972545	ND	ND	KR903327
<i>Tactitarna</i>	<i>baiderae</i> Hugel, 2014	GRYL	LDG 154	SH-2009-389	Mauritius	KR903945	KR903770	ND	KR904132	KR903606	KR903089	KR903255
<i>Tufaliscina</i>	sp. FCu	PODO-Pac	LDG 109	ENSIF3276	French Guiana, Arataye	KR903913	ND	KR903402	KR904102	ND	KR903065	KR903225
<i>Tarbinskiellus</i>	sp. India	GRYL-Gry	LDG 077	ENSIF3415	India, Kerala	KR903890	KR903722	ND	KR904081	KR903555	ND	KR903206
<i>Teleogryllus</i>	sp. India	GRYL-Gry	LDG 068	ENSIF3407	India, Kerala	KR903885	ND	KR903377	KR904076	KR903550	KR903043	KR903201
<i>Thetella</i>	sp. Com	ENEO-The	LDG 028	ENSIF3313	Comoros, Moheli	KR903853	KR903692	KR903348	KR904044	KR903520	KR903018	KR903169
<i>Thetella</i>	sp. Mau	NEMO-The	LDG 150	SH-2011-025	Mauritius	KR903942	KR903767	KR903428	KR904129	KR903603	KR903087	KR903252
<i>Tremellia</i>	sp. PNG	PHOR-Pho	LDG 251	ENSIF3323	PNG, Mt Wilhelm	KR904011	KR903819	KR903482	KR904193	KR903659	KR903136	ND
<i>Trigonidium</i>	sp. Moz	TRIG-Tri	LDG 126	ENSIF3392	Mozambique, Cabo Delgado	KR903923	KR903750	KR903411	KR904110	KR903584	KR903072	KR903233
<i>Trigonidium</i>	<i>ctandoloides</i> Rambur, 1838	TRIG-Tri	LDG 147	SH-2009-099	Mauritius	KR903939	KR903764	KR903426	KR904126	KR903600	KR903084	KR903249
<i>Trigonidium</i>	sp. Van	TRIG-Tri	LDG 169	ENSIF3369	Vanuatu, Espiritu Santo	KR903959	KR903781	KR903441	KR904145	KR903619	KR903097	KR903267
<i>Trigonidium</i>	<i>obscapipennis</i> (Chopard, 1957)	TRIG-Tri	LDG 145	SH-Reu2005-01	La Réunion	KR903937	ND	ND	KR904124	KR903598	ND	KR903247
<i>Triplata</i>	sp. Chi	PODO-Pod	LDG 234	ENSIF3295	China, Padang	ND	KR903809	KR903472	KR904182	KR903494	KR902992	KR903306
<i>Turanogryllus</i>	sp. India	GRYL-Tur	LDG 069	ENSIF3408	India, Karnataka	KR903886	KR903718	KR903378	KR904077	KR903551	KR903044	KR903202
<i>Unitheca</i>	<i>guadeloupensis</i> Desutter-Grandcolas, 1991	PARA-Par	LDG 004	ENSIF3328	West Indies, Guadeloupe	KR903839	KR903678	KR903335	ND	KR903507	KR903005	KR903157
<i>Uvaroviella</i>	<i>speleae</i> Desutter-Grandcolas, 1991	PHAL-Pha	LDG 046	ENSIF3251	French Guiana, Arataye	KR903867	KR903705	KR903362	KR904057	KR903533	KR903031	KR903182
<i>Uvaroviella</i>	<i>scandens</i> (Ote, 2006)	PHAL-Pha	LDG 058	ENSIF3334	Costa Rica	KR903878	ND	ND	KR904068	KR903543	ND	KR903193
<i>Uvaroviella</i>	<i>guyanensis</i> Desutter-Grandcolas, 1991	PHAL-Pha	LDG 108	ENSIF3266	French Guiana, Arataye	KR903912	KR903742	KR903401	KR904101	KR903576	KR903064	KR903224
<i>Velarifictorus</i>	sp. India	GRYL-Mod	LDG 070	ENSIF3409	India	KR903887	KR903719	KR903379	KR904078	KR903552	KR903045	KR903203
<i>Xenogryllus</i>	<i>ewacpteroides</i> Bolivar, 1890	ENEO-Xen	Xma2	ENSIF3159	CAR	KR904023	KR903829	KR903490	KR904205	KR903670	KR903148	KR903328
<i>Xenogryllus</i>	<i>marmoratus</i> (Haan, 1842)	ENEO-Xen	LDG 046	ENSIF3161/3562	Japan/China	KR904024	KR903830	KR903491	KR904206	KR903671	KR903149	KR903329
<i>Yoyuteris</i>	<i>iniei</i> Ote & Perez-Gelabert, 2009	PARA-Par	LDG 205	ENSIF3302	West Indies, Guadeloupe	ND	KR903797	KR903457	KR904167	ND	KR902991	KR903290
<i>Zebraeryllus</i>	<i>nouragu</i> Desutter-Grandcolas, 2014	GRYL	LDG 094	ENSIF3267	French Guiana, Arataye	KR903900	KR903729	KR903390	KR904088	KR903565	KR903055	KR903215
OUTGROUPS												
<i>Ceuthophilus</i>	sp	OG-RH	LDG 198	SH-2005-005	Quebec	KR903978	ND	ND	KR904162	KR903633	KR903111	KR903285
<i>Comitcus</i>	<i>campestris</i> Irish, 1986	OG-SC	C.cam	no	no	Z97608_1	Z97624_1	ND	Z97564_1	ND	ND	KR903285
<i>Locusta</i>	<i>migratoria</i> (Linnaeus, 1758)	OG-AC	L.mig	no	no	NC_001712.1	NC_001712.1	NC_001712.1	AF:370793	ND	ND	AF:370817
<i>Lutosa</i>	sp	OG-AN	LDG 099	ENSIF3734	West Indies, Guadeloupe	KR903904	KR903733	KR903394	KR904092	KR903569	KR903057	KR903219
<i>Niphetogryllacris</i>	<i>reunionis</i> (Karmy, 1932)	OG-GC	LDG 196	SH-2009-001	La Réunion	KR903977	ND	KR903453	KR904161	KR903632	KR903110	KR903284
<i>Schizodacryllus</i>	<i>monstruosus</i> (Drury, 1770)	OG-SC	S.mon	no	no	ND	ND	ND	AF:514545_1	ND	ND	ND
<i>Schistocerca</i>	<i>gregaria</i> (Forskål, 1775)	OG-AC	Sgre	MNHN_SG1	Africa, 1997	KR904022	GQ:491031	JX:033931.1	KR904204	ND	KR903147	ND

Table 2
(Continued)

Genus	Species	Subfam./tribe	Molecular codes	Voucher/repository	Locality	12S	16S	cyt b	18S	28SA	28SD	H3
<i>Tachyichnes</i>	<i>asynamora</i> (Adelung, 1902)	OG-RH	LDG 115	ENSIF2923	France	KR903918	KR903745	KR903406	KR904105	KR903579	KR903068	ND
<i>Xanthogryllacris</i>	<i>punctipennis</i> (Walker, 1869)	OG-GC	LDG 195	ENSIF2160	West Indies, Guadeloupe	KR903976	ND	KR903452	KR904160	KR903631	KR903109	KR903283

Voucher codes as indicated in Fig. 1 ND = No data. Subfamily abbreviations: CACH, Cachoplistinae; ENEO, Eneopterinae; EUSC, Euscyrtinae; GRMP, Gryllomorphae; GRTL, Gryllotalpinae; GRYL, Gryllinae; HAPI, Hapithinae; LAND, Landrevinae; LUZA, Luzarinae; MALG, Malgasinae; MOGO, Mogoplistinae; MYRM, Myrmecophilinae; NEMO, Nemobinae; OECA, Oecanthinae; PARA, Paragryllinae; PENT, Pentacentrinae; PHAL, Phalangopsinae; PHOR, Phalorinae; PODO, Podoscirtinae; PTER, Pteroplistinae; SCLE, Sclerogryllinae; TRIG, Trigonidiinae. Tribe abbreviations: Aph, Aphonoidini; Ara, Arachnocephalini; Cae, Ceatracasaini; Cep, Cephalogryllini; Cop, Cophogryllini; End, Endacustini; Ene, Eneopterini; Eur, Euripini; Grm, Gryllomorphiini; Gry, Gryllini; Hap, Hapithini; Hem, Hemigryllini; Het, Heterogryllini; Hom, Homoeogryllini; Lan, Landrevini; Leb, Lebinthini; Mod, Modicogryllini; Mog, Mogoplistini; Myr, Myrmecophilini; Nem, Nemobini; Nis, Nisitriini; Oec, Oecanthini; Pac, Paroecanthini; Par, Paragryllini; Pet, Petaloptilini; Pha, Phalangopsini; Pho, Phalorini; Phy, Phylloscirtini; Pod, Podoscirtini; Pte, Pteronemobiini; Ptr, Pteroplistini; Sci, Scioibini; Scl, Sclerogryllini; The, Thetellini; Tri, Trigonidiini; Tur, Turanogryllini; Xen, Xenogryllini. Repository abbreviations: ANIC, Australian National Insect Collection, Australia; ES, Collection E. Sardet, France; IAC, Institut Agronomique de Nouvelle-Calédonie, La Foa, New Caledonia; INBio, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; ENSIF, Ensifera collection of the MNHN, Paris; MEUV, Museo de Entomología del Universidad de la Valle, Cali, Colombia; RF, Collection Rob Felix, The Netherlands; SH, Collection Sylvain Hugel, Strasbourg, France; ZSI, Zoological Survey of India, Calcutta, India.

