Zootaxa 4424 (1): 001–064
http://www.mapress.com/j/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4424.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:9339A2CB-C106-4C0E-9A94-1E5BB220335A

ZOOTAXA

4424

A molecular phylogeny of the cicadas (Hemiptera: Cicadidae) with a review of tribe and subfamily classification

DAVID C. MARSHALL[1,15], MAX MOULDS[2], KATHY B. R. HILL[1], BENJAMIN W. PRICE[3],
ELIZABETH J. WADE[4], CHRISTOPHER L. OWEN[5], GEERT GOEMANS[1,10],
KIRAN MARATHE[6,11], VIVEK SARKAR[6,12], JOHN R. COOLEY[1,7], ALLEN F. SANBORN[8],
KRUSHNAMEGH KUNTE[6,13], MARTIN H. VILLET[9] & CHRIS SIMON[1,14]

[1]*Dept. of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA*
[2]*Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia. E-mail: msmoulds@gmail.com*
[3]*Natural History Museum, London, United Kingdom. E-mail: b.price@nhm.ac.uk*
[4]*Dept. of Natural Science and Mathematics, Curry College, Milton, MA 02186, USA. E-mail: elizabeth.wade@post03.curry.edu*
[5]*Systematic Entomology Laboratory, Agricultural Research Service, U.S. Dept. of Agriculture, Beltsville, MD 20705, USA. E-mail: clowen@email.gwu.edu*
[6]*National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK Campus,
Bellary Road, Bangalore 560 065, India*
[7]*College of Integrative Sciences, Wesleyan University, Middletown, CT 06459, USA. E-mail: cicada@magicicada.org*
[8]*Dept. of Biology, Barry University, 11300 NE Second Avenue, Miami Shores, FL 33161, USA. E-mail: asanborn@barry.edu*
[9]*Dept. of Biology, Rhodes University, Grahamstown 6140, South Africa. E-mail: M.Villet@ru.ac.za*
[10]*E-mail: ggoemans@gmail.com*
[11]*E-mail: kiran@ifoundbutterflies.org*
[12]*E-mail: vivek@ifoundbutterflies.org*
[13]*E-mail: krushnamegh@ncbs.res.in*
[14]*E-mail: chris.simon@uconn.edu*
[15]*Corresponding author. E-mail: david.marshall@uconn.edu*

Magnolia Press
Auckland, New Zealand

Accepted by C. Dietrich: 16 Feb. 2018; published: 28 May 2018

DAVID C. MARSHALL, MAX MOULDS, KATHY B. R. HILL, BENJAMIN W. PRICE, ELIZABETH J. WADE, CHRISTOPHER L. OWEN, GEERT GOEMANS, KIRAN MARATHE, VIVEK SARKAR, JOHN R. COOLEY, ALLEN F. SANBORN, KRUSHNAMEGH KUNTE, MARTIN H. VILLET, & CHRIS SIMON
A molecular phylogeny of the cicadas (Hemiptera: Cicadidae) with a review of tribe and subfamily classification
(*Zootaxa* 4424)

64 pp.; 30 cm.

28 May 2018

ISBN 978-1-77670-374-6 (paperback)

ISBN 978-1-77670-375-3 (Online edition)

FIRST PUBLISHED IN 2018 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

http://www.mapress.com/j/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Contents

ABSTRACT

A molecular phylogeny and a review of family-group classification are presented for 137 species (ca. 125 genera) of the insect family Cicadidae, the true cicadas, plus two species of hairy cicadas (Tettigarctidae) and two outgroup species from Cercopidae. Five genes, two of them mitochondrial, comprise the 4992 base-pair molecular dataset. Maximum-likelihood and Bayesian phylogenetic results are shown, including analyses to address potential base composition bias. *Tettigarcta* is confirmed as the sister-clade of the Cicadidae and support is found for three subfamilies identified in an earlier morphological cladistic analysis. A set of paraphyletic deep-level clades formed by African genera are together named as Tettigomyiinae **n. stat.** Taxonomic reassignments of genera and tribes are made where morphological examination confirms incorrect placements suggested by the molecular tree, and 11 new tribes are defined (Arenopsaltriini **n. tribe**, Durangonini **n. tribe**, Katoini **n. tribe**, Lacetasini **n. tribe**, Macrotristriini **n. tribe**, Malagasiini **n. tribe**, Nelcyndanini **n. tribe**, Pagiphorini **n. tribe**, Pictilini **n. tribe**, Psaltodini **n. tribe**, and Selymbriini **n. tribe**). Tribe Tacuini **n. syn.** is synonymized with Cryptotympanini, and Tryellina **n. syn.** is synonymized with an expanded Tribe Lamotialnini. Tribe Hyantiini **n. syn.** is synonymized with Fidicinini. Tribe Sinosenini is transferred to Cicadinae from Cicadettinae, Cicadatrini is moved to Cicadettinae from Cicadinae, and Ydiellini and Tettigomyiini are transferred to Tettigomyiinae **n. stat** from Cicadettinae. While the subfamily Cicadinae, historically defined by the presence of timbal covers, is weakly supported in the molecular tree, high taxonomic rank is not supported for several earlier clades based on unique morphology associated with sound production.

Key words: systematics, taxonomy, morphology, nuclear DNA, mtDNA, combined data analysis, Auchenorrhyncha, Hemiptera, Cicadoidea, biogeography

INTRODUCTION

Cicadas are hemipteran insects known for their multiple-year life cycles, some of which are the longest known in non-eusocial insects, and for their loud, complex, and usually species-specific acoustic sexual signals or songs (Myers 1929; Claridge 1985; Williams & Simon 1995). Cicadas have become useful model organisms for studies of speciation and biogeography, because songs allow rapid assessment of local cicada communities and facilitate the detection of cryptic taxa at early stages of divergence (Marshall *et al*. 2011; Hertach *et al*. 2016). Cicadas have also become a focus of studies of endothermy (e.g., Sanborn *et al.* 2003; Sanborn *et al.* 2017), of endosymbiosis, where extraordinary examples of genome evolution have been documented (McCutcheon *et al*. 2009; Van Leuven *et al*. 2014; Campbell *et al*. 2015), and in technology where the nanostructure of cicada wings has served as a template for nanolithography to create hydrophobic, antireflective and/or antibiotic surfaces (Zhang *et al*. 2006; Xie *et al*. 2008; Hasan *et al*. 2013; Zada *et al*. 2016; Lin *et al*. 2018). Although cicadas are not major agricultural pests, they are a significant concern for orchardists and growers of certain crops (e.g., sugarcane—Ito & Nagamine 1981; kiwifruit—Logan & Alspatch 2007; grapes—Mehdipour *et al*. 2016), and they are among the largest and most charismatic insects (Fig. 1).

Morphological features involved in sound production have been used in Cicadidae classification to distinguish taxa ranking as low as species and as high as family. In the first subfamily-level schemes, Distant (1889) distinguished two groups in part by the degree of development of structures covering the timbals, the specialized sound organs of male cicadas. Later, Distant (1906) expanded the classification to three groups, the subfamilies Cicadinae Latreille, Gaeaninae Distant, and Tibicininae Distant, with fully covered, partly covered, and uncovered timbals, respectively. Although these subfamily definitions are maintained in part today, the taxonomic utility of some song-related morphological features has been repeatedly challenged, and widely varying numbers of families and subfamilies have been proposed through the 20th century (see Boulard 1976a, 1986b, 1998; Duffels 1993; Moulds 2005) (Fig. 2). Distant's system of tribes has gone largely unexamined, although many tribes have since been added, and many recent changes have been proposed for tropical Asian genera (see below).

The first formal phylogenetic analysis of the family Cicadidae was published by Moulds (2005), who included genitalic and internal reproductive characters along with external morphology including sound-producing structures. His cladistic tree (Fig. 3) was used to support a three-subfamily system, partly matching Distant's groups, that has achieved general acceptance (e.g., Sanborn 2013). Moulds also concluded that the genus *Tettigarcta* White (the "hairy cicadas) forms a sister-clade to the rest of the cicadas, leading him to support a two-family classification of the Cicadoidea (Tettigarctidae and Cicadidae).

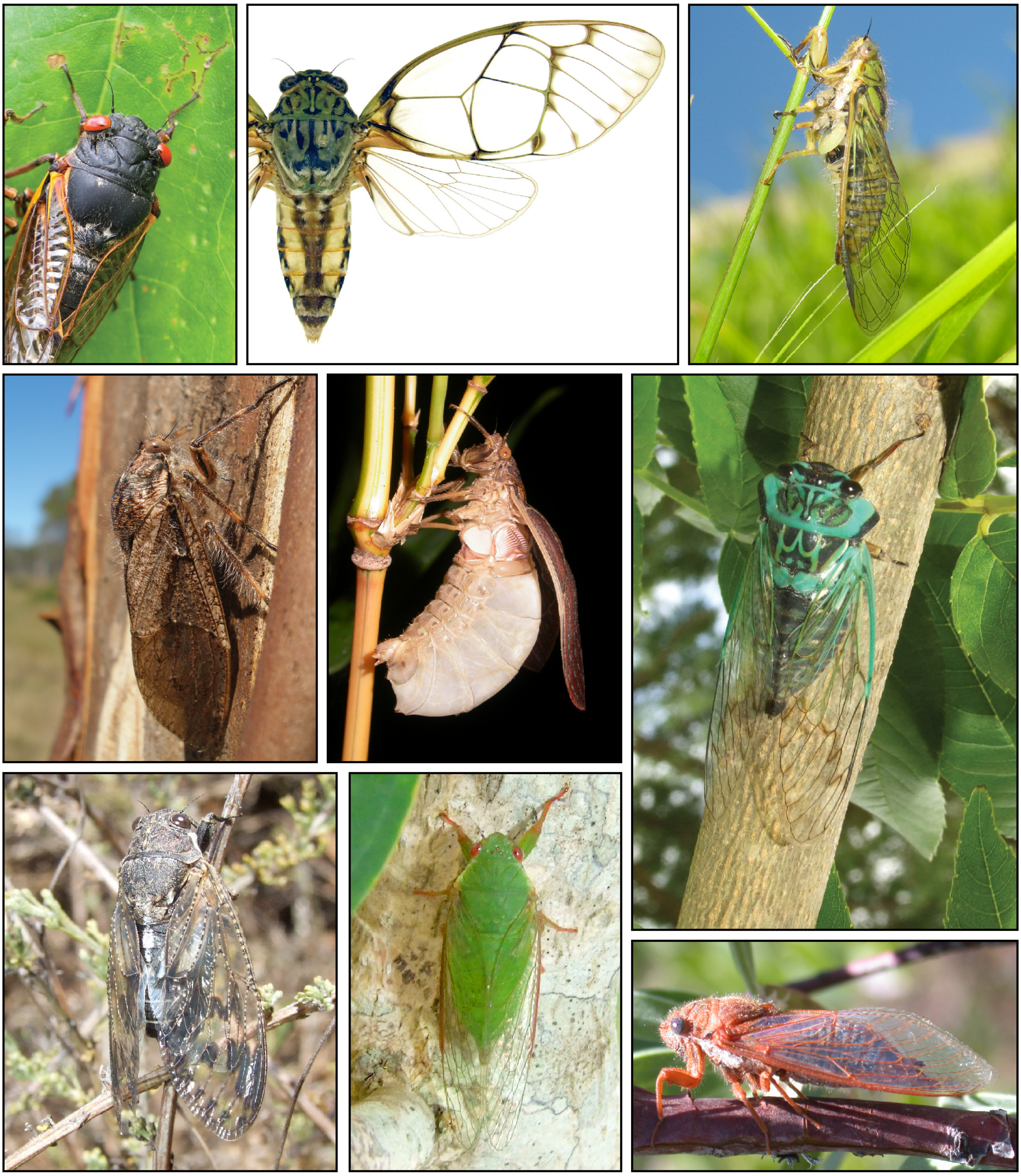


FIGURE 1. Superfamily Cicadoidea. Left to right, and top to bottom (all in Family Cicadidae except *Tettigarcta*): *Magicicada septendecim* L. (17-year cicada)—Cicadettinae, USA, photo C. Simon; *Psithyristria grandis* Lee & Hill—Cicadinae, Philippines; *Kikihia muta* (Fab.)—Cicadettinae, New Zealand; *Tettigarcta crinita* Distant—Tettigarctinae (Tettigarctidae), Australia, photo C. Simon; *Lembeja vitticollis* (Ashton)—Cicadettinae, Australia; *Odopoea insignifera* Berg—Cicadinae, Argentina; *Quintilia wealei* (Distant)—Tettigomyiinae **n. stat.**, South Africa; *Stagira* sp.—Tettigomyiinae **n. stat.**, South Africa; *Okanagana rubrovenosa* Davis—Tibicininae, USA. Images not at matching scale. Photos by K. Hill and D. Marshall unless specified.

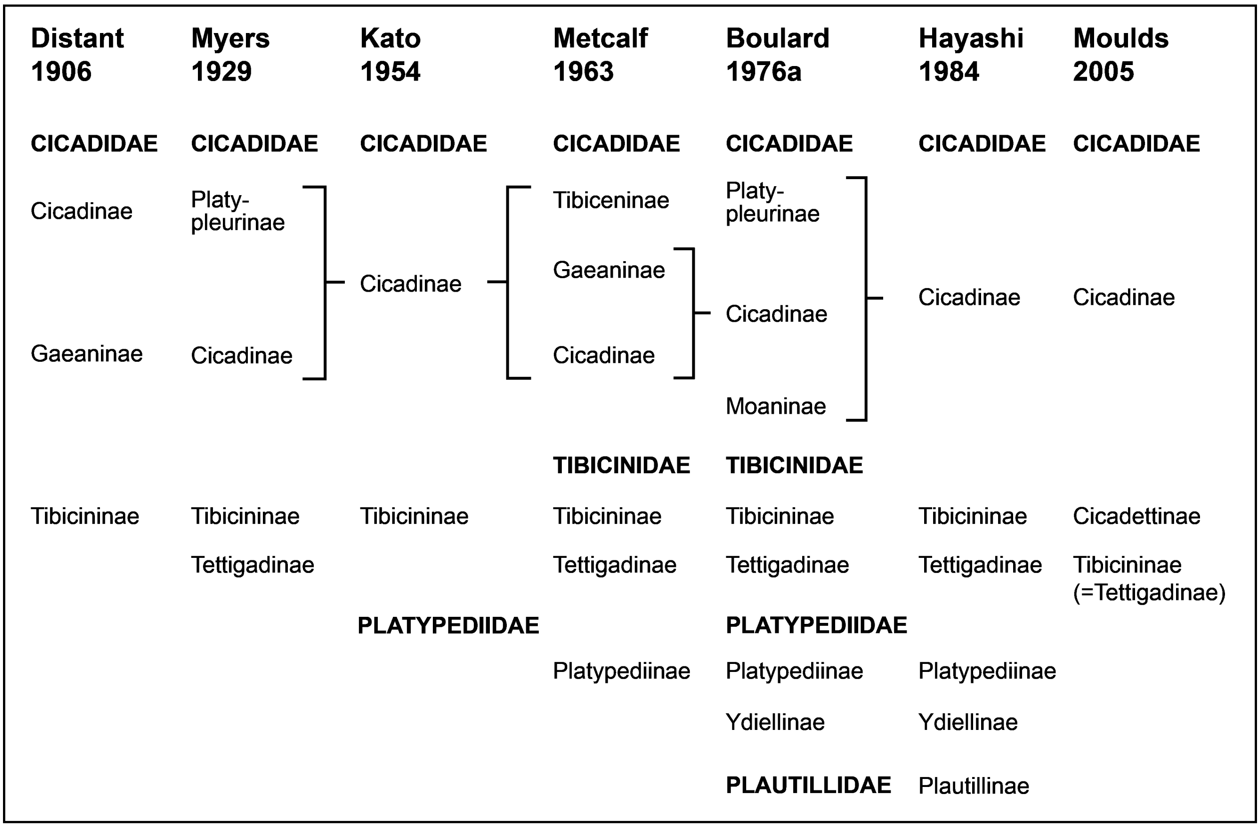


FIGURE 2. Historical shifts in the number of families and subfamilies in Cicadidae classification (excluding Tettigarctidae).

Several cicada genera and three tribes (e.g., Buckley & Simon 2007; Marshall *et al.* 2008; Marshall *et al.* 2012; Popple 2013; Sota *et al.* 2013; Hill *et al.* 2015, Owen *et al.* 2015; Marshall *et al.* 2016; Łukasik *et al.* 2017; Owen *et al.* 2017; Wang *et al.* 2017) have been examined in molecular phylogenetic studies, but no family-level genetic analysis has yet been completed to test Moulds's cladistic tree. Additional phylogenetic work is especially needed because Moulds's study incorporated just 70 current Cicadoidea genera of the approximately 450 known worldwide and 21 of the 44 tribes known before this study (see Sanborn 2013; Sanborn 2014a; Sanborn 2018), and the sampling was geographically biased toward Australasia. Few cicada genera were included from North America (2), South America (5), and Africa (1), although cicadas are diverse in all of those regions.

In this paper we present a molecular phylogeny of the true cicadas plus the hairy cicadas, together with a review of Cicadidae classification. Using nuclear and mitochondrial loci, we find strong support for the deep-level relationships in Moulds's morphological cladistic tree and its associated taxonomic changes. In part due to greater taxon sampling, we also find many strongly supported conflicts in the placement of genera within the subfamily and tribe classification. Where taxon placement in the molecular tree contradicts current classification, we make the necessary taxonomic transfers supported by morphological characters. We elevate the tribe Tettigomyiini in Cicadettinae to subfamily rank, and we describe 11 new tribes. We confirm only limited support for older proposed deep-level clades based on unique morphological features associated with sound production, as discussed by Boulard (1976a, 1998) and Moulds (2005).

MATERIALS AND METHODS

Taxon Sampling and Identification

For most species, cicada tissue was preserved in 95% ethanol at the time of collection and stored at room temperature or chilled on water ice until long-term storage at -20˚C or -80˚C. Some cicadas were preserved whole in ethanol, while in other cases one or more legs were removed at collection and preserved in ethanol, after which the remainder of the specimen was dried for pinning. A few species were sequenced from legs taken from dried museum specimens. Samples were obtained through a global network of collaborators (see Table 1 and

Acknowledgments) and identified by consulting primary literature and regional experts. Taxon sampling spanned the three described Cicadidae subfamilies (Moulds 2005) and the two extant species of the sister-family Tettigarctidae. Phylogenetic studies of some of the larger tribes (i.e., Cryptotympanini—Hill *et al.* 2015; Cicadettini—Marshall *et al.* 2016; Zammarini—Goemans 2016; Platypleurini—Price *et al.* in prep.; and Cicadini and related tribes—unpublished data) helped refine the final choice of taxa. Genbank sequences from two genera of froghoppers (Cercopidae) were selected as outgroups based on the Auchenorrhyncha phylogenies of Cryan & Urban (2012) and Cryan & Svenson (2010), bringing the total number of taxa in the analysis to 141. In some cases, sequences from two specimens of the same species (and/or sequences from Genbank) were combined to make one chimeric exemplar (see Table 1).

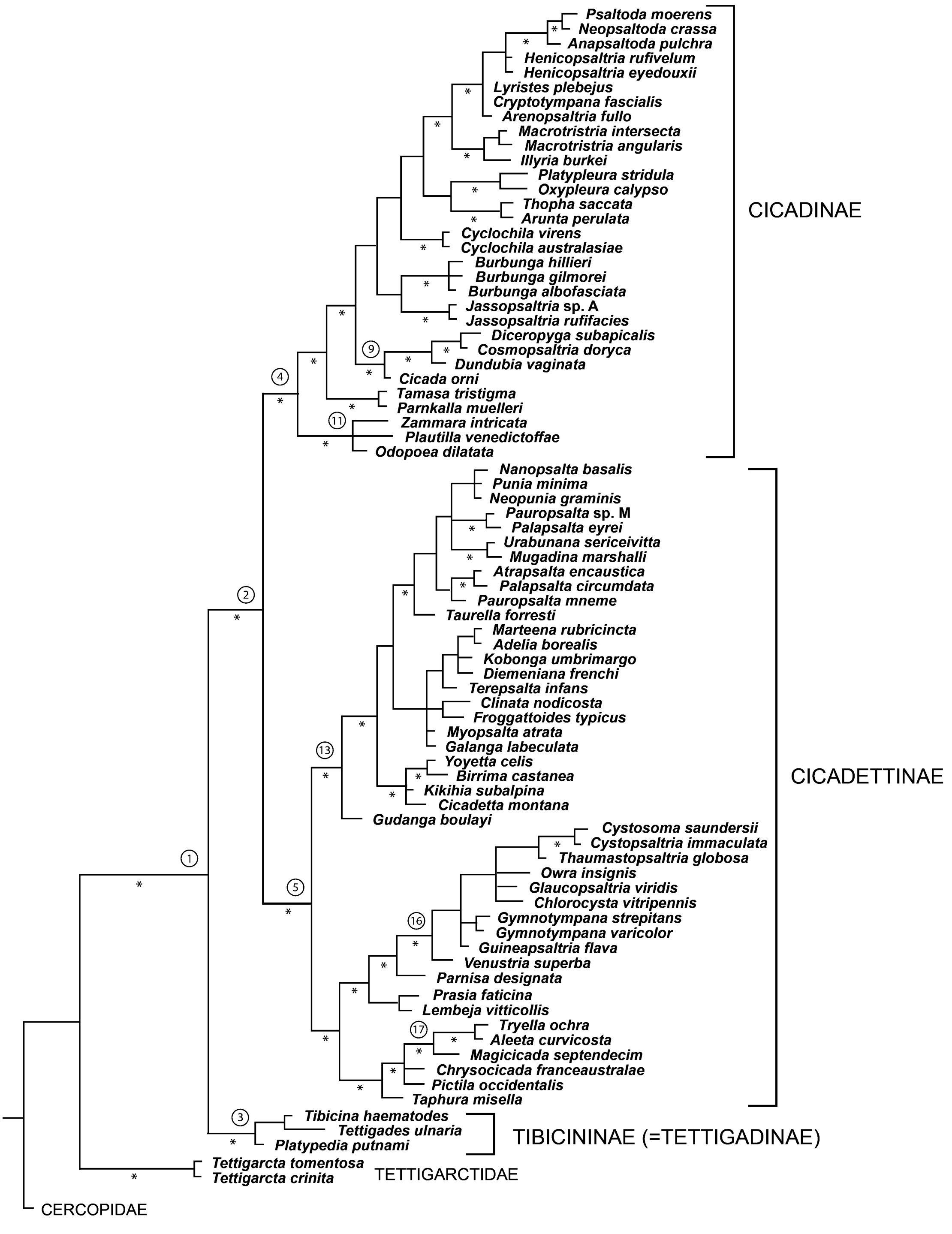


FIGURE 3. Cicadoidea phylogeny obtained from morphological cladistic analysis (adapted from Fig. 56 *in* Moulds 2005), with Cicadidae subfamilies shown. Stars at nodes indicate jackknife support above 50% and/or T-PTP support less than 0.07. Numbers refer to nodes shown in the molecular trees (see Results). Taxa are shown with nomenclature updated since 2005.

TABLE 1. Cicadoidea specimen, locality, and collection data, with loci sequenced for each sample. Asterisked taxa are outgroups from Cercopidae. Genbank numbers are shown when sequences were taken from that database and combined into chimeric exemplars; accession number sets for sequences obtained in this study (marked by 'x') are given in the Results (COI, COII, 18S) or the sequences are available in the Supplementary Data File (EF-1α, ARD1).

							Date		5'	3'				
Taxon Name	Author	Code	Lat.	Lon.	Location	Country	(D/M/Y)	Collectors	COI	COI	COII	ARD1	EF-1α	18s
**Catrimania semivitrea*	(Walker, 1858)	04-05-11-74	–	–	–	Peru	–	–	GU447000	GU447000	GU447079			GU446822
**Cosmoscarta heros*	(Fabr., 1803)	04-12-30-35	–	–	–	China	–	–	GU447018	GU447018	GU447094	x		GU446840
Aceropyga d. distans	(Walker, 1858)	03.FJ.CE.COL.01	-18.077	178.448	Viti Levu	Fiji	26/01/03	Simon Lab	GQ527084	x		x	GQ527128	x
Acuticephala alipuncta	Torres, 1958	08.AR.CC.CPS.01	-26.939	-59.675	Chaco	Argentina	18/01/08	Simon Lab				x	x	
Aleeta curvicosta	(Germar, 1834)	97.AU.NS.QEP.76	-33.867	151.133	NSW	Australia	08/02/97	D. Emery	AB740803	AB740803	x	x	x	x
Allobroma kedenburgi	Breddin, 1905	06.MY.SK.LAM.14	4.198	114.042	Sarawak	Malaysia	12/10/06	J. Cryan		x		x	x	x
Arenopsaltria fullo	(Walker, 1850)	02.AU.WA.YAR.03	-32.952	115.914	WA	Australia	31/12/02	Simon Lab	x	x		x	x	x
Arunta perulata	(G.-M., 1831)	07.AU.QL.RSN.01	-19.045	146.396	QLD	Australia	5/01/07	I. Hill	KR108349	KR108349		x	KR108375	x
Auritibicen japonicus	(Kato, 1925)	03.JP.YT.YAM.01	–	–	Honshu	Japan	08/2003	H. Honsya	x	x				
Auritibicen japonicus	(Kato, 1925)	CD12	35.260	138.360	Nagano	Japan	25/08/07	J. Yoshimura				x	x	x
Baeturia cf. *nasuta*	Blöte, 1960	01.PG.CH.HAI.01	–	–	Chimbu Pr.	PNG	2001	Whiting *et al.*		x	x		x	x
Beameria venosa	(Uhler, 1888)	07.US.UT.GOS.01	37.175	-109.927	Utah	USA	21/06/07	Heath, Hill, Marshall	x	x		x		x
Burbunga queenslandica	Moulds, 1994	02.AU.NS.TRA.01	-32.032	147.991	NSW	Australia	20/01/02	Moulds, Cooley, Hill	x	x		x		x
Calyria stigma	(Walker, 1850)	08.AR.MN.IES.05	-25.679	-54.450	Misiones	Argentina	6-7/1/08	Simon Lab	x	x		x	x	x
Calyria stigma	(Walker, 1850)	08.AR.MN.NCG.01	-27.169	-54.932	Misiones	Argentina	5/1/08	Simon Lab			x			
Carineta diardi	(G.-M., 1829)	08.BR.RJ.LUM.01	–	–	R.d. Jan.	Brazil	13/09/08	Daniela Takiya		x		x	x	x
Changa sita	(Distant, 1881)	NCBS_AC177	25.648	93.479	Nagaland	India	05/05/12	B. Price	x			x	x	
Chremistica cf. *matilei*	Boulard, 2000	MadLoc6_4	-25.006	46.303	Toliara Pr.	Madgascar	9-24/11/08	J. Cryan	x	x		x	x	x
Chremistica ochracea	(Walker, 1850)	0626	–	–	P.Hsien	Taiwan	08/07/03	J-H. Chen	KR674175			x	KR705791	x
Chremistica ribhoi	H. & Y., 2013	NCBS_AC788	25.862	91.842	Meghalaya	India	15/05/14	Kunte Lab	x	x	x	x	x	
Chremistica sp.	–	Laos_MtPan	–	–	Mt. Pan	Laos	2003	–	KR674240	KR674240			x	
Chrysocicada sp.	Boulard, 1989	06.AU.WA.MDE.01	-17.418	124.097	WA	Australia	07/02/06	Simon Lab	x	x	KT602300	x	KT713542	x
Cicada orni	Linnaeus, 1758	03.HR.SB.PIR.20	–	–	–	Croatia	--/09/03	T. Trilar, M. Gogala	GQ527102				GQ527142	
Cicada orni	Linnaeus, 1758	07.FR.BD.CLP.06	43.275	5.700	B-du-Rhône	France	09/07/07	J. Sueur, J.F.C. Windmill		x		x		x

… … continued on the next page

TABLE 1. (Continued)

							Date		5'	3'				
Taxon Name	Author	Code	Lat.	Lon.	Location	Country	(D/M/Y)	Collectors	COI	COI	COII	ARD1	EF-1α	18s
Cicada orni	Linnaeus, 1758	see Genbank ref.	–	–	–	–	–	–			EU401955			
Cicadatra atra	(Olivier, 1790)	07.FR.BD.CLP.07	43.275	5.700	B-du-Rhône	France	09/07/07	J. Sueur, J.F.C. Windmill	GQ527100	x		x	GQ527140	x
Cicadetta montana	(Scopoli, 1772)	02-034	–	–	Idrija	Slovenia	29/05/02	T. Trilar, M. Gogala	AF441815	KT602129	KT602328	x	KT713571	
Cicadettana calliope	(Walker, 1850)	04.US.KS.ATT.03	37.239	-98.053	Kansas	USA	26/06/04	K. Hill, D. Marshall	KF919587	KT602148	KT602347	x	KT713590	
Clidophleps vagans	Davis, 1925	03.US.CA.SBI.01	37.287	-118.374	California	USA	26/06/03	K. Hill, D. Marshall		AY997113	AY997113	x	X	x
Cornuplura nigroalbata	(Davis, 1936)	07.US.AZ.PBC.02	31.394	-111.090	Arizona	USA	24/06/07	K. Hill, D. Marshall	KR674179	KR674179			KR705795	x
Cosmopsaltria gestroei	(Distant, 1905)	08.PG.MR.KAM.01	-7.296	157.093	Morobe	P.N.Guinea	01/02/08	Bishop Museum	x	x		x	x	x
Cryptotympana atrata	(Fabr., 1775)	0624	–	–	T. Hsien	Taiwan	01/07/03	J-H. Chen	KR674174	KR674174	x	x	KR705790	x
Cryptotympana takasagona	Kato, 1925	0580	–	–	Taipei City	Taiwan	09/06/03	J-H. Chen	KR674167	KR674167	x		KR705781	
Cyclochila australasiae	(Donov., 1805)	02.AU.NS.NPF.04	-31.680	152.652	NSW	Australia	06/01/02	Simon Lab	x	x		x	x	x
Cystosoma saundersii	(Westw., 1842)	02.AU.QL.BBR.26	-26.888	152.214	QLD	Australia	09/01/02	Simon Lab		KT602157	KT602356	x	KT713599	x
Diceroprocta apache	(Davis, 1921)	03.US.CA.JUL.01	33.111	-116.503	California	USA	01/07/03	K. Hill, D. Marshall	x	x		x	x	x
Diemeniana euronotiana	(Kirkaldy, 1909)	98.AU.VI.BRI.06	-36.767	146.967	Victoria	Australia	20/01/98	Simon Lab		KT602085	KT602285	x	KT713526	x
Dundubia vaginata	(Fabr., 1787)	03.MY.SA.KIN.23	6.006	116.543	Sabah	Borneo	03/04/03	T. Trilar, K.P. Trilar	GQ527104	x		x	GQ527144	x
Durangona tigrina	Distant, 1911	09.EC.NA.HOL.01	-0.695	-77.731	Napo	Ecuador	21/01/09	G. Goemans	x	x		x	x	x
Euryphara dubia	(Rambur, 1840)	03.ES.ZG.CDV.01	–	–	C de Valdej.	Spain	31/05/03	S. Puissant		KT602124	KT602323		KT713566	
Fidicina cf. *ethelae*	(Goding, 1925)	04.PE.MD.PAZ.02	-12.802	-69.300	M de Dios	Peru	1-30/09/04	J. Cryan, J. Urban	x	x		x	x	x
Fijipsalta tympanistria	(Kirkaldy, 1907)	03.FJ.WE.NAL.01	-17.442	178.088	Viti Levu	Fiji	29/01/03	Simon Lab		KT602087	KT602287		KT713528	
Formosemia apicalis	(Matsu., 1907)	03.TW.KH.HSI.74	–	–	K. Hsien	Taiwan	20/09/03	J-H. Chen	GQ527098			x	GQ527138	
Gaeana maculata	(Drury, 1773)	08.CN.AH.TIA.07	–	–	Anhui	China	15/06/08	L. Jingke			x	x	x	x
Gaeana maculata	(Drury, 1773)	CL11	–	–	–	–	–	–	KM244671					
Gelidea torrida	(Erich., 1842)	06.AU.VI.MAR.01	-37.799	148.528	Victoria	Australia	23/11/06	Simon Lab		KT602045	KT602245	x	KT713486	x
gen. nr. *Cicada*	–	NCBS_AC226	26.65	89.55	W Bengal	India	24/05/12	T. Karmukar	x					
gen. nr. *Ligymolpa*	–	Madloc1_2	-21.254	47.422	Fianar. Pr	Madgascar	9-24/11/08	J. Cryan	x	x		x	x	x
gen. nr. *Tanna*	–	NCBS_AC211	8.647	77.167	Kerala	India	9/06/12	B. Price	x			x		
Graptopsaltria nigrofuscata	(de Mot., 1866)	03.JP.YN.MAC.08	–	–	Chubu	Japan	--/08/03	H.Karube,J.Yoshimura	x	x		x	x	x
Gudanga boulayi	Distant, 1905	03.AU.WA.LKD.10	-30.839	121.386	WA	Australia	16/01/03	Simon Lab		KT601993	KT602193	KY042187	KT713434	

……continued on the next page

TABLE 1. (Continued)