Table 3
PCR profiles and primers used, with their sources

Gene	Primer	Denaturation	Annealing	Elongation	Number of cycles	Final elongation	Reference
12SF	TACTATGTTACGACTTAT	30 s at 94 °C	30 s, 30 s at 47 °C, 48 °C	40 s, 30 s at 72 °C	10, 40	7 min at 72 °C	Kamphambati (1995)
12SR	AAACTAGGATTAGATACCC	30 s at 94 °C	40 s at 55 °C	40 s at 72 °C	45	5 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
16S-AG	CGCCTGTTTATCAAAAACATGT	50 s at 94 °C	50 s at 52 °C	50 s at 72 °C	50	7 min at 72 °C	Giribet et al. (1999)
16S-BG	AGATCAGTAAGAATTTAATGGTC	50 s at 94 °C	40 s at 58 °C	40 s at 72 °C	45	7 min at 72 °C	Svenson and Whiting (2004)
18S-A2	ATGGTTGCAAAGCTGAAAC	40 s at 94 °C	40 s at 50 °C	60 s at 72 °C	40	7 min at 72 °C	Whiting (2002)
18S-9R	GATCCTCCGAGGTTACACCTAC	35 s at 94 °C	35 s at 57 °C	50 s at 72 °C	40	7 min at 72 °C	Jarvis et al. (2004)
HisF	ATGGCTCGTACCAAGCAGACGGC	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
HisR	ATATCCTTGGGCATGATGGTGAC	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
28S--R1.2a	CCC SSG TAA TTT AAG CAT ATT A	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
28S-Rd3b	CGY TGA ACG GTT TCA CGT ACT	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
28SF4	CGA CAC GCC CCG ATC CTC AGA GCC A	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
28SR4	GATTCAGACGTGCAAAATCGATC	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
cytb427F	YTWGTWCAATGARTMTGAGG	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)
cytb800R	CCYARITTTAATAGGAATTGATCG	30 s at 94 °C	40 s at 48 °C	40 s at 72 °C	50	7 min at 72 °C	Robillard and Desutter-Grandcolas (2006)

Table 4
Descriptive statistics for the different sequence datasets with the outgroups included. Statistics were estimated after removal of primer sequences and the best model of evolution selected with the AIC criterion in jModelTest 2.1.3

Loci	No. taxa	No. characters	No/% variable sites	No/% parsimony informative sites (gap as missing character)	Model of evolution	AIC	(-) lnL	Average frequencies all sites/variable sites				Constancy of base frequencies (χ^2 values/ P values/d.f.)	
								A	C	G	T	All sites	Variable sites
18S	192	685	368/53.7	304/44.4	TIM2 + I + G	31301.042	15252.521	0.2/0.2	0.2/0.3	0.3/0.3	0.2/0.3	98.6/1/576	168.9/1/576
28SA	181	482	290/60.2	225/46.7	TIM2 + I + G	29250.050	14219.025	0.3/0.2	0.3/0.3	0.3/0.3	0.2/0.2	320.9/1/546	508.5/1/546
28SD	162	593	304/51.3	213/35.9	GTR + I + G	21538.126	10437.063	0.2/0.2	0.3/0.3	0.3/0.3	0.2/0.2	129.6/1/483	234.8/1/483
H3	180	328	142/43.3	130/39.6	TIM1 + I + G	25791.604	12491.802	0.2/0.1	0.3/0.5	0.3/0.3	0.2/0.1	322.8/1/549	793.6/0/549
12S	206	571	469/82.1	382/66.9	TIM2 + I + G	66519.833	32831.916	0.4/0.4	0.2/0.2	0.1/0.1	0.3/0.3	626.6/0/615	754.2/0/615
16S	174	592	443/74.8	382/64.5	TPM2uf + I + G	64338.811	31816.405	0.3/0.3	0.1/0.1	0.2/0.2	0.4/0.4	549.6/0.2/519	722.7/0/519
cytb	177	346	251/72.5	220/63.6	GTR + I + G	51714.423	25493.211	0.3/0.3	0.2/0.2	0.1/0.1	0.4/0.4	703.6/0/528	1027.3/0/528
Combined	214	3597	2262/62.8	1849/51.4	GTR + I + G	312107.864	155617.932	0.3/0.3	0.2/0.2	0.2/0.2	0.3/0.3	2930.8/0/639	3095.7/0/639

d.f., degrees of freedom.

Outgroup taxa were taken within the two suborders of Orthoptera, that is, Caelifera and Ensifera (Table 2). Caelifera were represented by two well-documented grasshopper species, *Schistocerca gregaria* Forskål, 1775 and *Locusta migratoria* Linnaeus, 1758. A wider panel of species was chosen for Ensifera, as the monophyly and phylogenetic structure of this clade is unclear (Legendre et al., 2010). It included representatives of the families Anostomatidae (one species), Rhaphidophoridae (two species) and Gryllacrididae (two species).

We assigned a voucher for number all the specimens we used. Most of them are recorded in the specimen database of the Muséum national d'Histoire naturelle (MNHN), where they can be found, together with all available geographical information at <http://science.mnhn.fr/institution/mnhn/collection/eo/search>; the others are deposited in the institutions and collections listed in Table 2.

Molecular methods

We generated 1219 sequences (95.6% of the total dataset) for this study (Table 2). When necessary, additional sequences were obtained from the vouchers used in previous phylogenetic studies (Robillard and Desutter-Grandcolas, 2006; Nattier et al., 2011b, 2012; Jaiswara et al., 2012). No sample could be obtained for *Schizodactylus monstrosus* and *Comicus campestris*. We therefore relied on sequences already published in GenBank (Benson et al., 2005) for these taxa.

We extracted total genomic DNA from middle or hind femora of dried, alcohol-preserved, or newly collected specimens. We used QIAamp DNA tissue microkit (QIAGEN) according to the manufacturer's instructions. Molecular work was performed at the Service de Systématique Moléculaire of the MNHN.

We sequenced seven markers, three mitochondrial and four nuclear, used in previous phylogenetic studies on insects (Table 3). These are the small (12SrRNA, ~400 bp) and large (16srRNA, ~500 bp) mitochondrial ribosomal subunits, the mitochondrial gene coding for cytochrome b protein (cytb, ~400 bp), a fragment of the small nuclear ribosomal subunit (18SrRNA, ~650 bp), two fragments of the large nuclear ribosomal unit (28SA, ~400 bp and 28SD, ~900 bp rRNA) and the gene coding for H3 protein (H3, ~330 bp). Primers and annealing temperatures are given in Table 3. Sequencing reactions were carried out on both DNA strands. Ambiguous results were checked by multiple sequencing either on a different DNA extraction from the same individual, or of an extraction from another conspecific individual. The quality of museum-preserved specimens varied considerably and DNA degradation did not allow the amplification of all target sequences for each species: however, 85% of the whole matrix was completed (Table 2).

Sequence analyses

Newly generated sequences were edited in Sequencher V. 4.9 (Gene Codes Corporation, Ann Arbor, MI, USA), blasted with NCBI blast tools, and submitted to GenBank (Table 2).

Multiple alignments were generated for each locus using Muscle 3.8 (Edgar, 2004) with default parameters, and refined manually in terminal regions. The positional homology of nucleotides in protein-coding genes was constrained manually in BioEdit 7.0.5.3 (Hall, 1999) using the codon reading frame information. For rDNA, we checked that our alignments were congruent with published models of secondary structure in insects (Flook and Rowell, 1997b; Buckley et al., 2000; Page, 2000; Kjer, 2004), which was the case for very conserved stems. Nevertheless, following the method proposed by Lutzoni et al. (2000), three hypervariable and ambiguously aligned regions (AARs), totalling 421 bp (positions 129–456, 548–556, and 628–711 of the 28SD initial alignment) were identified in the 28SD fragment. We coded the AARs as single multistate characters with the INAASE package (Lutzoni et al., 2000) for the parsimony analysis and removed it from the likelihood and Bayesian analyses.

We concatenated the different partitions with SequenceMatrix 1.7.7 (Vaidya et al., 2011), which resulted in an alignment of ~3600 bp (online Supporting Information).

Base composition, substitution rates, and rate heterogeneity across sites (Table 4) were estimated for each dataset under the most likely model of evolution suggested by the Akaike Information Criterion (AIC; Akaike, 1973; Posada and Buckley, 2004) in jmodeltest 2.1.3 (Guindon and Gascuel, 2003; Darriba et al., 2012). The constancy of base frequencies across taxa was evaluated with a chi-square (χ^2) “goodness of fit” test using PAUP 4.0b10 (Swofford, 1995). Tests were performed with all sites and variable sites only (Table 4) in order to assess the potential confounding effects of invariant sites (e.g. Buckley et al., 2001).

Phylogenetic analyses

We conducted maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) analyses on separate and combined datasets to address questions regarding the levels of homoplasy, tree incongruence, and information content within and among loci. We also conducted separate analyses to check for obvious artefacts or contaminations. In addition, we performed combined analyses (MP, BI)

of the whole dataset without the poorly documented taxa *Schizodactylus monstrosus* and *Comicus campestris*, to test their influence on the resultant topology. Trees were visualized with FigTree 1.4.0. (<http://tree.bio.ed.ac.uk/software/figtree/>).

In a probabilistic framework, we used jModelTest 2.1.3 under the AIC to select the best model for each marker among the models tested (Table 4). For all markers, the best model was GTR + I + Γ . We did not use though models mixing a proportion of invariant sites (I) with a gamma distribution shape parameter (Γ) because these two parameters are strongly correlated (Sullivan et al., 1999; Yang, 2006). Therefore each partition (i.e. marker) was analysed under a GTR + Γ model. We performed 500 ML replicates under the rapid hill-climbing algorithm as implemented in RAxML 7.4.2. (Stamatakis, 2006; Silvestro and Michalak, 2012), branch lengths being estimated together for all markers, and we selected the optimal solution (with and without *Schizodactylus monstrosus* and *Comicus campestris*). We ran two similar analyses for the nuclear and mitochondrial partitions, respectively. For the combined analyses, we also computed bootstrap support values with 500 pseudoreplicates. All these analyses were performed on a HP Z800 Workstation with 17.9 Gbits RAM and an Intel Xeon CPU E5520, using seven threads.