							Date		5'	3'				
Taxon Name	Author	Code	Lat.	Lon.	Location	Country	(D/M/Y)	Collectors	COI	COI	COII	ARD1	EF-1α	18s
Gymnotympana varicolor	(Distant, 1907)	04.AU.QL.RIF.04	-16.667	145.327	QLD	Australia	12/01/04	Simon Lab		x	x	x	x	x
Hadoa duryi	(Davis, 1917)	03.US.AZ.STR.04	34.422	-111.512	Arizona	USA	29/06/03	K. Hill, D. Marshall	x	x		x	KR705759	x
Haemopsalta aktites	(Ewart, 1989)	97.AU.NS.SEV.23	-34.750	150.750	NSW	Australia	20/01/97	D. Emery	KM377213	KT602082	KT602282		KT713523	x
Henicopsaltria rufivelum	Moulds, 1978	04.AU.QL.BFA.01	-16.825	145.631	QLD	Australia	09/01/04	Simon Lab	KR108354	KR108354		x	KR108380	x
Huechys sanguinea	(Degeer, 1773)	0544	–	–	T. Hsien	Taiwan	04/06/03	J-H. Chen	JN377636	KT602142	KT602341		KT713584	GQ406039
Hyalessa maculaticollis	(de Mot. 1866)	09.CN.ZJ.BUD.01	30.325	119.443	Zhejiang	China	26/07/09	Simon Lab				x	x	x
Hyalessa maculaticollis	(de Mot. 1866)	shindai-fe-a	36.253	137.979	Nagano	Japan	17/09/11	R. Yokochi	AB900923					
Illyria burkei	(Distant, 1882)	05.AU.QL.RVN.03	-23.380	147.703	QLD	Australia	07/01/05	Simon Lab	x	x		x	x	x
Jassopsaltria rufifacies	Ashton, 1914	03.AU.WA.CAT.01	-30.736	115.543	WA	Australia	19/01/03	Simon Lab	x	x		x	x	
Kaphsa sp.	–	NCBS_AC160	25.694	93.532	Nagaland	India	14/05/12	B. Price	x			x	x	
Karenia ravida	Distant, 1888	05.CN.SC.TGV.01	30.496	102.295	Sichuan	China	28/08/05	D. S. Sikes				x	x	x
Katoa sp.	–	11.VN.XX.XXX.01	–	–	–	Vietnam	2011	M.Schouten, A.Boer	x	x		x	x	
Katoa taibaiensis	C. & Lei, 1995	08.CN.AH.TIA.28	–	–	Anhui	China	15/06/08	Li Jingke	x	x	x	x	x	x
Kikihia cauta	(Myers, 1921)	94.NZ.WN.RIM.76	-41.115	175.232	Wellington	NZ	23/02/94	D. Lane		KT602132	KT602331		KT713574	x
Klapperichicen sp.	–	11.PK.BA.SAD.01	–	–	Panjgur	Pakistan	16-19/05/11	Z. Ahmed	x	x		x		
Kosemia radiator	(Uhler, 1896)	03.JP.CB.TOG.01	–	–	Chubu	Japan	23/09/03	R. Futahashi	AB902917	KT602117	KT602316	x	KT713559	x
Lacetas sp.	–	05.GH.AA.SHR.02	5.890	0.044	G Accra	Ghana	10/06/05	J. Cryan, J. Urban	x	x		x	x	x
Lahugada dohertyi	(Distant, 1891)	NCBS_PZ564	–	–	W Bengal	India	11/05/14	V. Sarkar	x	x		x		
Lamotialna condamini	Boulard, 1976	05.GH.WP.NKW.19	5.282	-2.641	Western Region	Ghana	7/06/05	J. Cryan, J. Urban		x	x	x	x	x
Lembeja vitticollis	(Ashton, 1912)	10.AU.QL.MAK.01	-16.815	145.643	QLD	Australia	20/02/10	Simon Lab		KT602159	KT602358	x	KT713601	x
Lyristes plebejus	(Scopoli, 1763)	03.HR.SB.PIR.19	43.817	15.667	Sibenik	Croatia	11/07/03	T. Trilar, M. Gogala	KR674238	KR674238	EU401956	x	KR705860	x
Macrotristria angularis	(Germar, 1834)	05.AU.QL.MAC.01	-28.166	148.715	QLD	Australia	02/01/05	Simon Lab	x	x		x	x	x
Magicicada neotredecim	M. & C., 2000	02.US.IN.VEC.A112	37.928	-87.311	Indiana	USA	24/06/05	Simon Lab		x	x	x	x	x
Majeorona truncata	Goding, 1925	09.EC.PA.SHB.03	-1.104	-76.734	Pastaza	Ecuador	23/01/09	G. Goemans	x	x		x	x	x
Malagasia inflata	Distant, 1882	Madloc_ECR_1	–	–	Fianar. Pr	Madgascar	9-24/11/08	J. Cryan				x	x	x
Malgachialna sp.	–	Madloc1_3	-21.254	47.422	Fianar. Pr	Madgascar	9-24/11/08	J. Cryan					x	
Maroboduus fractus	Distant, 1920	05.GH.WP.NKW.06	5.282	-2.641	W Region	Ghana	07/06/05	J. Cryan, J. Urban		x	x	x	x	x

……continued on the next page

TABLE 1. (Continued)

Taxon Name	Author	Code	Lat.	Lon.	Location	Country	Date (D/M/Y)	Collectors	5' COI	3' COI	COII	ARD1	EF-1α	18s
Megatibicen auletes	(Germar, 1834)	04.US.MD.ZYL.01	38.121	-76.364	Maryland	USA	2004	J. Zyla	KR674156	KR674156			KR705769.	
Meimuna opalifera	(Walker, 1850)	04.KR.GG.GNG.01	–	–	–	Korea	--/08/04	Y-J Lee	GQ527088			x	GQ527130	x
Meimuna sp.	–	NCBS_AC165	25.694	93.532	Nagaland	India	15/05/12	B. Price	x			x		
Mogannia hebes	(Walker, 1858)	03.TW.TP.UCH.54	–	–	T. Hsien	Taiwan	04/06/03	J-H. Chen	GQ527095	x		x	GQ527135	x
N. gen. [PERU]	–	04.PE.CS.COR.01	–	–	Cusco	Peru	2009	H. Mendel, M. Barclay	x	x			x	
Nablistes heterochroma	Boulard, 1986	05.GH.WP.NKW.04	5.282	-2.641	Western Region	Ghana	07/06/05	J. Cryan, J. Urban	x	x		x	x	x
Nelcyndana sp.	–	06.MY.SK.LAM.15	4.198	114.042	Sarawak	Malaysia	12/10/06	J. Cryan		x	x	x	x	x
Nelcyndana tener	(Stål, 1870)	Mindanao_1	7.728	126.288	Mindanao	Philippines	2008	J. Lourens		x	x		x	
Neocicada hieroglyphica	(Say, 1830)	11.US.OK.TAW.01	34.753	-95.068	Oklahoma	USA	17/06/11	K. Hill, D. Marshall	x	x		x	x	x
Neotibicen davisi	(S. & G., 1907)	11.US.FL.FIT.01	28.910	-82.681	Florida	USA	22/09/11	K.Hill, D.Marshall, R.Veal	KR674233	KR674233		x	KR705855	x
Nigripsaltria mouldsi	Boer, 1999	00.PG.MR.TEK.01	–	–	Morobe	P.N.Guinea	05/04/00	M. Moulds		KT602096	KT602296		KT713537	
Nosola paradoxa	Stål, 1866	07.BO.SC.BJV.01	–	–	Santa Cruz	Bolivia	2007	L.O'Brien, G.Goemans	x	x		x	x	
Notopsalta sericea	(Walker, 1850)	03.NZ.BP.WKW.03	-37.681	177.737	N. Island	NZ	22/03/03	Simon Lab	JX675276	JX675276				
Notopsalta sericea	(Walker, 1850)	93-202	-36.500	174.700	N. Island	NZ	04/02/93	C. Simon, S. Chiswell			KT602309		KT713552	
Odopoea insignifera	Berg, 1879	08.AR.JY.LEO.02	-24.045	-65.427	Jujuy	Argentina	17-18/01/08	Simon Lab	x	x			x	
Okanagana canadensis	(Prov., 1889)	02.US.MI.CLV.02	45.856	-84.727	Michigan	USA	15/07/02	J. Cooley		x	x	x	x	x
Okanagana canadensis	(Prov., 1889)	CNC#HEM401713	–	–	Manitoba	Canada	12/07/79	H. Goulet	KF919421					
Okanagana r. rubrovenosa	Davis, 1915	03.US.CA.EGR.02	37.836	-120.221	California	USA	25/06/03	K. Hill, D. Marshall		AY997111	AY997111			
Okanagana utahensis	Davis, 1919	03.US.CA.SBI.02	37.287	-118.374	California	USA	26/06/03	K. Hill, D. Marshall	KF920211	AY997112	AY997112	x	x	U06478
Okanagodes gracilis	Davis, 1919	03.US.CA.LPE.01	36.398	-117.808	California	USA	26/06/03	K. Hill, D. Marshall		AY997110	AY997110	x	x	x
Oncotympana pallidiventris	(Stål, 1870)	10.PH.DI.RED.04	10.377	125.635	Dinagat	Philippines	03/07/10	A. Mohagan, Simon Lab	x	x		x	x	x
Orialella aerizulae	Boulard, 1986	04.PE.MD.PAT.08	–	–	M de Dios	Peru	1-30/09/04	J. Cryan, J. Urban	x	x		x	x	x
Owra insignis	Ashton, 1912	04.AU.QL.JOP.01	-17.419	145.542	QLD	Australia	09/01/04	Simon Lab		x	x		x	x
Pagiphora aschei	Kartal, 1978	03.GR.GRE.RET.22A	–	–	Crete	Greece	21/08/03	T. Trilar, K.P. Trilar		x	x	x	x	x
Parnisa sp.	–	08.AR.MN.IES.03	-25.679	-54.450	Misiones	Argentina	6-7/01/2008	Simon Lab	x			x	x	x
Parnquila magna	(Distant, 1913)	06.AU.WA.EMG.03	-28.154	118.071	WA	Australia	16/02/06	Simon Lab	x	x		x	x	x

……*continued on the next page*

TABLE 1. (Continued)

Taxon Name	Author	Code	Lat.	Lon.	Location	Country	Date (D/M/Y)	Collectors	5' COI	3' COI	COII	ARD1	EF-1α	18s
Parnquila sp.	Distant, 1907	06.AU.WA.KUN.01	-24.488	119.651	WA	Australia	13/02/06	Simon Lab	x	x		x	x	
Pauropsalta mneme	(Walker, 1850)	06.AU.NS.DHA.01	-34.160	150.828	NSW	Australia	21/11/06	Simon Lab	KM377190	KM377190		KM377396	KM668354	x
Pauropsalta mneme	(Walker, 1850)	97.AU.NS.CRO.01	-33.333	149.167	NSW	Australia	10/02/97	Simon Lab			KT602280			
Pictila occidentalis	(G. & F., 1904)	03.AU.WA.VIC.05	-31.289	120.930	WA	Australia	17/01/03	Simon Lab		KT602100	KT602299	x	KT713541	x
Platylomia aff. *ficulnea*	(Distant, 1892)	NCBS_AB709	–	–	W Bengal	India	21/04/12	K. Kunte	x			x	x	
Platypedia putnami	(Uhler, 1877)	02-033	–	–	Oregon	USA	14/06/02	D. Vanderpool				x	x	x
Platypedia putnami	(Uhler, 1877)	CNC#HEM401733	–	–	Arizona	USA	30/05/91	J. O'Hara	KF919658					
Platypedia putnami	(Uhler, 1877)	Sanborn_putnami	–	–	Arizona	USA	–	A. Sanborn		AY997108	AY997108			
Platypleura octoguttata	(Fabr., 1798)	NCBS_AC187	13.072	77.581	Karnataka	India	23/05/12	A. Prakash, B. Price	x					
Platypleura polita	(Walker, 1850)	NCBS_PT207	–	–	Kerala	India	12/04/13	G. Agavekar	x				x	
Platypleura sp.	–	NCBS_PT209	–	–	Kerala	India	12/04/13	D. Agashe	x				x	
Platypleura takasagona	(Matsu., 1917)	0551	–	–	T. Hsien	Taiwan	04/06/03	J-H. Chen	KR674166	KR674166		x	KR705780	x
Pomponia cf. *linearis*	(Walker, 1850)	09.CN.ZJ.BUD.03	30.325	119.443	Zhejiang	China	26/07/09	Simon Lab	x	x		x	x	x
Psalmocharias plagifera	(Schum., 1922)	08.MA.SM.IMO.10	30.695	-9.449	S-M-Draa	Morocco	26/05/08	Pillet, Puissant, Sueur	GQ527105	x			GQ527145	x
Psaltoda moerens	(Germar, 1834)	04.AU.VI.DUF.02	-35.984	145.835	Victoria	Australia	04/02/04	Simon Lab	x	x		x	x	x
Psithyristria nodinervis	Stål, 1870	Psith8	–	–	Luzon	Philippines	--/08/2005	IRSNB, Belgium	GQ527120				GQ527156	
Purana cf. *tigrina*	(Walker, 1850)	NCBS_AC205	8.682	77.139	Kerala	India	08/06/12	B. Price	x			x		
Pycna sp.	–	NCBS_AC157	25.618	93.954	Nagaland	India	10/05/12	B. Price	x			x	x	
Quesada gigas	(Olivier, 1790)	04.US.TX.LAG.03	26.205	-97.352	Texas	USA	09/07/04	K. Hill & D. Marshall	x			x	x	x
Quintilia rufiventris	(Walker, 1850)	MHV_Quintilia	–	–	W Cape	S. Africa	–	M. Villet				x	x	x
Raiateana kuruduadua	(Distant, 1881)	03.FJ.WE.WEI.01	-17.560	177.947	Viti Levu	Fiji	27/01/03	Simon Lab	KR674147	KR674147		x	KR705753	x
Salvazana mirabilis	Distant, 1913	Laos_5	–	–	–	Laos	–	–	KR674239			x	KR705861	x
Scieroptera formosana	Schmidt, 1918	0555	–	–	T. Hsien	Taiwan	04/06/03	J-H. Chen		KT602118	KT602317	x	KT713560	
Selymbria stigmatica	(Germar, 1834)	04.PE.MD.TRC.06	-13.138	-69.608	M de Dios	Peru	1-30/9/04	J. Cryan, J. Urban	x		x	x	x	
Stagira segmentaria	Karsch, 1890	03.ZA.RSA.UNK.03	-32.583	26.933	Eastern Cape	S. Africa	07/12/97	M. Villet		x	x	x	x	
Subpsaltria yangi	Chen, 1943	Wei_yangi	–	–	Ningxia	China	20/06/11	C. Wei		x	x		x	
Tacua speciosa	(Illiger, 1800)	03.MY.SA.KIN.24	6.006	116.543	Sabah	Malaysia	03/04/03	T. Trilar, K.P. Trilar	KR674150	KR674150		x	KR705758	

… …*continued on the next page*

TABLE 1. (Continued)

Taxon Name	Author	Code	Lat.	Lon.	Location	Country	Date (D/M/Y)	Collectors	5' COI	3' COI	COII	ARD1	EF-1α	18s
Talcopsaltria olivei	Moulds, 2008	04.AU.QL.WAP.01	-15.596	145.297	QLD	Australia	12/01/04	Simon Lab	x	x	x	x	x	x
Tamasa tristigma	(Germar, 1834)	02.AU.QL.DAI.22	-27.641	153.162	QLD	Australia	06/01/02	S. Cowan		x	x	x	x	x
Tanna sozanensis	Kato, 1926	03.TW.TP.UCH.41	–	–	T. Hsien	Taiwan	04/06/03	J-H. Chen	GQ527094			x	GQ527134	x
Taphura attiguclava	Sanborn, 2017	04-11-15-29-1	-12.805	-69.293	M de Dios	Peru	--/09/04	Bartlett, Cryan, Urban		x	x	x	x	x
Taurella forresti	(Distant, 1882)	02.AU.NS.NPF.14	-31.680	152.652	NSW	Australia	06/01/02	Simon Lab		KT601960	KT602161	x	KT713401	x
Tettigades procera	Torres, 1958	06.CL.BI.LGL.03	-37.402	-71.438	Bío Bío	Chile	22/01/06	Simon Lab		x	x	x	x	x
Tettigades ulnaria	Distant, 1906	TETULN	-34.481	-71.975	O'Higgins	Chile	12/02/13	C. Zamora-Manzur	KM000128	KM000128	x		x	
Tettigarcta crinita	Distant, 1883	13.AU.NS.YBE	-35.746	148.520	NSW	Australia	04/03/13	Simon Lab		x				x
Tettigarcta tomentosa	White, 1845	00-09	–	–	Tasmania	Australia	01/01/00	M.Moulds, M.Claridge	x	x		x		x
Tettigomyia vespiformis	(A.&A-S., 1843)	MHV1213	–	–	E Cape	S. Africa	–	M. Villet	x	x		x	x	x
Thopha saccata	(Fabr., 1803)	01.AU.QL.HER.13	-19.361	146.454	QLD	Australia	03/01/01	M. & B. Moulds	KR108331	KR108331			KR108357	x
Tibicina haematodes	(Scopoli, 1763)	02-110	–	–	Cairanne	France	23/4/00	J. Sueur		AY997122	AY997122	x	x	x
Trismarcha excludens	(Walker, 1858)	05.GH.WP.NKW.03	5.282	-2.641	W Region	Ghana	07/06/05	J. Cryan, J. Urban		x	x	x	x	
Tryella willsi	(Distant, 1882)	02.AU.QL.MOZ.01	-24.477	148.613	QLD	Australia	11/01/02	Simon Lab		x	x	x	x	x
Ueana maculata	Distant, 1906	98-16	–	–	N Province	N.Caledonia	02/02/98	Simon Lab		KT602092	KT602292	x	KT713533	
Vagitanus terminalis	(Matsu., 1913)	0542	–	–	T. Hsien	Taiwan	04/06/03	J-H. Chen	x	x		x	x	x
Venustria superba	G. & F., 1904	04.AU.QL.KUR.02	-16.820	145.632	QLD	Australia	09/01/04	Simon Lab		x	x	x	x	x
Xosopsaltria annulata	(Germar, 1830)	MHV521	–	–	Eastern Cape	S. Africa	–	M. Villet				x	x	x
Xosopsaltria thunbergi	Metcalf, 1955	03.ZA.RSA.UNK.02	–	–	Eastern Cape	S. Africa	–	M. Villet		x	x	x	x	x
Yanga cf. *andriana*	(Distant, 1899)	MadLoc6_1	-25.006	46.303	Toliara Pr	Madgascar	9-24/11/08	J. Cryan	KR674245	KR674245		x	KR705866	x
Zammara smaragdina	Walker, 1850	03.CR.HE.LSB.01	10.431	-69.002	Heredia	Costa Rica	14/08/03	J. Cryan, J. Urban	x	x		x	x	x

Specimens collected on C. Simon-lab field trips were given a unique composite specimen code containing a two-digit year, a two-letter country, a two-letter district, a three-letter location, and a two-digit specimen number (Table 1). Codes established by collaborators were sometimes retained. Alcohol-preserved specimens are stored in the Simon research collection at the University of Connecticut and the pinned specimens are stored at the University of Connecticut Biodiversity Research Collection or in the collection of M. S. Moulds. Indian specimens are preserved in research collections of the Museum and Field Stations Facility at the National Centre for Biological Sciences, India (NCBS).

Genetic sequencing, alignment, and model selection

Genomic DNA was extracted from leg muscle or (rarely) other body tissue such as thorax or abdominal muscle using the Qiagen DNeasy Tissue kit (Qiagen, Valencia, California, USA), the Clontech Extract II kit (Clontech, Mountain View, CA, USA) or the Nucleospin Tissue kit (Macherey-Nagel, Bethlehem, PA, USA) following the manufacturers' instructions, with most digestions gently agitated overnight for approximately 18 hrs in a HYBAID Mini-hybridisation Oven (National Labnet Co., Woodbridge, NJ, USA).

Using the primers and annealing temperatures shown in Table 2, portions of five genes were amplified—mitochondrial cytochrome oxidase I (COI), mitochondrial cytochrome oxidase II (COII), nuclear elongation factor 1 alpha (EF-1α), nuclear acetyltransferase (ARD1, see Owen *et al.* 2015), and nuclear 18S ribosomal RNA (18S). Polymerase chain reaction (PCR) recipes and profiles were varied to optimize results across different cicada genera. PCR reactions mostly used Ex-taq or Titanium taq, with 25 µl volumes and 0.5-5 µl of template depending on sample concentration (usually 1-2 µl), 0.13 µl of taq, 1.25 µl of each primer (10 uM), and 2.5 µl each of 10X buffer and dNTPs. Some reactions were run at half- or quarter-scale. The basic PCR reaction was as follows: (1) 94˚C for 2 to 2.5 min; (2) 30 cycles of 94˚C for 45 sec, anneal temperature (see Table 2) for 45 sec, and 72˚C for 75 sec (90 sec to 3 min for 18S, some COI, EF-1α with long introns, and COI+COII co-amplification); (3) 72˚C for 5 min. Annealing temperatures for COI, COI+COII, and difficult cases were lowered as far as 45˚C (very rarely 40˚C). For ARD1 and COI+COII, a touchdown PCR protocol was routinely used as follows: (1) 95˚C for 1 min, (2) ten cycles of 95˚C for 1 min, 55-45˚C for 15 sec, and 68˚C for 75 sec to 1 min (2 min for COI+COII), dropping 1˚C for each cycle; (3) 30 cycles of 95˚C for 30 sec, 45˚C for 15 sec, and 68˚C for 75 sec (2 min for COI+COII); (4) 68˚C for 5 min. Touchdown was occasionally used for COI and EF-1α, commonly with longer extension times. Some specimens required re-amplification of a small amount of the initial PCR product (i.e., dipping a 10 µl pipet tip for transfer), occasionally combined with a touchdown protocol. In addition to the above protocols, some Cryptotympanini specimens were handled as described in Hill *et al.* (2015), and some samples (*Diemeniana*, *Kikihia*, *Notopsalta*) were handled as described in Arensburger *et al.* (2004).

PCR products were first run on 1% agarose gels to check amplicon size and then cleaned using the Qiagen, Clontech, or Nucleospin kits from the above manufacturers, according to the kit instructions, or with ExoSAP-IT (USB Corp., Cleveland, OH) at 1/1 to 1/4th the stock concentration. Some samples required cleanup from agarose gel bands cut and cleaned using Promega Wizard SV Gel and Cleanup kits (Promega Corp., Madison, WI, USA).

Cycle sequencing was conducted using the Applied Biosystems (Life Technologies Corp., Carlsbad, CA, USA) Big Dye Terminator v1.1 cycle sequencing kit at 1/8- to 1/4-scale reaction volume. For some specimens, a modified protocol used 0.25 µl BigDye 1.1 (Applied Biosystems), 0.75 µl BDX64 (MCLAB, South San Francisco, CA, USA), 1.5 µl BigDye 5x buffer, 0.7 µl of 2 uM primer stock, 2.2 µl of H2O, and 1-3.5 µl of cleaned PCR product. The general sequencing protocol was as follows: (1) hold at 96˚C for 2 min; (2) repeat 30 cycles of 96˚C for 30 sec, 50˚C for 15 sec, and 60˚C for 2.5 min; (3) hold at 60˚C for 5 min. Sequencing products were cleaned by Sephadex (Millipore) filtration and visualized on an Applied Biosystems ABI 3100 capillary sequencer. The Indian material was extracted and amplified in the Kunte Lab, and sequenced in the NCBS Sequencing Facility, usually using the protocols described above. The sequences of *Subpsaltria yangi* Chen were obtained in the laboratory of Cong Wei, Northwest A&F University, Shaanxi, China.

Sequences were analyzed using ABI Prism Sequencing Analysis software v3.7 (Applied Biosystems), aligned in Sequencher v3.1 (Gene Codes Corp., Ann Arbor, MI) or Geneious R6 (Biomatters Ltd., Auckland, New Zealand), and further aligned and checked by eye. Codon translation was used to confirm the absence of stop codons in coding regions. Most of the noncoding UTR region found in the ARD1 gene was discarded as unalignable, as were the intron sections of EF-1α. Six EF-1α exons were confirmed within the retained sites.

Heterozygous sites in nuclear-gene sequences were coded with their respective IUPAC ambiguity codes.

During alignment of the mitochondrial sequences, chromatograms were checked for double-peaked signals potentially indicating amplification of paralogous nuclear copies (numts) (Song *et al.* 2008). In these cases, PCR amplification was repeated at a higher temperature, or a longer fragment was amplified in order to exclude the putative paralog. In a limited number of these cases, amplified products were cloned with TOPO TA cloning kits, with the original PCRs repeated with PrimeSTAR HS DNA polymerase (Takara) or another high-fidelity taq.

TABLE 2. Primers and PCR conditions used.

Gene	Primer Name	Primer Sequence	Reference	Temperature
COI	HCO2198[6]	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al*. (1994)	45°C[5], 55-45[2]
COI	TL2-N-3014	TCCAATGCACTAATCTGCCATATTA	Simon *et al*. (1994)	
COI 5’	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer *et al*. (1994)	45°C
COI 5’	COIBar_cicadaF1	GAAAAAATGRTTTTTYTCAACTAAYC	Owen *et al*. (2015)	
COI 5’	COIBar_cicadaF2	TTYTCAACTAATCAYARRGAYATTGG	Owen *et al*. (2015)	
COI 5’	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al*. (1994)	
COI 3’	C1-J-2195	TTGATTTTTTGGTCATCCAGAAGT	Simon *et al*. (1994)	56°C[7]
COI 3’	TL2-N-3014	TCCAATGCACTAATCTGCCATATTA	Simon *et al*. (1994)	
COI	C1-J-1751	GGATCACCTGATATAGCATTCCC	Simon *et al*. (1994)	sequencing
COII	TL2-J-3032[4]	AATATGGCAGATTAGTGC	Sueur *et al*. (2007)	53°C, rare 45
	TK-N-3786cic	GTTTAAGAGACCATTACTT	C. Simon lab	
COII	TL2-J-3033[3]	AATATGGCAGATTAGTGCA	C. Simon & F. Frati	53°C
COII	A8-N-3914	TCATATTATTGGTGATATTTGAGG	Simon *et al*. (1994)	
COI+COII	tRNA_MetF1	GATAAGCTAAGWTTAAGCTAATGGG	Owen *et al*. (2015)	55-45°C[2]
	tRNA_MetF2	GCTAATGGGTTCATACCTCATTTATGG	Owen *et al*. (2015)	
	tRNA-TyrF1	CATAAATAAATTTACAGTTTATTGCYT	Owen *et al*. (2015)	
	TK-N-3786	GTTTAAGAGACCATTACTT	C. Simon lab	
COI+COII	C1-J-2195	TTGATTTTTTGGTCATCCAGAAGT	Simon *et al*. (1994)	45°C
	TK-N-3786	GTTTAAGAGACCATTACTT	C. Simon lab	
COI+COII	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al*. (1994)	45°C[8]
COI+COII	TK-N-3786	GTTTAAGAGACCATTACTT	C. Simon lab	
ARD1	1041F	TGGAAAGTGTTTCTGTCACATTTTCG	Owen *et al.* (2015)	55-45°C[2]
ARD1	1733R	ATCTCTTTTCATAGCGTATGCGTC	Owen *et al.* (2015)	
ARD1	ForShort	CGCTTTGTGAGAGAATTRC	This study	55-45°C[2]
ARD1	RevShort	GTATGCGTCTTCACCRTCTGC	This study	
ARD1	ForShort	CGCTTTGTGAGAGAATTRC	This study	55-45°C[2]

......continued on the next page

TABLE 2. (Continued)

Gene	Primer Name	Primer Sequence	Reference	Temperature
ARD1	RevShorter	CCRTCTGCATAATATTTTGG	This study	
EF-1α	F650-cicada	TGCTGCTGGTACTGGTGAAT	Arensburger *et al*. (2004)	58°C[5]
EF-1α	F650-ambig	TGCTGCKGGTACTGGTGAAT	This study	
EF-1α	R2855-cicada[1]	ACACCAGTTTCAACTCTGCC	Sueur *et al*. (2007)	
EF-1α	EM1For2	GTWGGWGTTAACAARATGGA	This study	46-54°C
EF-1α	EM1Rev1	CTSAGRGGCTTCTCAGTKGG	This study	
EF-1α	EM2For2	GARGAAATCAARAARGAAG	This study	
EF-1α	EM2Rev	CCTACWGGSACTGTTCCAATACC	This study	
EF-1α	calliopeEMint2	GCCTTAACCCGCCCTGTGCAG	This study	sequencing
EF-1α	calliopeEMintRev	CCATTTTGTTATGGAATTAAG	This study	sequencing
18S[9]	1F	TACCTGGTTGATCCTGCCAGTAG	Giribet *et al*. (1996)	54°C
18S	5R	CTTGGCAAATGCTTTCGC	Giribet *et al*. (1996)	
18S	5F	GCGAAAGCATTTGCCAAGAA	Giribet *et al*. (1996)	54°C
18S	9R	GATCCTTCCGCAGGTTCACCTAC	Giribet *et al*. (1996)	

[1] Note that EF1-R2855-cicada was identified as "EF1-N-1419" in Sueur et al. (2007); also sometimes called DV-EF-R1.
[2] Used touchdown protocol.
[3] Incorrectly referred to as "TL-2-3034" in some publications.
[4] Incorrectly referred to as "TL-2-3033", also sometimes called 3034b.
[5] as low as 1 min extension, occasionally up to 2:30.
[6] Sometimes referred to as C1-J-1490.
[7] Up to 2:00 extension time.
[8] Up to 3:00 extension time
[9] 18S protocol: 54° C anneal, 1:45 extension, 30 cycles.

Occasionally during the sequencing stage, and before beginning the final phylogenetic analyses, simple maximum-likelihood analyses were conducted separately for each amplicon in RAxML v8.1.17 (Stamatakis 2006), using the rapid bootstrap option and the GTR+Gamma substitution model. These topologies were examined to check for unexpected identical matches and conflicting relationships that could indicate specimen mixup or contamination. Such checks were performed at the amplicon level prior to concatenation into completed gene sequences.

Partitioning schemes and MrBayes-available substitution models for data subsets were selected using the "greedy" search algorithm and the BIC criterion in PartitionFinder v1.0.1 (Lanfear *et al.* 2012) with Python v2.7 (Python Software Foundation 2010), with thirteen subsets including individual codon positions of protein-coding data (with each gene separately treated at first) and the 18S ribosomal data. Data subsets were separately tested for base-composition bias, which can distort phylogenetic analyses (Felsenstein 2004), using a chi-square test of homogeneity in PAUP* v4.0 (Swofford 1998).

Phylogenetic estimation

Bayesian and maximum-likelihood (ML) phylogenetic trees for the combined genetic dataset were estimated using MrBayes v3.2.4 (Ronquist *et al.* 2012) and GARLI 2.0 (versions 2.0.1019 and 2.01.1067) (Zwickl 2006). For the MrBayes analysis, model settings were assigned following the partition scheme and substitution models shown in the Results, with all substitution model parameters (*statefreq*, *revmat*, *shape*, *pinvar*, and *tratio*) and relative subset rates (*ratepr=variable*) unlinked. Gamma distributions were given four rate categories as was assumed during model selection, and a default exponential branch length prior with a mean of 0.1 substitutions/site was assumed for all data subsets (*brlens=unconstrained:exponential[10]*). Two independent, simultaneous analyses (*nruns=2*), each with four chains, default heating, and a different random starting tree, were initially set to run for 3 x 10^8 generations, with MrBayes set to stop the analyses when the average standard deviation of split frequencies (a comparison of topological similarity between the paired analyses) dropped below 0.005 (*stoprule=yes*, *stopval=0.005*, with *diagnfreq*=30,000) with the default burnin of 25% (*relburnin=yes*, *burninfrac=0.25*). Autotune was also set to yes. Other parameters and settings not mentioned here were left at the MrBayes default values. Chains were sampled every 30,000 generations, and post-burnin effective sample sizes were checked using Tracer v1.5 (Rambaut & Drummond 2007) and confirmed to be above 200 for all parameters.

GARLI was used to estimate maximum-likelihood (ML) bootstrap supports for the branches in the MrBayes tree, using the same partitioning scheme and with the model parameters and relative rates separately estimated for each data subset. Gamma distributions were estimated with four rate categories. For each heuristic search replicate, the starting tree was obtained by stepwise addition under ML with *attachmentspertaxon* set to 50. *Genthreshfortopoterm* was set to 100,000 and *significanttopochange* and *scorethreshforterm* were set to 0.01 and 0.05, respectively, allowing for more thorough topology searches. All other settings were left as shown in default form. For each of 200 bootstrap replicates used to assess branch support, one heuristic search was completed under the above settings. The resulting ML bootstrap values were mapped onto the MrBayes consensus tree along with the Bayesian posterior probabilities.

To check for effects of missing data on the analyses above, the main dataset was trimmed to an 80-taxon dataset that was nearly 100% complete for 3' COI, EF-1α, and the ARD1 locus; the other gene segments were included if available for those taxa. The Cercopidae taxa were excluded, and one *Tettigarcta* sequence was assumed as the outgroup. This dataset was analyzed as above and the results compared to those from the 141-taxon dataset.

MrBayes v3.2.4 was also used to estimate the Cicadidae tree using the genetic data combined with the morphological dataset from Moulds (2005). First, the taxon sampling in the genetic dataset was reduced to include the 42 genera for which both data types were available (including the Cercopidae outgroup and *Tettigarcta*). One exemplar was used for each genus in the current analysis, and genetic and morphological data from different species of the same genus were combined when necessary. When more than one species was available from either dataset, the representative with the most complete character set was selected. State values within each character were adjusted to avoid missing states after taxon deletion, as necessary. The data were analyzed in MrBayes in the same manner as for the molecular data, but with the morphological characters grouped in a separate subset under the MkV model (with *coding=variable* to reflect the absence of invariant characters).

Accommodating base composition bias and potential heterotachy

The time-reversible DNA sequence models used in the above analyses assume base frequencies at equilibrium across the tree, but the chi-square test of base-composition heterogeneity was significant ($p<0.05$) for the mtDNA third codon-position data subset. Base composition bias can exacerbate the problem of long-branch attraction in phylogenetic analyses (Felsenstein 2004). As a result, two approaches were taken to examine potential effects of nonstationary nucleotide frequencies on our analyses. First, a new MrBayes analysis was conducted as above with the main dataset but with the third position mtDNA sites RY-coded (i.e., with the bases coded by purine or pyrimidine category), converted to binary state characters (0/1/?), and analyzed using the Mk+Gamma substitution model. Maximum-likelihood bootstrap values for the nodes in the MrBayes tree were obtained from 1000 bootstrap replicates of the same combined, partitioned dataset using RAxML version 8.1.17 (Stamatakis 2006)—Garli was not used because it does not allow estimation of among-site rate variation for binary character subsets, while RAxML offers a gamma distribution for such data. RAxML was invoked using the -f a option, with a GTR+Gamma+P_{invar} model estimated for each data subset (but Mk+Gamma+P_{invar} for the binary data), and with model parameters optimized to 0.001 lnL points (-e 0.001).

In the second analysis, heterogeneity in base composition was addressed using nh_PhyloBayes v0.2.3, which allows for the evolutionary model to vary in time along lineages as well as across sites (Blanquart & Lartillot

2006). For this more computationally intensive approach, the smaller dataset of 80 taxa (without missing data) was again used. The software was run with the bp model and four rate categories selected, with the chains sampled once every two cycles. Otherwise default settings were used, which allowed the Bayesian algorithm to estimate the number of break points along the tree (locations where base frequencies change). The *monitor* subroutine was used to plot the posterior log-likelihood over time and identify the number of burnin samples to be discarded (in this case, 1000). The *readtopo* subroutine was used to calculate the posterior consensus tree. Four independent replicates of this analysis were conducted, and each was run until plots of the posterior probabilities were stable over about 6000 samples.

Taxonomic analysis

Some relationships supported by the molecular analysis conflicted with the existing family-group classification of the Cicadidae as listed by Sanborn (2013) (see Results). Focusing on well-supported conflicts, we used the relationships in the molecular tree to guide a *post hoc* morphological reassessment of tribe and subfamily classification, with emphasis on the character set used by Moulds (2005). In some cases, this involved taxonomic reassignment of genera and/or tribes to existing groups, with or without redefinition of diagnostic characters. In other cases, construction of new family-level groups was necessary, especially for genera not included in earlier phylogenetic work. During this process we sought to create only the minimum number of new groups needed to accommodate the findings of the molecular analysis. Where possible, type species of type genera were examined for tribal definition, and identified material for some tribes was borrowed from the British Museum.

RESULTS

Molecular phylogenetics

Genetic data and model selection. The final alignment for 141 taxa contained 4992 sites distributed as follows: 1485 bp from COI (mtDNA), 684 bp from COII (mtDNA), 516 bp from ARD1, 423 bp from EF-1α, and 1884 bp from 18S. COI (MG953010-MG953094), COII (MG952981-MG953009), and 18S (MG953095-MG953188) sequences have been deposited with Genbank. Concatenated-exon sequences for EF-1α and ARD1 are available in the Supplementary Data File as part of the full DNA alignment. The fraction of the 141-taxon data matrix that was missing was 37.6%, as calculated by Mesquite v3.04 (Maddison & Maddison 2015). With the outgroup Cercopidae removed, 1537 sites were parsimony-informative, 261 were variable but parsimony-uninformative, and 3194 were invariant. Pairwise uncorrected p-distances within the ingroup were below 20% for the combined mtDNA sequences in most cases, with a maximum of 27%. Ingroup uncorrected distances ranged up to 19% for ARD1 (with a few exceptions), 17% for EF-1α, and 3% for 18S. PartitionFinder analysis of the dataset yielded a seven-subset scheme which is shown in Table 3 along with the recommended substitution models.