The BI analyses (with and without *Schizodactylus monstrosus* and *Comicus campestris*) were conducted using the same model strategy with MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) on the MNHN cluster. We ran the analyses for 50 millions of generations with the command stoprule = yes, sampling tree every 10 000 generations. We used Tracer 1.5 (Rambaut and Drummond, 2009) to check that our effective sample size was large enough for a meaningful estimation of parameters and to assess the burn-in. Finally, we checked for convergence of our results ensuring that the potential scale-reduction factor approached 1.0 for all parameters.

Heuristic searches, on nuclear and mitochondrial data, separated or combined (with and without *Schizodactylus monstrosus* and *Comicus campestris*), with or without the coded AAR, were implemented in PAUP* under the MP criteria with unordered (Fitch) characters, 100 random sequence addition replicates, the TBR branch-swapping, and gaps treated as missing data. Strict consensus trees were then reconstructed. Support for internal branches was assessed in PAUP* by nonparametric bootstrapping (Felsenstein, 1985; Efron et al., 1996) with 100 pseudoreplicates, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition (e.g. DeBry and Olmstead, 2000).



Fig. 1. Phylogeny of crickets based on 205 terminals and seven DNA markers, obtained by Bayesian inference. Support values (BI/ML/MP) are indicated for the deeper nodes and the clades A to G. Taxa codes (i.e. voucher codes) as in Table 2, and made explicit in Figs 2–6.

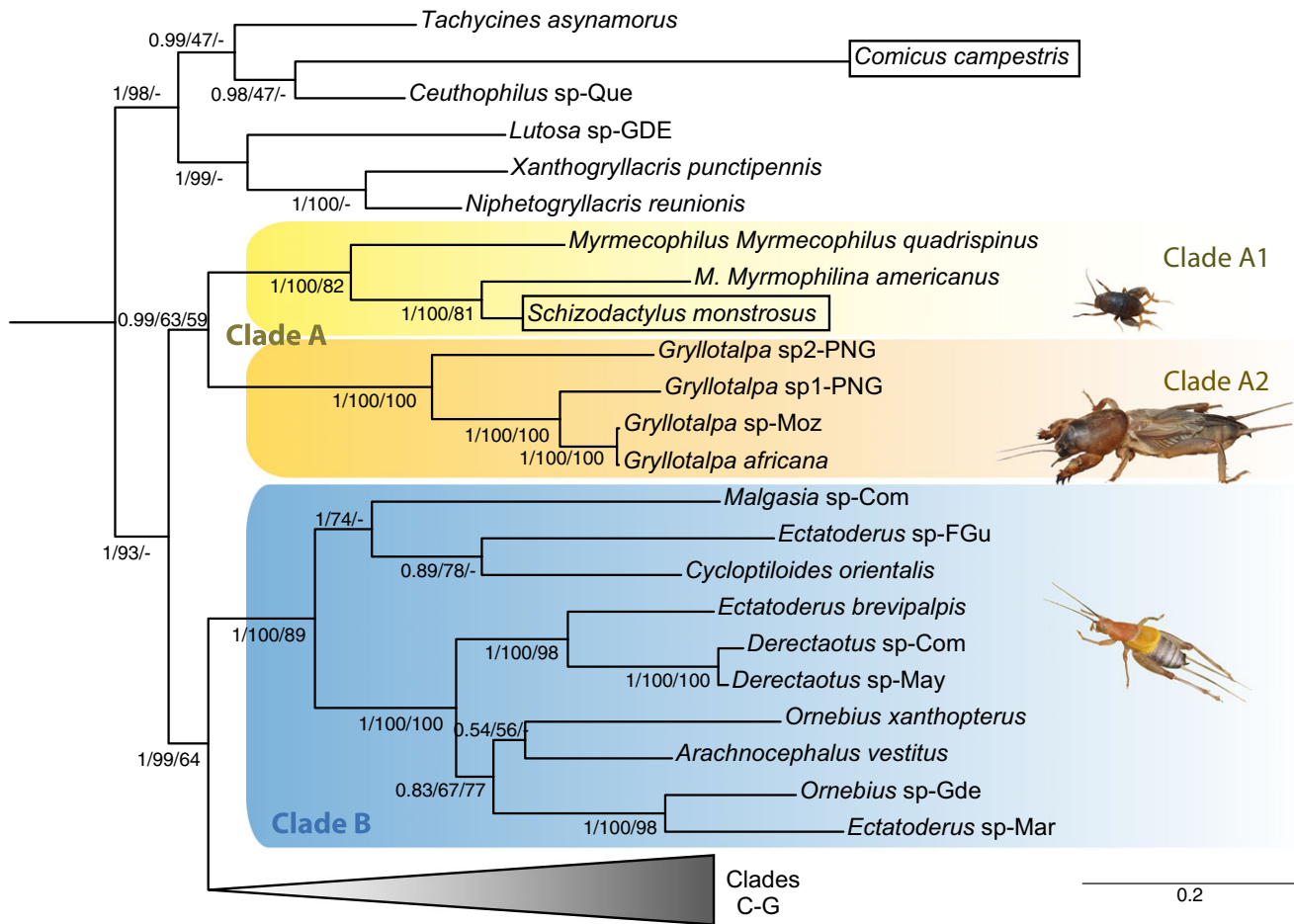


Fig. 2. Phylogeny of crickets based on 205 terminals and seven DNA markers in Bayesian inference: detailed topology for clades A and B (see Fig. 1). Support values (BI/ML/MP) are indicated for all nodes. Ensiferan outgroups are displayed to show the position of the two schizodactylid species, *Comicus campestris* Irish, 1986 and *Schizodactylus monstrosus* Drury, 1770 (squared). The analyses without these two taxa are provided as Supplementary Figs 15–17.

Taxonomic hypotheses

Although we sampled many cricket species, we consider that we did not sample enough genera to accurately represent cricket diversity below the subfamilial level. The subfamilial rank is the classification category that has been most commonly retained by the successive authors of classificatory systems for crickets, although they have been used in various systems comprising from one to thirteen families according to the authors. For the sake of stability, and as a first contribution to cricket classification, we consequently chose to test the monophyly of the subfamilies currently used in the OSF and to propose a new, phylogeny-based, classification of crickets from and above the subfamilial level.

Additional studies will be required to build comprehensive phylogenies below the subfamilial level. A detailed analysis of the present results in terms of

cricket classification will be published elsewhere (L. Desutter-Grandcolas, unpublished data).

Results

Sequence analyses

The sequences used have a high content of G/C (60–80%) and A/T (70%) for the nuclear and mitochondrial DNA respectively (Table 4), in agreement with values previously reported for other orthopterans (e.g. Chintauan-Marquier et al., 2011, 2014) and insects in general (Simon et al., 1994, 2006). Base frequencies were constant for all nuclear partitions taking all sites, and for the ribosomal nuclear partitions taking variable sites only. Across all fragments, 2262 sites (62.8%) were variable and 1849 sites (51.4%) were parsimony-informative. The nuclear and mitochondrial