TABLE 3. Partition scheme and substitution models used for subsets of the genetic dataset.

Subset	Number of sites	Substitution Model
mtDNA - 1st coding position	723	GTR+I+Gamma
mtDNA - 2nd coding position	723	GTR+I+Gamma
mtDNA - 3rd coding position	723	HKY+I+Gamma
ARD1 & EF-1α 1st position, ARD1 2nd position	485	K80+I+Gamma
EF-1α 2nd coding position	141	SYM+I+Gamma
ARD1 & EF-1α 3rd coding position	313	GTR+I+Gamma
18S	1884	SYM+I+Gamma

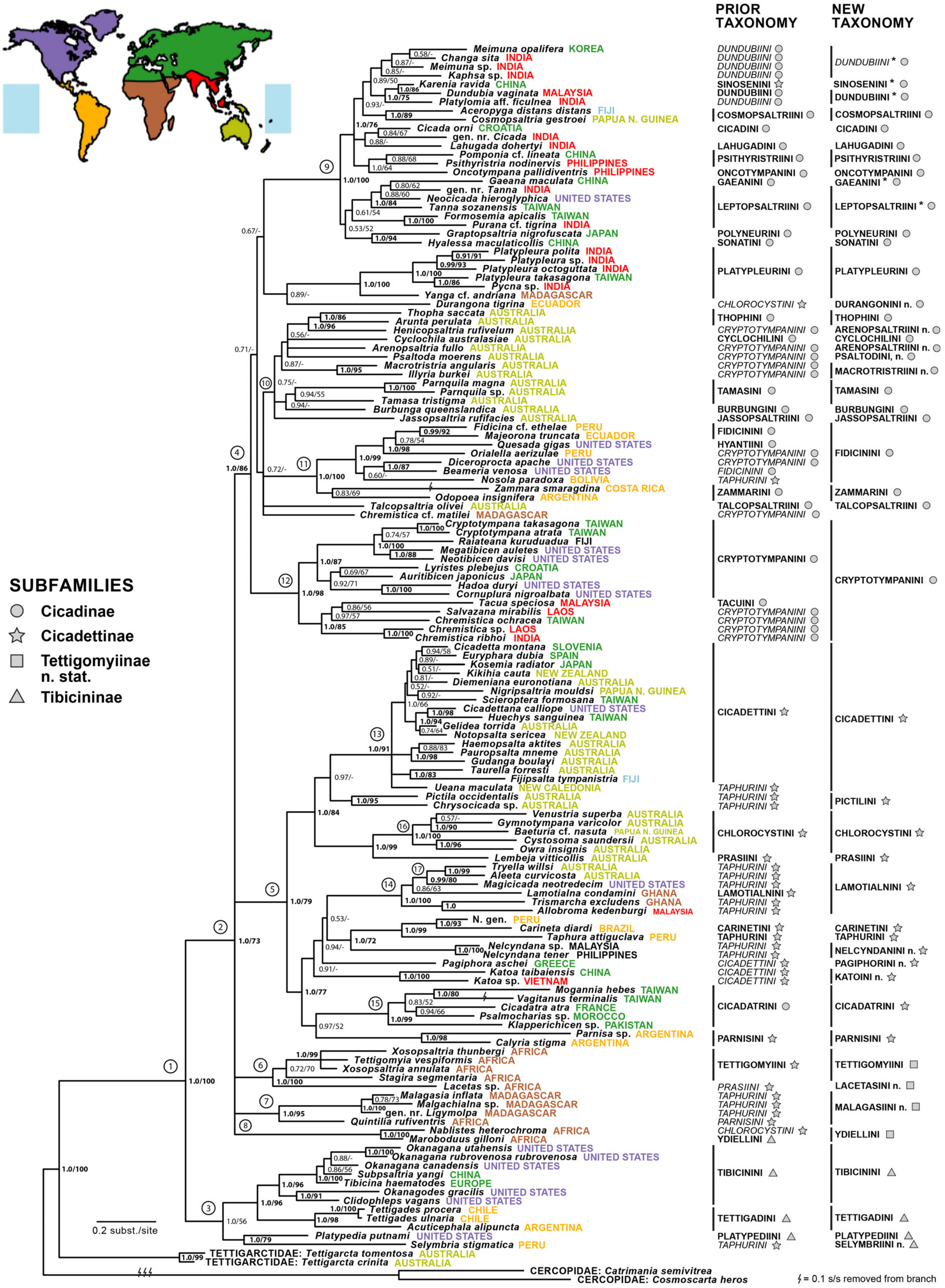


FIGURE 4. MrBayes 50% majority rule tree ("five-gene tree") from the final partitioned analysis of the DNA dataset, with posterior probabilities and ML bootstrap supports shown. Taxonomic assignments before and resulting from this study are shown to the right, as well as countries of origins of the samples following the species names, colored by biogeographic region (see map inset). Italics are used with the former taxonomy to emphasize species that require new tribal assignments due to a distant relationship from the type genus. *The paraphyletic conditions of Dundubiini and Leptopsaltriini in the tree are discussed in the Comments sections for those tribes and under *Comments on the Asian fauna* in the Discussion.

Phylogenetic estimation. The MrBayes analysis concluded at 46.6 million generations, leading to 11.65 million generations being excluded as burnin. Analysis of the posterior sample yielded an arithmetic mean log likelihood of -83566.85 and a harmonic mean log likelihood of -83650.11. Final PSRF statistics for all parameters were 1.002 or less, with most at 1.0.

Figure 4, the "five-gene tree", shows the final MrBayes consensus tree based on DNA data alone, with posterior probabilities and ML bootstrap supports for all branches. Here, strong genetic support for a branch is inferred from Bayesian posterior probabilities of 1.0 and ML bootstrap percentages above 75. Taxonomic assignments prior to and following our results are shown and discussed in detail below. From this point we use the new taxonomic assignments.

All of the deep level family-group relationships found using morphology (numbered clades 1-5 in all figures) are strongly supported in the five-gene tree (Fig. 4) and in the combined DNA + morphology analysis (Fig. 5), except clade 3 (Tibicininae) which received only 56% ML bootstrap support in the five-gene tree. The Cicadidae samples (clade 1) form a strongly supported sister-clade to the Tettigarctidae. Within this clade, genera currently classified in Tibicininae (clade 3, denoted by triangle symbols) are sister to the remainder. The large sister clade to the Tibicininae (clade 2) contains five well-supported groups with uncertain branching order, two of which correspond to the subfamilies Cicadinae (clade 4 and circle symbols) and Cicadettinae (clade 5 and star symbols).

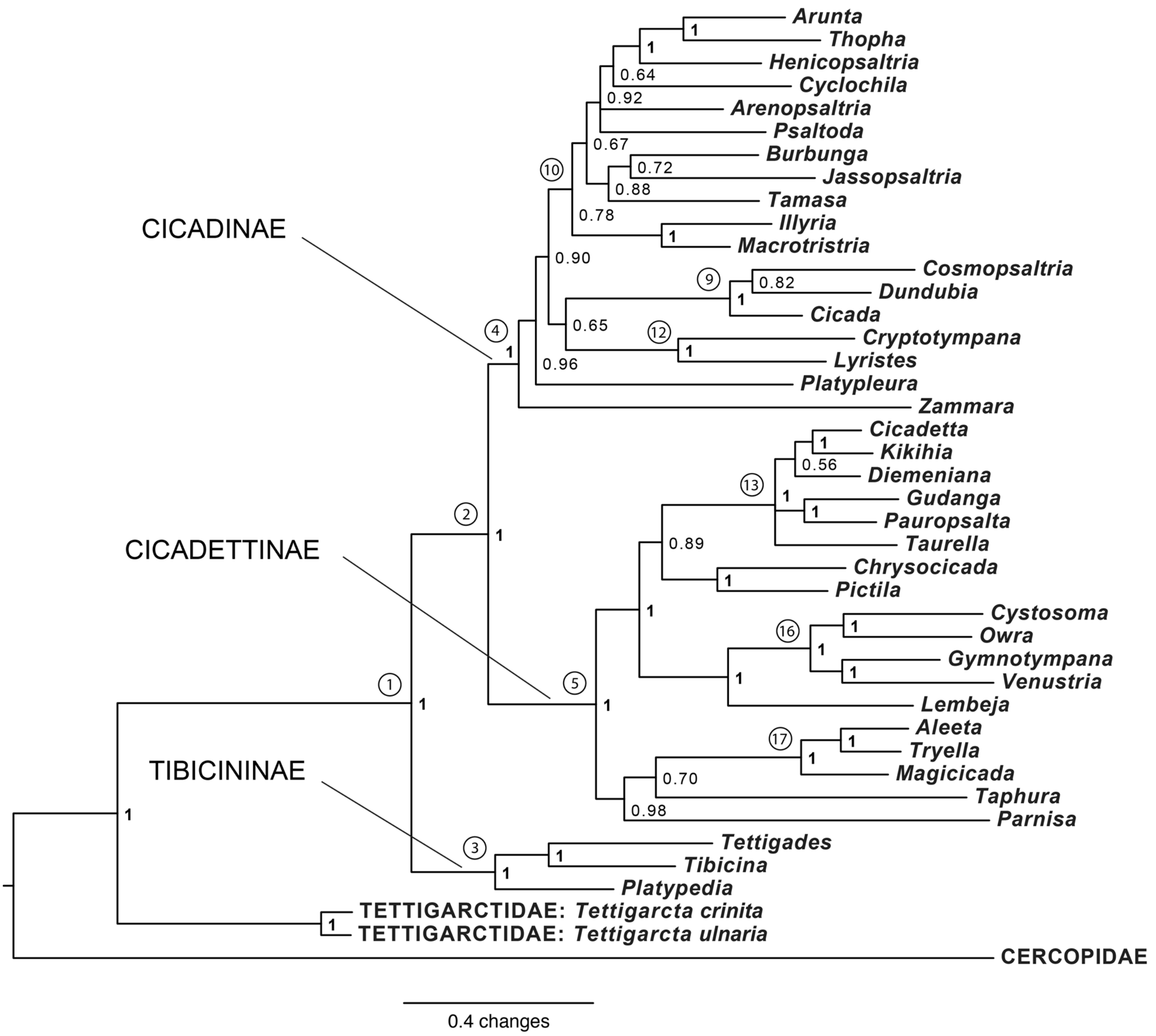


FIGURE 5. Exploratory MrBayes 50% majority rule consensus tree from a combined analysis of the DNA dataset and 117 morphological characters from Moulds (2005), restricted to genera from Moulds's analysis. Note that Moulds's analysis did not include any taxa for Tettigomyiinae **n. stat.** Values at nodes are posterior probabilities of clades. Taxa are shown with nomenclature updated since 2005.

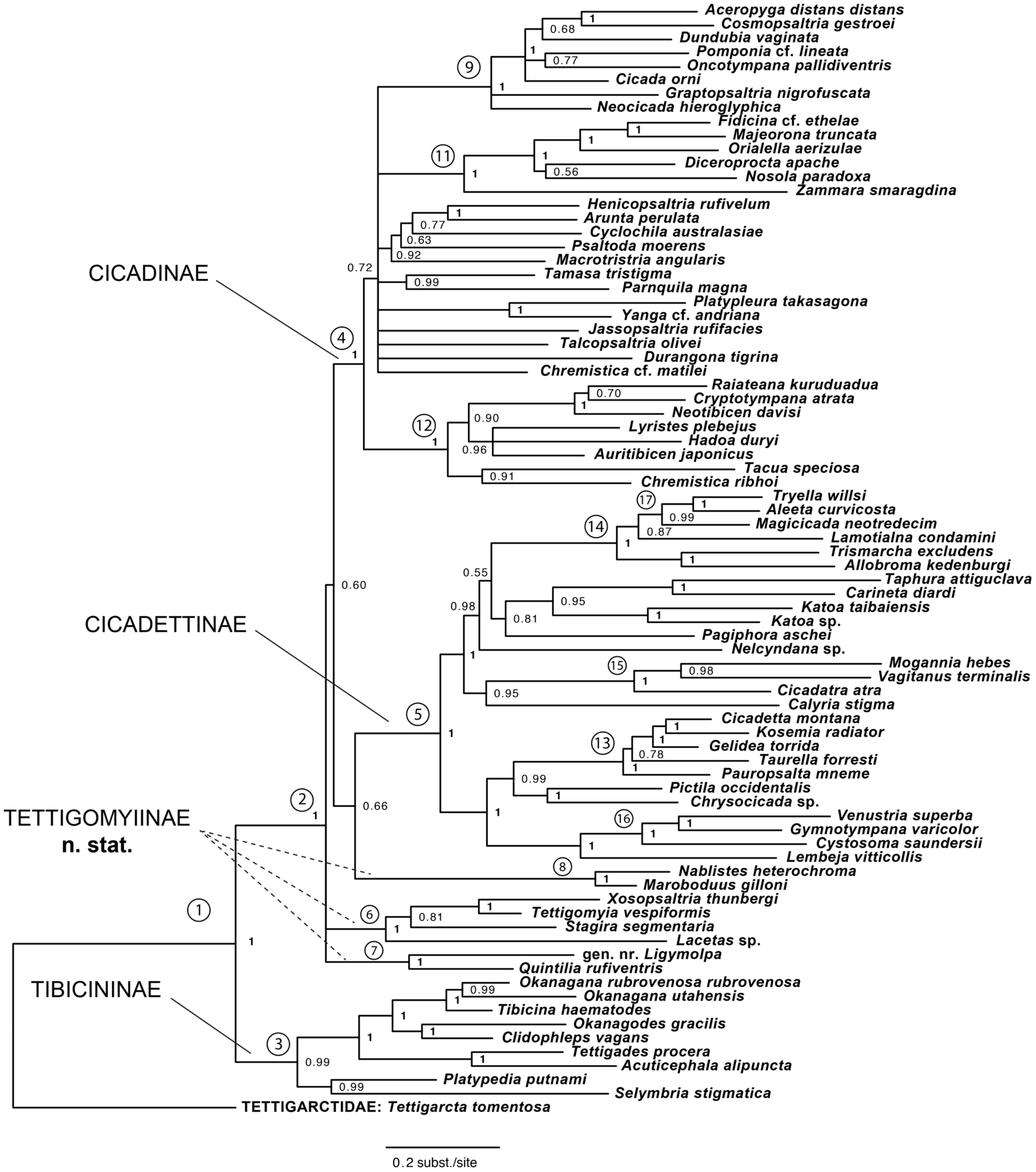


FIGURE 6. Exploratory MrBayes analysis of a smaller 80-taxon DNA dataset created to reduce missing data. Values at nodes are posterior probabilities of clades.

The remaining three deep-level clades (6-8) in Fig. 4 contain African genera that were not studied in Moulds's morphological treatment of the family. All of these were previously classified in Cicadettinae and Tibicininae, and all are now assigned to subfamily Tettigomyiinae **n. stat.** as explained below. In six additional cases, current subfamily classification strongly conflicts with the position of specific taxa or clades in the DNA tree. *Karenia* Distant, *Durangona* Distant, and *Nosola* Stål have been previously placed in Cicadettinae but group with genera from Cicadinae. *Selymbria* Stål (previously in Cicadettinae) falls within the Tibicininae (Fig. 4). Finally, all of the genera in the tribe Cicadatrini (previously in Cicadinae) form a group (clade 15) related to genera from Cicadettinae, and the monogeneric tribe Sinosenini (previously in Cicadettinae) groups within the Cicadinae (see clade 9). The positions of many genera in the five-gene tree also conflict with their existing tribal placement, especially involving tribes Cryptotympanini Handlirsch, Taphurini Distant, and Cicadettini Buckton. These cases are discussed in detail in the taxonomic outcomes section below.

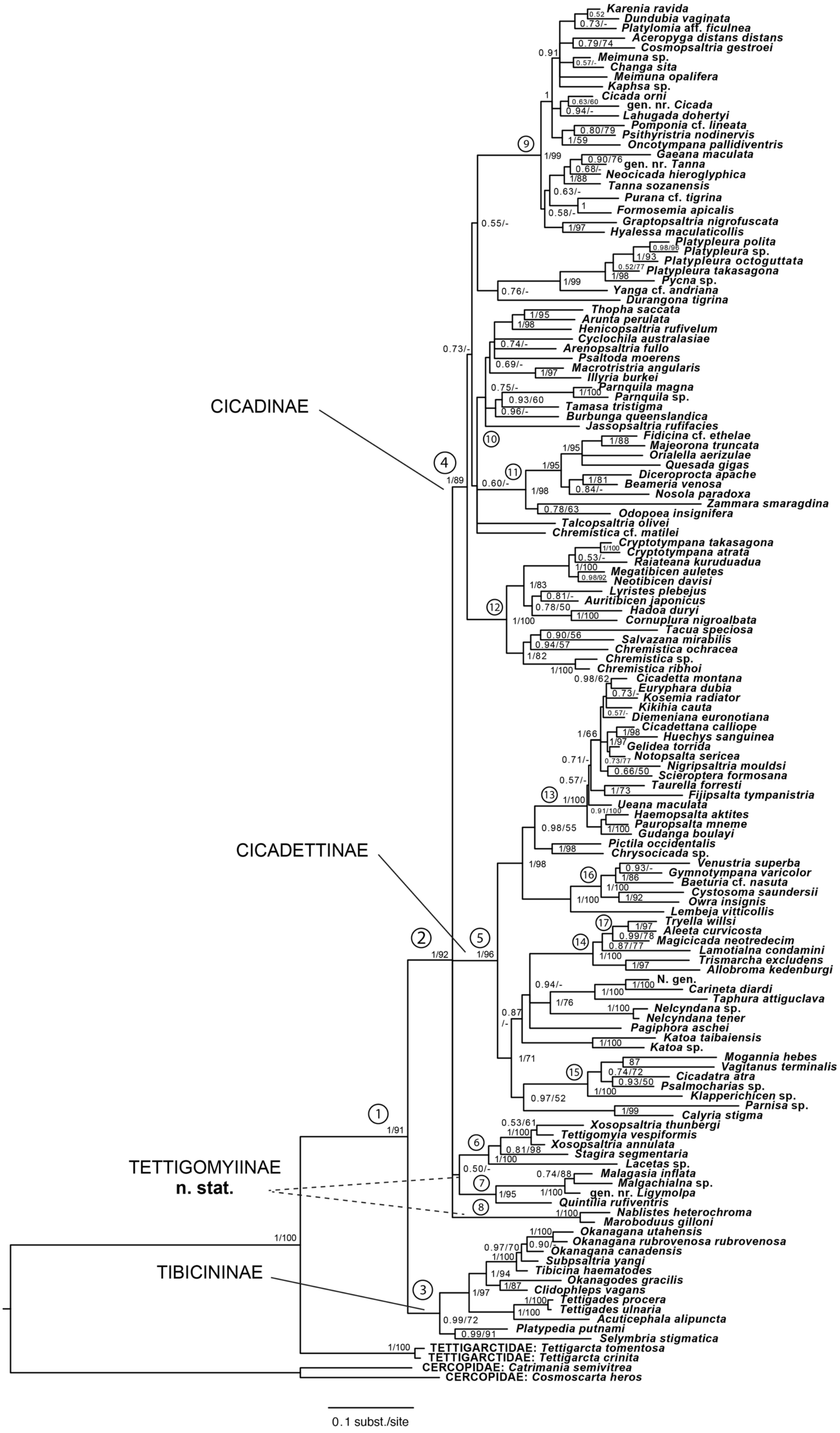


FIGURE 7. Exploratory MrBayes analysis of the DNA dataset with mitochondrial third positions RY-coded, with posterior probabilities and ML bootstrap values shown.

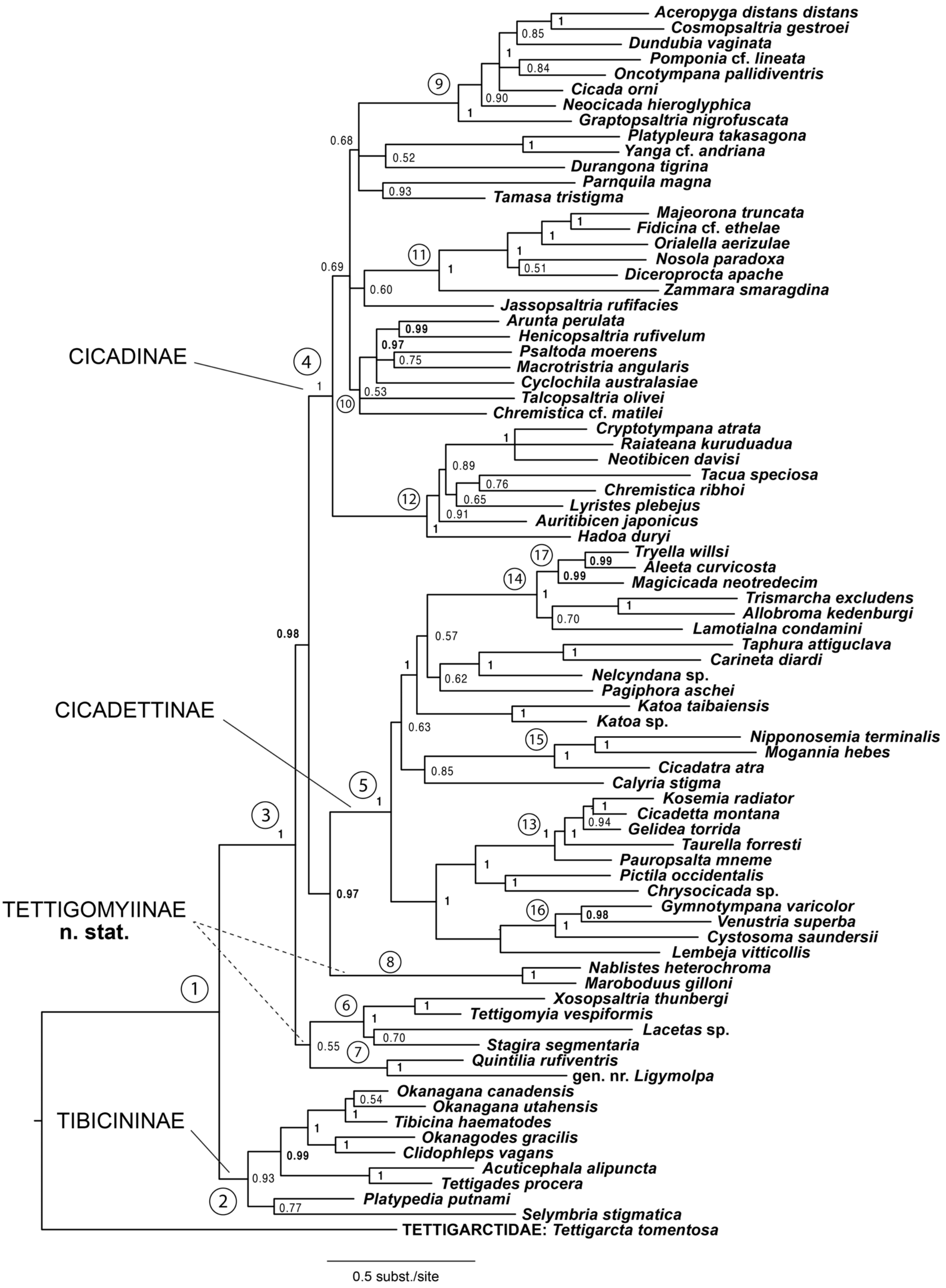


FIGURE 8. Exploratory nh_PhyloBayes analysis of the DNA dataset allowing accommodation of base frequency nonhomogeneity. Values at nodes are posterior probabilities of clades.

Analyses of larger single-amplicon datasets (not shown), intended to check for errors from contamination and/or mislabelling of specimens or sequences, found no conflicts with well-supported nodes in the combined-data tree. MrBayes analysis of the dataset pared to reduce missing data also yielded the same well-supported branches (Fig. 6).

Accommodating base composition bias and potential heterotachy. The MrBayes analysis of the nucleotide dataset with RY-coded mtDNA third codon positions ended at 62.9 million generations. After the first 15.7 million generations were excluded as burnin, the posterior arithmetic mean log likelihood was -60410.96 and the harmonic mean was -60508.44. The consensus tree (Fig. 7) shows no well-supported differences from the main analysis without RY coding, although most deep-level branches are supported by slightly greater ML bootstrap values.

Although the four nt_PhyloBayes analyses appeared to have found stable solutions, the resulting posterior probabilities varied from ln L = -33795.6 to -33978.6, indicating a substantial starting-point dependence and a need for impractically long analyses and/or improved MCMC tuning. The nh_PhyloBayes analysis with the best score (Fig. 8) found the same pattern of branch support as the standard partitioned Bayesian and ML analyses, with one exception—the three well-supported African clades numbered 6-8 did not cluster together at the base of the main radiation (after the divergence of the Tibicininae). Instead, *Maroboduus* Distant + *Nablistes* Karsch appeared in a sister-clade position to the Cicadettinae (clade 5) with moderately strong Bayesian support. In the two analyses with lower posterior probabilities (not shown), all of the African genera clustered into a monophyletic clade that branched off sister to the Cicadettinae + Cicadinae.

Taxonomic revision

Examination of the classification within existing subfamilies and tribes of the Cicadidae and morphological patterns in light of the molecular results has led to the following revised scheme. Below, we present a summary of the scheme, followed by detailed reviews of the subfamilies and tribes. All four current Cicadidae subfamilies, 53 tribes, and 456 genera are listed. Morphological descriptions use the revised terminology of Moulds (2005), which contains labeled diagrams of all morphological structures discussed here. Specific comments, often pertaining to taxonomic rearrangements published since the catalogue of Sanborn (2013), are included in a short section for many groups, and more general discussion is placed later in the main Discussion section. Unless otherwise stated, current subtribes are left unchanged in the revised classification. Fig. 9 illustrates all of the taxonomic transfers and synonymies discussed below.

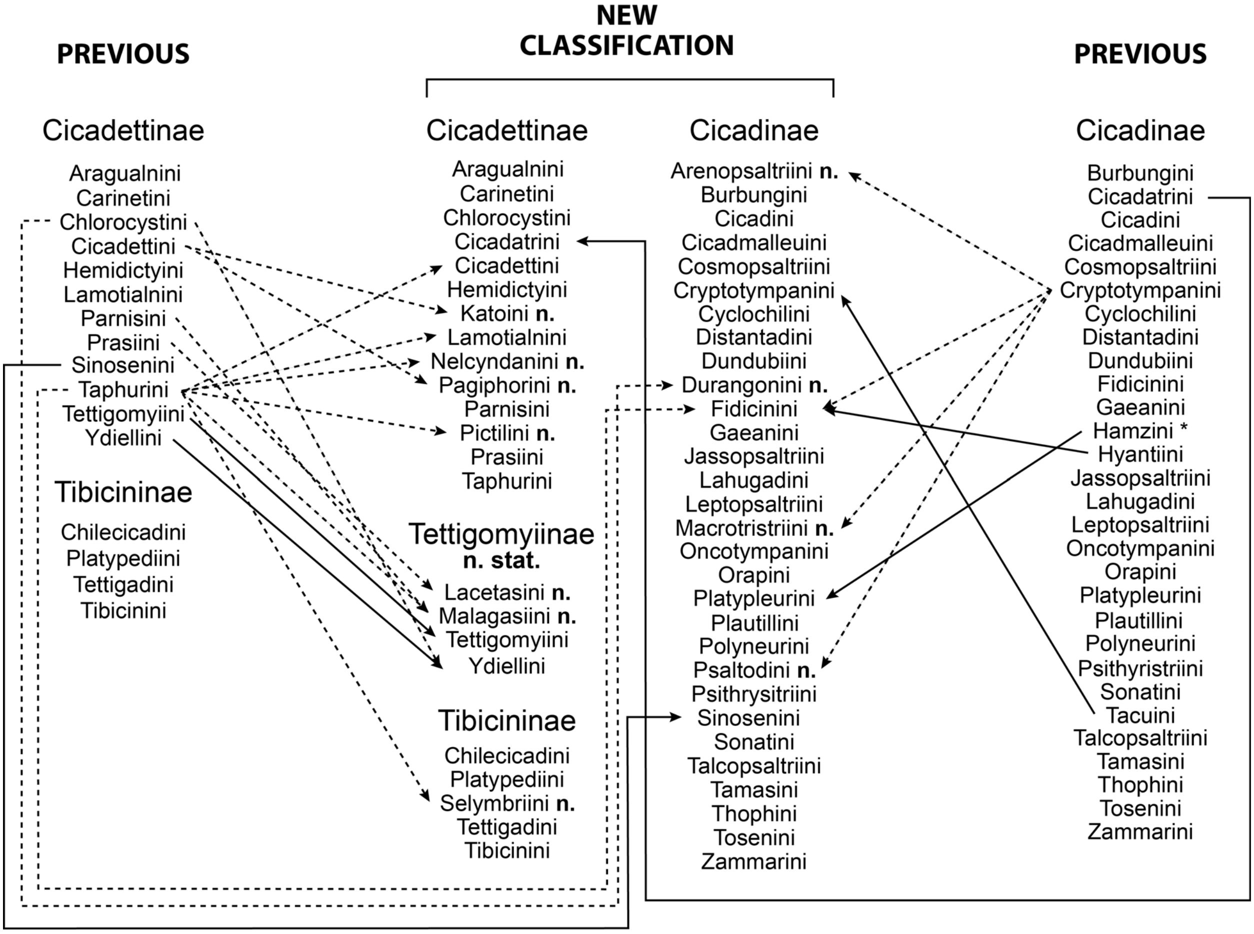


FIGURE 9. Taxonomic transfers made in this paper, as explained in the Taxonomic Revision section in Results. Solid lines indicate complete movement of a tribe between subfamilies and/or synonymization, and dotted lines indicate partial transfer. *Suppression of priority of Hamzini, which has priority over Platypleurini, is currently the subject of Case 3761 before the ICZN (see Tribe Platypleurini).

The subfamily classification follows Moulds (2005) with the addition of a new subfamily for African genera that were not available during Moulds's morphological revision, a concept highlighted by the new molecular data. Some modifications are made to the diagnostic features of the Cicadettinae, Cicadinae, and Tibicininae (see also Table 4). For subfamily synonymies see Moulds (2005) except that we follow Sanborn (2013) and use the name Tibicininae over Tettigadinae despite its confusing connotations (see Comments under subfamily Tibicininae).

For tribal synonymies see Sanborn (2013), Moulds (2005), Metcalf (1963) and Duffels & van der Laan (1985). The tribal descriptions below are based on characters identified as meaningful at tribal level in Moulds (2005) supplemented by additional characters found relevant to the new tribes being described. We have not been able to examine representatives of all genera and it has therefore been necessary to leave such genera unchanged in their tribal placement pending future study.

TABLE 4. Characters for the four subfamilies of the family Cicadidae. Autapomorphies are highlighted in gray. Note that the Tettigomyiinae **n. stat.** lacks an autapomorphy and is diagnosable only by a combination of attributes.

	SUBFAMILY			
CHARACTER	Cicadinae	Cicadettinae	Tettigomyiinae **n. stat.**	Tibicininae
Metanotum	Entirely concealed at dorsal midline.	Partly visible at dorsal midline.	Exposed or concealed (in Lacetasini **n. tribe**) at dorsal midline.	Concealed at dorsal midline (except in *Platypedia*, *Tibicina*).
Forewing veins CuP and 1A	Fused in part.	Fused in part.	Fused in part.	Unfused (fused in *Platypedia* and *Neoplatypedia*).
Hindwing veins RP and M	Fused at their bases.	Fused at their bases.	Fused at their bases.	Unfused at their bases.
Male opercula shape	Not strongly S-shaped and not with lateral margins deeply concave.	Not strongly S-shaped and not with lateral margins deeply concave.	Not strongly S-shaped and not with lateral margins deeply concave.	A distinctive S-shape with lateral margins deeply concave, and with distal margins not reaching distal margins of tympanal cavities.
Male timbal covers	Present but lost in a few genera.	Lacking timbal covers or with a partial turned-back rim.	Lacking timbal covers or with a partial turned-back rim.	Lacking timbal covers or with a partial turned-back rim.
Pygofer distal shoulder	Well developed, often the most distal part of pygofer.	Undeveloped.	Well developed, often the most distal part of pygofer.	Undeveloped.
Pygofer upper lobe	Absent or present.	Present.	Absent.	Usually absent (present in Selymbriini **n. tribe**).
Uncus	Of moderate length and retractable within pygofer.	Absent or very small and duck-bill shaped, and retractable within pygofer.	Long, directed distally, not retractable within pygofer.	Very long and not retractable within pygofer.
Claspers	Absent, but present in some Dundubiini (if present, spined).	Usually large (small in Kaotini **n. tribe**), not spined.	Absent.	Absent.
Ventrobasal pocket of aedeagus	Absent.	Absent.	Absent.	Present.
Aedeagal restraint	Before or below uncus.	By claspers.	Before or below uncus.	By tubular encapsulation below uncus.
Apical part of theca	Without leaf-like lateral lobes.	Without leaf-like lateral lobes.	Without leaf-like lateral lobes.	With a pair of leaf-like lateral lobes.

SUMMARY OF SUBFAMILIES, TRIBES AND GENERA

Subfamily Cicadettinae Buckton

Tribe Aragualnini Sanborn
Aragualna Champanhet, Boulard & Gaiani.

Tribe Carinetini Distant
Ahomana Distant; *Carineta* Amyot & Audinet-Serville; *Guaranisaria* Distant; *Herrera* Distant; *Novemcella* Goding; *Paranistria* Metcalf; *Toulgoetalna* Boulard.

Tribe Chlorocystini Distant
Aedeastria Boer; *Akamba* Distant; *Baeturia* Stål; *Cephalalna* Boulard; *Chlorocysta* Westwood; *Conibosa* Distant; *Cystopsaltria* Goding & Froggatt; *Cystosoma* Westwood; *Decebalus* Distant; *Dinarobia* Mamet; *Euthemopsaltria* Moulds; *Fractuosella* Boulard; *Glaucopsaltria* Goding & Froggatt; *Guineapsaltria* Boer; *Gymnotympana* Stål; *Kumanga* Distant; *Mirabilopsaltria* Boer; *Muda* Distant; *Musoda* Karsch; *Owra* Ashton; *Papuapsaltria* Boer; *Scottotympana* Boer; *Thaumastopsaltria* Kirkaldy; *Venustria* Goding & Froggatt.

Tribe Cicadatrini Distant
Bijaurana Distant; *Chloropsalta* Haupt; *Cicadatra* Kolenati; *Emathia* Stål; *Klapperichicen* Dlabola; *Mogannia* Amyot & Audinet-Serville; *Pachypsaltria* Stål; *Psalmocharias* Kirkaldy; *Shaoshia* Wei, Ahmed & Rizvi; *Taungia* Ollenbach; *Triglena* Fieber; *Vagitanus* Distant.