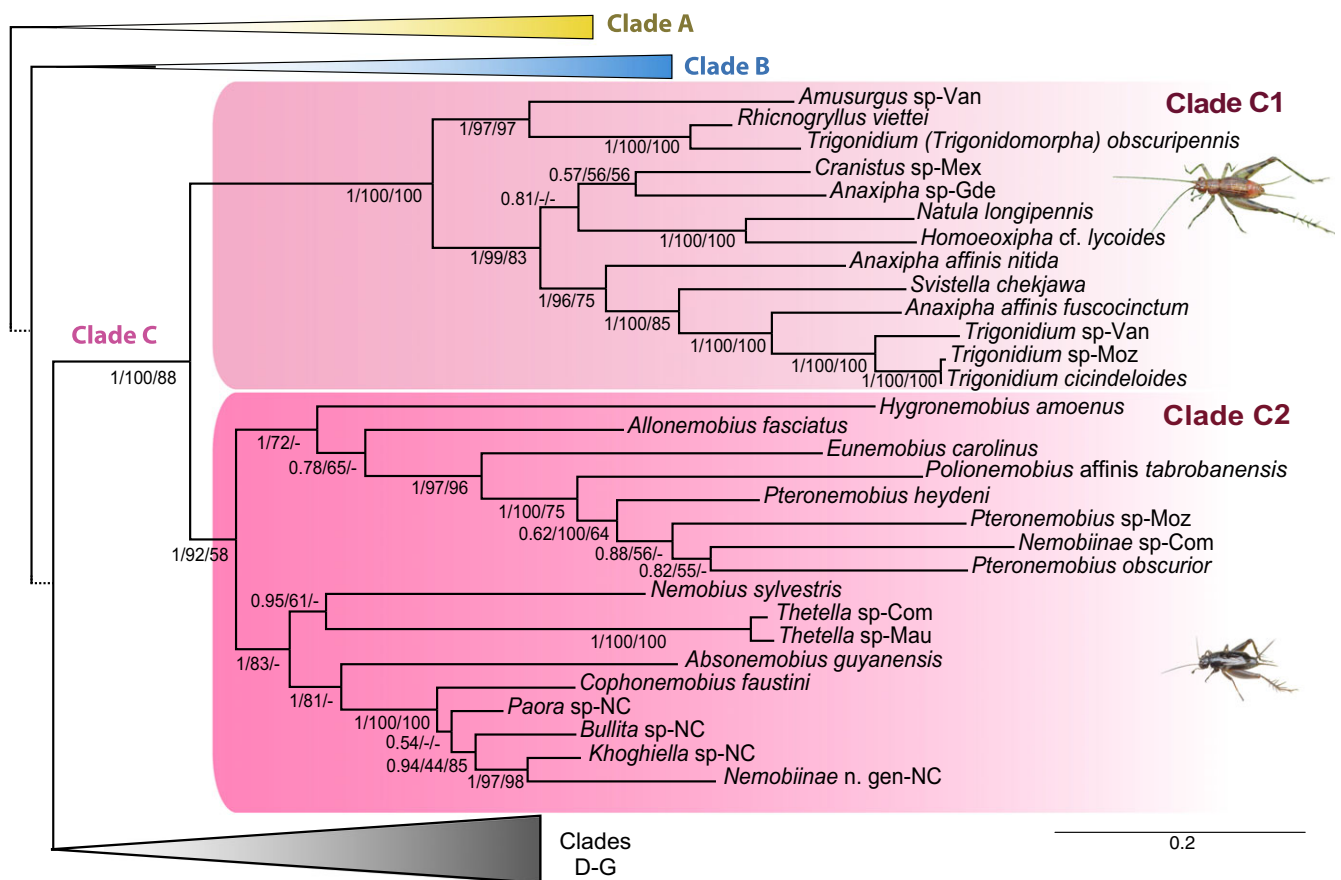


Fig. 3. Phylogeny of crickets based on 205 terminals and seven DNA markers in Bayesian inference: detailed topology for clade C (see Fig. 1). Support values as in Fig. 2.

partitions represent 47.1% and 52.9% of the informative sites, respectively. Models of evolution and associated parameters for the probabilistic analyses are given in Table 4.

Phylogenetic analyses

For all phylogenetic methods, combining the nuclear and mitochondrial data improved tree resolution and nodal support (Figs 1–6; Figs S8–S10) by comparison with separate analyses (e.g. Figs S1–S7). The nuclear and mitochondrial partitions yielded very similar trees (Figs S11–S14), except for a few taxa (namely sand crickets and Pteroplantinae), the positions of which remain unsupported in the combined analysis. The addition of the coded AAR (in the MP analysis) had no significant effect on tree topologies. The MP, ML, and BI methods yielded similar topologies for most of the main clades (see below and Figs S8 and S10). Removing *Schizodactylus monstrosus* and *Comicus campestris* from the data did not modify the results of the ML and BI analyses significantly (see Figs S15 and S16). In MP, it resulted in a less resolved strict consen-

sus that still shows most of the main clades (i.e. clades A, B, C, D, E and F+G); a trifurcation between ensiferan outgroups, clade A and the rest of the crickets forbids finding crickets *sensu lato* monophyletic.

Support values (posterior probabilities and nonparametric bootstrap values) are given in Fig. 1 for the deeper nodes, and in Figs 2–6 for the other nodes.

Our results with the complete data set (Fig. 1) suggest that, within the monophyletic Ensifera, the crickets *sensu lato* form a clade strongly supported in BI (PP = 1.00) and ML analyses (ML = 93), provided they include *Schizodactylus*. They are the sister group to the other sampled Ensifera (i.e. Rhaphidophoridae, Gryllacrididae, Anostostomatidae). The sand crickets are not recovered as a monophyletic group: the genus *Comicus* gathered with the Rhaphidophoridae (ML, BI – Fig. 2; MP, Fig. S10), while *Schizodactylus* comes within the ant-loving cricket clade. The position of these two taxa may be, however, an artefact due to incomplete data. Among the outgroups, the Gryllacrididae are always monophyletic and sister-group to the Anostostomatidae. All these relationships are very well supported (PP ≥ 0.99). The analyses per-

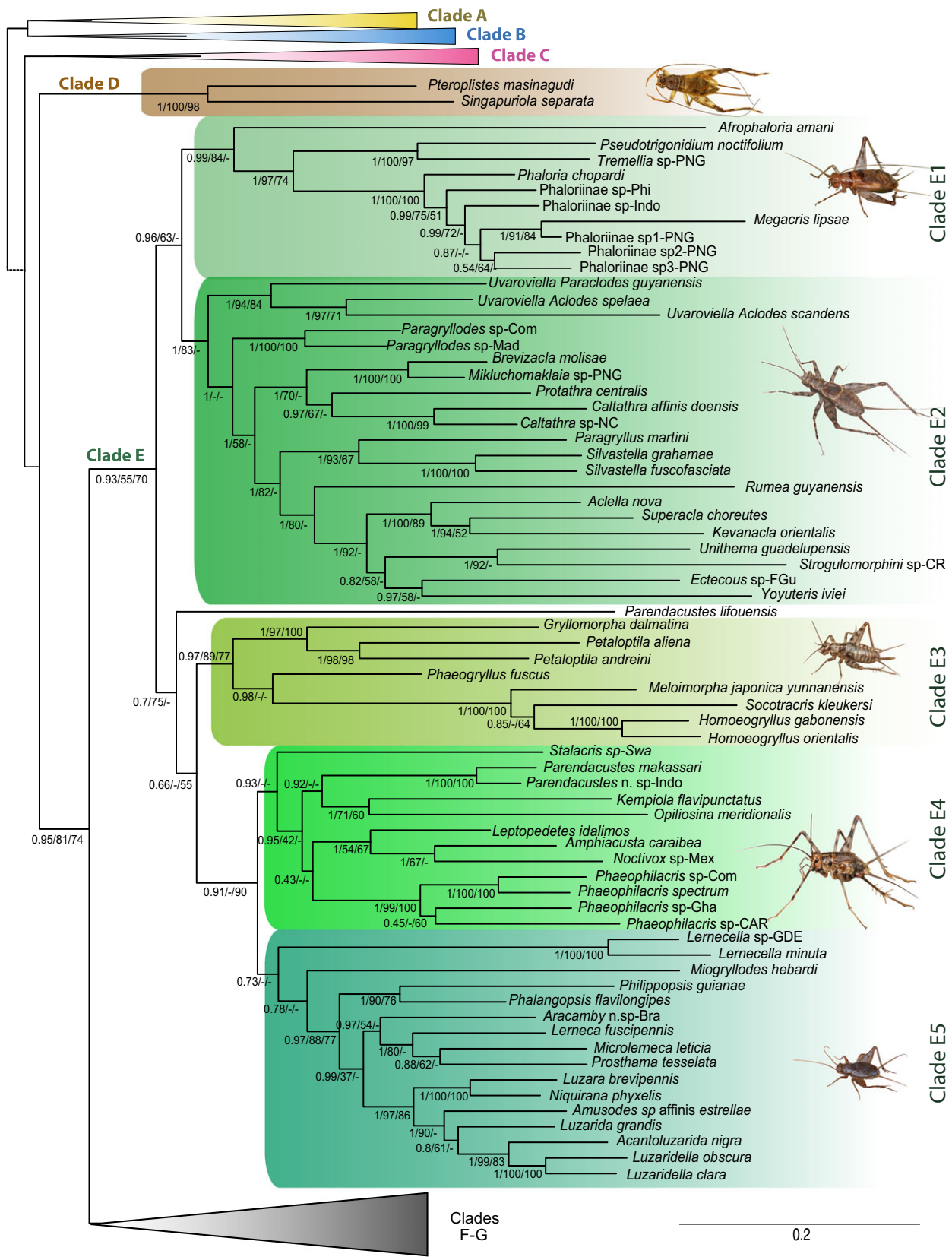


Fig. 4. Phylogeny of crickets based on 205 terminals and seven DNA markers in Bayesian inference: detailed topology for clades D and E (see Fig. 1). Support values as in Fig. 2.