Tribe Cicadettini Buckton
Adelia Moulds; *Aestuansella* Boulard; *Amphipsalta* Fleming; *Atrapsalta* Owen & Moulds; *Auscala* Moulds; *Auta* Distant; *Berberigetta* Costa, Nunes, Marabuto, Mendes & Simões; *Birrima* Distant; *Bispinalta* Delorme; *Buyisa* Distant; *Caledopsalta* Delorme; *Caliginopsalta* Ewart; *Chelapsalta* Moulds; *Cicadetta* Kolenati; *Cicadettana* Marshall & Hill; *Clinata* Moulds; *Clinopsalta* Moulds; *Crotopsalta* Ewart; *Curvicicada* Chou & Lu; *Diemeniana* Distant; *Dimissalna* Boulard; *Dipsopsalta* Moulds; *Drymopsalta* Ewart; *Erempsalta* Moulds; *Euboeana* Gogala, Trilar & Drosopoulos; *Euryphara* Horváth; *Ewartia* Moulds; *Falcatpsalta* Owen & Moulds; *Fijipsalta* Duffels; *Froggattoides* Distant; *Gagatopsalta* Ewart; *Galanga* Moulds; *Gelidea* Moulds; *Germalna* Delorme; *Ggomapsalta* Lee; *Graminitigrina* Ewart & Marques; *Graptotettix* Stål; *Gudanga* Distant; *Haemopsalta* Owen & Moulds; *Heliopsalta* Moulds; *Hilaphura* Webb; *Huechys* Amyot & Audinet-Serville; *Kanakia* Distant; *Kikihia* Dugdale; *Kobonga* Distant; *Kosemia* Matsumura; *Limnopsalta* Moulds; *Linguacicada* Chou & Lu; *Maoricicada* Dugdale; *Marteena* Moulds; *Melampsalta* Kolenati; *Melanesiana* Delorme; *Mouia* Distant; *Mugadina* Moulds; *Murmurillana* Delorme; *Myersalna* Boulard; *Myopsalta* Moulds; *Nanopsalta* Moulds; *Neopunia* Moulds; *Nigripsaltria* Boer; *Noongara* Moulds; *Notopsalta* Dugdale; *Oligoglena* Horvath, 1912; *Pakidetta* Sanborn & Ahmed; *Palapsalta* Moulds; *Panialna* Delorme; *Paradina* Moulds; *Parvittya* Distant; *Paulaudalna* Delorme; *Pauropsalta* Goding & Froggatt; *Philipsalta* Lee, Marshall & Hill; *Physeema* Moulds; *Pinheya* Dlabola; *Pipilopsalta* Ewart; *Platypsalta* Moulds; *Plerapsalta* Moulds; *Popplepsalta* Owen & Moulds; *Poviliana* Boulard; *Pseudokanakia* Delorme; *Pseudotettigetta* Puissant; *Punia* Moulds; *Pyropsalta* Moulds; *Relictapsalta* Owen & Moulds; *Rhodopsalta* Dugdale; *Rouxalna* Boulard; *Samaecicada* Popple & Emery; *Saticula* Stål; *Scieroptera* Stål; *Scolopita* Chou & Lei; *Simona* Moulds; *Stellenboschia* Distant; *Strepuntalna* Delorme; *Sylphoides* Moulds; *Takapsalta* Matsumura; *Taurella* Moulds; *Telmapsalta* Moulds; *Terepsalta* Moulds; *Tettigetta* Kolenati; *Tettigettacula* Puissant; *Tettigettalna* Puissant; *Tettigettula* Puissant; *Tibeta* Lei & Chou; *Toxala* Moulds; *Toxopeusella* Schmidt; *Tympanistalna* Boulard; *Ueana* Distant; *Urabunana* Distant; *Uradolichos* Moulds; *Vastarena* Delorme; *Xossarella* Boulard; *Yoyetta* Moulds.

Tribe Hemidictyini Distant
Hemidictya Burmeister; *Hovana* Distant.

Tribe Katoini Moulds & Marshall, n. tribe
Katoa Ouchi.

Tribe Lamotialnini Boulard
Abricta Stål; *Abroma* Stål; *Aleeta* Moulds; *Allobroma* Duffels; *Chrysolasia* Moulds; *Hylora* Boulard; *Lamotialna* Boulard; *Lemuriana* Distant; *Magicicada* Davis; *Monomatapa* Distant; *Musimoia* China; *Neomuda* Distant; *Oudeboschia* Distant; *Panka* Distant; *Sundabroma* Duffels; *Trismarcha* Karsch; *Tryella* Moulds; *Unduncus* Duffels; *Viettealna* Boulard.

Tribe Nelcyndanini Moulds & Marshall, n. tribe
Nelcyndana Distant.

Tribe Pagiphorini Moulds & Marshall, n. tribe
Pagiphora Horváth.

Tribe Parnisini Distant
Abagazara Distant; *Acyroneura* Torres; *Adeniana* Distant; *Arcystasia* Distant; *Calopsaltria* Stål; *Calyria* Stål; *Crassisternalna* Boulard; *Derotettix* Berg; *Henicotettix* Stål; *Jafuna* Distant; *Kageralna* Boulard; *Koranna* Distant; *Luangwana* Distant; *Lycurgus* China; *Malgotilia* Boulard; *Mapondera* Distant; *Masupha* Distant; *Parnisa* Stål; *Prunasis* Stål; *Psilotympana* Stål; *Rhinopsalta* Melichar; *Taipinga* Distant; *Zouga* Distant.

Tribe Pictilini Moulds & Hill, n. tribe
Chrysocicada Boulard; *Pictila* Moulds.

Tribe Prasiini Matsumura
Arfaka Distant; *Bafutalna* Boulard; *Iruana* Distant; *Jacatra* Distant; *Lembeja* Distant; *Mariekea* Jong & Boer; *Murphyalna* Boulard; *Prasia* Stål; *Sapantanga* Distant.

Tribe Taphurini Distant
Anopercalna Boulard; *Chalumalna* Boulard; *Dorachosa* Distant; *Dulderana* Distant; *Elachysoma* Torres; *Imbabura* Distant; *Malloryalna* Sanborn; *Prosotettix* Jacobi; *Psallodia* Uhler; *Taphura* Stål.

Subfamily Cicadinae Latreille

Tribe Arenopsaltriini Moulds, n. tribe
Arenopsaltria Ashton; *Henicopsaltria* Stål.

Tribe Burbungini Moulds
Burbunga Distant.

Tribe Cicadini Latreille
Cicada Linnaeus.

Tribe Cicadmalleuini Boulard & Puissant
Cicadmalleus Boulard & Puissant.

Tribe Cosmopsaltriini Kato
Aceropyga Duffels; *Brachylobopyga* Duffels; *Cosmopsaltria* Stål; *Diceropyga* Stål; *Dilobopyga* Duffels; *Inflatopyga* Duffels; *Moana* Myers; *Rhadinopyga* Duffels.

Tribe Cryptotympanini Handlirsch
Antankaria Distant; *Auritibicen* Lee; *Cacama* Distant; *Chremistica* Stål; *Cornuplura* Davis; *Cryptotympana* Stål; *Hadoa* Moulds; *Hea* Distant; *Heteropsaltria* Jacobi; *Lyristes* Horváth; *Megatibicen* Sanborn & Heath; *Neotibicen* Hill & Moulds; *Nggeliana* Boulard; *Raiateana* Boulard; *Salvazana* Distant; *Tacua* Amyot & Audinet-Serville.

Tribe Cyclochilini Distant
Cyclochila Amyot & Audinet-Serville.

Tribe Distantadini Orian
Distantada Orian.

Tribe Dundubiini Distant
Aola Distant; *Ayesha* Distant; *Biura* Lee & Sanborn; *Champaka* Distant; *Changa* Lee; *Cochleopsaltria* Pham & Constant; *Crassopsaltria* Boulard; *Dundubia* Amyot & Audinet-Serville; *Haphsa* Distant; *Kaphsa* Lee; *Khimbya* Distant; *Lethama* Distant; *Macrosemia* Kato; *Megapomponia* Boulard; *Meimuna* Distant; *Minilomia* Lee; *Orientopsaltria* Kato; *Platylomia* Stål; *Sinapsaltria* Kato; *Sinosemia* Matsumura; *Sinotympana* Lee; *Songga* Lee; *Unipomponia* Lee; *Zaphsa* Lee & Emery.

Tribe Durangonini Moulds & Marshall, n. tribe
Durangona Distant.

Tribe Fidicinini Distant
Ariasa Distant; *Beameria* Davis; *Bergalna* Boulard & Martinelli; *Cracenpsaltria* Sanborn; *Diceroprocta* Stål; *Dorisiana* Metcalf; *Elassoneura* Torres; *Fidicina* Amyot & Audinet-Serville; *Fidicinoides* Boulard & Martinelli; *Guyalna* Boulard & Martinelli; *Hemisciera* Amyot & Audinet-Serville; *Hyantia* Stål; *Majeorona* Distant; *Mura* Distant; *Nosola* Stål; *Ollanta* Distant; *Orialella* Metcalf; *Pacarina* Distant; *Pompanonia* Boulard; *Prasinosoma* Torres; *Proarna* Stål; *Quesada* Distant; *Tympanoterpes* Stål.

Tribe Gaeanini Distant
Ambragaeana Chou & Yao; *Balinta* Distant; *Becquartina* Kato; *Callogaeana* Chou & Yao; *Gaeana* Amyot & Audinet-Serville; *Paratalainga* He; *Sulphogaeana* Chou & Yao; *Talainga* Distant; *Taona* Distant; *Trengganua* Moulton.

Tribe Jassopsaltriini Moulds
Jassopsaltria Ashton.

Tribe Lahugadini Distant
Lahugada Distant.

Tribe Leptopsaltriini Moulton
Aetanna Lee; *Cabecita* Lee; *Calcagninus* Distant; *Euterpnosia* Matsumura; *Formocicada* Lee & Hayashi; *Formosemia* Matsumura; *Galgoria* Lee; *Gudaba* Distant; *Inthaxara* Distant; *Leptopsaltria* Stål; *Leptosemia* Matsumura; *Manna* Lee & Emery; *Masamia* Lee & Emery; *Maua* Distant; *Minipomponia* Boulard; *Miniterpnosia* Lee; *Mosaica* Lee & Emery; *Nabalua* Moulton; *Neocicada* Kato; *Neoterpnosia* Lee & Emery; *Paranosia* Lee; *Paratanna* Lee; *Purana* Distant; *Puranoides* Moulton; *Qurana* Lee; *Rustia* Stål; *Taiwanosemia* Matsumura; *Tanna* Distant; *Yezoterpnosia* Matsumura.

Tribe Macrotristriini Moulds, n. tribe
Illyria Moulds; *Macrotristria* Stål.

Tribe Oncotympanini Ishihara
Mata Distant; *Neoncotympana* Lee; *Oncotympana* Stål.

Tribe Orapini Boulard
Orapa Distant.

Tribe Platypleurini Schmidt
Afzeliada Boulard; *Albanycada* Villet; *Attenuella* Boulard; *Azanicada* Villet; *Brevisiana* Boulard; *Canualna* Boulard; *Capcicada* Villet; *Esada* Boulard; *Hainanosemia* Kato; *Hamza* Distant; *Ioba* Distant; *Kalabita* Moulton; *Karscheliana* Boulard; *Koma* Distant; *Kongota* Distant; *Muansa* Distant; *Munza* Distant; *Oxypleura* Amyot & Audinet-Serville; *Platypleura* Amyot & Audinet-Serville; *Pycna* Amyot & Audinet-Serville; *Sadaka* Distant; *Sechellalna* Boulard; *Severiana* Boulard; *Soudaniella* Boulard; *Strumosella* Boulard; *Strumoseura* Villet; *Suisha* Kato; *Tugelana* Distant; *Ugada* Distant; *Umjaba* Distant; *Yanga* Distant.

Tribe Plautillini Distant
Plautilla Stål.

Tribe Polyneurini Amyot & Audinet-Serville
Angamiana Distant; *Formotosena* Kato; *Graptopsaltria* Stål; *Polyneura* Westwood.

Tribe Psaltodini Moulds, n. tribe
Anapsaltoda Ashton; *Neopsaltoda* Distant; *Psaltoda* Stål.

Tribe Psithyristriini Distant
Basa Distant; *Kamalata* Distant; *Onomacritus* Distant; *Pomponia* Stål; *Psithyristria* Stål; *Semia* Matsumura; *Terpnosia* Distant.

Tribe Sinosenini Boulard
Karenia Distant.

Tribe Sonatini Lee
Hyalessa China.

Tribe Talcopsaltriini Moulds
Talcopsaltria Moulds.

Tribe Tamasini Moulds
Parnkalla Distant; *Parnquila* Moulds; *Tamasa* Distant.

Tribe Thophini Distant
Arunta Distant; *Thopha* Amyot & Audinet-Serville.

Tribe Tosenini Amyot & Audinet-Serville
Ayuthia Distant; *Distantalna* Boulard; *Tosena* Amyot & Audinet-Serville.

Tribe Zammarini Distant
Borencona Davis; *Chinaria* Davis; *Daza* Distant; *Juanaria* Distant; *Miranha* Distant; *Odopoea* Stål; *Onoralna* Boulard; *Orellana* Distant; *Procollina* Metcalf; *Uhleroides* Distant; *Zammara* Amyot & Audinet-Serville; *Zammaralna* Boulard & Sueur.

Subfamily Tettigomyiinae Distant, n. stat.

Tribe Lacetasini Moulds & Marshall, n. tribe
Lacetas Karsch.

Tribe Malagasiini Moulds & Marshall, n. tribe
Ligymolpa Karsch; *Malagasia* Distant; *Malgachialna* Boulard; *Nyara* Villet; *Quintilia* Stål.

Tribe Tettigomyiini Distant
Bavea Distant; *Gazuma* Distant; *Paectira* Karsch; *Spoerryana* Boulard; *Stagea* Villet; *Stagira* Stål; *Tettigomyia* Amyot & Audinet-Serville; *Xosopsaltria* Kirkaldy.

Tribe Ydiellini Boulard
Maroboduus Distant; *Nablistes* Karsch.

Subfamily Tibicininae Distant

Tribe Chilecicadini Sanborn
Chilecicada Sanborn.

Tribe Platypediini Kato
Neoplatypedia Davis; *Platypedia* Uhler.

Tribe Selymbriini Moulds & Marshall, n. tribe
Selymbria Stål.

Tribe Tettigadini Distant
Acuticephala Torres; *Alarcta* Torres; *Babras* Jacobi; *Calliopsida* Torres; *Chonosia* Distant; *Coata* Distant; *Mendozana* Distant; *Psephenotettix* Torres; *Tettigades* Amyot & Audinet-Serville; *Tettigotoma* Torres; *Torrescada* Sanborn & Heath.

Tribe Tibicinini Distant
Clidophleps Van Duzee; *Okanagana* Distant; *Okanagodes* Davis; *Paharia* Distant; *Subpsaltria* Chen; *Subtibicina* Lee; *Tibicina* Kolenati; *Tibicinoides* Distant.

SUBFAMILY CICADETTINAE BUCKTON, 1890

Type genus. *Cicadetta* Kolenati, 1857 (type species *Cicada montana* Scopoli, 1772).

Included tribes. Aragualnini Sanborn, 2018; Carinetini Distant, 1905; Chlorocystini Distant, 1905; Cicadatrini Distant, 1905; Cicadettini Buckton, 1890; Hemidictyini Distant, 1905; Katoini Moulds & Marshall **n. tribe**; Lamotialnini Boulard, 1976; Nelcyndanini Moulds & Marshall **n. tribe**; Pagiphorini Moulds & Marshall **n. tribe**; Parnisini Distant, 1905; Pictilini Moulds & Hill **n. tribe**; Prasiini Matsumura, 1917; Taphurini Distant, 1905.

Diagnosis (modified from Moulds, 2005). Metanotum partly visible at dorsal midline. Forewing veins CuP and 1A fused in part. Hindwing veins RP and M fused at their bases. Male opercula not strongly S-shaped and not with lateral margins deeply concave. Rim of male timbal cavity lacking a turned-back rim or timbal cover. Pygofer with distal shoulder undeveloped; pygofer upper lobe present. Uncus absent or very small and duck-bill shaped, and retractable within pygofer. Claspers present and usually large (small in Katoini **n. tribe**), dominating the whole 10th abdominal segment, not spined. Aedeagus without ventrobasal pocket; aedeagus restrained by claspers. Apical part of theca without leaf-like lateral lobes.

Distinguishing features (Table 4). Uncus absent or very small and duck-bill shaped, and retractable within pygofer; claspers present and usually large, dominating the whole 10th abdominal segment.

Distribution. Global.

Comments. Cicadatrini is transferred from the Cicadinae to the Cicadettinae following the molecular phylogenetic results, confirmed by the presence of claspers which are diagnostic for this subfamily. The remaining tribes in the Cicadettinae conform to Moulds (2005) definition of the subfamily (see clade 5, Fig. 4). In a dissertation, Goemans (2016, see also in prep.), showed that Dazini Kato, 1932 is synonymous with Zammarini; the transfer was formalized and further supported by Sanborn (2018).

Tribe Aragualnini Sanborn, 2018

Type genus. *Aragualna* Champanhet, Boulard & Gaiani, 2000.

Included genera. *Aragualna* Champanhet, Boulard & Gaiani, 2000.

Diagnosis. As in Sanborn (2018).

Distribution. Venezuela.

Comments. Molecular data in Goemans (2016, also in prep.) showed *Aragualna* to be unrelated to the type genus of Dazini. Sanborn (2018) erected the new tribe Aragualnini.

Tribe Carinetini Distant, 1905

Type genus. *Carineta* Amyot & Audinet-Serville, 1843 (type species *Cicada formosa* Germar, 1830 = *Carineta diardi* Guérin-Méneville, 1829).

Included genera. *Ahomana* Distant, 1905; *Carineta* Amyot & Audinet-Serville, 1843; *Guaranisaria* Distant, 1905; *Herrera* Distant, 1905; *Novemcella* Goding, 1925; *Paranistria* Metcalf, 1952; *Toulgoetalna* Boulard, 1982.

Diagnosis and distinguishing features. For Carinetini, Distant (1905c) describes a robust body that narrows both anteriorly and posteriorly, with a short pronotum having oblique margins, and with usually hyaline wings. The genitalia are here illustrated in Fig. 11.

Distribution. Neotropics.

Comments. Only the type genus of Carinetini was represented in our study and the type species could not be obtained. The tribal concept (with subtribes) remains as in Sanborn (2013, 2014a) except that Sanborn (2014a) recently transferred *Ahomana* from the Tibicinini.

Tribe Chlorocystini Distant, 1905

Type genus. *Chlorocysta* Westwood, 1851 (type species *Cystosoma vitripennis* Westwood, 1851).

Included genera. *Aedeastria* Boer, 1990; *Akamba* Distant, 1905; *Baeturia* Stål, 1866; *Cephalalna* Boulard, 2006; *Chlorocysta* Westwood, 1851; *Conibosa* Distant, 1905; *Cystopsaltria* Goding & Froggatt, 1904; *Cystosoma* Westwood, 1842; *Decebalus* Distant, 1920; *Dinarobia* Mamet, 1957; *Euthemopsaltria* Moulds, 2014; *Fractuosella* Boulard, 1979; *Glaucopsaltria* Goding & Froggatt, 1904; *Guineapsaltria* Boer, 1993; *Gymnotympana* Stål, 1861; *Kumanga* Distant, 1905; *Mirabilopsaltria* Boer, 1996; *Muda* Distant, 1897; *Musoda* Karsch, 1890; *Owra* Ashton, 1912; *Papuapsaltria* Boer, 1995; *Scottotympana* Boer, 1991; *Thaumastopsaltria* Kirkaldy, 1900; *Venustria* Goding & Froggatt, 1904.

Diagnosis. The tribe is defined by Boer (1995) and Moulds (2005). Male genitalia of the type are also illustrated in Moulds (2012).

Distribution. Primarily South-East Asia, Australasia, and the Western Pacific, with isolated genera in Africa/Madagascar, South America, and the Mascarene Islands and Mauritius.

Comments. *Durangona* and *Nablistes* are morphologically incompatible with Boer's definition of Chlorocystini, a conclusion supported by the molecular phylogenetic results. *Durangona* is transferred to form the tribe Durangonini **n. tribe,** while *Nablistes* is transferred to Ydiellini. The assignment of American (*Conibosa*) and African genera (e.g., *Akamba*, *Cephalalna*, *Musoda*), as well as *Fractuosella*, may require re-examination.

Tribe Cicadatrini Distant, 1905

Type genus. *Cicadatra* Kolenati, 1857 (type species *Cicada atra* Olivier, 1790).

Included genera. *Bijaurana* Distant, 1912; *Chloropsalta* Haupt, 1920; *Cicadatra* Kolenati, 1857; *Emathia* Stål, 1866; *Klapperichicen* Dlabola, 1957; *Mogannia* Amyot & Audinet-Serville, 1843; *Pachypsaltria* Stål, 1861; *Psalmocharias* Kirkaldy, 1908; *Shaoshia* Wei, Ahmed & Rizvi, 2010; *Taungia* Ollenbach, 1929; *Triglena* Fieber, 1875; *Vagitanus* Distant, 1918.

Distinguishing features. Wang *et al*. (2017) derived three synapomorphies for the tribe from a cladistic analysis using *Paharia* (Tibicinini), *Meimuna* (Dundubiini), and *Cicadetta* (Cicadettini) as outgroups: Male opercula enlarged at subapical portion towards body centre; aedeagus with several processes apically and subapically; apical part of aedeagus bifurcate.

Distribution. Palearctic, Indomalaya. *Pachypsaltria*, from South America, is doubtfully placed in Cicadatrini but we have not been able to examine specimens.

Comments. Moganniini was synonymized with Cicadatrini by Lee & Hill (2010), but Boulard (2013) listed the group at subtribe level in Cicadini. Lee (2014) synonymized *Nipponosemia* with *Vagitanus* and moved *Chloropsalta* to Cicadatrini from Gaeanini; Lee also moved *Bijaurana* to Cicadatrini. Wang *et al.* (2017) placed *Cicadalna* Boulard as a junior synonym of *Emathia* Stål, simultaneously transferring it from the Cicadini to the Cicadatrini.

Tribe Cicadettini Buckton, 1890

Type genus. *Cicadetta* Kolenati, 1857 (type species *Cicada montana* Scopoli, 1772).

Included genera. *Adelia* Moulds, 2012; *Aestuansella* Boulard, 1981; *Amphipsalta* Fleming, 1969; *Atrapsalta* Owen & Moulds, 2016; *Auscala* Moulds, 2012; *Auta* Distant, 1897; *Berberigetta* Costa, Nunes, Marabuto, Mendes & Simões, 2017; *Birrima* Distant, 1906; *Bispinalta* Delorme, 2017; *Buyisa* Distant, 1907; *Caledopsalta* Delorme, 2017; *Caliginopsalta* Ewart, 2005; *Chelapsalta* Moulds, 2012; *Cicadetta* Kolenati, 1857; *Cicadettana* Marshall & Hill, 2017; *Clinata* Moulds, 2012; *Clinopsalta* Moulds, 2012; *Crotopsalta* Ewart, 2005; *Curvicicada* Chou & Lu, 1997; *Diemeniana* Distant, 1906; *Dimissalna* Boulard, 2007; *Dipsopsalta* Moulds, 2012; *Drymopsalta* Ewart, 2005; *Erempsalta* Moulds, 2012; *Euboeana* Gogala, Trilar & Drosopoulos, 2011; *Euryphara* Horváth, 1912; *Ewartia* Moulds, 2012; *Falcatpsalta* Owen & Moulds, 2016; *Fijipsalta* Duffels, 1988; *Froggattoides* Distant, 1910; *Gagatopsalta* Ewart, 2005; *Galanga* Moulds, 2012; *Gelidea* Moulds, 2012; *Germalna* Delorme; *Ggomapsalta* Lee, 2009; *Graminitigrina* Ewart & Marques, 2008; *Graptotettix* Stål, 1866; *Gudanga* Distant, 1905; *Haemopsalta* Owen & Moulds, 2016; *Heliopsalta* Moulds, 2012; *Hilaphura* Webb, 1979; *Huechys* Amyot & Audinet-Serville, 1843; *Kanakia* Distant, 1892; *Kikihia* Dugdale, 1972; *Kobonga* Distant, 1906; *Kosemia* Matsumura, 1927; *Limnopsalta* Moulds, 2012; *Linguacicada* Chou & Lu, 1997; *Maoricicada* Dugdale, 1972; *Marteena* Moulds, 1986; *Melampsalta* Kolenati, 1857; *Melanesiana* Delorme, 2017; *Mouia* Distant, 1920; *Mugadina* Moulds, 2012; *Murmurillana* Delorme, 2016; *Myersalna* Boulard, 1988; *Myopsalta* Moulds, 2012; *Nanopsalta* Moulds, 2012; *Neopunia* Moulds, 2012; *Nigripsaltria* Boer, 1999; *Noongara* Moulds, 2012; *Notopsalta* Dugdale, 1972; *Oligoglena* Horvath, 1912; *Pakidetta* Sanborn & Ahmed, 2017; *Palapsalta* Moulds, 2012; *Panialna* Delorme, 2016; *Paradina* Moulds, 2012; *Parvittya* Distant, 1905; *Paulaudalna* Delorme, 2017; *Pauropsalta* Goding & Froggatt, 1904; *Philipsalta* Lee, Marshall & Hill, 2016; *Physeema* Moulds, 2012; *Pinheya* Dlabola, 1963; *Pipilopsalta* Ewart, 2005; *Platypsalta* Moulds, 2012; *Plerapsalta* Moulds, 2012; *Popplepsalta* Owen & Moulds, 2016; *Poviliana* Boulard, 1997; *Pseudokanakia* Delorme, 2016; *Pseudotettigetta* Puissant, 2010; *Punia* Moulds, 2012; *Pyropsalta* Moulds, 2012; *Relictapsalta* Owen & Moulds, 2016; *Rhodopsalta* Dugdale, 1972; *Rouxalna* Boulard, 1999; *Samaecicada* Popple & Emery, 2010; *Saticula* Stål, 1866; *Scieroptera* Stål, 1866; *Scolopita* Chou & Lei, 1997; *Simona* Moulds, 2012; *Stellenboschia* Distant, 1920; *Strepuntalna* Delorme, 2017; *Sylphoides* Moulds, 2012; *Takapsalta* Matsumura, 1927; *Taurella* Moulds, 2012; *Telmapsalta* Moulds, 2012; *Terepsalta* Moulds, 2012; *Tettigetta* Kolenati, 1857; *Tettigettacula* Puissant, 2010; *Tettigettalna* Puissant, 2010; *Tettigettula* Puissant, 2010; *Tibeta* Lei & Chou, 1997; *Toxala* Moulds, 2012; *Toxopeusella* Schmidt, 1926; *Tympanistalna* Boulard, 1982; *Ueana* Distant, 1905; *Urabunana* Distant, 1905; *Uradolichos* Moulds, 2012; *Vastarena* Delorme, 2016; *Xossarella* Boulard, 1980; *Yoyetta* Moulds, 2012.

Diagnosis. The tribe is defined by having thecal pseudoparameres while other notable features are timbals that only rarely extend below the level of the wing bases and flat upper pygofer lobes (Moulds, 2005). Male genitalia of the type are illustrated in Moulds (2012).

Distribution. All regions except the Neotropics. One species of uncertain status is doubtfully reported from Suriname (*Cicadetta surinamensis* Kirkaldy, 1909).

Comments. This is the first complete assignment of the genera in this large tribe following the molecular analysis of Marshall *et al*. (2016). *Ueana* (see clade 13, Fig. 4) as well as *Kanakia*, *Panialna*, *Pseudokanakia* and *Vastarena* are transferred from Taphurini to Cicadettini because they possess the diagnostic thecal pseudoparameres (Delorme 2016; Delorme *et al.* 2016; Delorme 2017). There are now 110 genera in Cicadettini.

The monotypic genus *Samaecicada* (not included in this study) has been previously considered a part of the Cicadettini although its attributes are not entirely compatible with that tribe (Popple & Emery 2010; Moulds 2012). Genetic evidence suggests that *Samaecicada* is part of a closely related sister-group to the main Cicadettini clade (Marshall *et al.* 2016). *Samaecicada* lacks two attributes found in other Cicadettini, thecal pseudoparameres and flat basal lobes, but in other respects has attributes typical of the Cicadettini including complete fusion of forewing veins M and CuA on meeting the basal cell, claw-like claspers, a substantially reduced uncus and male opercula that have the lateral margin substantially raised above the level of the tympanal cavity. We leave *Samaecicada* in the Cicadettini pending our further study of allied species not yet described.

The authorship of Cicadettini dates from Buckton (1890), and not Buckton (1889), *contra* Moulds (2005) and Boulard (1988, 1998), because no new family group taxon is given in Buckton (1889), whereas "Cicadetta is explicitly named at sub-family level in Buckton (1890). The name is corrected to Cicadettinae following Articles 11.7.1.3 and 11.7.2.

Lee *et al*. (2016) placed Huechysini Distant as a junior synonym of Cicadettini. *Mezammira* Fieber, 1876 was recently resurrected by Gogala *et al.* (2017) with type species *Tibicen flaveolus* Brullé, 1832, but Dmitriev (2017) has shown this name to be a *nomen nudum* and that *Oligoglena* takes precedence.

Tribe Hemidictyini Distant, 1905

Type genus. *Hemidictya* Burmeister, 1835 (type species *Hemidictya frondosa* Burmeister, 1835).

Included genera. *Hemidictya* Burmeister, 1835; *Hovana* Distant, 1905.

Diagnosis. Distant's (1905e) original description is broad and includes many disparate genera that have since been transferred.

Distribution. Neotropics, Afrotropics (Madagascar).

Comments. This tribe was not sampled in this study.

Tribe Katoini Moulds & Marshall, n. tribe

Type genus. *Katoa* Ouchi, 1938 (type species *Katoa tenmokuensis* Ouchi, 1938).

Included genera. *Katoa* Ouchi, 1938.

Diagnosis. Head with supra-antennal plates meeting eyes. Postclypeus shape in transverse cross-section rounded; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margins weakly ampliate; lateral tooth absent. Forewing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is longest. Hindwing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking large inner protuberances. Meracanthus tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, partly covering tympanal cavity. Male abdominal tergites with sides straight in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below level of wing bases; timbal covers absent. Pygofer (Fig. 12) with upper lobe present, thickened; basal lobe small; dorsal beak absent. Uncus absent. Claspers short, usually separated. Aedeagus with theca recurved basally through less than 90º, otherwise straight or gently curved; conjunctival claws absent but theca usually with distal spine-like appendages; and ventral rib of basal plate rod-like, suspended with attachment only at ends.

Distinguishing features. Katoini **n. tribe** are distinguished from all other tribes in having, in combination, a narrow head so that the supra-antennal plates meet the eyes, male genitalia with no uncus, no dorsal beak, very small claspers, and no pseudoparameres, and a basal plate with the ventral rib attached only at its ends.

Distribution. China, Indomalaya.

Comments. The status of this tribe is supported by its deep origins within the Cicadettinae in the molecular analysis (see clade 5, Fig. 4) and by divergent morphology. Lee (2012a) placed *Katoa* in the Cicadettini and noted the presence of claspers and thecal pseudoparameres. We have examined the male genitalia of *K. taibaiensis* Lei & Chou and a small undetermined species, but we could find no trace of pseudoparameres, structures that are definitive for the Cicadettini. Nor are pseudoparameres evident in the genitalia figures in Chou *et al.* (1997) for *K. neokanagana*, (Liu), *K. paucispina* Lei & Chou, *K. chlorotica* Chou & Lu, and *K. paura* Chou & Lu. We were unable to examine the genitalia of the type species, *K. tenmokuensis* Ouchi, but as its facies is consistent with other species in the genus it is reasonable to assume its genitalia will also be similar. Lee (2012a) does not say which species he found pseudoparameres in so we cannot verify this observation.

Tribe Lamotialnini Boulard, 1976

Tryellina Moulds, 2005. **n. syn.**

Type genus. *Lamotialna* Boulard, 1976 (type species *Lamotialna condamini* Boulard, 1976).

Included genera. *Abricta* Stål, 1866; *Abroma* Stål, 1866; *Aleeta* Moulds, 2003; *Allobroma* Duffels, 2011; *Chrysolasia* Moulds, 2003; *Hylora* Boulard, 1971; *Lamotialna* Boulard, 1976; *Lemuriana* Distant, 1905; *Magicicada* Davis, 1925; *Monomatapa* Distant, 1879; *Musimoia* China, 1929; *Neomuda* Distant, 1920; *Oudeboschia* Distant, 1920; *Panka* Distant, 1905; *Sundabroma* Duffels, 2011; *Trismarcha* Karsch, 1891; *Tryella* Moulds, 2003; *Unduncus* Duffels, 2011; *Viettealna* Boulard, 1980.

Hylora, *Musimoia*, *Oudeboschia*, *Panka*, *Unduncus* and *Viettealna* may be incorrectly included here as it was not possible to examine specimens.

Diagnosis. Head with distance between supra-antennal plate and eye about equal to length of antennal plate. Postclypeus shape in transverse cross-section rounded; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margins confluent with adjoining pronotal sclerites; lateral tooth absent (except in *Magicicada*). Forewing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is shortest. Hindwing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, partly or completely covering tympanal cavity. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites either rounded to ventral surface or reflexed without an inward V-shaped kink. Timbals extended below level of wing bases; timbal covers absent. Pygofer with upper lobe present, flat, sometimes ill-defined; basal lobe moderately developed; dorsal beak a part of chitinized pygofer. Uncus absent. Claspers large, dominating the whole 10th abdominal segment, often widely separated. Aedeagus with theca recurved basally through some 90-140°; conjunctival claws present; ventral rib of basal plate rod-like, suspended with attachment only at ends. Male reproductive system with accessory glands long in *Aleeta*, otherwise unknown. Female reproductive system with accessory glands of common oviduct long in *Aleeta*, otherwise unknown.

Distinguishing features. The tribe can be defined by having aedeagal conjunctival claws. Other notable features are the lack of a developed uncus and the ventral rib on the underside of the basal plate which is rod-like and suspended with attachments only at ends, the claspers that are usually widely spaced, and the male timbals that extend below the level of the wing bases.

Distribution. Global except South America.

Comments. The five-gene tree places the Lamotialnini within a group of genera previously representing the subtribe Tryellina Moulds, 2005 **n. syn.** (in the tribe Taphurini as originally proposed by Boulard)—see clade 14, Fig. 4. Because Lamotialnini has priority, Tryellina is here synonymized. *Chrysolasia* was left out of Tryellina when the subtribe was proposed, but it is included here with Lamotialnini because of the diagnostic conjunctival claws (Moulds, 2003). *Lemuriana* is now included for the same reason (see Duffels, 2011).

Boulard (1976b) originally placed the Lamotialnini in his subfamily Platypediinae. Then Boulard (1986a) abandoned the family Platypediidae (and thus the Platypediinae) and transferred the Lamotialnini into the then family Tibicinidae. Later Boulard (1993, 2002) reduced the Lamotialnini to subtribal rank in the tribe Taphurini, subfamily Tibicininae. Moulds (2005) reinstated the tribe Lamotialnini, retaining it in the subfamily Tibicininae, but renamed the subfamily Cicadettinae. However, Sanborn (2013) in his world catalogue inadvertently placed the Lamotialnini in the new meaning of the Tibicininae, not the Tibicininae intended by Boulard (1986a) and Moulds (2005) that was renamed the Cicadettinae. A similar error occurred when Sanborn placed the Ydiellini in the current Tibicininae, rather than the Cicadettinae (see also Ruschel 2015). Moulds (2005) showed that the type genus of the then Tibicininae (now Cicadettinae) actually belonged to a small group of genera very different from the speciose Cicadettinae and, to avoid confusion for this new concept of the Tibicininae, proposed replacement of the name by its junior synonym Tettigadinae, but the idea failed to gain universal acceptance, including by Sanborn, and remains a point of confusion.

Tribe Nelcyndanini Moulds & Marshall, n. tribe

Type genus. *Nelcyndana* Distant, 1906 (type species *Tibicen tener* Stål, 1870).

Included genera. *Nelcyndana* Distant, 1906.