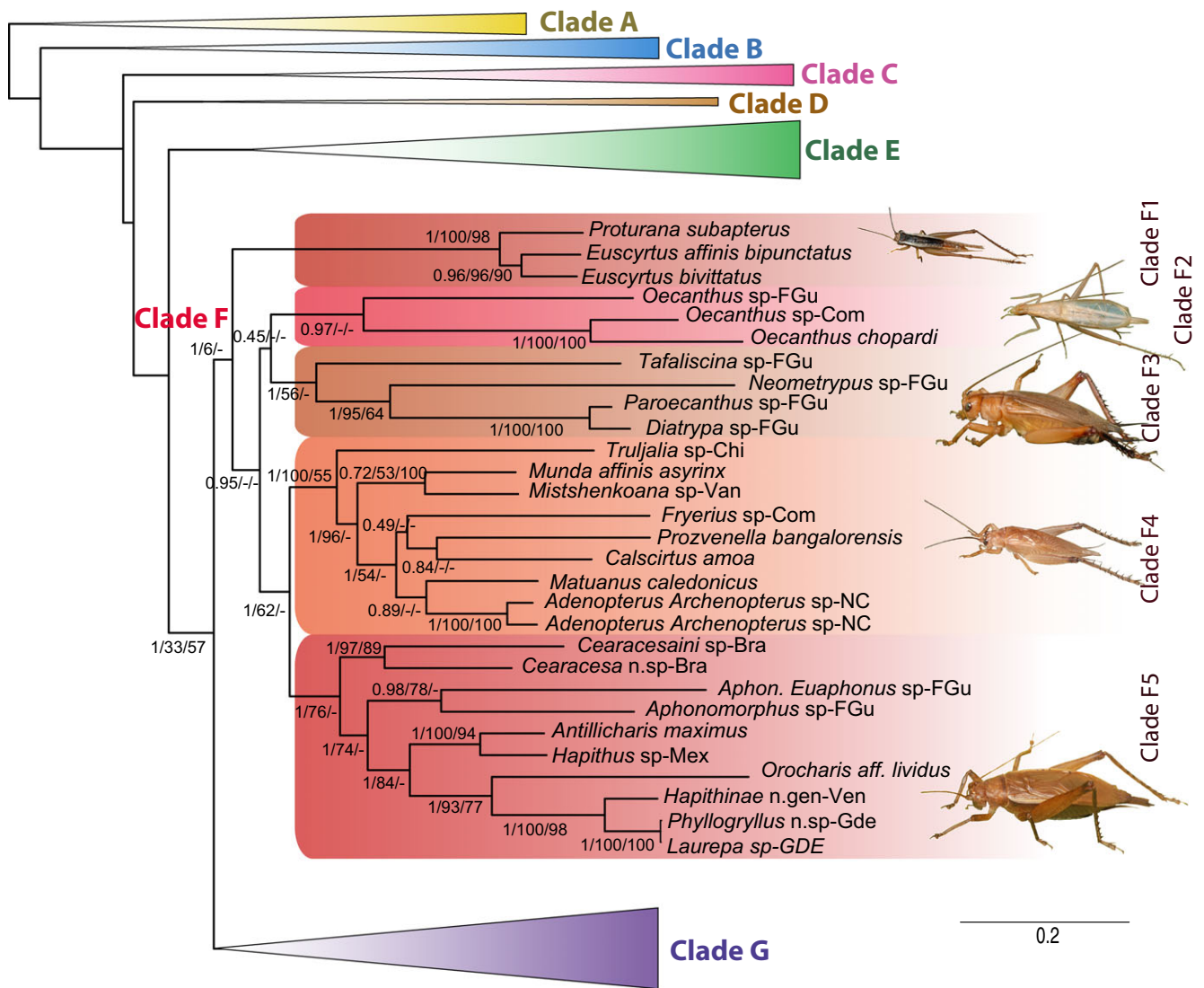


Fig. 5. Phylogeny of crickets based on 205 terminals and seven DNA markers in BI: detailed topology for clade F (see Fig. 1). Support values as in Fig. 2.

formed without the partition 28SD gave the same relationships with a weaker support ($0.5 < PP < 0.7$) (Fig. S9).

Within the cricket clade (Figs 2–6), three main clades are identified. They correspond to (i) ant-loving crickets and mole crickets (Clade A), (ii) scaly crickets (plus the Malagasy genus *Malgasia*) (clade B), and (iii) true crickets, separated into five clades named C to G, with the clade C being the sister group to all the others. These clades and this structure are recovered in all analyses: all the clades have a very high PP, but clades E, F and G are not so well supported in MP and ML, as are their internal relationships. The main differences concern the clades F and G in MP (see infra) and in the position of clade D: in ML, the clade D is the sister group of all true crickets (Fig. S8), while it is the sister group of the clade (E + F + G) in MP and BI

(PP = 0.69, Fig. 1; Fig. S10); in ML analysis performed without the marker 28SD, the clade D is the sister group of the clade C (PP = 0.58, Fig. S9).

Within clade A (Fig. 2), the mole crickets and the ant-loving crickets (+*Schizodactylus*) form two very well-supported clades (A1 and A2, PP = 1.00 for both). Clade B, gathering the scaly crickets and *Malgasia* (Fig. 1, PP = 1.00), is subdivided into two sister groups, which invalidates the separation of *Malgasia* as a separate subfamily. Clade C (Fig. 3, PP = 1.00) is made of two very well-supported sister groups, which comprise all the sampled species of the subfamilies Trigonidiinae (clade C1, PP = 1.00) and Nemobiinae (clade C2, PP = 1.00), at the exception of the genus *Hemigrillus* Saussure, 1877, which is nested in clade G. The current tribes of Trigonidiinae are not found to be

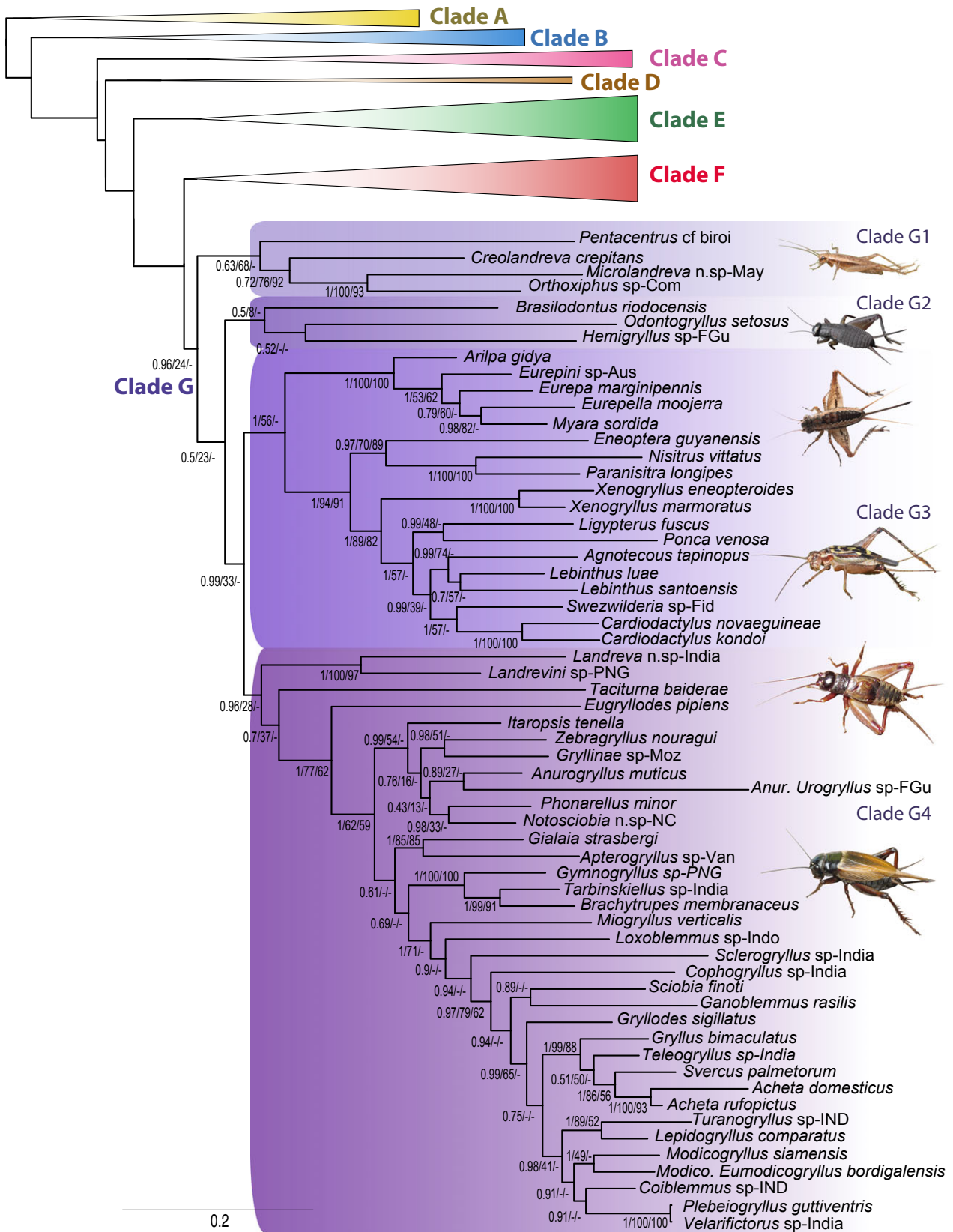


Fig. 6. Phylogeny of crickets based on 205 terminals and seven DNA markers in Bayesian inference: detailed topology for clade G (see Fig. 1). Support values as in Fig. 2.

monophyletic, as the Phylloscyrtini, represented by *Cranistus* sp., are nested within the Trigonidiini.

Nemobiinae separates into two groups (PP = 1.00, both): the first one includes mostly Pteronemobiini, whereas the second includes mostly Nemobiini. This result supports the monophyly of these two tribes, providing that *Absonemobius* is transferred from the Pteronemobiini to the Nemobiini. Also, the nested position of the genus *Thetella* in the *Nemobius* group invalidates the Thetellini tribe. The genus *Cophonemobius*, not classified in the OSF, is nested within the *Nemobius* group. In MP topology, the pteronemobiine genus *Allonemobius* is the sister group of the *Nemobius* clade, while *Absonemobius* is nested within the pteronemobiine clade (Fig. S10).

Clade D (Fig. 4) comprises the crickets belonging to the tribe Pteroplistini of the subfamily Pteroplistinae. This small clade is very well supported, unlike its exact position within crickets (PP < 0.7 – Fig. 1; Figs S8–S10). Clade E (Fig. 4, PP = 0.93) includes mostly taxa presently classified in the “Phalangopsinae subfamily group”. It comprises five well-supported clades (E1 to E5), recovered in all analyses (except E1 in MP). The species *Parendacustes lifouensis* is the sister group of Trigonidiinae + Nemobiinae on ML topology, and nested with taxa of clade E2 on MP topology: this position maybe due to a lack of data, this taxon being here documented for 12S and cytb only. The clades E1 to E5 do not fit with the subfamilies of the “Phalangopsinae subfamily group”, which are all but one (viz. Phaloriinae) recovered as polyphyletic. Moreover, the genera *Gryllomorpha* and *Petaloptila*, which are currently classified in the tribes Gryllomorphini and Petaloptelini of the Gryllomorphinae subfamily inside the “Gryllinae subfamily group”, are clearly nested within clade E.

Clade E1 (PP = 0.99) comprises genera classified in the Phaloriinae (i.e. *Afrophaloria*, *Phaloria*, *Pseudotrigonidium* and *Tremellia*), together with the genera *Megacris*, not assigned to a subfamily in the OSF but originally described as a Phaloriinae.

Clade E2 (PP = 1.00) comprises two sister clades. The first one corresponds to the wide Neotropical genus *Uvaroviella* (Phalangopsinae, Phalangopsini), and the second includes taxa classified in the polyphyletic Endacustini tribe (*Paragrylloides*, *Protathra*) and all the sampled taxa presently classified in the Paragryllinae. This second clade (PP = 1.00) could be congruent with the definition of several taxonomic groups described as tribes or subtribes, that is, Paragryllini (*Paragryllus*), Benoistellini (*Silvastella*), Rumeini (*Rumea*), and a mix of Neoacolini + Strogulomorphini (*Aclella*, *Superacla*, *Kevanacla*, *Ectecous*, *Unithema*, Strogulomorphini sp, *Yoyuteris*).

Clade E3 (PP = 0.97) includes all sampled Gryllomorphini except *Eugrylloides* (nested in clade G4), in addition to *Phaeogryllus* (classified in Phalangopsinae, Heterogryllini), *Meloimorpha* and *Homoeogryllus* (Cachoplistinae, Homoeogryllini), and *Socotraxis* (Phalangopsinae).

Clade E4 (PP = 0.93) gathers *Stalacris* and *Opiliosina* (respectively classified within the “Phalangopsinae subfamily group” and the Phalangopsinae subfamily), with *Parendacustes* (Phalangopsinae, Phalangopsini), *Kempiola* (Cachoplistinae, Homoeogryllini), *Leptopedetes*, *Amphiacusta* and *Noctivox* (Luzarinae, Amphiacustina), and the wide African genus *Phaeophilacris* (“Phalangopsinae subfamily group”, Endacustini). Internal relationships of clade E4 are strongly supported, except for the sister relationship between the neotropical Amphiacustina and *Phaeophilacris* (PP < 0.5).

Clade E5 includes all the sampled taxa presently classified in the subfamily Luzarinae, except *Amphiacusta*, *Leptopedetes*, and *Noctivox* (in clade E4). Apart from *Lernecella* and *Miogrylloides*, the positions of which within the clade are weakly supported (PP < 0.8), the internal structure of E5 is strongly supported: a clade made of *Phalangopsis* and *Philippopsis* (PP = 1.00; Phalangopsinae, Phalangopsini) is the sister group of a clade comprising on one hand *Aracambly*, *Lerneca*, *Microlerneca*, and *Prostama* (PP = 0.97), and on the other hand *Luzara*, *Luzarida*, *Acantoluzarida*, *Luzaridella*, *Niquirana*, and *Amusodes* (PP = 1.00) (all Luzarinae).

In the MP topology (Fig. S10), clades E4 and E5 vary for the position of *Lernecella* and *Miogrylloides*.

Clade F (Fig. 5, PP = 1.00) broadly corresponds to the “Podoscirtinae subfamily group”; it is composed of five main clades, which correspond roughly to five subfamilies used in the OSF, provided their content and definition are slightly modified. Clade F1 (PP = 1.00) is the sister-group of the other clades and corresponds to the Euscirtinae (“Podoscirtinae subfamily group”). Clades (F2 + F3) and (F4 + F5) are sister-groups (PP = 0.95), with a weak (PP < 0.5) and strong (PP = 1.00) support, respectively. Clade F2 (PP = 0.97) includes the Oecanthinae (not classified), whereas clade F3 (PP = 1.00) includes the genera *Neometrypus*, *Paroecanthus*, *Tafalisca*, and *Diatrypa*, which are today scattered in three different tribes of the Podoscirtinae subfamily (Podoscirtini Neometrypina, Paroecanthini Paroecanthina and Tafaliscina, and Aphonoidini Diatrypina, respectively). Clade F4 (PP = 1.00) includes the Podoscirtinae (minus the taxa listed above), and clade F5 (PP = 1.00) corresponds to the Hapithinae plus some of the taxa presently classified in the Eneopterinae.

Finally, Clade G (Fig. 6) is strongly supported (PP = 0.96), but its internal relationships are not all well supported. Four clades proposed by our results partially cover the “Gryllinae subfamily group” used in the OSF, but do not support the monophyly of the subfamilies. Only two clades (G3, G4) are well supported (PP \geq 0.96), the other two (G1, G2) having a support $<$ 0.7. Clade G1 includes taxa currently classified either in the Pentacentrinae (“Podoscirtinae subfamily group”) or in the Landrevinae (“Gryllinae subfamily group”). Clade G2 includes taxa once classified in the tribe Odontogryllini (since then synonymized with the Landrevini), together with the genus *Hemigryllus*, currently classified in the Nemobiinae (see clade C2). Clade G3 includes the Eneopterinae *sensu stricto*. Four tribes among the five acknowledged today are recovered as monophyletic, the Eneopterini being polyphyletic, and the genus *Swezwilderia*, classified as *incertae sedis* in the OSF, is nested within the Lebinthini. Clade G4 includes two monophyletic groups: the first includes some Landrevinae (but see above, clade G1) and the taxa presently classified in the Gryllinae, Sclerogryllinae, and Gryllo-morphinae pro parte (p.p.) (genus *Eugryllodes*); the second shows a sistership relation between *Eugryllodes* and all the other taxa (minus the grylline genus *Taciturna*). Finally, none of the sampled tribes of the Gryllinae subfamily (Cephalogryllini, Cophogryllini, Gryllini, Modicogryllini, Sciobiini, Turanogryllini) are recovered as monophyletic, the genera *Cophogryllus*, *Sciobia*, and *Turanogryllus* being nested among the other genera.

In the MP topology (Fig. S10), the clades F and G are not sister-groups, but they form a paraphyletic assemblage, where the clades F1 (Euscyrtinae), F3 (Tafaliscinae), F4 (Podoscirtinae) and F5 (Hapithinae) are recovered, while the clades F2 (Oecanthinae), G1 (Pentacentrinae + Landrevinae p.p.) and G4 (Gryllinae + *Sclerogryllus* + *Eugryllodes*) are almost recovered.

Figure 7 and Table 5 sum up how our results support the currently used classification of crickets. We can distinguish four different situations, according to the congruence between the OSF classification and our phylogenetic hypothesis (Table 5): (i) groups recovered as monophyletic in their current meaning; (ii) groups that could be recovered as monophyletic providing minor changes in cricket classification (most often, this means to move a few genera from one clade to another); (iii) groups recovered as polyphyletic; (iv) groups (most often isolated genera) nested within larger clades. Six subfamilies are thus monophyletic (Euscyrtinae, Oecanthinae, Phaloriinae, Pteroplistinae, Trigonidiinae, Gryllotalpinae), while five others are almost recovered as monophyletic (Gryllinae, Paragryllinae, Nemobiinae, Mogoplistinae, Myrmecophilinae).

Discussion

Monophyly of the cricket clade, and its main subdivisions

Our results are congruent with the current grouping of crickets and their allies: in all analyses, crickets, scaly crickets, ant-loving crickets, and mole crickets are grouped together, attesting this long-lasting hypothesis. *Schizodactylus* and *Comicus*, currently gathered in the ensiferan family Schizodactylidae (sand crickets), are not monophyletic here, a result that could be an artefact, ensuing from an incomplete data set for the sand crickets (Table 2). Overall, our data confirm the phylogenetic affinity of sand crickets with crickets *sensu lato*, but are insufficient to propose a clear phylogenetic pattern of basal relationships between the cricket clade and its potential sister group (but see Song et al., 2015).

The cricket clade is composed of seven main monophyletic groups (Fig. 1, clades A to G). These clades, together with their main subdivisions, support part of the currently hypothesized families, “subfamily groups”, or subfamilies (Fig. 7 and Table 5).

The higher rank categories, that is, families or “subfamily groups”, correspond to the broad morphological categories used since the beginning of modern cricket classification. Three of the four families used in the OSF are recovered as monophyletic (Table 5, Fig. 7), but their relationships are not consistent with a similar taxonomic level (see below). These families are: the mole crickets (OSF Gryllotalpidae), the scaly crickets (OSF Mogoplistidae), and the true crickets (OSF Gryllidae). The monophyly of the fourth family, the Myrmecophilidae, sampled here for the Myrmecophilini tribe only, is also well supported in the analyses without *Schizodactylus* (see above and Figs S15–S17). Out of the three “subfamily groups” used in the OSF, only one corresponds to a well-supported clade (“Phalangopsinae subfamily group”, clade E); the “Podoscirtinae subfamily group” and the “Gryllinae subfamily group” are included in our clades F and G respectively.

Among the 22 sampled subfamilies, only six are monophyletic, that is, the Gryllotalpinae, Trigonidiinae, Pteroplistinae, Euscyrtinae, Oecanthinae (sampled here for the Oecanthini tribe only), and Phaloriinae. They correspond to the smallest groups currently recognized in terms of cricket classification, except the Trigonidiinae, and the most homogeneous morphologically. All the other subfamilies are para- or polyphyletic. Some “nearly monophyletic” subfamilies correspond to morphologically well-characterized groups, the definitions for which have been made confused by the wrong placement of a few genera: their monophyly may be obtained with slight taxonomic