Diagnosis. Head with supra-antennal plates meeting eyes. Postclypeus shape in transverse cross-section rounded; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margins weakly ampliate; lateral tooth absent. Forewing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal and proximal portions about equal. Hindwing anal lobe narrow with vein 3A short, curved at distal end and separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Meracanthus tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, partly covering tympanal cavity. Male abdominal tergites with sides curved in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below level of wing bases; timbal covers absent. Pygofer (Fig. 11) with basal lobe large, positioned on distal half of pygofer, well beyond midlength; upper lobe very small, not sclerotized, superimposed over basal lobe; dorsal beak present. Uncus absent. Claspers small, basally bulbous, distally slender. Aedeagus with theca recurved basally through some 180°, otherwise straight or gently curved; without pseudoparameres; conjunctival claws absent; and ventral rib of basal plate rod-like, suspended with attachment only at ends.

Distinguishing features. The superimposing of the upper pygofer lobe over the basal lobe is unique. The uncus has apparently divided as it has in the closely allied tribes Taphurini and Carinetini, but the two halves have migrated laterally across segment 10 to locate at the lateral extremities of the segment thus appearing as if an accessory to the claspers. The Nelcyndanini differ from the Taphurini and Carinetini in not having an ornamented basal lobe.

Distribution. South-East Asia, including the Philippines.

Comments. Duffels (2010) discussed the position of *Nelcyndana* and retained its earlier assignment to Taphurini. The need for this tribe is now apparent from its deep origins within the Cicadettinae in the molecular phylogeny (see clade 5, Fig. 4). Given that related tribes are scattered globally (Neotropical, Nearctic, Ethiopian, Palearctic and Oriental), it deserves further study.

Tribe Pagiphorini Moulds & Marshall, n. tribe

Type genus. *Pagiphora* Horváth, 1912 (type species *Tibicen annulata* Brullé, 1832).

Included genera. *Pagiphora* Horváth, 1912.

Diagnosis. Head with supra-antennal plates meeting eyes. Postclypeus shape in transverse cross-section rounded; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margins weakly ampliate; lateral tooth absent. Forewing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for only part of its length, much diverged distally; vein CuA_1 divided by crossvein at about midlength. Hindwing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance.

Meracanthus tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, partly covering tympanal cavity. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites rounded to ventral surface, without an inward V-shaped kink. Timbals extended below level of wing bases; timbal covers absent. Pygofer (Fig. 11) with upper lobe present, positioned on distal half of pygofer, well beyond midlength; basal lobe small, fused with pygofer margin; dorsal beak present. Uncus absent. Claspers short. Aedeagus with theca recurved basally through some 140º, otherwise straight or gently curved; without appendages (pseudoparameres absent); conjunctival claws absent; and ventral rib of basal plate rod-like, suspended with attachment only at ends.

Distinguishing features. The Pagiphorini **n. tribe** are distinguished from all other tribes in having, in combination, vein RA_1 distally much diverged from subcosta (Sc); male abdomen rounded in cross-section so that epipleurites are rounded to ventral surface rather than reflexed; pygofer with upper lobe present, positioned on distal half of pygofer, well beyond midlength; and aedeagus with theca recurved basally through some 140º.

Distribution. Western Palearctic.

Comments. *Pagiphora* was previously included within the tribe Cicadettini (Metcalf, 1963), and this placement has never been questioned. However, the molecular results (see clade 5, Fig. 4) and absence of pseudoparameres show that *Pagiphora* does not belong with the Cicadettini (clade 13).

Tribe Parnisini Distant, 1905

Type genus. *Parnisa* Stål, 1862 (type species *Cicada proponens* Walker, 1858).

Included genera. *Abagazara* Distant, 1905; *Acyroneura* Torres, 1958; *Adeniana* Distant, 1905; *Arcystasia* Distant, 1882; *Calopsaltria* Stål, 1861; *Calyria* Stål, 1862; *Crassisternalna* Boulard, 1980; *Derotettix* Berg, 1882; *Henicotettix* Stål, 1858; *Jafuna* Distant, 1912; *Kageralna* Boulard, 2012; *Koranna* Distant, 1905; *Luangwana* Distant, 1914; *Lycurgus* China, 1925; *Malgotilia* Boulard, 1980; *Mapondera* Distant, 1905; *Masupha* Distant, 1892; *Parnisa* Stål, 1862; *Prunasis* Stål, 1862; *Psilotympana* Stål, 1861; *Rhinopsalta* Melichar, 1908; *Taipinga* Distant, 1905; *Zouga* Distant, 1906.

Diagnosis and distinguishing features. A summary diagnosis was provided by Moulds (2005). The genitalia are illustrated here in Fig. 12.

Distribution. Neotropics, Palearctic, Afrotropics, Madagascar.

Comments. Of the genera in this tribe, we have been able to study only *Parnisa* and *Calyria* (although not the type species of *Calyria*). We leave the tribe unchanged with one exception: *Quintilia* is transferred to the subfamily Tettigomyiinae **n. stat.** following the results from the five-gene tree and confirmation of diagnostic morphological features. The extensive distribution of the tribe suggests that further study is needed.

Tribe Pictilini Moulds & Hill, n. tribe

Type genus. *Pictila* Moulds, 2012 (type species *Tibicen occidentalis* Goding & Froggatt, 1904).

Included genera. *Chrysocicada* Boulard, 1989; *Pictila* Moulds, 2012.

Diagnosis. Head including eyes as wide as lateral margins of pronotum and almost as wide as lateral angles but with supra-antennal plates meeting or nearly meeting eyes. Postclypeus shape in transverse cross-section rounded; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margins confluent with adjoining pronotal sclerites; lateral tooth absent. Forewing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is longest. Hindwing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, partly covering tympanal cavity but extending distally beyond timbal cavity. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals not extended below level of wing bases; timbal covers absent. Pygofer (Fig. 11) with upper lobe present, thickened, positioned on distal half of pygofer, well beyond mid length; basal lobe moderately developed; dorsal beak absent or present as a part of chitinized pygofer. Uncus absent. Claspers large, dominating the whole 10th abdominal segment. Aedeagus with theca recurved basally through some 140°, otherwise straight or gently curved; without appendages; ventral rib of basal plate rod-like, suspended with attachment only at ends.

Distinguishing features. Distinguished from all other tribes by having, in combination, a head that is almost as wide as the lateral angles of pronotal collar but with supra-antennal plates meeting or nearly meeting the eyes, no timbal covers, the male pygofer with the basal lobe positioned on distal half of pygofer well beyond mid length, and the basal plate of the aedeagus with the ventral rib rod-like, suspended with attachment only at ends.

Distribution. Australia.

Comments. Two undescribed Australian species, probably different genera, appear likely to belong to this tribe, as shown in Marshall *et al.* (2016).

Tribe Prasiini Matsumura, 1917

Type genus. *Prasia* Stål, 1863 (type species *P. faticina* Stål, 1863).

Included genera. *Arfaka* Distant, 1905; *Bafutalna* Boulard, 1993; *Iruana* Distant, 1905; *Jacatra* Distant, 1905; *Lembeja* Distant, 1892; *Mariekea* Jong & Boer, 2004; *Murphyalna* Boulard, 2012; *Prasia* Stål, 1863; *Sapantanga* Distant, 1905.

Diagnosis. A diagnosis of Asian/Australian taxa based on Boer (1995) was provided by Moulds (2005), who considered the inclusion of African genera here as tentative.

Distribution. Afrotropics, Australasia, Neotropics (*Sapatanga*).

Comments. Only *Lembeja* and *Lacetas* were treated in this study. Although we were unable to sample the type genus or species, genitalic illustrations of *Prasia faticima* Stål in Jong (1985) clearly show the claspers that are diagnostic of the Cicadettinae, so there is no question of the subfamily placement.

Lacetas is here transferred to the tribe Tettigomyiini, which we have moved to the subfamily Tettigomyiinae **n. stat.** (see clade 6, Fig. 4), in accordance with morphological traits. Otherwise the tribe remains as given in Sanborn (2013).

Tribe Taphurini Distant, 1905

Type genus. *Taphura* Stål, 1862 (type species *Cicada misella* Stål, 1854).

Included genera. *Anopercalna* Boulard, 2008; *Chalumalna* Boulard, 1998; *Dorachosa* Distant, 1892; *Dulderana* Distant, 1905; *Elachysoma* Torres, 1964; *Imbabura* Distant, 1911; *Malloryalna* Sanborn, 2016; *Prosotettix* Jacobi, 1907; *Psallodia* Uhler, 1903; *Taphura* Stål, 1862.

Diagnosis and distinguishing features. Of the genera included above we have only studied *Taphura*. The following attributes are highlighted as potentially defining the Taphurini based on *Taphura* and allied tribes (see also Sanborn 2017). The uncus is absent but in some species the anal tube is lobed laterally (Fig. 11); the claspers are long and slender; the theca is basally turned through some 90°; the upper pygofer lobes are very small and substantially unsclerotized; the basal lobe is large, flat and ornamented with one or more protrusions; the opercula curve towards the abdominal midline but are very small, narrow and remain widely separated and far from the distal margins of the tympanal cavities. As these attributes are based solely on *Taphura* they should be consider as a guide only in defining the Taphurini pending a comprehensive review of all Taphurini genera.

Distribution. Neotropics.

Comments. Taphurini has a long history as a repository for usually small-bodied genera of uncertain classification. Following the molecular phylogenetic results, most genera from the tribe Taphurini are being transferred to the tribes Cicadettini, Lamotialnini, Nelcyndanini **n. tribe**, and Pictilini **n. tribe** of the Cicadettinae (clade 5, Fig. 4). *Ligymolpa*, *Malagasia* and *Malgachialna* are transferred to the tribe Malagasiini **n. tribe** of the subfamily Tettigomyiinae **n. stat.** (see clade 7). *Selymbria* is transferred to the tribe Selymbriini **n. tribe** of the subfamily Tibicininae (clade 3). *Nosola* is transferred to the tribe Fidicinini of the subfamily Cicadinae (see clade 11). Additional genera remaining in the tribe may also be misplaced.

SUBFAMILY CICADINAE LATREILLE, 1802

Type genus. *Cicada* Linnaeus, 1758 (type species *C. orni* Linnaeus, 1758).

Included tribes. Arenopsaltriini Moulds **n. tribe**; Burbungini Moulds, 2005; Cicadini Latreille, 1802; Cicadmalleuini Boulard & Puissant, 2013; Cosmopsaltriini Kato, 1932; Cryptotympanini Handlirsch, 1925; Cyclochilini Distant, 1904; Distantadini Orian, 1963; Dundubiini Distant, 1905; Durangonini Moulds & Marshall **n. tribe**; Fidicinini Distant, 1905; Gaeanini Distant, 1905; Jassopsaltriini Moulds, 2005; Lahugadini Distant, 1905; Leptopsaltriini Moulton, 1923; Macrotristriini Moulds **n. tribe**; Oncotympanini Ishihara, 1961; Orapini Boulard, 1985; Platypleurini Schmidt, 1918; Plautillini Distant, 1905; Polyneurini Amyot & Audinet-Serville, 1843; Psaltodini Moulds **n. tribe**; Psithyristriini Distant, 1905; Sinosenini Boulard, 1975; Sonatini Lee, 2010; Talcopsaltriini Moulds, 2008; Tamasini Moulds, 2005; Thophini Distant, 1904; Tosenini Amyot & Audinet-Serville, 1843; Zammarini Distant, 1905.

Diagnosis (modified from Moulds, 2005). Metanotum entirely concealed at dorsal midline. Forewing veins CuP and 1A fused in part. Hindwing veins RP and M fused at their bases. Male opercula not strongly S-shaped and not with lateral margins deeply concave. Abdominal timbal covers present in most genera. Pygofer with distal shoulder well developed, often the most distal part of pygofer and either broad and rounded or distally extended into a pointed lobe; pygofer upper lobe either absent or present. Uncus of moderate length and retractable within pygofer. Claspers absent or present (some Dundubiini), if present then spined apically. Aedeagus without ventrobasal pocket; aedeagus restrained before or below uncus. Apical part of theca without leaf-like lateral lobes.

Distinguishing features (Table 4). The following attributes define the Cicadinae: metanotum concealed at dorsal midline; male abdominal timbal covers present but lost in a few genera; male pygofer with distal shoulder well developed, often the most distal part of pygofer, either broad and rounded or distally extended into a pointed lobe; uncus of moderate length and retractable within pygofer.

Distribution. Global.

Comments. The previously held concept of the Cicadinae (Moulds 2005) remains unchanged (see clade 4, Fig. 4). Tacuini **n. syn.** is synonymized with Cryptotympanini. *Karenia* and its tribe Sinosenini are transferred to Cicadinae from Cicadettinae. Cicadatrini is transferred from Cicadinae to Cicadettinae. *Nosola* and *Durangona* are transferred from Cicadettinae to Fidicinini and Durangonini **n. tribe**, respectively, both in Cicadinae. Hamzini Distant, 1905 is treated here as a junior synonym of Platypleurini pending Case 3761 which is before the ICZN (see Comments under Tribe Platypleurini).

Tribe Arenopsaltriini Moulds, n. tribe

Type genus. *Arenopsaltria* Ashton, 1921 (type species *Fidicina fullo* Walker, 1850).

Included genera. *Arenopsaltria* Ashton, 1921; *Henicopsaltria* Stål, 1866.

Diagnosis. Head including eyes with vertex laterally elongate so that the distance between the supra-antennal plate and eye is much longer than the length of the supra-antennal plate. Postclypeus shape in transverse cross-section rounded. Pronotal collar with lateral margin moderately ampliate, at dorsal midline moderately broad, about as wide as lateral margin; weakly spined along much of margin. Forewing pterostigma present; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is shortest or dividing about equally. Hindwing with anal lobe broad and vein 3A curved, long, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Male opercula completely encapsulating meracanthus, completely covering tympanal cavity and overlapping. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 much enlarged, 2+3 equal to approximately half abdominal length; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below wing bases. Timbal covers flat; reaching metathorax, fully rounded dorsally, meeting opercula ventrally and tightly closing timbal cavity; lower margin extending anteriorly from or very near auditory capsule. Pygofer (Fig. 10) dorsal beak present in *Arenopsaltria* as a part of chitinized pygofer but absent in *Henicopsaltria*; upper lobe present in *Henicopsaltria*, absent in *Arenopsaltria*; basal lobe moderately to well developed. Uncus with median lobe large, dominant, distally bifurcate; aedeagus restrained by tubular encapsulation on ventral surface of uncus; accessory spines (claspers) absent; ventrally restraining aedeagus by a pair of ventral apophyses. Aedeagus with ventral rib completely fused with basal plate; theca with shaft recurved basally through 180° or more; without appendages. Male reproductive system with accessory glands short.

Distinguishing features. Arenopsaltriini **n. tribe** are distinguished from all other tribes in having, in combination, a head with an elongate vertex where the distance between the supra-antennal plate and eye is much longer than the length of the supra-antennal plate, male timbal covers that are flat, fully rounded dorsally, and tightly close the timbal cavity, a pronotal collar that is moderately ampliate with a weakly spined margin, and an uncus that ventrally restrains the aedeagus by tubular encapsulation on ventral surface of uncus.

Distribution. Australia.

Comments. See 'Comments on the Australian fauna' in the Discussion.

Tribe Burbungini Moulds, 2005

Type genus. *Burbunga* Distant, 1905 (type species *Tibicen gilmorei* Distant, 1882).

Included genera. *Burbunga* Distant, 1905.

Diagnosis and distinguishing features. As in Moulds (2005, 2012).

Distribution. Australia.

Tribe Cicadini Latreille, 1802

Type species. *Cicada* Linnaeus, 1758 (type species *Cicada orni* Linnaeus, 1758).

Included genera. *Cicada* Linnaeus, 1758.

Diagnosis and distinguishing features. Currently as in Lee & Hayashi (2003a) (as subtribe Cicadina).

Distribution. Primarily western Palearctic, although many neglected names from other regions remain under *Cicada*.

Comments. Wang *et al.* (2017) placed *Cicadalna* Boulard, 2006 as a junior synonym of *Emathia* Stål, 1866, simultaneously transferring it from the Cicadini to the Cicadatrini.

Lee & Hayashi (2003a,b; 2004), Lee (2008), Lee & Hill (2010) and Lee (2010) rearranged the Cicadini to eventually include seven subtribes (Cicadina, Cosmopsaltriina, Dundubiina, Leptopsaltriina, Oncotympanina, Psithyristriina and Tosenina). Soon after this, Lee & Emery (2013, 2014) reinstated the Leptopsaltriina as the Leptopsaltriini and the Dundubiina as the Dundubiini respectively. Then Lee (2014) gave the remaining subtribes that he had placed in the Cicadini tribal rank (in the discussion headed 'Taxonomic list of Cicadidae from Laos', p. 61). Several of these changes were made with little or no explanation, and recently Boulard (2013) presented a substantially different arrangement of the subtribes of Cicadini and Dundubiini, so further evaluation is needed (see also Wang *et al.* 2017). Table 5 illustrates the historical changes in Cicadini and related tribes (see clade 9, Fig. 4, and see also Ruschel 2015, p. 22).

Tribe Cicadmalleuini Boulard & Puissant, 2013

Type genus. *Cicadmalleus* Boulard & Puissant, 2013 (type species *Cicadmalleus micheli* Boulard & Puissant, 2013).

Included genera. *Cicadmalleus* Boulard & Puissant, 2013.

Diagnosis and distinguishing features. As in Boulard & Puissant (2013, 2016).

Distribution. Indomalaya (Thailand).

Comments. Specimens of *Cicadmalleus micheli*, the only species in this tribe, were not available for study.

Tribe Cosmopsaltriini Kato, 1932

Type genus. *Cosmopsaltria* Stål, 1866 (Type species *Cicada doryca* Boisduval, 1835).

Included genera. *Aceropyga* Duffels, 1977; *Brachylobopyga* Duffels, 1982; *Cosmopsaltria* Stål, 1866; *Diceropyga* Stål, 1870; *Dilobopyga* Duffels, 1977; *Inflatopyga* Duffels, 1997; *Moana* Myers, 1928; *Rhadinopyga* Duffels, 1985.

Diagnosis and distinguishing features. Duffels & Turner (2002) derived synapomorphies for the then subtribe Cosmopsaltriina from a cladistic analysis of all included genera.

Distribution. SE Asia, Australasia, Oceania

Comments. Lee (2014) elevated this from subtribe status without comment.

Tribe Cryptotympanini Handlirsch, 1925

Tacuini Distant, 1904: 300. **n. syn.**

Type genus. *Cryptotympana* Stål, 1861 (type species *Tettigonia pustulata* Fabricius, 1787 = *C. atrata* Fabricius, 1775).

Included genera. *Antankaria* Distant, 1904; *Auritibicen* Lee, 2015; *Cacama* Distant, 1904; *Chremistica* Stål, 1870; *Cornuplura* Davis, 1944; *Cryptotympana* Stål, 1861; *Hadoa* Moulds, 2015; *Hea* Distant, 1906; *Heteropsaltria* Jacobi, 1902; *Lyristes* Horváth, 1926; *Megatibicen* Sanborn & Heath, 2016; *Neotibicen* Hill & Moulds, 2015; *Nggeliana* Boulard, 1979; *Raiateana* Boulard, 1979; *Salvazana* Distant, 1913; *Tacua* Amyot & Audinet-Serville, 1843.

Diagnosis and distinguishing features. Handlirsch (1925) includes no description. Moulds (2005) provided a diagnosis but redescription may be necessary following the removal of many genera.

Distribution. Nearctic, Palearctic, Indomalaya, Oceania, Afrotropics.

Comments. The five-gene tree showed that several taxa currently classified as Cryptotympanini are unrelated to *Cryptotympana*. *Diceroprocta* and *Orialella* have attributes suggesting that they are best placed in Fidicinini, a position supported by the molecular tree, while *Arenopsaltria* and *Henicopsaltria* are transferred to Arenopsaltriini **n. tribe**, *Illyria* and *Macrotristria* are transferred to Macrotristriini **n. tribe**, and *Psaltoda, Anapsaltoda* and *Neopsaltoda* are transferred to Psaltodini **n. tribe.** *Antankaria*, *Hea*, *Heteropsaltria*, and *Nggeliana* were not included in this study and are left in Cryptotympanini. A Madagascar species tentatively identified as close to *matilei* Boulard is listed under *Chremistica* but unrelated to *Cryptotympana* in the five-gene tree. We were unable to examine sufficient material of this species to place it and so we leave these in Cryptotympanini.

Tacua (representing the monotypic Tacuini **n. syn.**) fell within the true Cryptotympanini clade on the five-gene tree (see clade 12, Fig. 4). Distant (1904) erected Tacuini based on the 'wings more or less opaquely coloured' and the rounded lateral margins of the pronotum, but colour is not a satisfactory tribal attribute and the shape of the pronotal collar is not definitive alone. *Tacua speciosa* Illiger has attributes clearly compatible with the Cryptotympanini, namely timbal covers that completely close the timbal cavity, opercula that pass the distal rim of the tympanal cavity, abdominal tergites 2 and 3 that are wider than segments 4-7, an aedeagus that is restrained by a pair of lobe-like ventral protrusions of the uncus, a theca that is basally turned through 180°, and a basal plate that is basally turned through 180° and with the apical lateral corners distally extended. Consequently the Tacuini are here synonymized.

A case has been resurrected before the Commission (case 239) to suppress *Tibicen* Latreille, 1825 and its derivatives (e.g. Tibicenini Van Duzee, 1916) so that priority is given to its junior synonym *Lyristes* (see Boulard & Puissant 2014; Marshall & Hill 2014; Sanborn 2014b); this has implications for the use of the name Cryptotympanini. We follow Puissant *et al.* (2015) and Marshall (2015) in using *Lyristes* and Cryptotympanini while the case is pending.

Tribe Cyclochilini Distant, 1904

Type genus. *Cyclochila* Amyot & Audinet-Serville, 1843 (type species: *Tettigonia australasiae* Donovan, 1805).

Included genera. *Cyclochila* Amyot & Audinet-Serville, 1843.

Diagnosis and distinguishing features. As in Moulds (2005).

Distribution. Australia.

Tribe Distantadini Orian, 1963

Type genus. *Distantada* Orian, 1963 (type species *Cicada thomasseti* China, 1924).

Included genera. *Distantada* Orian, 1963.

Diagnosis and distinguishing features. As in the generic description.

Distribution. Mascarene Islands

Comments. This tribe was not sampled in this study. Unpublished genetic data support its position within Cicadinae.

Tribe Dundubiini Distant, 1905

Type genus. *Dundubia* Amyot & Audinet-Serville, 1843 (type species *Tettigonia vaginata* Fabricius, 1787).

Included genera. *Aola* Distant, 1905; *Ayesha* Distant, 1905; *Biura* Lee & Sanborn, 2015; *Champaka* Distant, 1905; *Changa* Lee, 2016; *Cochleopsaltria* Pham & Constant, 2017; *Crassopsaltria* Boulard, 2008; *Dundubia* Amyot & Audinet-Serville, 1843; *Haphsa* Distant, 1905; *Kaphsa* Lee, 2012; *Khimbya* Distant, 1905; *Lethama* Distant, 1905; *Macrosemia* Kato, 1925; *Megapomponia* Boulard, 2005; *Meimuna* Distant, 1905; *Minilomia* Lee, 2013; *Orientopsaltria* Kato, 1944; *Platylomia* Stål, 1870; *Sinapsaltria* Kato, 1940; *Sinosemia* Matsumura, 1927; *Sinotympana* Lee, 2009; *Songga* Lee, 2016; *Unipomponia* Lee, 2014; *Zaphsa* Lee & Emery, 2014.

Distribution. Paleartic, Indomalaya, Australasia, Western Pacific

Diagnosis and distinguishing features. The tribe has been defined by Beuk (2002), Moulds (2005), and Lee & Emery (2014).

Comments. The molecular tree very weakly supports the current identity of the Dundubiini except for the inclusion of *Karenia*, tribe Sinosenini (see clade 9, Fig. 4). Morphological examination showed *Karenia* to be incompatible with Lee & Emery's (2014) diagnosis of the tribe Dundubiini and with the genera included there, especially in the development of the timbal covers and abdominal structure. However, the exact placement of *Karenia* here, along with the position of the Dundubiini taxa relative to Cosmopsaltriini and other groups within clade 9, is poorly supported due in part to our inability to amplify mitochondrial DNA without nuclear copies for *Karenia* (mtDNA is most informative for shallow relationships). We therefore recognize the possibility that *Karenia* is not exactly placed in the tree, and as *Karenia* is morphologically incompatible with other tribes we leave its tribal classification unchanged.

Lee & Emery (2014) moved *Lethama* to Dundubiini from Cosmopsaltriina without comment. Authorship of Dundubiini was attributed to Atkinson (1886) by Metcalf (1963), but the name "DUNDUBIA group" from that publication does not conform to Article 11.7.1.1 (ICZN, 1999) pertaining to the formation of family group names. (The same argument pertains to family group names based on *Tibicen*, which are not currently in use but have been attributed to Atkinson's "TIBICEN group".)

Tribe Durangonini Moulds & Marshall, n. tribe

Type genus. *Durangona* Distant, 1911 (type species *Durangona tigrina* Distant, 1911).

Included genera. *Durangona* Distant, 1911.

Diagnosis. Head with supra-antennal plate meeting eye. Postclypeus shape in transverse cross-section angular; postclypial ridges with transverse grooves. Pronotal collar with lateral margins confluent with adjoining pronotal sclerites; lateral tooth absent. Forewing veins C and R+Sc close together; vein RA_1 abutting subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is longest. Hindwing with anal lobe narrow and vein 3A straight, short, adjacent to wing margin. Foreleg femoral primary spine lying flat, prostrate. Hindcoxae lacking a large inner protuberance. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity, not meeting. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below wing bases. Timbal covers reduced to a narrow marginal ridge. Pygofer (Fig. 10) dorsal beak absent; upper lobe absent; basal lobe moderately to well developed. Uncus with median lobe broad, long, dominant, apically divided; restraining aedeagus by ventral expansion of the uncal wall; lacking a pair of ventral apophyses; accessory spines (claspers) absent. Aedeagus basal plate not depressed centrally and with ventral rib completely fused; theca meeting basal plate almost vertically, the shaft long and slender, pseudoparameres absent.-

Distinguishing features. Durangonini **n. tribe** are distinguished from all other tribes in having, in combination, postclypial ridges with transverse grooves; vein RA_1 abutting the subcosta (Sc) for its length; and male timbal covers reduced to a narrow marginal ridge.

Distribution. South America.

Comments. Molecular data support this as a deeply divergent lineage within Cicadinae. The Durangonini **n. tribe** differ from their weakly supported sister clade, the Platypleurini, in having timbal covers reduced to a narrow marginal ridge, a pronotal collar with lateral margins confluent with adjoining pronotal sclerites rather than strongly flanged, and a forewing margin that is not dilated.

Tribe Fidicinini Distant, 1905

Hyantiini Distant, 1905: 304. **n. syn.**

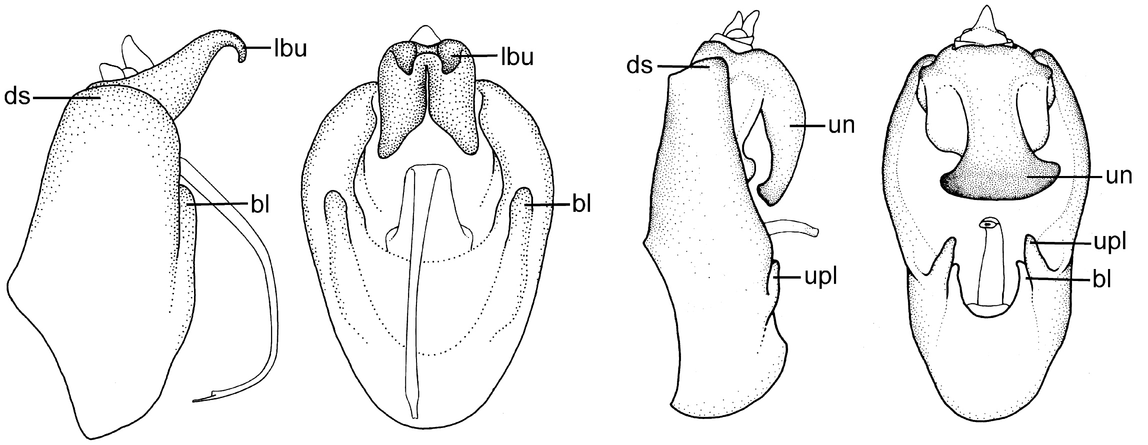
Type genus. *Fidicina* Amyot & Audinet-Serville, 1843 (type species *Tettigonia mannifera* Fabricius, 1803).

Included genera. *Ariasa* Distant, 1905; *Beameria* Davis, 1934; *Bergalna* Boulard & Martinelli, 1996; *Cracenpsaltria* Sanborn, 2016; *Diceroprocta* Stål, 1870; *Dorisiana* Metcalf, 1952; *Elassoneura* Torres, 1964; *Fidicina* Amyot & Audinet-Serville, 1843; *Fidicinoides* Boulard & Martinelli, 1996; *Guyalna* Boulard & Martinelli, 1996; *Hemisciera* Amyot & Audinet-Serville, 1843; *Hyantia* Stål, 1866; *Majeorona* Distant, 1905; *Mura* Distant, 1905; *Nosola* Stål, 1866; *Ollanta* Distant, 1905; *Orialella* Metcalf, 1952; *Pacarina* Distant, 1905; *Pompanonia* Boulard, 1982; *Prasinosoma* Torres, 1963; *Proarna* Stål, 1864; *Quesada* Distant, 1905; *Tympanoterpes* Stål, 1861.

Diagnosis. Head with supra-antennal plate shorter than, longer than, or equal to distance between supra-antennal plate and eye. Postclypeus shape in transverse cross-section bulbous, rounded or flattened. Pronotal collar with lateral margin moderately ampliate to confluent with adjoining pronotal sclerites, at dorsal midline moderately broad to wide but narrower than or equal to lateral angles. Forewing pterostigma present; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal part shortest or about equally divided; node at about mid-length of wing or a little closer to the base than apex. Hindwing with anal lobe narrow or tending narrow with vein 3A straight or gently curved for most of its length, separated from wide margin. Foreleg femoral primary spine erect or prostrate. Hindcoxae with large inner protuberance. Male opercula completely encapsulating meracanthus, covering tympanal cavity and either almost meeting, meeting, or overlapping medially. Male abdominal tergites with sides nearly straight to convex in cross-section; tergites 2 and 3 either a little larger or similar in size to at least one subsequent tergite; epipleurites without an inward V-shaped kink; epipleurites reflexed to ventral surface. Timbals extended below level of wing bases. Timbal covers flat or tending domed; reduced dorsally and either reaching or not reaching metathorax, the lower margin extending from or very near auditory capsule. Male genitalia (Fig. 10, see also Fig. 11) with pygofer dorsal beak present, barely developed, or absent; upper pygofer lobe absent; basal lobe moderately to well developed; distal shoulder well developed, sometimes hook-like. Uncus with median lobe large, dominant, with a pair of dorsal crests, in some genera fused and in *Beameria* much reduced; restraining aedeagus by a pair of ventral apophyses; accessory spines (claspers) absent. Aedeagus with ventral rib of basal plate completely fused; theca meeting basal plate almost vertically; basal plate deeply depressed centrally.

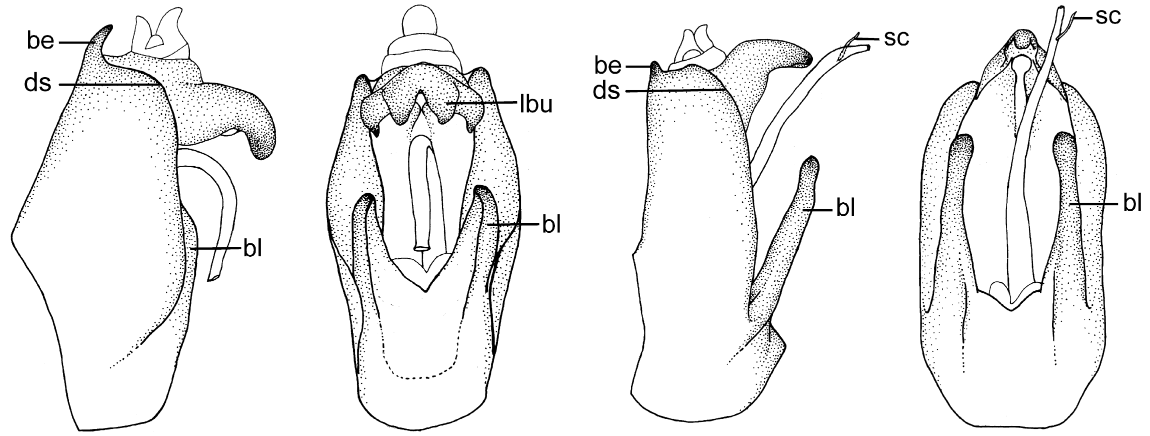
Distinguishing features. The Fidicinini differ from all other tribes in having, in combination, hindcoxae with a large inner protuberance, timbal covers reduced dorsally, the uncus with a dorsal crest and ventral apophyses restraining the aedeagus. Differs from the Zammarini in having a dorsal crest on the uncus and well developed pygofer distal shoulders. Also the basal lobe is never bifurcate in Fidicinini but usually so in Zammarini. The Fidicinini also lack the characteristic medially angulate lateral pronotal margin found in many Zammarini.

Distribution. Nearctic, Palearctic.