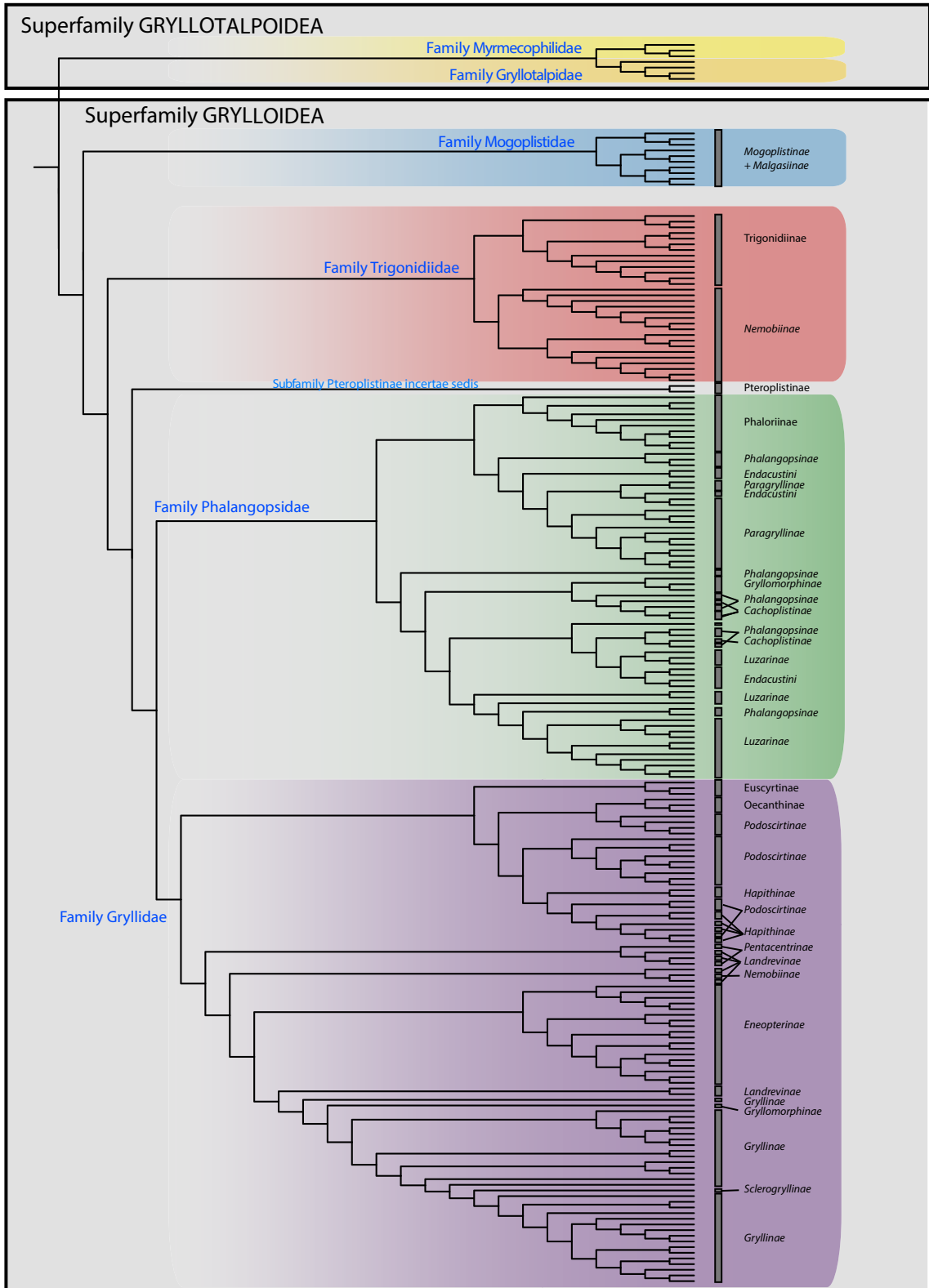


Fig. 7. Phylogeny of crickets based on 205 terminals and seven DNA markers in Bayesian inference, and derived classification of crickets, with two superfamilies (Gryllotalpoidea, Grylloidea), including, respectively, two (Gryllotalpidae, Myrmecophilidae) and four families (Mogoplistidae, Trigonidiidae, Phalangopsidae, Gryllidae). The current position of each terminal species in the subfamilies used by the OSF is indicated on the right of the tree.

Table 5

Results of the phylogenetic test of the current classification used in the OSF, and its potential match with the phylogenetic topology

OSF classification	Topology	
OSF Families/Subfamilies	Monophyly status	Resultant clades
GRYLLIDAE		
“Gryllinae subfamily group”		
Gryllinae	Monophyletic without <i>Gryllomorpha</i> , <i>Petaloptila</i> , and with <i>Sclerogryllus</i>	Included in clade G4
Gryllomiminae	Not tested (1 genus)	–
Gryllomorphinae	Polyphyletic	Dispatched in clades E3 and G4
Itarinae	Not tested (2 genera)	–
Landrevinae	Polyphyletic	Dispatched in clades G1, G2 and G4
Sclerogryllinae	Nested clade	Included in clade G4
“Podoscirtinae subfamily group”		
Euscirtinae	Monophyletic	Equal to clade F1
Hapithinae	Polyphyletic	Included in clade F5
Podoscirtinae	Polyphyletic	Dispatched in clades F3, F4 and F5
Pentacentrinae	Polyphyletic	Included in clade G1
No hypothesized “subfamily group”		
Eneopterinae	Nested clade	Dispatched in clades F5 and G3
Oecanthinae	Monophyletic	Equal to clade F2
“Phalangopsinae subfamily group”		
Cachoplistinae	Polyphyletic	Dispatched in clades E2, E3 and E4
Luzarinae	Polyphyletic	Dispatched in clades E1, E4 and E5
Paragryllinae	Monophyletic with <i>Caltathra</i> and <i>Protathra</i>	Included in clade E2
Phalangopsinae	Polyphyletic	Dispatched in clades E2, E3, E4 and E5
Phaloriinae	Monophyletic	Included in clade E1
Pteroplistinae	Monophyletic	Equal to clade D
Endacustini	Polyphyletic	Dispatched in clades E2 and E4
No hypothesized “subfamily group”		
Nemobiinae	Monophyletic without <i>Hemigryllus</i>	Dispatched in clades C2 and G2
Trigonidiinae	Monophyletic	Equal to clade C1
MOGOPLISTIDAE		
Malgasiinae	Nested clade	Included in clade B
Mogoplistinae	Monophyletic with <i>Malgasia</i>	Included in clade B
GRYLLOTALPIDAE		
Gryllotalpinae	Monophyletic	Equal to clade A1
Scapteriscinae	Not tested (2 genera)	–
MYRMECOPHILIDAE		
Myrmecophilinae	Paraphyletic due to <i>Schizodactylus</i> , otherwise monophyletic	Included in clade A2

changes, that is, provided some particular genera are moved from their current definition in the OSF. This is the case of the Nemobiinae, which form a well-supported clade, from which the genus *Hemigryllus* is excluded. Gorochov (1986) and Desutter (1987, 1988) previously suggested that *Hemigryllus* is not a Nemobiinae: Gorochov (1986) had erected the Hemigryllinae subfamily within an “Eneopteridae group” comprising the Eneopterinae, Landrevinae, and Phalangopsinae, and Desutter (1987, 1988) had tentatively placed *Hemigryllus* within the newly erected Tafaliscinae subfamily comprising the Neotropical Tafaliscini, Paroecanthini, Neometrypini, and Diatrypini. In the same way, the genus *Malgasia* is nested within the Mogoplistinae from which it cannot be separated as a distinct subfamily. The Pentacentrinae are monophyletic provided they include some genera currently classified within the Landrevinae, a reorganization suggested by

several morphological characters (S. Hugel, unpublished data). However, because these two subfamilies belong to different “subfamily groups”, this modification implies their complete reassessment. Finally, the Eneopterinae are monophyletic provided that they are narrowed according to Robillard and Desutter-Grandcolas (2008); the genera added in this group by Otte and Perez-Gelabert (2009) must be transferred to the Hapithinae.

The other subfamilies should be more deeply reassessed: the Gryllinae should include the Sclerogryllinae and some of the Gryllomorphinae (at least *Eugryllodes* among the sampled genera). The Luzarinae, Phalangopsinae, Cachoplistinae, and Paragryllinae of the “Phalangopsinae subfamily group” should be fully redefined and the genera reclassified. The subfamilies proposed by Gorochov (2014) for the “Phalangopsinae subfamily group” on a taxonomic basis are not vali-

dated here, his “Phalangopsinae” gathering taxa belonging to our clades E2, E4, and E5. The position of the taxa yet to be classified within the Podoscirtinae and the Hapithinae of the “Podoscirtinae subfamily group” should be revised.

At a lower taxonomic level, most of the 37 sampled tribes are para- or polyphyletic. These non-monophyletic tribes belong to the “Phalangopsinae subfamily group”, the “Podoscirtinae subfamily group”, and the “Gryllinae subfamily group”, which are scattered across our clades E, F and G, but also to the Trigonidiinae and the Nemobiinae (clade C).

The vast majority of the phylogenetic relationships discussed above are well supported (PP > 0.80), except for the definition of the clades F and G (see above). These results will imply deep modifications in the current cricket classification, even if the general framework looks preserved. The bulk of cricket diversity will have to be reorganized to design a phylogeny-based classification of crickets, which also calls for a reassessment of the morphological characters used to define the different taxa.

Laying the foundation of a phylogenetic classification

Our results (Fig. 7) support the monophyly of the cricket clade (\pm *Schizodactylus*), and its subdivision into two main clades: mole crickets and ant-loving crickets on the one hand, and all the other crickets on the other. In the framework of the OSF classification of Ensifera, the separation of (Gryllotalpidae + Myrmecophilidae) from the Grylloidea justifies the erection of a superfamily Gryllotalpoidea Leach, 1815, while the Grylloidea Laicharting, 1781 is restricted to scaly crickets and true crickets. The whole cricket clade should consequently be elevated at the infraorder level, that is, the Gryllidea, as proposed by several authors in the past (Vickery, 1977; Desutter, 1987, 1988; Gorochov, 1995; see also Song et al., 2015). The monophyly of Gryllidea, which is ascertained here for extant taxa, will have to be checked relative to ensiferan fossils, with a reanalysis of morphological characters in fossils and extant taxa (see Béthoux and Nel (2002) for fossil taxa only).