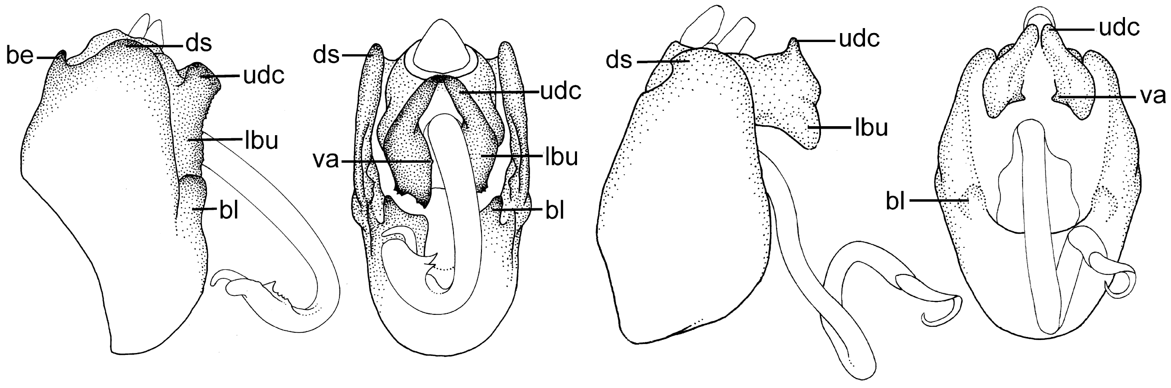
Durangona tigrina
Cicadinae: Durangonini

Psaltoda moerens
Cicadinae: Psaltodini



Arenopsaltria fullo
Cicadinae: Arenopsaltriini

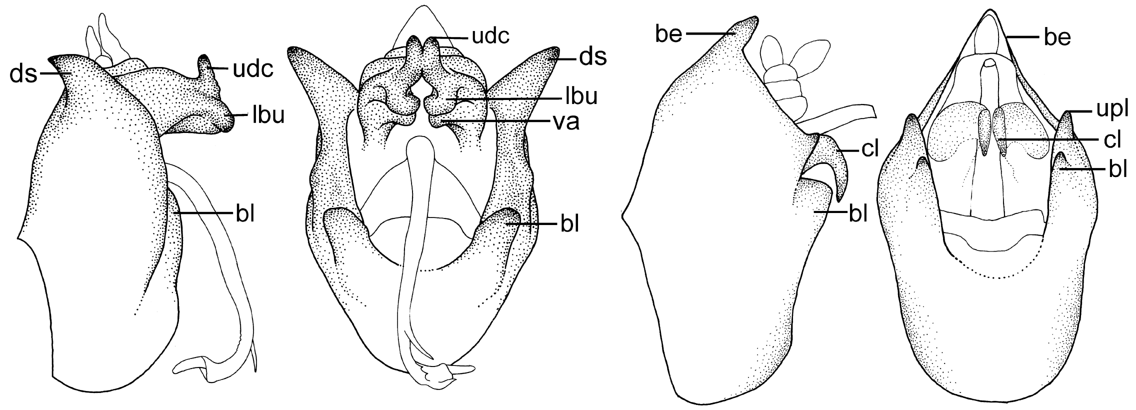
Macrotristria angularis
Cicadinae: Macrotristriini



Fidicina mannifera
Cicadinae: Fidicinini

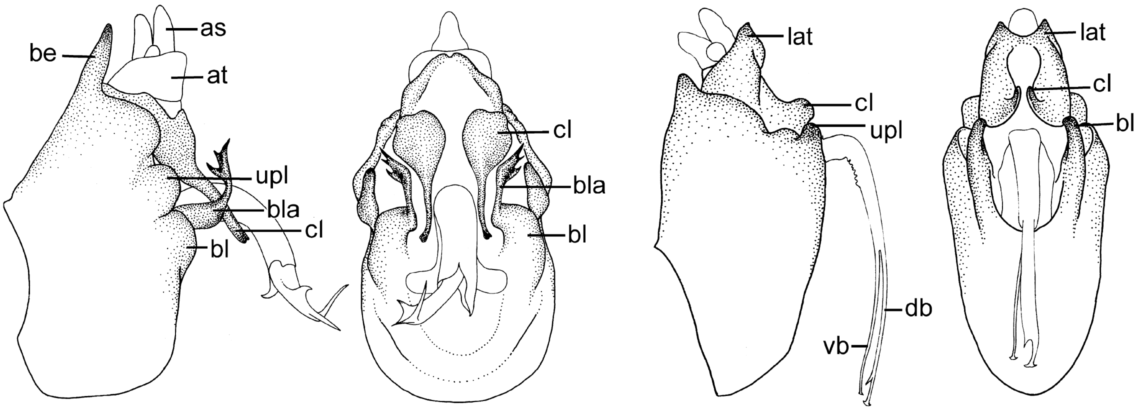
Nosola paradoxa
Cicadinae: Fidicinini

FIGURE 10. Male genitalia, lateral and ventral views, for type species of Durangonini **n. tribe**, Psaltodini **n. tribe**, Arenopsaltriini **n. tribe**, Macrotristriini **n. tribe**, Fidicinini, and for genus *Nosola* (transferred to Fidicinini), see upper part of Fig. 4. (*be*) dorsal beak; (*bl*) basal lobe; (*ds*) distal shoulder; (*lbu*) lateral branch of uncus; (*sc*) subapical cercus; (*udc*) uncal dorsal crest; (*un*) uncus; (*upl*) upper pygofer lobe; (*va*) ventral apophysis.



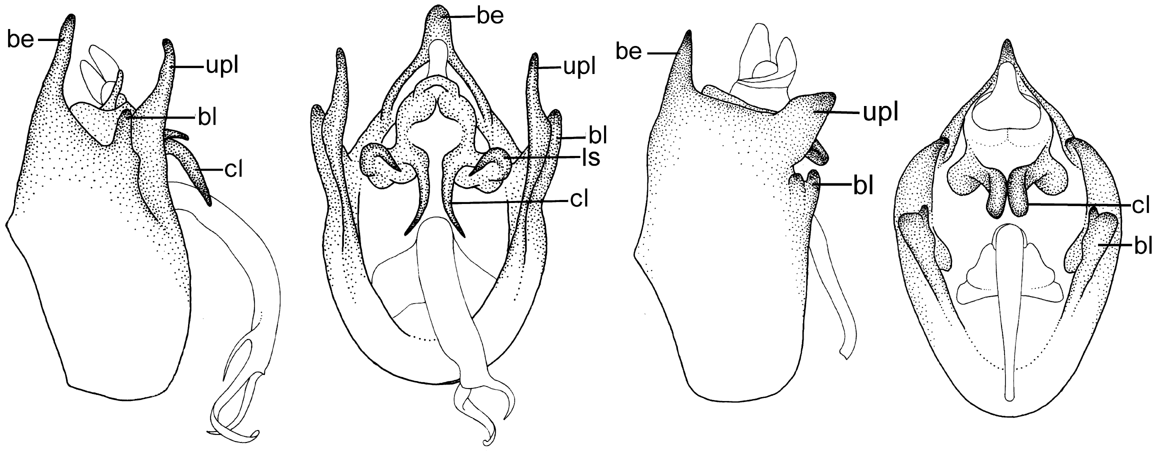
Diceroprocta alacris
Cicadinae: Fidicinini

Pictila occidentalis
Cicadettinae: Pictilini



Carineta diardi
Cicadettinae: Carinetini

Taphura misella
Cicadettinae: Taphurini



Nelcyndana tener
Cicadettinae: Nelcyndanini

Pagiphora annulata
Cicadettinae: Pagiphorini

FIGURE 11. Male genitalia, lateral and ventral views, for type species of *Diceroprocta* (transferred to Fidicinini), Pictilini **n. tribe**, Carinetini, Taphurini, Nelcyndanini **n. tribe**, and for Pagiphorini **n. tribe**, see central part of Fig. 4. (*as*) anal style; (*at*) anal tube; (*be*) dorsal beak; (*bl*) basal lobe; (*bla*) basal lobe appendage; (*cl*) clasper; (*db*) dorsal branch of aedeagus; (*ds*) distal shoulder; (*lat*) lateral branch of anal tube; (*lbu*) lateral branch of uncus; (*ls*) lateral spine; (*udc*) uncal dorsal crest; (*upl*) upper pygofer lobe; (*va*) ventral apophysis; (*vb*) ventral branch of aedeagus.

Comments. Although the timbal covers of all genera are reduced dorsally there is considerable variation in the extent of the forward development, barely so in *Beameria* to fully covering the timbal cavity in *Diceroprocta*, the latter never the less still reduced at its base. The dorsal crest is well developed in all genera except *Beameria* where it is much reduced but structurally evident at the base of the uncus. The considerably modified forewings of *Nosola*, where the forewing costa is strongly bowed and the node less than mid-length on the wing, are considered adaptations associated with sexual communication and like other such adaptions in other tribes not relevant at tribal rank.

Tribe Gaeanini Distant, 1905

Type genus. *Gaeana* Amyot & Audinet-Serville, 1843 (type species *Cicada maculata* Drury, 1773).

Included genera. *Ambragaeana* Chou & Yao, 1985; *Balinta* Distant, 1905; *Becquartina* Kato, 1940; *Callogaeana* Chou & Yao, 1985; *Gaeana* Amyot & Audinet-Serville, 1843; *Paratalainga* He, 1984; *Sulphogaeana* Chou & Yao, 1985; *Talainga* Distant, 1890; *Taona* Distant, 1909; *Trengganua* Moulton, 1923.

Distribution. Palearctic, Indomalaya.

Diagnosis. As modified by Lee (2014) from Distant (1905b).

Comments. Only *Gaeana maculata* was represented in the analysis, so the concept of the Gaeanini is unmodified here. Lee (2014) synonymized Talaingini Myers, 1929 with Gaeanini. Subtribe Becquartinina (tribe Gaeanini) was mentioned at tribal rank in Lee (2014, p. 61), but this appears to have been inadvertent because it was not among the list of Cicadini subtribes listed earlier in the paper as intended for tribe status. We leave Becquartinina at subtribal rank within Gaeanini (but see Boulard 2013, which lists Becquartinina, Gaeanina, and Talaingina as subtribes of Cicadini).

Tribe Jassopsaltriini Moulds, 2005

Type genus. *Jassopsaltria* Ashton, 1914 (type species *Jassopsaltria rufifacies* Ashton, 1914).

Included genera. *Jassopsaltria* Ashton, 1914.

Diagnosis and distinguishing features. As in Moulds (2005).

Distribution. Australia.

Tribe Lahugadini Distant, 1905

Type genus. *Lahugada* Distant, 1905 (type species *Pomponia dohertyi* Distant, 1891).

Included genera. *Lahugada* Distant, 1905.

Diagnosis and distinguishing features. Distant (1905a) distinguished this tribe from its close relatives in the Dundubiini by the non-dentate lateral margins of the pronotum, the largely covered tympana, the “tympanal flaps” broader than long, and the short and somewhat globose opercula that are wider than the abdominal margin (visible dorsally). No recent refinement of this concept is available.

Distribution. India (Assam and N. West Bengal).

Comments. None.

Tribe Leptopsaltriini Moulton, 1923

Type genus. *Leptopsaltria* Stål, 1866 (type species *Cicada tuberosa* Signoret, 1847).

Included genera. *Aetanna* Lee, 2014; *Cabecita* Lee, 2014; *Calcagninus* Distant, 1892; *Euterpnosia* Matsumura, 1917; *Formocicada* Lee & Hayashi, 2004; *Formosemia* Matsumura, 1917; *Galgoria* Lee, 2016; *Gudaba* Distant, 1906; *Inthaxara* Distant, 1913; *Leptopsaltria* Stål, 1866; *Leptosemia* Matsumura, 1917; *Manna* Lee & Emery, 2013; *Masamia* Lee & Emery, 2013; *Maua* Distant, 1905; *Minipomponia* Boulard, 2008;

Miniterpnosia Lee, 2013; *Mosaica* Lee & Emery, 2013; *Nabalua* Moulton, 1923; *Neocicada* Kato, 1932; *Neoterpnosia* Lee & Emery, 2014; *Paranosia* Lee, 2014; *Paratanna* Lee, 2012; *Purana* Distant, 1905; *Puranoides* Moulton, 1917; *Qurana* Lee, 2009; *Rustia* Stål, 1866; *Taiwanosemia* Matsumura, 1917; *Tanna* Distant, 1905; *Yezoterpnosia* Matsumura, 1917.

Diagnosis and distinguishing features. As in Lee & Emery (2013).

Distribution. Nearctic, Palearctic, Indomalaya.

Comments. This tribe was recently raised from subtribal rank by Lee & Emery (2013). The position of *Gaeana maculata* (Gaeanini), nested within Leptopsaltriini (see clade 9 in Fig. 4), renders the tribe paraphyletic, but because the genera in clade 9 have undergone extensive recent changes in classification we leave Leptopsaltriini unchanged pending more detailed analysis of the clade.

Tribe Macrotristriini Moulds, n. tribe

Type genus. *Macrotristria* Stål, 1861 (type species *Cicada angularis* Germar, 1834).

Included genera. *Illyria* Moulds, 1985; *Macrotristria* Stål, 1870.

Diagnosis. Head including eyes with vertex laterally elongate so that the supra-antennal plate is shorter than distance between supra-antennal plate and eye. Postclypeus shape in transverse cross-section rounded. Pronotal collar with lateral margin strongly ampliate, sloping in lateral view, evenly rounded in dorsal view, at dorsal midline broad, equal to about diameter of eye or greater or less so; lateral tooth absent. Forewing pterostigma present; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is shortest. Hindwing with anal lobe broad and vein 3A curved, long, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity, almost meeting, meeting or overlapping. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below wing bases. Timbal covers flat; reaching metathorax but reduced dorsally and not tightly closing the timbal cavity; lower margin extending anteriorly from or very near auditory capsule. Pygofer (Fig. 10) dorsal beak present and a part of chitinized pygofer; upper lobe absent; basal lobe moderately to well developed. Uncus with median lobe digitate or basically tubular, long, dominant; accessory spines (claspers) absent. Aedeagus with ventral rib completely fused with basal plate; theca with shaft recurved basally through 180° or more; pseudoparameres absent; subapical cerci present. Male reproductive system with accessory glands long.

Distinguishing features. Macrotristriini **n. tribe** are distinguished from all other tribes in having, in combination, a head with an elongate vertex where the distance between the eye and supra-antennal plate is much longer than the length of the supra-antennal plate, male timbal covers that are flat and reach the metathorax but are a little reduced dorsally, and a theca with one or two subapical cerci.

Distribution. Australia.

Comments. See 'Comments on the Australian fauna' in the Discussion.

Tribe Oncotympanini Ishihara, 1961

Type genus. *Oncotympana* Stål, 1870 (type species *Pomponia pallidiventris* Stål, 1870).

Included genera. *Mata* Distant, 1906; *Neoncotympana* Lee, 2010; *Oncotympana* Stål, 1870.

Diagnosis and distinguishing features. Lee (2010) stated that Oncotympanini can be distinguished from Cicadini and its other former subtribes by prominently globose male timbal covers.

Distribution. China, southeast Asia.

Comments. Lee (2010) reduced Oncotympanini to subtribe level and transferred it to Cicadini, then later returned the group to tribe status (Lee, 2014).

Tribe Orapini Boulard, 1985

Type genus. *Orapa* Distant, 1905 (type species *Pycna numa* Distant, 1904).

Included genera. *Orapa* Distant, 1905.

Diagnosis. As in Boulard (1985).

Distribution. Afrotropics.

Comments. This tribe was not sampled in this study.

Tribe Platypleurini Schmidt, 1918

Type genus. *Platypleura* Amyot & Audinet-Serville, 1843 (type species *Cicada stridula* L.).

Included genera. *Afzeliada* Boulard, 1973; *Albanycada* Villet, 1989; *Attenuella* Boulard, 1973; *Azanicada* Villet, 1989; *Brevisiana* Boulard, 1973; *Canualna* Boulard, 1985; *Capcicada* Villet, 1989; *Esada* Boulard, 1973; *Hainanosemia* Kato, 1927; *Hamza* Distant, 1904; *Ioba* Distant, 1904; *Kalabita* Moulton, 1923; *Karscheliana* Boulard, 1990; *Koma* Distant, 1904; *Kongota* Distant, 1904; *Muansa* Distant, 1904; *Munza* Distant, 1904; *Oxypleura* Amyot & Audinet-Serville, 1843; *Platypleura* Amyot & Audinet-Serville, 1843; *Pycna* Amyot & Audinet-Serville, 1843; *Sadaka* Distant, 1904; *Sechellalna* Boulard, 2010; *Severiana* Boulard, 1973; *Soudaniella* Boulard, 1973; *Strumosella* Boulard, 1973; *Strumoseura* Villet, 1999; *Suisha* Kato, 1928; *Tugelana* Distant, 1912; *Ugada* Distant, 1904; *Umjaba* Distant, 1904; *Yanga* Distant, 1904.

Diagnosis and distinguishing features. As summarized in Moulds (2005).

Distribution. Afrotropics, Palearctic, Indomalaya.

Comments. Lee (2014), following Price (2010), formally recognized the priority of Hamzini Distant, 1905 over Platypleurini. Case 3761 has been submitted to the ICZN, under Article 23.9.3 of the Code of Zoological Nomenclature (ICZN 1999), to maintain priority of Platypleurini (Marshall *et al.* 2018), and accordingly we maintain usage of the junior synonym (Art. 82.1). The type species of the tribe was not available for this study, and no modification to the concept is proposed.

Tribe Plautillini Distant, 1905

Type genus. *Plautilla* Stål, 1865 (type species *Plautilla stalagmoptera* Stål, 1865).

Included genera. *Plautilla* Stål, 1865.

Diagnosis and distinguishing features. As in Distant (1906).

Distribution. Neotropics.

Comments. This tribe was not examined in this study. In a doctoral dissertation, Goemans (2016) proposed that Plautillini may be synonymous with Zammarini.

Tribe Polyneurini Amyot & Audinet-Serville, 1843

Type genus. *Polyneura* Westwood, 1840 (type species *Polyneura ducalis* Westwood, 1840).

Included genera. *Angamiana* Distant, 1890; *Formotosena* Kato, 1925; *Graptopsaltria* Stål, 1866; *Polyneura* Westwood, 1840.

Diagnosis and distinguishing features. Amyot & Audinet-Serville's (1843) original concept included two unrelated genera (*Cystosoma*, *Hemidictya*) that have since been transferred, but no refined tribal description is available.

Distribution. Palearctic, Indomalaya.

Comments. Only *Graptopsaltria* was represented here.

Tribe Psaltodini Moulds, n. tribe

Type genus. *Psaltoda* Stål, 1861 (type species *Cicada moerens* Germar, 1834).

Included genera. *Anapsaltoda* Ashton, 1921; *Neopsaltoda* Distant, 1910; *Psaltoda* Stål, 1861.

Diagnosis. Head including eyes with vertex laterally elongate so that the supra-antennal plate is shorter than the distance between the supra-antennal plate and eye. Postclypeus shape in transverse cross-section rounded. Pronotal collar with lateral margin strongly ampliate, sloping in lateral view, evenly rounded in dorsal view; at dorsal midline broad, equal to about diameter of eye or greater; lateral tooth absent. Forewing pterostigma present; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein about equally or with proximal portion shortest. Hindwing with anal lobe broad and vein 3A curved, long, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity, overlapping. Male abdominal tergites flat in cross-section; tergites 2 and 3 much enlarged so that 2+3 accounts for half or more abdominal length; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below wing bases. Timbal covers flat; reaching metathorax, fully rounded dorsally and tightly closing the timbal cavity; lower margin extending anteriorly from or very near auditory capsule. Pygofer (Fig. 10) dorsal beak absent; upper lobe present; basal lobe moderately to well developed. Uncus with median lobe digitate with expanded apex, long, dominant; accessory spines (claspers) absent; restraining aedeagus by membrane prior to ventral surface of uncus. Aedeagus ventral rib completely fused with basal plate; theca with shaft recurved basally through 180° or more; pseudoparameres absent; subapical cerci absent. Male reproductive system with accessory glands short.

Distinguishing features. Psaltodini **n. tribe** are distinguished from all other tribes in having, in combination, a head with an elongate vertex where the distance between the eye and supra-antennal plate is much longer than the length of the supra-antennal plate, a very broad pronotal collar as wide as diameter of eye with its lateral margin strongly ampliate, sloping in lateral view, evenly rounded in dorsal view and without lateral teeth, male tergites 2 and 3 much enlarged so that 2+3 accounts for half or more abdominal length, and a male uncus that is spatulate.

Distribution. Australia.

Comments. See 'Comments on the Australian fauna' in the Discussion.

Tribe Psithyristriini Distant, 1905

Type genus. *Psithyristria* Stål, 1870 (type species *Psithyristria specularis* Stål, 1870).

Included genera. *Basa* Distant, 1905; *Kamalata* Distant, 1889; *Onomacritus* Distant, 1912; *Pomponia* Stål, 1866; *Psithyristria* Stål, 1870; *Semia* Matsumura, 1917; *Terpnosia* Distant, 1892.

Diagnosis and distinguishing features. As for Psithyristriina in Lee & Hill (2010).

Distribution. Philippines.

Comments. Lee & Hill (2010) synonymized Distant's original concept with tribe Cicadini and provided a new definition for their subtribe Psithyristriina, following molecular evidence. Lee (2014) returned Psithyristriini to tribe status without comment.

Tribe Sinosenini Boulard, 1975

Type genus. *Karenia* Distant, 1888 (type species *Karenia ravida* Distant, 1888).

Included genera. *Karenia* Distant, 1888.

Diagnosis and distinguishing features. As in Boulard (1975a).

Distribution. Asia, Indomalaya.

Comments. *Karenia*, and its tribe Sinosenini are moved to Cicadinae from Cicadettinae following the 5-gene tree and morphological evidence (see clade 9, Fig. 4) showing a well-developed (but divided) uncus, the absence of claspers, a well-developed distal shoulder, and partial development of timbal covers. Further, *Karenia* has the pygofer dorsal beak positioned on a membrane rather than being a part of the sclerotized pygofer, a synapomorphy for a group of tribes that include the Dundubiini (*sensu* Lee & Emery 2014), Cicadini (Moulds, 2005) and others.

Sinosenini had been synonymized with Carinetini (Duffels & van der Laan 1985) but was recognized by Wei *et al.* (2009) and Pham & Yang (2012). See also Comments under tribe Dundubiini.

Tribe Sonatini Lee, 2010

Type genus. *Hyalessa* China, 1925 (type species *Hyalessa ronshana* China, 1925).

Included genera. *Hyalessa* China, 1925.

Diagnosis and distinguishing features. As in Lee (2010).

Distribution. Palearctic, Indomalaya.

Comments. *Sonata* has been previously placed as a junior synonym of *Hyalessa* China, 1925, but its family-group name retains priority (Art. 40.1; ICZN 1999).

Tribe Talcopsaltriini Moulds, 2008

Type genus. *Talcopsaltria* Moulds, 2008 (type species *Talcopsaltria olivei* Moulds, 2008).

Included genera. *Talcopsaltria* Moulds, 2008.

Diagnosis and distinguishing features. As in Moulds (2008).

Distribution. Australia.

Tribe Tamasini Moulds, 2005

Type genus. *Tamasa* Distant, 1905 (type species *Cicada tristigma* Germar, 1834).

Included genera. *Parnkalla* Distant, 1905; *Parnquila* Moulds, 2012; *Tamasa* Distant, 1905.

Diagnosis and distinguishing features. As in Moulds (2005).

Distribution. Australia.

Tribe Thophini Distant, 1904

Type genus. *Thopha* Amyot & Audinet-Serville, 1843 (type species *Tettigonia saccata* Fabricius, 1803).

Included genera. *Arunta* Distant, 1904; *Thopha* Amyot & Audinet-Serville, 1843.

Diagnosis and distinguishing features. As in Moulds (2005).

Distribution. Australia.

Tribe Tosenini Amyot & Audinet-Serville, 1843

Type genus. *Tosena* Amyot & Audinet-Serville, 1843 (type species *Tettigonia fasciata* Fabricius, 1787).

Included genera. *Ayuthia* Distant, 1919; *Distantalna* Boulard, 2009; *Tosena* Amyot & Audinet-Serville, 1843.

Diagnosis and distinguishing features. As in Amyot & Audinet-Serville (1843).

Distribution. Palearctic, Indomalaya.

Comments. This tribal concept remains unchanged since none of the genera were represented in this study.

Tribe Zammarini Distant, 1905

Type genus. *Zammara* Amyot & Audinet-Serville, 1843 (type species *Tettigonia tympanum* Fabricius, 1803).

Included genera. *Borencona* Davis, 1928; *Chinaria* Davis, 1934; *Daza* Distant, 1905; *Juanaria* Distant, 1920; *Miranha* Distant, 1905; *Odopoea* Stål, 1861; *Onoralna* Boulard, 1996; *Orellana* Distant, 1905; *Procollina* Metcalf, 1952; *Uhleroides* Distant, 1912; *Zammara* Amyot & Audinet-Serville, 1843; *Zammaralna* Boulard & Sueur, 1996.

Diagnosis. Head with distance between supra-antennal plate and eye equal to or shorter than length of supra-antennal plate. Postclypeus shape in transverse cross-section rounded or flattened. Pronotal collar with lateral margin ampliate and often angular, at dorsal midline moderately broad to moderately wide and never narrower than lateral angles. Forewing pterostigma present; vein RA_1 aligned closely or diverging from subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal part shortest or about equally divided; node at about mid-length of wing, sometimes a little closer to the base than apex and sometimes a little further from base. Hindwing with anal lobe narrow with vein 3A short, gently curved for most of its length, separated from wide margin. Foreleg femoral primary spine erect or prostrate. Hindcoxae with large inner protuberance. Male opercula completely encapsulating meracanthus, covering tympanal cavity and almost meeting. Male abdominal tergites with sides nearly straight; tergites 2 and 3 either a little larger or similar in size to at least one subsequent tergite; epipleurites without an inward V-shaped kink; epipleurites reflexed to ventral surface. Timbals extended below level of wing bases. Timbal covers domed; reduced dorsally and either reaching or not reaching metathorax, the lower margin extending from or very near auditory capsule. Male genitalia with pygofer dorsal beak present; upper pygofer lobe absent; basal lobe moderately developed, bi-lobed or tending so; distal shoulder not well developed. Uncus either singularly lobed or bi-lobed, without a pair of dorsal crests; restraining aedeagus by a pair of ventral apophyses; accessory spines (claspers) absent. Aedeagus with ventral rib of basal plate completely fused; theca meeting basal plate almost vertically; basal plate deeply depressed centrally.

Distinguishing features. The Zammarini differ from all other tribes in having, in combination, hindcoxae with a large inner protuberance, timbal covers reduced dorsally, the uncus without a dorsal crest and ventral apophyses restraining the aedeagus. Differs from the Fidicinini in having no dorsal crest on the uncus and undeveloped pygofer distal shoulders. Also the basal lobe is never bifurcate in Fidicinini but usually so in Zammarini. The Zammarini also commonly have an ampliate pronotal lateral margin (reduced in *Uhleroides*) that is often medially angulate that is never found in the Fidicinini.

Distribution. Neotropics.

Comments. In a dissertation, Goemans (2016) used genetic and morphological data to show a close relationship between *Daza, Plautilla*, and *Zammara*, and proposed synonymization of Dazini, Plautillini, and Zammarini. Dazini was formally transferred to Zammarini by Sanborn (2018).

SUBFAMILY TETTIGOMYIINAE DISTANT, 1905, N. STAT.

Type genus. *Tettigomyia* Amyot & Audinet-Serville, 1843 (type species *T. vespiformis* Amyot & Audinet-Serville, 1843).

Included tribes. Lacetasini Moulds & Marshall **n. tribe**; Malagasiini Moulds & Marshall **n. tribe**; Tettigomyiini Distant, 1905; Ydiellini Boulard, 1973.

Diagnosis. Metanotum either exposed or concealed (in Lacetasini **n. tribe**) at dorsal midline. Forewing veins CuP and 1A fused in part. Hindwing veins RP and M fused at their bases. Abdominal timbal cavity lacking a timbal cover, or with a partial turned-back rim. Male opercula not strongly S-shaped and not with lateral margins deeply concave. Pygofer distal shoulder developed, often the most distal part of pygofer; pygofer upper lobe absent. Uncus long, directed distally, not retractable within pygofer; with a mid lateral flange but much reduced in *Tettigomyia.* Claspers absent. Aedeagus lacking a ventrobasal pocket; aedeagus restrained before or below uncus. Apical part of theca either simple or tending spatulate (modified in Malagasiini **n. tribe**), lacking leaf-like lateral lobes.

Distinguishing features (Table 4). The Tettigomyiinae **n. stat.** (see clades 6-8, Fig. 4) have a mid lateral flange on the uncus that may be an apomorphy for this subfamily; regardless they can be recognized by a combination of features. They have distinctive genitalia in common with the Tibicininae in their long, non-retractable uncus. However, the male opercula of Tettigomyiinae differ from those of the Tibicininae in not having a distinctive S-shape with their lateral margins deeply concave. The Tettigomyiinae also lack the ventrobasal pocket of the aedeagus found in Tibicininae, and the hindwing veins RP and M are fused in Tettigomyiinae but not in Tibicininae. The Tettigomyiinae differ from both the Cicadettinae and the Cicadinae in having a non-retractable uncus. The Tettigomyiinae differ from the Cicadettinae in lacking claspers.

Distribution. Afrotropics.

Comments. Tettigomyiini and Ydiellini are transferred to Tettigomyiinae **n. stat.** from the Cicadettinae. See also ‘Comments on the African fauna’ in the Discussion.

Tribe Lacetasini Moulds & Marshall, n. tribe

Type genus. *Lacetas* Karsch, 1890 (type *species Lacetas annulicornis* Karsch, 1890).

Included genera. *Lacetas* Karsch, 1890.

Diagnosis. Head including eyes very narrow, the supra-antennal plates compressed between postclypeus and eye. Postclypeus shape in transverse cross-section angular, in dorsal view about as long as head; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margins not ampliate, ill-defined; lateral tooth absent. Forewings opaque green; veins C and R+Sc wide apart; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is longest. Hindwing with anal lobe narrow with vein 3A tending straight, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Meracanthus long, gradually tapering to a point. Male opercula not completely encapsulating meracanthus, not covering tympanal cavity, not meeting. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below level of wing bases; timbal covers absent. Pygofer (Fig. 12) with upper lobe absent; distal shoulders developed but fused as one due to apical narrowing of the pygofer; basal lobe small, positioned beyond midlength; dorsal beak absent. Uncus long, undivided, not retractable within pygofer, restraining aedeagus by ventral encapsulation. Aedeagus with theca meeting basal plate near 90º, gently curved throughout its length, apically ornamented with a broad turned-back plate; lacking pseudoparameres; conjunctival claws absent; ventral rib of basal plate strongly keeled at about midlength.

Distinguishing features. The Lacetasini **n. tribe** differ from other tribes in the Tettigomyiinae **n. stat.** in having forewing veins C and R+Sc widely separated and in the pronounced fin-like keel on the basal plate. The tribe differs from all other tribes in having, in combination, forewing veins C and R+Sc widely separated, and a male uncus that is long, undivided, and not retractable within the pygofer.

Distribution. Africa.

Comments. None.

Tribe Malagasiini Moulds & Marshall, n. tribe

Type genus. *Malagasia* Distant, 1882 (type species *Malagasia inflata* Distant, 1882).

Included genera. *Ligymolpa* Karsch, 1890; *Malagasia* Distant, 1882; *Malgachialna* Boulard, 1980; *Nyara* Villet, 1999; *Quintilia* Stål, 1866.

Diagnosis. Head with distance between supra-antennal plate and eye about equal to length of antennal plate. Postclypeus in transverse cross-section rounded, in dorsal view short, much less than length of head; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar narrow, with lateral margins moderately ampliate; lateral tooth absent. Forewing pterostigma absent. Forewing veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein at about midlength or with distal portion longest. Hindwing with anal lobe narrow to wide with vein 3A tending straight, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Meracanthus long, gradually tapering to a point. Male opercula completely encapsulating meracanthus, covering tympanal cavity, not meeting. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites rounded to ventral surface, without an inward V-shaped kink. Timbals level with or extended below level of wing bases; timbal covers absent. Pygofer (Fig. 12) with upper lobe absent; distal shoulder well developed; basal lobe broad, flat, adhered to pygofer; dorsal beak present. Uncus long, undivided, not retractable within pygofer, restraining aedeagus by ventral encapsulation not extending to uncal apex. Aedeagus with theca meeting basal plate near vertically, apically tending spatulate; lacking pseudoparameres; conjunctival claws absent; ventral rib of basal plate fused along its length.

Distinguishing features. In the subfamily Tettigomyiinae **n. stat.**, the Malagasiini **n. tribe** differ from the Lacetasini **n. tribe** in having forewing veins C and R+Sc close together rather than widely separated; from the Tettigomyiini in having a dorsal beak and the aedeagus restrained by ventral encapsulation of the uncus that does not extend to the uncal apex, and from the Ydiellini in lacking its distinctive male genitalia where the uncus is large, very wide and duck-bill shaped and the aedeagus is ornamented with a large, wide apical 'cover' that shields a pair of very large, leaf-like lobes.

Distribution. Africa and Madagascar.

Comments. We were unable to study all African genera and others may belong here, especially some currently placed in the Tettigomyiini. See also 'Comments on the African fauna' under Discussion. *Nyara* Villet is transferred from Taphurini to Malagasiini **n. tribe** following genitalia illustrations in Villet (1999) and comments by Villet that the genus is allied to *Quintilia*.

Tribe Tettigomyiini Distant, 1905

Type genus. *Tettigomyia* Amyot & Audinet-Serville, 1843 (type species *T. vespiformis* Amyot & Audinet-Serville, 1843)

Included genera. *Bavea* Distant, 1905; *Gazuma* Distant, 1905; *Paectira* Karsch, 1890; *Spoerryana* Boulard, 1974; *Stagea* Villet, 1994; *Stagira* Stål, 1861; *Tettigomyia* Amyot & Audinet-Serville, 1843; *Xosopsaltria* Kirkaldy, 1904.

Diagnosis. Distant (1905e) described the Tettigomyiini as having a broad and short forewing, not scarcely longer than the body, sometimes scarcely longer than the abdomen, and an abdomen usually inflated ("always thickened"). Other notable features include a bulbous male abdomen but one that has the epipleurites reflexed to the ventral surface, a male pygofer (Fig. 12) with a flat rounded basal lobe adhered to the pygofer margin and no dorsal beak, the aedeagus restrained by ventral encapsulation of the uncus that reaches the apex of the uncus, and a theca that meets the basal plate vertically. Villet (1997) noted that a "bottle-necked" shape of the major rib of the timbal is found in *Bavea*, *Paectira*, *Stagea*, *Stagira*, *Tettigomyia*, and *Xosopsaltria*, and Villet (1994) listed additional characters linking some of these genera.

Distinguishing features. In the subfamily Tettigomyiinae **n. stat.** (clades 6-8, Fig. 4), the Tettigomyiini differ from the Lacetasini **n. tribe** in having the forewings hyaline instead of opaque green and forewing veins C and R+Sc close together rather than widely separated; from the Malagasiini **n. tribe** in having no dorsal beak and the aedeagus restrained by ventral encapsulation of the uncus that extends to the uncal apex; and from the Ydiellini in lacking its distinctive male genitalia in which the uncus is large, very wide and duck-bill shaped and the aedeagus is ornamented with a large, wide apical 'cover' that shields a pair of very large, leaf-like lobes.

Distribution. Africa and Madagascar

Comments. Villet (1993, 1997) noted the morphological similarities between *Stagira* and *Tettigomyia* and suggested that they may be phylogenetically allied.

Tribe Ydiellini Boulard, 1973

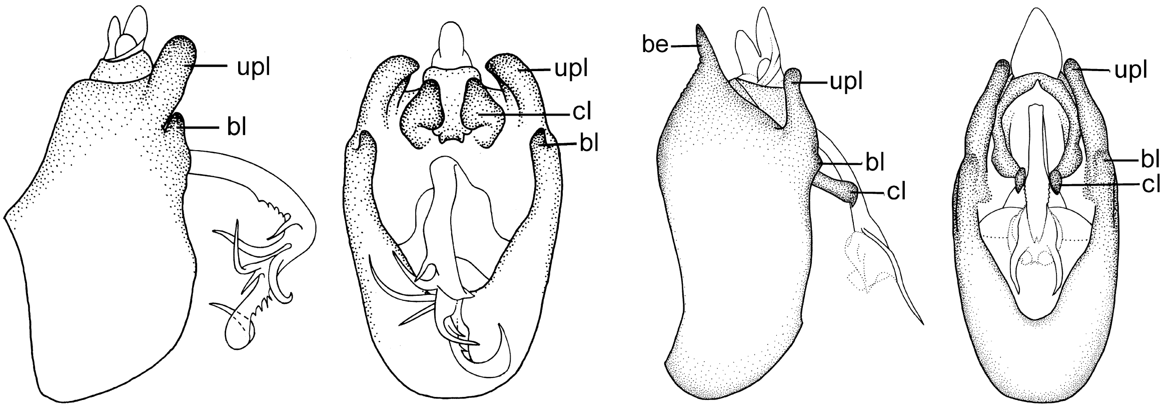
Type genus. *Maroboduus* Distant, 1920 (=*Ydiella* Boulard, 1973) (type species *Ydiella gilloni* Boulard, 1973).

Included genera. *Maroboduus* Distant, 1920; *Nablistes* Karsch, 1891.

Diagnosis and distinguishing features. Boulard (1973) distinguished the tribe Ydiellini for *Maroboduus* based on the presence of thickened forewing veins adjoining the apical and ulnar cells of the forewing (the ulnar cells being enlarged) and a row of teeth on the hindwing costa, both of these characters apparently being involved in the generation of sound. The five gene tree shows *Nablistes* to be closely related to *Maroboduus* (clade 8, Fig. 4), so it is here transferred from Chlorocystini. While *Nablistes* lacks Boulard's diagnostic attributes associated with sound production it shares with *Maroboduus* a remarkable and very distinctive male genitalia; the uncus is large, very wide and duck-bill shaped and the aedeagus of both is similarly and extensively ornamented with a large, wide apical 'cover' that is spined basally on either side, which in turn shields a pair of very large, leaf-like lobes.

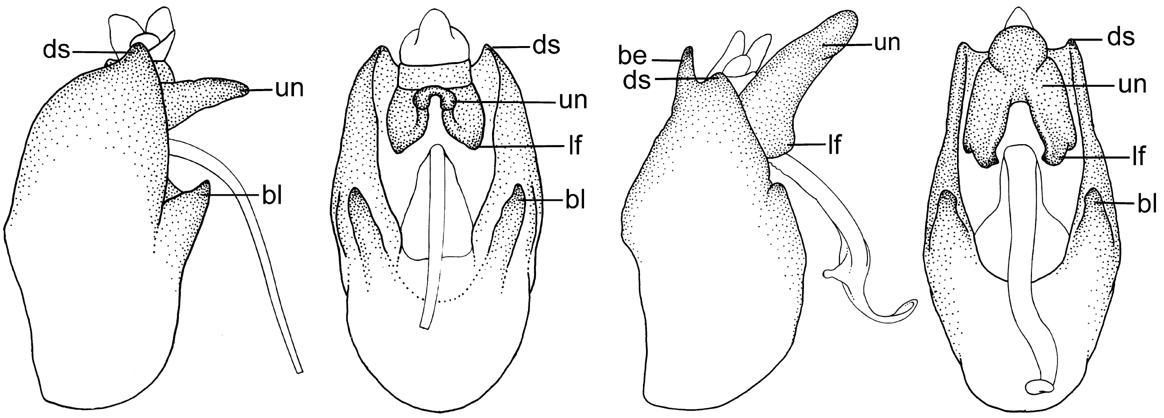
Distribution. Africa.

Comments. The need for this tribe is apparent from its deep origins within the Cicadettinae, following the molecular phylogenetic results. Morphological distinctiveness precludes combining *Maroboduus* and *Nablistes* with their nearest relatives in the tree. *Ydiella* was synonymized with *Maroboduus* but the family-group name retains priority (Article 40.1; ICZN 1999). The tribe was inadvertently listed in subfamily Tibicininae in the catalogue by Sanborn (2013), as discussed under Tribe Lamotialnini (see also Ruschel, 2015).



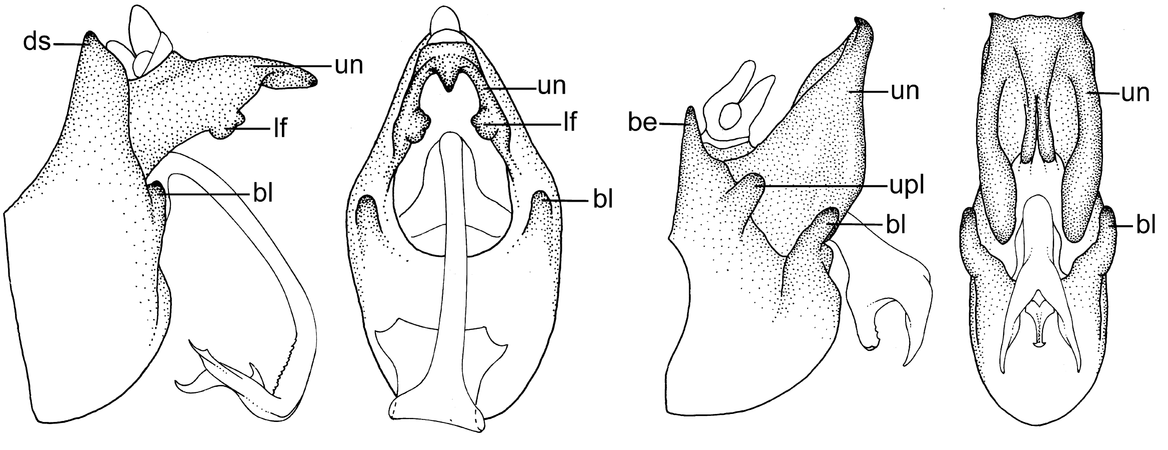
Katoa tenmokuensis
Cicadettinae: Katoini

Parnisa designata
Cicadettinae: Parnisini



Tettigomyia vespiformis
Tettigomyiinae: Tettigomyiini

Malagasia inflata
Tettigomyiinae: Malagasiini



Lacetas annulicornis
Tettigomyiinae: Lacetasini

Selymbria stigmatica
Tibicininae: Selymbryiini

FIGURE 12. Male genitalia, lateral and ventral views, for type species of Katoini **n. tribe**, Parnisini (type not available), Tettigomyiini, Malagasiini **n. tribe**, Lacetasini **n. tribe**, and Selymbriini **n. tribe**, see lower part of Fig. 4. (*be*) dorsal beak; (*bl*) basal lobe; (*cl*) clasper; (*ds*) distal shoulder; (*lf*) lateral flange; (*un*) uncus; (*upl*) upper pygofer lobe.

SUBFAMILY TIBICININAE DISTANT, 1905

Type genus. *Tibicina* Kolenati, 1857 (type species *Cicada haematodes* Scopoli, 1763).

Included tribes. Chilecicadini Sanborn, 2014; Platypediini Kato, 1932; Selymbriini Moulds & Marshall **n. tribe**; Tettigadini Distant, 1905; Tibicinini Distant, 1905.

Diagnosis (modified from Moulds, 2005). Metanotum entirely concealed at dorsal midline (except in *Platypedia* and *Tibicina*). Forewing veins CuP and 1A unfused (fused in *Platypedia* and *Neoplatypedia*). Hindwing veins RP and M unfused at their bases. Male opercula with distinctive S-shape and deeply concave lateral margins, and with distal margins not reaching distal margins of tympanal cavities. Abdominal timbal cavity lacking timbal covers or with a partial turned-back rim. Pygofer with distal shoulder undeveloped; pygofer upper lobe usually absent (present in Selymbriini **n. tribe**). Uncus exceedingly long and non-retractable within pygofer. Claspers absent. Aedeagus with ventrobasal pocket present; aedeagus restrained by tubular encapsulation below uncus. Apical part of theca with a pair of leaf-like lateral lobes.

Distinguishing features (Table 4). Hindwing veins RP and M unfused at base. Uncus exceedingly long and non-retractable within pygofer. Aedeagus with ventrobasal pocket present. Aedeagus with apical part of theca bearing a pair of leaf-like lateral lobes and a non-retractable tubular vesica. Male opercula with a distinctive S-shape, their lateral margins deeply concave, their distal margins not reaching distal margins of tympanal cavities, and basally not extending beyond meracantha.

Distribution. Neotropics, Neacrtic, Palearctic.

Comments. *Selymbria* is transferred to Tibicininae (see clade 3, Fig. 4) from the Cicadettinae to form the Selymbriini **n. tribe.**

The Tibicininae, with type genus *Tibicina,* acquired a completely different concept in the revised classification of Moulds (2005) by removal of *Tibicina* from the subfamily it was traditionally associated with, now the Cicadettinae. To avoid confusion in the application of this name, Moulds proposed using the name of its junior synonym Tettigadinae, a proposal that required a submission to the International Commission of Zoological Nomenclature to suppress the name Tibicininae. However, the proposal was not universally accepted following Moulds's revision so no appeal was made for suppression.

Family group names based on *Tibicina* have sometimes been attributed to Buckton (1889) (e.g., Tibicinidae in Metcalf 1963). However, Buckton's name "Tibicinae", based on the stem "Tibic-", cannot be unambiguously linked to either *Tibicen* or *Tibicina*, both of which were available, and the text of the paper offers no additional evidence. An application to the ICZN will be necessary to formally reject Buckton's name.

Tribe Chilecicadini Sanborn, 2014

Type genus. *Chilecicada* Sanborn, 2014 (type species *Cicada occidentis* Walker, 1850).

Included genera. *Chilecicada* Sanborn, 2014.

Diagnosis and distinguishing features. As in Sanborn (2014a).

Distribution. South America.

Comments. This tribe was not sampled in this study. Unpublished molecular data support its position within Tibicininae.

Tribe Platypediini Kato, 1932

Type genus. *Platypedia* Uhler, 1888 (type species *Cicada areolata* Uhler, 1861).

Included genera. *Neoplatypedia* Davis, 1920; *Platypedia* Uhler, 1888.

Diagnosis. As in Kato (1932).

Distribution. Nearctic.

Comments. This concept is consistent with the results of this study and no changes are proposed.

Tribe Selymbriini Moulds & Marshall, n. tribe

Type genus. *Selymbria* Stål, 1861 (type species *Cicada stigmatica* Germar, 1834).

Included genera. *Selymbria* Stål, 1861.

Diagnosis. Head including eyes wide, nearly as wide or wider than lateral angles but with supra-antennal plates nearly meeting eyes. Postclypeus shape in transverse cross-section rounded; postclypial ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margins moderately ampliate, rounded, broadly U-shaped; lateral tooth absent. Metanotum lacking auxiliary sound-producing structures. Forewing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length; vein CuA_1 divided by crossvein so that distal portion is longest. Hindwing with anal lobe broad and vein 3A curved at distal end, short, separated from wing margin. Foreleg femoral primary spine erect. Hindcoxae lacking a large inner protuberance. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, completely covering tympanal cavity but not meeting. Male abdominal tergites with sides convex in cross-section; tergites 2 and 3 similar in size to tergites 4-7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extended below level of wing bases; timbal cavity with a turned-back rim. Pygofer (Fig. 12) with upper lobe present, flat; distal shoulder not developed; basal lobe moderately developed; dorsal beak a part of chitinized pygofer. Uncus exceedingly long, undivided, not retractable within pygofer. Aedeagus with theca not unlike that of the Tettigarctidae, very short, curved in a gentle arc, in lateral view distally broadened with broad rounded apex, in vertical profile narrow, bearing two pairs of flat triangular lobes dorsally, lacking any other appendages; vesica presumed absent; conjunctival claws and pseudoparameres absent; ventral rib of basal plate fused.

Distinguishing features. The Selymbriini **n. tribe** differ from other tribes in the subfamily Tibicininae in having the supra-antennal plate almost reaching the eye, no male auxiliary auditory structure, the male aedeagal basal plate undulated and not right-angled distally, and a very short theca that is laterally expanded distally and ornamented. The tribe differs from all other tribes in having, in combination, a male uncus that is exceedingly long, undivided, not retractable within pygofer, and an aedeagus that has the theca very short and with a broad, flat, laterally expanded distal end ornamented with triangular wings not unlike in Tettigarctidae.

Distribution. Neotropics.

Comments. A deep position within the five-gene tree and a lack of shared attributes with its sister Platypediini support this tribe (see clade 3, Fig. 4). The basal position of *Selymbria* is reflected in the remarkable similarity of its aedeagus to that of its near sister *Tettigarcta* (Family Tettigarctidae). *Selymbria* is the only genus known within the Cicadidae showing this similarity, which shows how the basal plate in Cicadidae could be derived from that of Tettigarctidae.

Tribe Tettigadini Distant, 1905

Type genus. *Tettigades* Amyot & Audinet-Serville, 1843 (type species *Tettigades chilensis* Amyot & Audinet-Serville, 1843).

Included genera. *Acuticephala* Torres, 1958; *Alarcta* Torres, 1958; *Babras* Jacobi, 1907; *Calliopsida* Torres, 1958; *Chonosia* Distant, 1905; *Coata* Distant, 1906; *Mendozana* Distant, 1906; *Psephenotettix* Torres, 1958; *Tettigades* Amyot & Audinet-Serville, 1843; *Tettigotoma* Torres, 1942; *Torrescada* Sanborn & Heath, 2017.

Diagnosis and distinguishing features. Distant's (1905c) original description, based largely on the medially angulate pronotal margin and exposed timbals, is now of limited value and redefinition is needed.

Distribution. Neotropics.

Comments. This concept is consistent with the results of this study. *Torrescada* was proposed as a replacement name for *Torresia* Sanborn & Heath, 2014, which was preoccupied (Sanborn & Heath 2017).

Tribe Tibicinini Distant, 1905

Type genus. *Tibicina* Kolenati, 1857 (type species *Cicada haematodes* Scopoli, 1763).

Included genera. *Clidophleps* Van Duzee, 1915; *Okanagana* Distant, 1905; *Okanagodes* Davis, 1919; *Paharia* Distant, 1905; *Subpsaltria* Chen, 1943; *Subtibicina* Lee, 2012; *Tibicina* Kolenati, 1857; *Tibicinoides* Distant, 1914.

Diagnosis and distinguishing features. As in Distant (1905d).

Distribution. Holarctic.

Comments. This concept is consistent with the results of this study and no changes are proposed (see clade 3, Fig. 4). See under subfamily Tibicininae for comments on authorship.

DISCUSSION

Molecular phylogeny of the Cicadoidea

The five-gene tree of the Cicadoidea (Fig. 4) contains well-supported relationships that support Moulds's (2005) results based on morphology (Fig. 3), especially clades 1-5. These patterns were also found when the genetic and morphological characters were analyzed together (Fig. 5). *Tettigarcta* (Tettigarctidae) falls outside the true cicadas (clade 1), as expected (Duffels 1993; Moulds 1990), and the subfamilies Tibicininae, Cicadinae, and Cicadettinae are recovered as clades 3, 4, and 5, respectively. Support is somewhat weaker for the subfamily Tibicininae in the ML analysis. A forthcoming study using anchored phylogenomic data finds stronger support for the clade (C. Simon *et al.* unpublished). Other patterns in the five-gene tree depart notably from Moulds's phylogeny—for example, several South American Cicadinae genera were placed in a clade sister to the rest of Cicadinae by Moulds (2005), while they are nested within the subfamily here (as clade 11).

This study sampled Cicadidae genera more broadly than Moulds's analysis, leading to the discovery of new, geographically restricted deep level clades in Fig. 4. Many of the African and Madagascar genera appear in a set of clades (6-8) branching off in unresolved order from the base of clade 2, separate from the groups corresponding to the existing subfamilies (see Taxonomy discussion below). Other intriguing geographic trends are apparent. The early-diverging Tibicininae are absent from Africa and Australia while the Cicadinae and Cicadettinae are global in distribution (minus Antarctica), and the North American periodical cicada genus *Magicicada* is remarkably closely related to *Tryella* and *Aleeta* from Australia (see clade 17), confirming results from analysis of genitalic features (Moulds 2003). While Moulds (2005, p. 424) suggested a potential connection between *Parnisa* from South America and the Australian Chlorocystini and Prasiini based on morphology, the molecular tree with better taxon sampling shows these lineages to be deeply divergent within Cicadettinae (clade 5). Other patterns within Cicadettinae continue to suggest an Australasian origin for the large tribe Cicadettini (clade 13), which contains about 15% of described cicada species, and which has radiated to a nearly global distribution during the late Cenozoic (Marshall *et al.* 2015, Owen *et al.* 2017).

Many newer phylogenetic analyses use genomic datasets with hundreds of loci. This analysis uses five gene segments (two mitochondrial) and the full data matrix was just 62% complete, although for three core genes (3' COI, ARD1, and EF-1α) sequence data are available for a given gene 78% of the time. Our conclusions are limited to the well-supported relationships in the five-gene tree, all of which were recovered in additional analyses intended to check for effects of missing data (compare Figs. 4 and 6). Furthermore, analyses intended to correct for base composition bias (RY coding, use of nonstationary models), which was a concern here due to the large amount of fast-evolving mtDNA data, similarly showed no differences in the well-supported relationships that form the basis of all conclusions of this paper (Figs. 7, 8).

Evolution of morphology associated with sound production

Several family group taxa in Cicadidae have been proposed based on unique features of the sound-producing apparatus, with only limited success. For example, subfamily Moaninae, proposed based on a unique scutellar-stridulatory method of sound production (Boulard 1976a), was synonymized by Duffels (1993) who used genitalic morphology to show a link to *Aceropyga* (Cosmopsaltriini), which has the usual timbal-based sound mechanism. Although *Moana* is not in our tree, Cosmopsaltriini is here found to be part of a radiation of closely related genera from Asia and India (Fig. 4, clade 9). Tribe Plautillini, once placed at family level based on a unique form of timbal cover (Boulard 1975b; see also Duffels 1993; Moulds 2005) has been proposed as synonymous with the Zammarini by Goemans (2016) and Goemans *et al.* (in prep.) based on molecular and morphological data. The tribe Ydiellini (with type genus *Maroboduus*, and originally a subfamily) is here found on a deep branch in the five-gene tree (clade 8) and is closely related to *Nablistes*, which does not share its loss of timbals and unique wing-stridulatory mode of sound production. Most of the genera classified in the subfamily Cicadinae, which have been diagnosed by the presence of well-developed timbal covers since the time of Distant (1906), intriguingly appear as a well-supported clade despite a short supporting branch (clade 4). However, the five-gene tree shows that this clade also contains *Durangona*, *Karenia*, and *Nosola*, which appear to have lost timbal covers. Another group, the well-supported Cicadatrini tribe (clade 15), was previously placed in Cicadinae because it does possess timbal covers, but in our trees is nested in Cicadettinae (see also Wang *et al.* 2017), plausibly implying a convergent gain of timbal covers. Taxonomic changes associated with these findings and others are given in the Results. Together, these examples confirm that changes in morphology associated with sound production can occur rapidly and convergently in cicadas (see also Sanborn *et al.* 2016).

Taxonomy

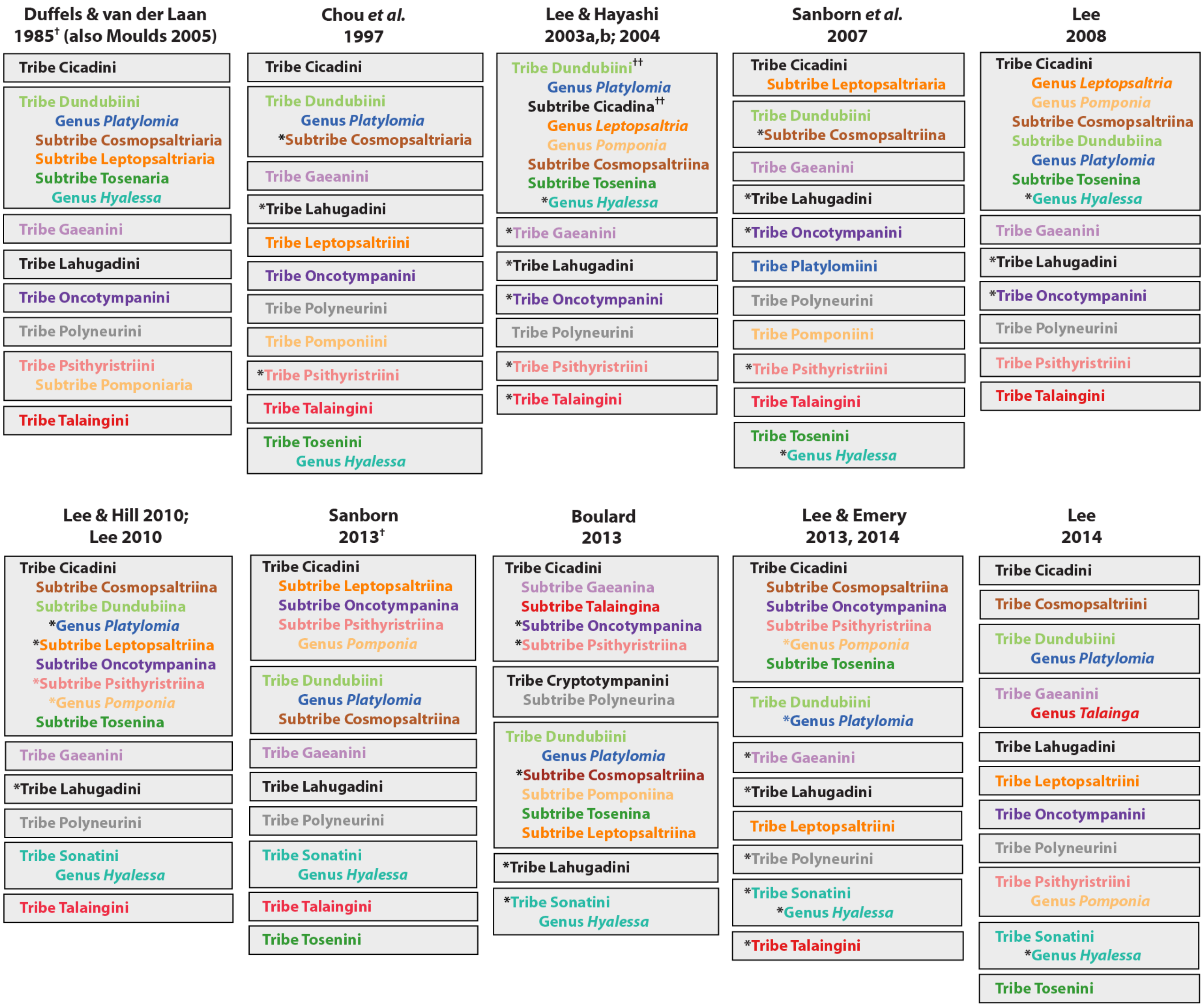
Comments on the Australian fauna. Twelve of the thirteen Australian Cicadinae genera (all but *Talcopsaltria*) that were sampled, all largely endemic, form a very weakly supported clade in the five-gene tree (clade 10). Most of these genera have long branches (not due to our taxon sampling) that branch from an early rapid radiation, with no clear generic subgroups. Seven have been previously allocated to endemic tribes based on morphology. Only *Talcopsaltria* falls just outside the cluster of other Australian Cicadinae, but the branch is not well supported.

The five Australian Cicadinae genera not allocated to endemic tribes have been previously placed in the Cryptotympanini because of their partial morphological similarity to *Cryptotympana* (Moulds 2005). However, the five-gene tree now shows that *Cryptotympana* and its allies (clade 12) are not closely related to the Australian genera, so *Henicopsaltria*, *Arenopsaltria*, *Psaltoda*, *Macrotristria* and *Illyria* each require allocation to a new tribe or tribes. Finding an attribute, or combination of attributes, to uniquely define these five genera as a single tribe has proven elusive, which is not surprising given the lack of well-supported phylogenetic structure within clade 10. For example, all but *Psaltoda* have similar male tympanal cavities but other attributes such as development of the timbal covers are variable. Likewise, all but *Illyria* and *Macrotristria* have very broad male abdominal tergites 2 and 3 occupying half the abdomen but tympanal cavities and other attributes are not compatible. We therefore reluctantly erect three additional tribes for these deep Australian lineages. *Macrotristria* and *Illyria* form a distinctive morphological entity and are placed in the Macrotristriini **n. tribe**. *Psaltoda*, together with *Neopsaltoda* and *Anapsaltoda*, also are distinctive and are placed in the Psaltodini **n. tribe** while *Henicopsaltria* and *Arenopsaltria* have features in common sufficient enough to combine them into a third tribe, Arenopsaltriini **n. tribe**.

Comments on the African fauna. The subfamily Tettigomyiinae **n. stat.** is here loosely conceived for those African genera that clearly fall outside the Cicadinae, Cicadettinae and Tibicininae. In our five-gene tree they comprise clades 6-8, which are well supported individually but unresolved together. One could recognize each as a separate subfamily with some differing synapomorphies, e.g. the metanotum either exposed or concealed at the dorsal midline, but we consider such action premature without a comprehensive review of African genera. Instead we accept here a broad Tettigomyiinae awaiting refinement in a future study. In our concept of the subfamily Tettigomyiinae are several lineages suggestive of tribal rank. However, there are other African genera not included in our study that may change these tribal concepts and without an exhaustive study we place all these tentatively in just four tribes within Tettigomyiinae, two of them new.

Comments on the South American fauna.The five-gene tree identifies a relatively deep clade of mostly South American genera with conflicting tribal placements in Cicadinae (clade 11). Close examination of morphology showed that *Diceroprocta*, *Nosola*, *Orialella*, and *Quesada* could be combined with *Fidicina* in a redefined Fidicinini. South American cicadas in the subfamily Cicadettinae are represented in our tree by genera in the tribes Carinetini, Taphurini, and Parnisini. Genera previously considered belonging to the Taphurini are widely dispersed throughout the five-gene tree; most cannot belong to this tribe. The genus *Taphura*, found only in South America (see Sanborn 2017), has several distinctive features and we hypothesize that the Taphurini *sensu stricto* are restricted to South America. Finally, the subfamily Tibicininae contains an extensive radiation of South American cicadas in the tribe Tettigadini represented in this paper by *Tettigades* and *Acuticephala*. This tribe dominates the cicada fauna of temperate South America and forms a disjunct sister group to North American Tibicinini (*Okanagana* and relatives). Sister to Tibicinini + Tettigadini is another Northern-Southern Hemisphere pair, *Platypedia* and *Selymbria*, respectively.

TABLE 5. Historical shifts in classification for cicadas in the Cicadini (subfamily Cicadinae) and allied tribes (clade 9 in Figs. 3-8)§. Only names (or type genera of family group names) that have been used at tribal rank at some point are shown; additional subtribes exist for some groups. Nominotypical subtribe names are omitted for simplicity. Asterisks denote taxa that were not addressed in the given publication and are therefore shown with their status at the time of the study. Where multiple papers are cited, the changes occurred over multiple publications. Only Lahugada and Cicadini have remained at tribal rank from 1985-present.



Duffels & van der Laan 1985[†] (also Moulds 2005)	Chou *et al.* 1997	Lee & Hayashi 2003a,b; 2004	Sanborn *et al.* 2007	Lee 2008
Tribe Cicadini	Tribe Cicadini	Tribe Dundubiini[††] Genus *Platylomia* Subtribe Cicadina[††] Genus *Leptopsaltria* Genus *Pomponia* Subtribe Cosmopsaltriina Subtribe Tosenina *Genus *Hyalessa*	Tribe Cicadini Subtribe Leptopsaltriaria	Tribe Cicadini Genus *Leptopsaltria* Genus *Pomponia* Subtribe Cosmopsaltriina Subtribe Dundubiina Genus *Platylomia* Subtribe Tosenina *Genus *Hyalessa*
Tribe Dundubiini Genus *Platylomia* Subtribe Cosmopsaltriaria Subtribe Leptopsaltriaria Subtribe Tosenaria Genus *Hyalessa*	Tribe Dundubiini Genus *Platylomia* *Subtribe Cosmopsaltriaria	*Tribe Gaeanini	Tribe Dundubiini *Subtribe Cosmopsaltriina	Tribe Gaeanini
Tribe Gaeanini	Tribe Gaeanini	*Tribe Lahugadini	Tribe Gaeanini	*Tribe Lahugadini
Tribe Lahugadini	*Tribe Lahugadini	*Tribe Oncotympanini	*Tribe Lahugadini	*Tribe Oncotympanini
Tribe Oncotympanini	Tribe Leptopsaltriini	Tribe Polyneurini	*Tribe Oncotympanini	Tribe Polyneurini
Tribe Polyneurini	Tribe Oncotympanini	*Tribe Psithyristriini	Tribe Platylomiini	Tribe Psithyristriini
Tribe Psithyristriini Subtribe Pomponiaria	Tribe Polyneurini	*Tribe Talaingini	Tribe Polyneurini	Tribe Talaingini
Tribe Talaingini	Tribe Pomponiini		Tribe Pomponiini	
	*Tribe Psithyristriini		*Tribe Psithyristriini	
	Tribe Talaingini		Tribe Talaingini	
	Tribe Tosenini Genus *Hyalessa*		Tribe Tosenini *Genus *Hyalessa*	

Lee & Hill 2010; Lee 2010	Sanborn 2013[†]	Boulard 2013	Lee & Emery 2013, 2014	Lee 2014
Tribe Cicadini Subtribe Cosmopsaltriina Subtribe Dundubiina *Genus *Platylomia* *Subtribe Leptopsaltriina Subtribe Oncotympanina *Subtribe Psithyristriina *Genus *Pomponia* Subtribe Tosenina	Tribe Cicadini Subtribe Leptopsaltriina Subtribe Oncotympanina Subtribe Psithyristriina Genus *Pomponia*	Tribe Cicadini Subtribe Gaeanina Subtribe Talaingina *Subtribe Oncotympanina *Subtribe Psithyristriina	Tribe Cicadini Subtribe Cosmopsaltriina Subtribe Oncotympanina Subtribe Psithyristriina *Genus *Pomponia* Subtribe Tosenina	Tribe Cicadini
Tribe Gaeanini	Tribe Dundubiini Genus *Platylomia* Subtribe Cosmopsaltriina	Tribe Cryptotympanini Subtribe Polyneurina	Tribe Dundubiini *Genus *Platylomia*	Tribe Cosmopsaltriini
*Tribe Lahugadini	Tribe Gaeanini	Tribe Dundubiini Genus *Platylomia* *Subtribe Cosmopsaltriina Subtribe Pomponiina Subtribe Tosenina Subtribe Leptopsaltriina	*Tribe Gaeanini	Tribe Dundubiini Genus *Platylomia*
Tribe Polyneurini	Tribe Lahugadini	*Tribe Lahugadini	*Tribe Lahugadini	Tribe Gaeanini Genus *Talainga*
Tribe Sonatini Genus *Hyalessa*	Tribe Polyneurini	*Tribe Sonatini Genus *Hyalessa*	Tribe Leptopsaltriini	Tribe Lahugadini
Tribe Talaingini	Tribe Sonatini Genus *Hyalessa*		*Tribe Polyneurini	Tribe Leptopsaltriini
	Tribe Talaingini		*Tribe Sonatini *Genus *Hyalessa*	Tribe Oncotympanini
	Tribe Tosenini		*Tribe Talaingini	Tribe Polyneurini
				Tribe Psithyristriini Genus *Pomponia*
				Tribe Sonatini *Genus *Hyalessa*
				Tribe Tosenini

[§] Kareniina (=Sinosenini) is in clade 9 of Fig. 4 but is not included here because it was classified in Cicadettinae during the period shown.

[†] Catalogue.

[††] Lee & Hayashi (2003b) placed Cicadina as a subtribe of Dundubiini but Cicadini has priority.

Comments on the Asian fauna. A large number of mostly Asian and Indian genera, some of which exhibit striking morphological evolution in color pattern and wing venation (e.g., *Gaeana*, *Polyneura*), form a distinctive, well-supported clade in the five-gene tree (clade 9). Despite the relatively shallow depth of this clade, its genera have been classified into no fewer than six tribes since the early 20th century, and recent years have seen rapid and sometimes erratic changes to the classification (Table 5), with the recent elevation of some groups (Lee 2014) bringing the number of tribes to ten before this study (see also Comments under tribe Cicadini). Two tribes, Dundubiini and Leptopsaltriini, are paraphyletic on the five-gene tree as discussed after the tribal definitions (see clade 9). With the classification of Cicadini and its related tribes in flux, and considering the low clade supports in that section of the tree, we leave the arrangements unchanged (with the exception of *Karenia* and its tribe Sinosenini as discussed earlier).

FUTURE DIRECTIONS

Our study highlights the need for additional review and redescription of some cicada tribes following changes in their lists of included genera, especially older tribes such as Cryptotympanini and Parnisini. In addition, systematic analysis of the African groups created here is needed, with more thorough taxon sampling.

A large number of Chinese and Indian genera and species still remain to be analyzed. Considering that this region has the highest generic diversity of cicadas, and the cicada faunas of these areas are likely a mixture of Oriental, Palaearctic and African elements, it is essential to study how these faunas have originated in relation to biogeography and diversification patterns of neighboring zoogeographic subregions. This will also shed light on the colonization and diversification of cicadas of the Indian Subcontinent.

The results of this paper add to growing evidence that the widespread distributions of some taxonomically older cicada tribes are an artefact of inadequate classification (e.g., Chlorocystini, Cryptotympanini, Parnisini, Taphurini). Most tribes are regional in distribution, with notable exceptions in some cases attributable to the exploitation of expanding late Cenozoic habitats (e.g., Cicadettini; Marshall *et al.* 2016). Further study of tribes such as Parnisini, Chlorocystini, Lamotialnini, and Taphurini (and other cases noted in the tribal review) is needed to test the placement of genera that could not be included here.

ACKNOWLEDGMENTS

This study would not have been possible without the help of an extensive network of global collaborators including Z. Ahmed, P. Arensburger, M. Barclay, Y. Basset, V. Bhaumik, A. de Boer, M. Boulard, T. Buckley, J-H. Chen, S. Chiswell, M. Claridge, S. Cowan, J. Cryan, C. Dietrich, D. Emery, S. Emery, T. Erwin, R. Futahashi, M. Gogala, I. Hill, H. Honsya, M. Humphrey, J. Jones, L. Jingke, T. Karmakar, G. S. Girish Kumar, D. Lane, Y. Lee, Z. Lei, L. O'Brien, H. Mendel, A. Mohagan, D. Mohagan, J. Morgan, B. Moulds, T. Moulds, F. Mozaffarian, J. Olive, L. Popple, S. Puissant, M. Schouten, D. Sikes, F. Skillman, Society for Insect Studies (Sydney, Australia), T. Sota, J. Sueur, D. Takiya, P-H. Thai, K. Trilar, T. Trilar, J. Urban, D. Vanderpool, R. Veal, C. Wei, M. Whiting, J. Windmill, J. Xiang, J. Yoshimura, C. Zamora-Manzur, J. Zyla, and the Bishop Museum. Jason Cryan and Julie Urban provided numerous essential samples from sites in Africa, South America, and southeast Asia. Jian-Hong Chen, C. Dietrich, T. Sota, J. Yoshimura, M. Gogala, T. Trilar, J. Sueur, S. Puissant, and Young June Lee also provided samples from important regions. Mike Whiting and Brigham Young University's Monte L. Bean Life Science Museum contributed a large collection that will support ongoing research. Hans Duffels, Masami Hayashi, Young June Lee, and Pham Hong Thai assisted with specimen identification. Mick Webb (British Museum) assisted with specimen loans.

Financial support was provided by NSF grants DEB1655891, DEB0955849, DEB0720664, DEB0529679, and DEB0089946 to CS, MM, DM, JC, MV, and collaborators. The Indian work was partially funded by a USAID PEER Science Program grant (AID-OAA-A-11-00012), a Ramanujan Fellowship (Department of Science and Technology, Govt. of India) and a National Centre for Biological Sciences (NCBS) research grant to KK. Logistical support and facilities for specimen deposition were provided by the University of Connecticut (UConn) Biodiversity Research Collection and the Museum and Field Stations Facility at the NCBS; the latter also supported the sequencing of the Indian material. The UConn Biocomputing Facility supported time-consuming data analysis.

Assistance with historical literature was obtained from the Biodiversity Heritage Library (https://www.biodiversitylibrary.org) and by an online bibliography of the Cicadoidea (http://www.tmcnary.com/CicadaBibliography.htm). A. Ewart, L. Popple, C. Dietrich, and two anonymous reviewers provided helpful comments on the manuscript. Dmitry Dmitriev provided advice on questions of nomenclature, and Ivan Nozaic drew the genitalia sketches.