A very similar classification was proposed by Vickery (1977), who kept, however, the Myrmecophilidae within the Grylloidea. Gorochov (1995) separated the Gryllotalpidae and possibly the Myrmecophilidae from the Mogoplistidae and all other crickets within the Gryllidea, but put *Malgasia* in a subfamily of the Myrmecophilidae. Also his Gryllidea included both extant and fossil taxa, but some of his clades were paraphyletic (see Gorochov, 1995, his fig. 1149).

Within the Grylloidea *sensu stricto*, we propose to consider four families: the Mogoplistidae Brunner von Wattenwy, 1873 (clade B), the Trigonidiidae Saussure,

1874 (clade C), the Phalangopsidae Blanchard, 1845 (clade E), and the Gryllidae Laicharting, 1781 (clade F + G). The first three are robust and highly supported, while the latter has variable support and its inner structure needs to be studied more deeply. Clade D (Pteroplistinae Chopard, 1936), which is supported by all analyses but its phylogenetic position remains unstable, should be kept *incertae sedis* within Grylloidea. These families fit variously with morphological characters.

The monophyly of the Trigonidiidae, and of their two traditional subfamilies, the Trigonidiinae and the Nemobiinae (without *Hemigryllus*), is corroborated by many morphological characters (Gorochov, 1986; Desutter, 1987, 1988). The morphological definition of the Phalangopsidae, which has been recognized as a main cricket group since Blanchard (1845), will have to be checked to take into account at least *Gryllomorpha* and *Petaloptila*, and possibly other genera of the Petaloptilini tribe. Finally, the Gryllidae, as defined here, is not compatible with the morphological characters currently used: it will have to be reanalysed to clarify the situation. Except for the Trigonidiinae and Nemobiinae (Desutter, 1987, 1988), the Eneopterinae (Robillard and Desutter-Grandcolas, 2008), and the Pentacentrinae (S. Hugel, unpublished data), the putative subfamilies will have to be reconsidered from the point of view of their morphological diagnosis, a valid concern for nearly all the groups of crickets below the familial rank (L. Desutter-Grandcolas, unpublished data).

The classification system proposed here fits the structure of the phylogeny better than the OSF, and uses the best-supported clades as a backbone for a future classification of crickets. It is intermediary between the very split system proposed by several authors, with up to 12 or 13 hypothesized families (Bruner, 1916; Chopard, 1949; Vickery, 1977; McE Kevan, 1982; Desutter, 1988), and the lumped system with all crickets gathered in one family subdivided in as many subfamilies (Scudder, 1897; Otte and Alexander, 1983). This system is not incompatible with the OSF, but beyond an apparent consistency, the classification of crickets needs to be deeply revised to achieve a classification system that accommodates monophyletic units of evolution.

Laying the foundation of future evolutionary studies

The proposed phylogenetic hypothesis brings new perspectives for understanding cricket evolution, especially on communication, for which these insects are important models (Gerhardt and Huber, 2002).

Acoustic evolution in Ensifera should be reconsidered, as previous analyses of acoustic evolution in Ensifera focused on the structural homology between crickets *sensu lato* on the one hand, and katydids (Tet-

tigonioidea) on the other. The question was then to decide whether acoustic communication has evolved once (ancestral communication) or twice (convergent evolution) within Ensifera as a whole: “crickets” being considered an acoustically homogeneous group (see e.g. Bailey, 1991). Structural analyses of forewing venation revealed an unsuspected diversity in crickets *sensu lato*, supporting a hypothesis of convergence between the mole crickets and the crickets *sensu stricto*; in other words, the primary homology hypothesis was not supported (Desutter-Grandcolas, 2003; Desutter-Grandcolas et al., 2005; but see Béthoux, 2012). By definition, such a hypothesis cannot be tested by a phylogeny, but it may imply more or less complex patterns of character change according to the phylogenetic topology. Our present phylogeny is parsimoniously consistent with the convergence hypothesis between crickets and mole crickets, and is also consistent with the fact that crickets *sensu lato* may have structurally diverse acoustic structure (see below); their early acoustic evolution may then not have been straightforward, especially as acoustic communication may have developed in Ensifera within a general framework of communication by vibration and/or sound (Desutter-Grandcolas, 2003 and references therein; Strauss and Lakes-Harlan, 2008a,b; Stritih and Cokl, 2012).

Cricket *sensu stricto* moreover present a wide acoustic diversity, both in terms of structures and in terms of functional properties. The few species used to generate the basic model of sound production in crickets, that is, *Acheta*, *Gryllus*, or *Teleogryllus* grylline species (Nocke, 1972; Elliott and Koch, 1985; Montealegre-Z et al., 2011; but see Bennet-Clark and Bailey, 2002), all belong to a small apical group nested within our clade G. Recent bioacoustic analyses of more distantly related Eneopterinae species questioned this basic cricket model: Eneopterinae emit high-frequency calls using the second or third harmonic as a dominant frequency (Robillard et al., 2013), or produce several kinds of syllables using complex stridulatory behaviours and structures (Robillard and Desutter-Grandcolas, 2011b). Yet, Eneopterinae are quite close to Gryllinae, both belonging to clade G, and the two groups taken together do not reflect the high diversity of sound-production structures in crickets. For example, the sound generating system of an *Oecanthus* species analysed with laser Doppler vibrometry proved recently really different from the usual cricket model when considering the vibratory properties of the wings (Mhatre et al., 2012). To further study cricket bioacoustics, good targets to begin with could be the Trigonidiidae, the sister group of all other crickets, and non-mute Phalangopsidae, the sister group of our Gryllidae. These two groups have very peculiar stridulums that do not fit well with the usual acoustic structures of crickets according to the current basic model

of sound production. Trigonidiidae are characterized by a wide harp area, crossed by one vein and bordered by a high diagonal vein that may extend the resonant area of the wing to almost the whole forewing surface (Desutter-Grandcolas and Nischk, 2000). Yet, Trigonidiidae emit either very loud calls (Trigonidiinae), or soft, courting-like calls (Nemobiinae): this situation reflects the presence versus absence of the mirror on the forewings, whereas this structure is supposed to be inactive in sound radiation (e.g. Nocke, 1972; Bennet-Clark, 2003; Montealegre-Z et al., 2011). In addition, many Phalangopsidae have a corneous, stiff right forewing, and a soft and fragile left forewing, and they are able to emit calling songs, which are either loud and high-pitched, or soft and non-resonant. Such a highly asymmetrical stridulum may not vibrate the same way as a typical grylline stridulum (e.g. Simmons and Ritchie, 1996; Bennet-Clark, 2003; Montealegre-Z et al., 2011), and this situation is not as yet fully understood. To study cricket call evolution deeper, or even predict cricket calls in extant and fossil taxa from the study of their stridulatory apparatus, as undertaken for katydids (Montealegre-Z, 2009; Gu et al., 2012), it is now essential to study the large diversity of cricket bioacoustics within a phylogenetic perspective, considering the explicit diversity documented by behavioural observations, and the implicit diversity suggested by the phylogeny.

In addition to acoustics, the Gryllotalpoidea includes taxa inhabiting specialized acoustic burrows (mole crickets), taxa living in symbiosis with ants (Myrmecophilinae, Myrmecophilini), and taxa found in deserts (Myrmecophilinae, Bothriophylacini). These habitats and life habits require specific morphological, physiological, and behavioural adaptations, for which the main lines of evolution could be better deciphered in a tree-thinking perspective.

Finally, cricket biogeography and diversification have never been analysed in a wide-scale context due to the lack of properly defined monophyletic groups, but our study brings valuable insights in this respect. Whereas familial and most subfamilial cricket clades are distributed worldwide, some subfamilial taxa, as modified according to our phylogenetic hypothesis, show interesting new biogeographical patterns. This is the case, for example, of the sister-groups Podoscirtinae and Hapitinae in clade F, which now both show a biogeographical coherence: the former is distributed in the Palearctic and in Oceania, while the latter is present in the Neotropics only. In the same way, the nested positions of *Gryllomorpha* and *Petaloptila* within the Phalangopsidae attest for the first time the presence, in the Mediterranean region, of cricket taxa that diversified from a wide intertropical group. These examples suggest new biogeographical scenarios, which should be tested further as typically undertaken for all

organisms, with well-supported phylogenetic hypotheses (Sanmartin et al., 2001; Sanmartin, 2003; Crisp et al., 2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figures S1–S7. Results of the separate phylogenetic analyses in ML for 12S, 16S, 18S, 28SA, 28SD, cytb and H3 markers, respectively. $\ln L_{12S} = -32572.585003$; $\ln L_{16S} = -32702.581814$; $\ln L_{18S} = -15462.852866$; $\ln L_{28SA} = -13704.500232$; $\ln L_{28SD} = -10522.780197$; $\ln L_{cytb} = -25817.127967$; $\ln L_{H3} = -12141.167417$.

Figure S8. Result of the combined phylogenetic analysis in ML ($\ln L = -150351.480431$).

Figure S9. Results of the combined (without marker 28SD) phylogenetic analysis in ML ($\ln L = -137828.405642$).

Figure S10. Result of the combined phylogenetic analysis in parsimony (strict-consensus of four trees of 37341 steps).

Figure S11. Result of the phylogenetic analysis of the nuclear data in MP.

Figure S12. Result of the phylogenetic analysis of the nuclear data in ML.

Figure S13. Result of the phylogenetic analysis of the mitochondrial data in MP.

Figure S14. Result of the phylogenetic analysis of the mitochondrial data in ML.

Figure S15. Result of the combined phylogenetic analysis in ML ($\ln L = -149666.340159$) without *Comicus campestris* and *Schizodactylus monstrosus*.

Figure S16. Result of the combined phylogenetic analysis in BI without *Comicus campestris* and *Schizodactylus monstrosus*.

Figure S17. Result of the combined phylogenetic analysis in MP (strict-consensus of 333 trees of 37155 steps) without *Comicus campestris* and *Schizodactylus monstrosus*.

Data S1. Phylogenetic matrix used in this study.