Specimens collected by the authors were obtained in several countries, and we wish to thank the many contacts and officials who assisted our research through the permitting process (in alphabetical order by country): Argentina (Administracion de Parques Nacionales); Australia (Michelle Scott, Dept. of the Environment and Water Resources; Tracey Connelly and Brett Easton, Dept. of Environment and Natural Resources, NT; Michelle Nissen, Dept. of Environment and Heritage Protection, QLD; Kate Lloyd, Dept. of Environment, Water, and Natural Resources, SA; Sue Hadden, Dept. of Sustainability and Environment, VIC; Danny Stefoni, Dept. of Environment Regulation, WA), Chile (Administracion de Parques Nacionales), China (Z. Lei, Institute of Plant Protection, Chinese Academy of Agricultural Sciences); Costa Rica, Ministry of Environment and Energy and the National Institute of Biodiversity (I.J. Guevara Sequeira and H. Ramirez Murillo), permit nos 128-2003-OFAU and 2529201; Ghana, Wildlife Division, Forestry Commission (V. Attah), permit nos WD/A.185/Vol.6/22 and 005833; Madagascar, Ministry of the Environment, Forests, and Tourism (L.H. Rasoavahiny), permit no. 271/08/MEFT/SG/DGEF/DSAP/SSE. Malaysia, Economic Planning Unit, UPE (Munirah Abd. Manan), permit nos. 40/200/19 SJ.1040 (permit ID no. 1389), 40/200/19/1481 (permit ID no.1933), and 40/200/19/1476; New Zealand (Department of Conservation, Te Papa Atawhai); Peru, Instituto Nacional de Recursos Naturales (G. Suarez de Freitas and A. Morizaki Taura) and Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (G. Lamas Müller); Philippines, Protected Areas and Wildlife Bureau (Theresa Mundita S. Lim). Craig Morley of the University of the South Pacific, Fiji, also assisted with logistics and permits.

Research and collection permits for the Indian part of this project were issued by the state forest departments in Kerala (permit no. WL 10-3781/2012 dated 18/12/2012, and GO (RT) No. 376/2012/F and WLD dated 26/07/2012), Karnataka (permit no. 227/2014-2015 dated 2015/04/16), Goa (permit no. 2/21/GEN/WL and ET(S)/2013-14/387 dated 2013/06/20), Nagaland (permit no. CWL/GEN/240/522-39, dated 14/08/2012), Meghalaya (permit no. FWC/G/173/Pt-II/474-83, dated 27/05/2014), Arunachal Pradesh (permit no. CWL/G/13(95)/2011-12/Pt-III/2466-70, dated 16/02/2015), and West Bengal (permit no. 2115(9)/WL/4K-1/13/BL41, dated 06/11/2013), for which we thank the Principal Chief Conservator of Forest, Deputy Conservators of Forest, Wildlife Wardens and field officers of those states.

REFERENCES

Amyot, C.-J.-B. & Serville, J.G.A. (1843) *Histoire naturelle des Insectes. Hémiptères*. Librairie encyclopédique de Roret, Paris, 675 pp.
https://doi.org/10.5962/bhl.title.8471

Arensburger, P., Buckley, T.R., Simon, C., Moulds, M. & Holsinger, K.E. (2004) Biogeography and phylogeny of the New Zealand cicada genera (Hemiptera: Cicadidae) based on nuclear and mitochondrial DNA data. *Journal of Biogeography*, 31, 557–569.
https://doi.org/10.1046/j.1365-2699.2003.01012.x

Atkinson, E.T. (1886) Notes on Indian Rhynchota, no. 6. Addenda and index. *Journal of the Asiatic Society of Bengal*, 55, 143–223.

Beuk, P.L. Th. (2002) *Cicadas Spreading by Island or by Spreading the Wings? Historic Biogeography of Dundubiine Cicadas of the Southeast Asian Continent and Archipelagos*. University of Amsterdam, Amsterdam, 323 pp.

Blanquart, S. & Lartillot, N. (2006) A Bayesian compound stochastic process for modeling nonstationary and nonhomogeneous sequence evolution. *Molecular Biology and Evolution*, 23, 2058–2071.
https://doi.org/10.1093/molbev/msl091

Boer, A.J.de. (1995) The phylogeny and taxonomic status of the Chlorocystini (sensu stricto) (Homoptera, Tibicinidae). *Bijdragen tot de Dierkunde*, 65, 201–231.

Boulard, M. (1973) Les Ydiellinae: sous-famille nouvelle de cigales Platypediidae. Clé des familles et sous-familles des Homopteres Cicadoidea. *Annales de la Société entomologique de France*, 9, 841–852.

Boulard, M. (1975a) Une nouvelle tribu de cigales Platypediinae (Hom.). *Doriana*, 219, 1–3.

Boulard, M. (1975b) Un nouvel Homoptere jassidomorphe des cacaoyeres camerounaises. *Café, Cacao, Thé*, 19, 137–138.

Boulard, M. (1976a) Un type nouveau d'appareil stridulant accessoire pour les Cicadoidea. Révision de la classification supérieure de la superfamille (Hom.). *Journal of Natural History*, 10, 399–407.
https://doi.org/10.1080/00222937600770301

Boulard, M. (1976b) Sur une deuxieme cigale africaine depourvue d'appareil sonore (Homoptera). *Bulletin de l'Institut Fondamental d'Afrique Noire*, Series A, 37, 629–636.

Boulard, M. (1985) Apparence et mimétisme chez les Cigales (Hom. Cicadoidea). *Bulletin de la Société entomologique de France*, 90, 1016–1051.

Boulard, M. (1986a) Cigales de la Foret de Tai (Cote d'Ivoire) et complements a la faune cicadeenne Aftrotropicale (Homoptera, Cicadoidea). *Revue Francaise d'Entomologie*, New Series, 7, 223–239.

Boulard, M. (1986b) Une singulière évolution morphologique: celle d'un appareil stridulant sur les genitalia des males de *Carineta*. Description de cinq espèces nouvelles (Hom. Tibicinidae). *Annales de la Société Entomologique de France*, New Series, 22, 191–204.

Boulard, M. (1988) Taxonomie et nomenclature supérieures des Cicadoidea. Histoire problèmes et solutions. *Ecole pratique des hautes Etudes, travaux du Laboratoire Biologie et Evolution des Insectes Hémipteroidea*, 1, 1–89.

Boulard, M. (1993) *Bafutalna mirei*, n. gen., n. sp. de cicale acymbalique (Homoptera, Cicadoidea, Tibicinidae). *Ecole pratique des hautes Etudes, travaux du Laboratoire Biologie et Evolution des Insectes Hémipteroidea*, 6, 87–92.

Boulard, M. (1998) Nomenclature et taxonomie supérieures des Cicadoidea ou vraies cigales: histoire, problèmes et solutions (Rhynchota Homoptera Cicadomorpha). *Ecole pratique des hautes Etudes, Biologie et Evolution des Insectes*, 10, 79–129. Boulard, M. (2002) Diversite des Auchenorhynchques Cicadomorphes Formes, couleurs et comportements (Diversite structurelle ou taxonomimique Diversite particuliere aux Cicadides). *Denisia*, 4, 171–214.

Boulard, M. (2013) *The cicadas of Thailand. Vol. 2*. Siri Scientific Press, Manchester, 436 pp.

Boulard, M. & Puissant, S. (2013) Une cigale-marteau chez les Cicadidae. Nouvelle espèce, nouveau genre, nouvelle sous-tribu. *EPHE, Biologie et Évolution des Insectes*, 20, 3–8.

Boulard, M. & Puissant, S. (2014) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 71, 119–131.

Boulard, M. & Puissant, S. (2016) Description du mâle de la Cigale-marteu, *Cicadmalleus micheli* Boulard & Puissant, 2013, et position systématique de l'espèce (Hemiptera, Cicadoidea, Cicadidae). *Bulletin de la Société entomologique de France*, 131, 313–321.

Buckley, T.R. & Simon, C. (2007) Evolutionary radiation of the cicada genus *Maoricicada* Dugdale (Hemiptera: Cicadoidea) and the origins of the New Zealand alpine biota. *Biological Journal of the Linnean Society*, 91, 419–435. https://doi.org/10.1111/j.1095-8312.2007.00807.x

Buckton, G.B. (1889) Notes on the classification of Cicadidae. *Entomologist*, 22, 269–270.

Buckton, G.B. (1890) *Monograph of the British Cicadidae or Tettigidae. Vol. 1*. Macmillan and Co., London, 133 pp.

Campbell, M.A., Van Leuven, J.T., Meister, R.C., Carey, K.M., Simon, C. & McCutcheon, J.P. (2015) Genome expansion via lineage splitting and genome reduction in the cicada endosymbiont *Hodgkinia*. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 10192–10199. https://doi.org/10.1073/pnas.1421386112

Chou, I., Lei, Z., Li, X.L. & Yao, W. (1997) *The Cicadidae of China (Homoptera: Cicadoidea).* Tianze Eldoneio, Hong Kong, 385 pp.

Claridge, M.F. (1985) Acoustic signals in the Homoptera: behavior, taxonomy, and evolution. *Annual Review of Entomology*, 30, 297–317. https://doi.org/10.1146/annurev.en.30.010185.001501

Cryan, J.R. & Svenson, G.J. (2010) Family-level relationships of the spittlebugs and froghoppers (Hemiptera: Cicadomorpha: Cercopoidea). *Systematic Entomology*, 35, 393–415. https://doi.org/10.1111/j.1365-3113.2009.00520.x

Cryan, J.R. & Urban, J.M. (2012) Higher-level phylogeny of the insect order Hemiptera: is Auchenorrhyncha really paraphyletic? *Systematic Entomology*, 37, 7–21. https://doi.org/10.1111/j.1365-3113.2011.00611.x

Delorme, Q. (2016) *Vastarena*, a new genus for the New Caledonian cicada *Abroma pumila* Distant (Insecta: Hemiptera, Cicadoidea, Cicadidae). *Zootaxa*, 4162 (1), 197–200. https://doi.org/10.11646/zootaxa.4162.1.13

Delorme, Q. (2017) Description of four new genera and five new species of cicadas from New Caledonia (Insecta: Hemiptera, Cicadoidea, Cicadidae). *Zootaxa*, 4243 (1), 97–124. https://doi.org/10.11646/zootaxa.4243.1.4

Delorme, Q., Mille, C. & Jourdain, H. (2016) A review of the genus *Kanakia* Distant, 1892 (Insecta: Hemiptera, Cicadoidea, Cicadidae) from New Caledonia. *Zootaxa*, 4092 (3), 301–338. https://doi.org/10.11646/zootaxa.4092.3.1

Distant, W.L. (1889) *A monograph of Oriental Cicadidae*. Indian Museum, Calcutta, 157 pp.

Distant, W.L. (1904) Rhynchotal notes.–XXVI. *Annals and Magazine of Natural History*, 14, 293–303. https://doi.org/10.1080/03745480409443011

Distant, W.L. (1905a) Rhynchotal notes.–XXX. *Annals and Magazine of Natural History*, 15, 304–319. https://doi.org/10.1080/03745480509443047

Distant, W.L. (1905b) Rhynchotal notes.–XXXI. *Annals and Magazine of Natural History*, 15, 379–87. https://doi.org/10.1080/03745480509443064

Distant, W.L. (1905c) Rhynchotal notes.–XXXII. *Annals and Magazine of Natural History*, 15, 478–86. https://doi.org/10.1080/03745480509442837

Distant, W.L. (1905d) Rhynchotal notes.–XXXIII. *Annals and Magazine of Natural History*, 16, 22–35.

https://doi.org/10.1080/03745480509443650

Distant, W.L. (1905e) Rhynchotal notes.–XXXV. *Annals and Magazine of Natural History*, 16, 265–80. https://doi.org/10.1080/03745480509442862

Distant, W.L. (1906) *A Synonymic Catalogue of Homoptera. Part 1. Cicadidae*. British Museum, London, 207 pp.

Dmitriev, D.A. (2017) Unavailability of the genus group name *Mezammira* (Hemiptera: Cicadidae). *Acta Entomological Slovenica*, 25, 159–164.

Duffels, J.P. (1993) The systematic position of *Moana expansa* (Homoptera: Cicadidae), with reference to sound organs and the higher classification of the superfamily Cicadoidea. *Journal of Natural History*, 27, 1223–1237. https://doi.org/10.1080/00222939300770731

Duffels, J.P. (2010) The genus *Nelcyndana* Stål (Hemiptera, Cicadidae, Taphurini) with description of three new species from Borneo. *ZooKeys*, 61, 11–31. https://doi.org/10.3897/zookeys.61.487

Duffels, J.P. (2011) New genera and species of the tribe Taphurini (Hemiptera, Cicadidae) from Sundaland. *Deutsche entomologische Zeitschrift*, 58, 77–104. https://doi.org/10.1002/mmnd.201100006

Duffels, J.P. & van der Laan, P.A. (1985) *Catalogue of the Cicadoidea (Homoptera, Auchenorrhyncha) 1956–1980. Series Entomologica. Vol. 34.* Junk, Dordrecht, 414 pp.

Duffels, J.P. & Turner, H. (2002) Cladistic analysis and biogeography of the cicadas of the Indo-Pacific subtribe Cosmopsaltriina (Hemiptera: Cicadoidea: Cicadidae). *Systematic Entomology*, 27, 235–261. https://doi.org/10.1046/j.1365-3113.2002.00177.x

Felsenstein, J. (2004) *Inferring Phylogenies.* Sinauer Associates, Sunderland, 664 pp.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–297.

Giribet, G., Carranza, S., Baguña, J., Riutort, M. & Ribera, C. (1996) First molecular evidence for the existence of a Tardigrada + Arthropoda clade. *Molecular Biology and Evolution*, 13, 76–84. https://doi.org/10.1093/oxfordjournals.molbev.a025573

Goemans, G. (2016) *The classification and phylogeny of the neotropical cicada tribe Zammarini (Hemiptera, Cicadidae) and a revision of its type genus* Zammara *Amyot & Audinet Serville, 1843 and its sister genus* Zammaralna *Boulard & Sueur, 1996.* Ph.D. dissertation, University of Connecticut, Storrs, 206 pp. Available from: http://digitalcommons.uconn.edu/dissertations/1033 (accessed 27 May 2017)

Goemans, G., Wade, E.J. & Simon, C. (2018) *Molecular phylogenetics of the neotropical cicada tribe Zammarini (Hemiptera: Cicadidae).* [in preparation]

Gogala, M., Puissant, S. & Trilar, T. (2017) Revision and resurrection of the genus name *Mezammira* Fieber, 1876 (Hemiptera: Cicadidae) with special focus on its species from Greece and the description of two new species. *Acta Entomological Slovenica*, 25, 5–64.

Handlirsch, A. (1925) Ordung: Homoptera (Latr.) Westw. (Homopteren). *In* Schroder, C.W.M. (Ed.), *Systematische Übersicht (Schluss.). Schröder's Handbuch der Entomologie*, Series 3 (17–18), pp. 1102–1126.

Hasan, J., Crawford, R.J. & Ivanova, E.P. (2013) Antibacterial surfaces: the quest for a new generation of biomaterials. *Trends in Biotechnology*, 31, 295–304. https://doi.org/10.1016/j.tibtech.2013.01.017

Hayashi, M. (1984) A review of the Japanese Cicadidae. *Cicada (Transactions of the Japanese Cicada Club)*, 5, 25–51.

Hertach, T., Puissant, S., Gogala, M., Trilar, T., Hagmann, R., Baur, H., Kunz, G., Wade, E.J., Loader, S.P., Simon, C. & Nagel, P. (2016) Complex within a complex: Integrative taxonomy reveals hidden diversity in *Cicadetta brevipennis* (Hemiptera: Cicadidae) and unexpected relationships with a song divergent relative. *PLoS One*, 11, e0165562. https://doi.org/10.1371/journal.pone.0165562

Hill, K.B.R., Marshall, D.C., Moulds, M.S. & Simon, C. (2015) Molecular phylogenetics, diversification, and systematics of *Tibicen* Latreille, 1825 and allied cicadas of the tribe Cryptotympanini, with three new genera and emphasis on species from the USA and Canada (Hemiptera: Auchenorrhyncha: Cicadidae). *Zootaxa*, 3985 (2), 219–251. https://doi.org/10.11646/zootaxa.3985.2.3

ICZN (1999) *International Code of Zoological Nomenclature. 4th Edition.* The International Trust for Zoological Nomenclature, London, 306 pp.

Ito, Y. & Nagamine, M. (1981) Why a cicada, *Mogannia minuta* Matsumura, became a pest of sugarcane: an hypothesis based on the theory of 'escape'. *Ecological Entomology*, 6, 273–283. https://doi.org/10.1111/j.1365-2311.1981.tb00614.x

Jong, M.R.de. (1985) Taxonomy and biogeography of oriental Prasiini 1: The genus *Prasia* Stål, 1853 (Homoptera: Tibicinidae). *Tijdschrift voor entomologie*, 128, 165–191.

Kato, M. (1954) On the classification of Cicadoidea (Homoptera: Auchenorrhyncha). *Kontyû*, 21, 97–100.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701. https://doi.org/10.1093/molbev/mss020

Lee, Y.J. (2008) A checklist of Cicadidae (Insecta: Hemiptera) from Vietnam, with some taxonomic remarks. *Zootaxa*, 1787, 1–27.

Lee, Y.J. (2010) New genus and two new species of Oncotympanina stat. nov. (Hemiptera: Cicadidae: Cicadini) and the erection of Sonatini new tribe. *Journal of Asia-Pacific Entomology*, 14, 167–171.
https://doi.org/10.1016/j.aspen.2010.12.001

Lee, Y.J. (2012a) Descriptions of two new genera and species of Cicadidae (Hemiptera) from India with some notes on tribal classification. *Deutsche Entomologische Zeitschrift*, 59, 225–231.

Lee, Y.J. (2014) Cicadas (Hemiptera: Cicadidae) of Laos, with the description of four new genera and two new species. *Annales de la Société entomologique de France*, 50, 59–81.
https://doi.org/10.1080/00379271.2014.934038

Lee, Y.J. & Emery, D. (2013) New genera and species of Leptopsaltriini (Hemiptera: Cicadidae: Cicadinae) from India and Tibet, with the descriptions of five new subtribes. *Zoosystema*, 35, 525–535.
https://doi.org/10.5252/z2013n4a6

Lee, Y.J. & Emery, D. (2014) Description of a new genus and species of the tribe Dundubiini (Hemiptera: Cicadidae: Cicadinae) from India, with taxonomic notes on Dundubiini including the description of two new subtribes. *Zoosystema*, 36, 73–80.
https://doi.org/10.5252/z2014n1a5

Lee, Y.J. & Hayashi, M. (2003a) Taxonomic review of Cicadidae (Hemiptera, Auchenorrhyncha) from Taiwan, Part 1. Platypleurini, Tibicenini, Polyneurini, and Dundubiini (Dundubiina). *Insecta Koreana*, 20, 149–185.

Lee, Y.J. & Hayashi, M. (2003b) Taxonomic review of Cicadidae (Hemiptera, Auchenorrhyncha) from Taiwan, Part 2. Dundubiini (A Part of Cicadina) with two new species. *Insecta Koreana*, 20, 359–392.

Lee, Y.J. & Hayashi, M. (2004) Taxonomic review of Cicadidae (Hemiptera: Auchenorrhyncha) from Taiwan, Part 3. Dundubiini (Two other genera of Cicadina), Moganiini, and Huechysini with a new genus and two new species. *Journal of Asia-Pacific Entomology*, 7, 45–72.
https://doi.org/10.1016/S1226-8615(08)60200-9

Lee, Y.J. & Hill, K.B.R. (2010) Systematic revision of the genus *Psithyristria* Stål (Hemiptera: Cicadidae) with seven new species and a molecular phylogeny of the genus and higher taxa. *Systematic Entomology*, 35, 277–305.
https://doi.org/10.1111/j.1365-3113.2009.00509.x

Lee, Y.J., Marshall, D.C., Mohagan, A. & Hill, K.B.R. (2016) Cicadas (Hemiptera: Cicadidae) from Camiguin of Mindanao Province and Dinagat Island in the Philippines, with a new genus and three new species. *Zootaxa*, 4097 (2), 187–202.
https://doi.org/10.11646/zootaxa.4097.2.2

Lin, N., Berton, P., Moraes, C., Rogers, R.D. & Tufenkji, N. (2018) Nanodarts, nanoblades, and nanospikes: Mechano-bactericidal nanostructures and where to find them. *Advances in Colloid and Interface Science*, 252, 55–68.
https://doi.org/10.1016/j.cis.2017.12.007

Logan, D.P. & Alspatch, P.A. (2007) Negative association between chorus cicada, *Amphipsalta zelandica*, and armillaria root disease in kiwifruit. *New Zealand Plant Protection*, 60, 235–240.

Łukasik, P., Nazario, K., Van Leuven, J.T., Campbell, M.A., Meyer, M., Michalik, A., Pessacq, P., Simon, C., Veloso, C. & McCutcheon, J.P. (2017) Multiple origins of interdependent endosymbiotic complexes in a genus of cicadas. *Proceedings of the National Academy of Sciences of the United States of America*, 115 (2), 226–235. [E226–E235]
https://doi.org/10.1073/pnas.1712321115

Maddison, W.P. & Maddison, D.R. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.04. http://mesquiteproject.org (accessed 7 March 2015)

Marshall, D.C. (2015) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 72, 217–219.

Marshall, D.C. & Hill, K.B.R. (2014) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 71, 103–107.

Marshall, D.C., Hill, K.B.R., Cooley, J.R. & Simon, C. (2011) Hybridization, mitochondrial DNA taxonomy, and prediction of the early stages of reproductive isolation: Lessons from New Zealand cicadas of the genus *Kikihia*. *Systematic Biology*, 60, 482–502.
https://doi.org/10.1093/sysbio/syr017

Marshall, D.C., Hill, K.B.R., Marske, K.A., Chambers, C., Buckley, T.R. & Simon, C. (2012) Limited, episodic diversification and contrasting phylogeography in a New Zealand cicada radiation. *BMC Evolutionary Biology*, 12, 177.
https://doi.org/10.1186/1471-2148-12-177

Marshall, D.C., Hill, K.B.R., Moulds, M.S., Vanderpool, D., Cooley, J.R., Mohagan, A.B. & Simon, C. (2016) Inflation of molecular clock rates and dates: Molecular phylogenetics, biogeography, and diversification of a global cicada radiation from Australasia (Hemiptera: Cicadidae: Cicadettini). *Systematic Biology*, 65, 16–34.
https://doi.org/10.1093/sysbio/syv069

Marshall, D.C., Moulds, M.S., Boulard, M., Sanborn, A., Ewart, A., Wei, C., Price, B., Marathe, K., Popple, L.W., Price, B.W. & Simon, C. (2018) PLATYPLEURINI Schmidt, 1918: Proposed precedence over HAMZARIA Distant, 1905 to conserve nomenclatural stability in the CICADIDAE (Insecta: Hemiptera: Auchenorrhyncha: Cicadoidea). *Bulletin of Zoological Nomenclature*. [in review]

Marshall, D.C., Slon, K., Cooley, J.R., Hill, K.B.R. & Simon, C. (2008) Steady Plio-Pleistocene diversification and a 2-million-year sympatry threshold in a New Zealand cicada radiation. *Molecular Phylogenetic and Evolution*, 48, 1054–1066. https://doi.org/10.1016/j.ympev.2008.05.007

McCutcheon, J.P., McDonald, B.R. & Moran, N.A. (2009) Origin of an alternative genetic code in the extremely small and GC–rich genome of a bacterial symbiont. *PLoS Genetics*, 5, e1000565. https://doi.org/10.1371/journal.pgen.1000565

Mehdipour, M., Zamanian, H., Farazmand, H. & Hosseini-Gharalari, A. (2016) Disruption of reproductive behavior of grapevine cicada, *Cicadatra alhageos*, by acoustic signals playback. *Entomologia Experimentalis et Applicata*, 158, 210–216. https://doi.org/10.1111/eea.12394

Metcalf, Z.P. (1963) *General catalogue of the Homoptera. Fascicle VIII. Cicadoidea. Part 1. Cicadidae. Section I. Tibiceninae. Paper No. 1502*. North Carolina State College, Raleigh, 585 pp.

Moulds, M.S. (1990) *Australian cicadas.* New South Wales University Press, Kensington, 217 pp.

Moulds, M.S. (2003) An appraisal of the cicadas of the genus *Abricta* Stål and allied genera (Hemiptera: Auchenorrhyncha: Cicadidae). *Records of the Australian Museum*, 55, 245–304. https://doi.org/10.3853/j.0067-1975.55.2003.1386

Moulds, M.S. (2005) An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. *Records of the Australian Museum*, 57, 375–446. https://doi.org/10.3853/j.0067-1975.57.2005.1447

Moulds, M.S. (2008) Talcopsaltriini, a new tribe for a new genus and species of Australian cicada (Hemiptera: Cicadoidea: Cicadidae). *Records of the Australian Museum*, 60, 207–214. https://doi.org/10.3853/j.0067-1975.60.2008.1496

Moulds, M.S. (2012) A review of the genera of Australian cicadas (Hemiptera: Cicadoidea). *Zootaxa*, 3287, 1–262.

Myers, J.G. (1929) *Insect singers: a natural history of the cicadas.* George Routledge and Sons, London, 304 pp.

Owen, C.L., Marshall, D.C., Hill, K.B.R. & Simon, C. (2015) The phylogenetic utility of acetyltransferase (ARD1) and glutaminyl tRNA synthetase (QtRNA) for reconstructing Cenozoic relationships as exemplified by the large Australian cicada *Pauropsalta* generic complex. *Molecular Phylogenetics and Evolution*, 83, 258–277. https://doi.org/10.1016/j.ympev.2014.07.008

Owen, C.L., Marshall, D.C., Hill, K.B.R. & Simon, C. (2017) How the aridification of Australia structured the biogeography and influenced the diversification of a large lineage of Australian cicadas. *Systematic Biology*, 66, 569–589. https://doi.org/10.1093/sysbio/syw078

Pham, H.T. & Yang, J-T. (2012) First record of the cicada genus *Karenia* Distant, 1888 (Hemiptera: Cicadidae) from Vietnam, with description of a new species. *Zootaxa*, 3153, 32–38.

Popple, L.W. (2013) A revision of the *Pauropsalta annulata* Goding & Froggatt species group (Hemiptera: Cicadidae) based on morphology, calling songs and ecology, with investigations into calling song structure, molecular phylogenetic relationships and a case of hybridisation between two subspecies. *Zootaxa*, 3730 (1), 1–102. https://doi.org/10.11646/zootaxa.3730.1.1

Popple, L.W. & Emery, D.L. (2010) A new cicada genus and a redescription of *Pauropsalta subolivacea* Ashton (Hemiptera: Cicadidae) from eastern Australia. *Australian Entomologist*, 30, 107–114.

Price, B.W. (2010) *Historical biogeography of the tribe Platypleurini Schmidt, 1918 (Hemiptera: Cicadidae) with a focus on southern Africa*. Ph.D. dissertation, Rhodes University, Grahamstown, 133 pp.

Price B.W., Marshall, D., Barker, N.P., Simon, C. & Villet, M.H. (2018) Out of Africa: a molecular phylogeny of the tribe Platypleurini Schmidt, 1918 (Hemiptera: Cicadidae), with a focus on the genus *Platypleura* (Amyot & Seville, 1843) in Africa. [in preparation]

Puissant, S., Boulard, M., Lee, Y.J., Hayashi, M. & Sueur, J. (2015) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 72, 219–220.

Python Software Foundation (2010) Python version 2.7. Available from: http://www.python.org/psf (accessed 1 March 2013)

Rambaut, A. & Drummond, A.J. (2007) Tracer v1.5. Available from http://evolve.zoo.ox.ac.uk (accessed 12 December 2013)

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. https://doi.org/10.1093/sysbio/sys029

Ruschel, T.P. (2015) *Revisão taxonômica de* Dorisiana *Metcalf, 1952 (Hemiptera, Auchenorrhyncha, Cicadidae, Cicadinae, Fidicinini).* M.Sc. dissertation, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, 159 pp. Available from: http://hdl.handle.net/10923/7325 (accessed 22 July 2015).

Sanborn, A.F. (2013). *Catalogue of the Cicadoidea (Hemiptera: Auchenorrhyncha).* Academic Press, San Diego, 1001 pp. Printed with publication date 2014 but published on 14 November 2013, according to Elsevier website. Available from: https://www.elsevier.com/books/catalogue-of-the-cicadoidea-hemiptera-auchenorrhyncha/sanborn/978-0-12-416647-9

(accessed 25 September 2017)

Sanborn, A.F. (2014a) A new genus and new tribe of cicada from South America (Hemiptera: Cicadoidea: Cicadidae) with a note on the taxonomic position of *Ahomana* Distant, 1905. *Proceedings of the Entomological Society of Washington*, 116, 339–348.
https://doi.org/10.4289/0013-8797.116.3.339

Sanborn, A.F. (2014b) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 71, 108–118.

Sanborn, A.F. (2017) Generic redescription, seven new species and a key to the *Taphura* Stål, 1862 (Hemiptera: Cicadidae: Cicadettinae: Taphurini). *Zootaxa*, 4324 (3), 451–481.
https://doi.org/10.11646/zootaxa.4324.3.3

Sanborn, A.F. (2018) The cicada genus *Procollina* Metcalf, 1952 (Hemiptera: Cicadidae): redescription including fourteen new species, with a key to the species of the subtribe Dazina Kato, 1932 rev. stat., the description of the Aragualnini n. tribe, and one new combination. *Zootaxa*, 4389 (1), 1–65.
https://doi.org/10.11646/zootaxa.4389.1.1

Sanborn, A.F. & Heath, M.S. (2017) Replacement name for the cicada genus *Torresia* Sanborn and Heath, 2014 (Hemiptera: Cicadidae: Tibicininae: Tettigadini) and two new combinations. *Zootaxa*, 4286, 115.
https://doi.org/10.11646/zootaxa.4286.1.6

Sanborn, A.F., Heath, J.E., Heath, M.S. & Phillips, P.K. (2017) Thermal adaptation in North American cicadas (Hemiptera: Cicadidae). *Journal of Thermal Biology*, 69, v–xviii.
https://doi.org/10.1016/j.jtherbio.2017.07.011

Sanborn, A.F., Phillips, P.K. & Sites, R.W. (2007) Biodiversity, biogeography, and bibliography of the cicadas of Thailand (Hemiptera: Cicadoidea: Cicadidae). *Zootaxa*, 1413, 1–46.

Sanborn, A.F., Phillips, P.K. & Villet, M.H. (2016) Song analysis of South African pygmy bladder cicadas (Hemiptera: Cicadidae: Cicadettinae: Tettigomyiini). *Annals of the Entomological Society of America*, 109, 526–533.
https://doi.org/10.1093/aesa/saw024

Sanborn, A.F., Villet, M.H. & Phillips, P.K. (2003) Hot-blooded singers: endothermy facilitates crepuscular signaling in African platypleurine cicadas (Hemiptera: Cicadidae: *Platypleura* spp.). *Naturwissenschaften*, 90, 305–308.
https://doi.org/10.1007/s00114-003-0428-1

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87, 651–701.
https://doi.org/10.1093/aesa/87.6.651

Song, H., Buhay, J.E., Whiting, M.F. & Crandall, K.A. (2008) Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. *Proceedings of the National Academy of Sciences*, 105, 13486–13491.
https://doi.org/10.1073/pnas.0803076105

Sota, T., Yamamoto, S., Cooley, J.R., Hill, K.B.R., Simon, C. & Yoshimura, J. (2013) Independent divergence of 13- and 17-yr life cycles among three periodical cicada lineages. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 6919–6924.
https://doi.org/10.1073/pnas.1220060110

Stamatakis, A. (2006) Phylogenetic models of rate heterogeneity: a high performance computing perspective. *In* IPDPS 2006 (Ed.), *Proceedings 20th IEEE International Parallel & Distributed Processing Symposium, Rhodos Island, Greece.* IEEE, San Diego, 8 pp.
https://doi.org/10.1109/IPDPS.2006.1639535

Sueur, J., Vanderpool, D., Simon, C., Ouvrard, D. & Bourgoin, T. (2007) Molecular phylogeny of the genus *Tibicina* (Hemiptera, Cicadidae): rapid radiation and acoustic behaviour. *Biological Journal of the Linnean Society*, 91, 611–626.
https://doi.org/10.1111/j.1095-8312.2007.00823.x

Swofford, D.L. (1998) PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4. Sinauer Associates, Sunderland.

Van Leuven, J.T., Meister, R.C., Simon, C. & McCutcheon, J.P. (2014) Sympatric speciation in a bacterial endosymbiont results in two genomes with the functionality of one. *Cell*, 158, 1270–1280.
https://doi.org/10.1016/j.cell.2014.07.047

Villet, M. (1993) The cicada genus *Bavea* Distant 1905 (Homoptera Tibicinidae): redescription, distribution and phylogenetic affinities. *Tropical Zoology*, 6, 435–440.
https://doi.org/10.1080/03946975.1993.10539232

Villet, M.H. (1994) The cicada genus *Stagea* n. gen. (Homoptera Tibicinidae): systematics. *Tropical Zoology*, 7, 293–297.
https://doi.org/10.1080/03946975.1994.10539259

Villet, M.H. (1997) The cicada genus *Stagira* Stål 1861 (Homoptera: Tibicinidae): systematic revision. *Tropical Zoology*, 10, 347–392.
https://doi.org/10.1080/03946975.1997.10539347

Villet, M.H. (1999) The cicada genus *Nyara* n. gen. (Homoptera Cicadidae): systematics, behaviour and conservation status. *Tropical Zoology*, 12, 157–163.
https://doi.org/10.1080/03946975.1999.10539385

Wang, X., He, Z. & Wei, C. (2017) A new species of *Cicadatra* Kolenati, 1857 from China, with primary phylogenetic analyses of the tribe Cicadatrini (Hemiptera: Cicadidae). *Zootaxa*, 4242, 174–184.
https://doi.org/10.11646/zootaxa.4242.1.9

Wei, C., Tang, G., He, H. & Zhang, Y. (2009) Review of the cicada genus *Karenia* (Hemiptera: Cicadidae), with a description of one new species trapped by clapping hands and its entomogenous fungus. *Systematics and Biodiversity*, 7, 337–343.
https://doi.org/10.1017/S147720000999003X

Williams, K.S. & Simon, C. (1995) The ecology, behavior, and evolution of periodical cicadas. *Annual Review of Entomology*, 40, 269–295.
https://doi.org/10.1146/annurev.en.40.010195.001413

Xie, G., Zhang, G., Lin, F., Zhang, J., Liu, Z. & Mu, S. (2008) The fabrication of subwavelength anti-reflective nanostructures using a bio-template. *Nanotechnology* 19 (095605), 1–5.
https://doi.org/10.1088/0957-4484/19/9/095605

Zada, I., Zhang, W., Li, Y., Sun, P., Cai, N., Gu, J., Liu, Q., Su, H. & Zhang, D. (2016) Angle dependent antireflection property of TiO2 inspired by cicada wings. *Applied Physics Letters*, 109, 153701.
https://doi.org/10.1063/1.4962903

Zhang, G., Xhang, J., Xie, G., Liu, Z. & Shao, H. (2006) Cicada wings: a stamp from nature for nanoimprint lithography. *Small*, 2, 1440–1443.
https://doi.org/10.1002/smll.200600255

Zwickl, D.J. (2006) *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion.* Ph.D. dissertation. The University of Texas, Austin, 115 pp.