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The molecular systematics and diversification of a taxonomically unstable group of Asian cicada tribes related to Cicadini Latreille, 1802 (Hemiptera : Cicadidae)

Kathy B. R. Hill[A,1], *David C. Marshall*[A,P,1], *Kiran Marathe*[B,M], *Maxwell S. Moulds*[C], *Young June Lee*[D], *Thai-Hong Pham*[E,F], *Alma B. Mohagan*[G], *Vivek Sarkar*[B,I,N], *Benjamin W. Price*[J], *J. P. Duffels*[K], *Marieke A. Schouten*[O], *Arnold J. de Boer*[L], *Krushnamegh Kunte*[B] and *Chris Simon*[A]

[A]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA. Email: david.marshall@uconn.edu; chris.simon@uconn.edu
[B]National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK Campus, Bellary Road, Bengaluru 560 065, Karnataka, India. Email: kiran@ifoundbutterflies.org; vivek@ifoundbutterflies.org; krushnamegh@ncbs.res.in
[C]Australian Museum Research Institute, 1 William Street, Sydney, NSW 2010, Australia. Email: msmoulds@gmail.com
[D]Bolton, CT 06043, USA. Email: cicaderolee@gmail.com
[E]Mientrung Institute for Scientific Research, Vietnam Academy of Science and Technology, Hue, Vietnam.
[F]Vietnam National Museum of Nature and Graduate School of Science and Technology, Vietnam Academy of Science and Technology, Hanoi, Vietnam. Email: phamthai1976@yahoo.com
[G]Central Mindanao University, Sayre Highway, Maramag, Bukidnon, Philippines. Email: almohagan@gmail.com
[I]Wildlife Institute of India – Category 2 Centre (WII-C2C) for World Natural Heritage Management and Training for Asia and the Pacific Region, under the auspices of UNESCO, Wildlife Institute of India, Chandrabani, Dehradun, Uttarakhand-248001, India.
[J]Life Sciences Department, Natural History Museum, London, SW7 5BD, UK. Email: b.price@nhm.ac.uk
[K]Naturalis Biodiversity Center, PO Box 9517, NL-2300 RA Leiden, Netherlands. Email: hans.duffels@naturalis.nl
[L]Zoological Museum, Department of Entomology, University of Amsterdam, Plantage Middenlaan 64, NL-1018 DH Amsterdam, Netherlands.
[M]Present address: Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC, V6T 1Z4, Canada.
[N]Present address: Department of Zoology, North Orissa University, Sri Ram Chandra Vihar, Takatpur, Mayurbhanj, Baripada, Odisha 757 003, India.
[O]Deceased. Formerly at Eurofins MITOX BV, Science Park 408, 1098XH Amsterdam, Netherlands.
[P]Corresponding author. Email: david.marshall@uconn.edu

Abstract. The cicadas (Hemiptera: Cicadidae) related to tribe Cicadini exhibit some of the most remarkable phenotypes in the family, with many genera possessing striking colour patterns and unusual morphological features. This largely Asian group of 13 tribes has proven challenging for cicada taxonomists, in part because of likely convergent evolution or losses of these phenotypes. We present the first focused molecular phylogeny of this clade, including ~60 described genera. The genetic dataset contains 839 ingroup-informative sites (out of 2575) from mitochondrial cytochrome *c* oxidase subunit I, nuclear elongation factor-1 α, and nuclear acetyltransferase. We use Bayesian and maximum likelihood trees to test recent changes in tribe- and subtribe-level classification, and we reconstruct ancestral character states for potentially convergent traits influencing tribe descriptions. We use fossil and molecular clock calibrations to estimate the temporal and geographic context of the radiation. The tribes Gaeanini, Leptopsaltriini, Platypleurini, Psithyristriini, and Tosenini appear polyphyletic and in need of revision, in part because of convergent evolution of opaque wings and multiple convergent gains or losses of abdominal tubercles. *Kalabita* Moulton, 1923 is transferred from Platypleurini to Leptopsaltriini. *Vittagaeana* **gen. nov.** is established for *Vittagaeana paviei* **comb. nov.** and *Vittagaeana dives* **comb. nov.**, formerly in *Tosena*. Sinosenini **syn. nov.** is synonymised with

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[1]The two senior authors contributed equally to this work.

Dundubiina. Ayuthiini **trib. nov.** is established with two **new subtribes** for *Ayuthia* Distant, 1919 and *Distantalna* Boulard, 2009, formerly in Tosenini. For the earliest split in the tree, one common ancestor appears to have been Indian + Asian in geographic distribution and the other Asian. We estimate that the radiation began in the middle Cenozoic Era, possibly as recently as the early Miocene. The recent and steady pattern of diversification suggests that refinement of tribe diagnoses will prove challenging.

http://zoobank.org:urn:lsid:zoobank.org:pub:5A6C16F4-5269-453B-BA5C-B29C3394683A

Keywords: wing morphology, tubercles, character state reconstruction, convergence, family group classification, nomenclature, biogeography, divergence times, Cenozoic Era, India, Auchenorrhyncha.

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Introduction

Cicadas (Hemiptera: Cicadidae Latreille, 1802) are diverse, charismatic, and well known insects in Asia, where many books on the regional fauna have been published (e.g. Kato 1932; Lee 1995, 2005; Chou *et al*. 1997; Chen 2004; Boulard 2007, 2013; Hayashi and Saisho 2011). Nearly 70 genera and over 250 species in at least 18 tribes are known in China (Chou *et al*. 1997); Hainan Island alone hosts at least 28 genera (Yang and Wei 2013). By comparison, 15 genera, 191 species or subspecies, and 6 tribes are known from the United States (Sanborn and Heath 2012). Subtropical habitats in south-east Asia are especially rich, with over 60 genera known for Thailand, Laos, Cambodia, and Vietnam combined (Sanborn *et al*. 2007; Lee 2008, 2010*a*, 2014; Boulard 2013). A recent checklist for the Indian subcontinent recorded over 280 species in 73 genera and 20 tribes (Price *et al*. 2016). Many cicadas from Asia are large-bodied, like Malaysia's *Megapomponia imperatoria* (Westwood, 1842), the world's largest. Some have striking patterns of wing colouration (Fig. 1) and other intriguing derived phenotypes (Boulard and Puissant 2013, 2016). Many have extraordinarily loud, high-pitched, metallic, or acoustically complex songs (e.g. Kos and Gogala 2000; Leong 2012; Puissant and Lee 2016). One new genus is reported to change colour slowly after capture while alive (Wei *et al*. 2020).

In a recent family-level molecular study, half of the sampled Cicadidae tribes found in Asia belonged to one monophyletic group affiliated with the nominotypical tribe Cicadini Latreille, 1802 in subfamily Cicadinae (see Clade 9 in Marshall *et al*. 2018). This clade contains ~725 species-level taxa in 88 genera and 13 of the 53 world-wide cicada tribes (Sanborn 2013; Marshall *et al*. 2018; Sanborn *et al*. 2020). It accounts for up to 70% of the Asian species and about one-fifth of all cicadas globally. With just two of its genera and a handful of species extending beyond Asia, the group is one of several examples of high geographic affinity of tribe-level clades, and we refer to it here as the Asian cicada clade. Other cicada tribes found in Asia have more global distributions.

Higher taxonomy within the Asian cicada clade has undergone extensive change in recent decades, with many tribes or subtribes being synonymised and later resurrected or changed in composition or hierarchical level (Fig. 2). Only three of 13 tribes have remained at tribal level throughout this

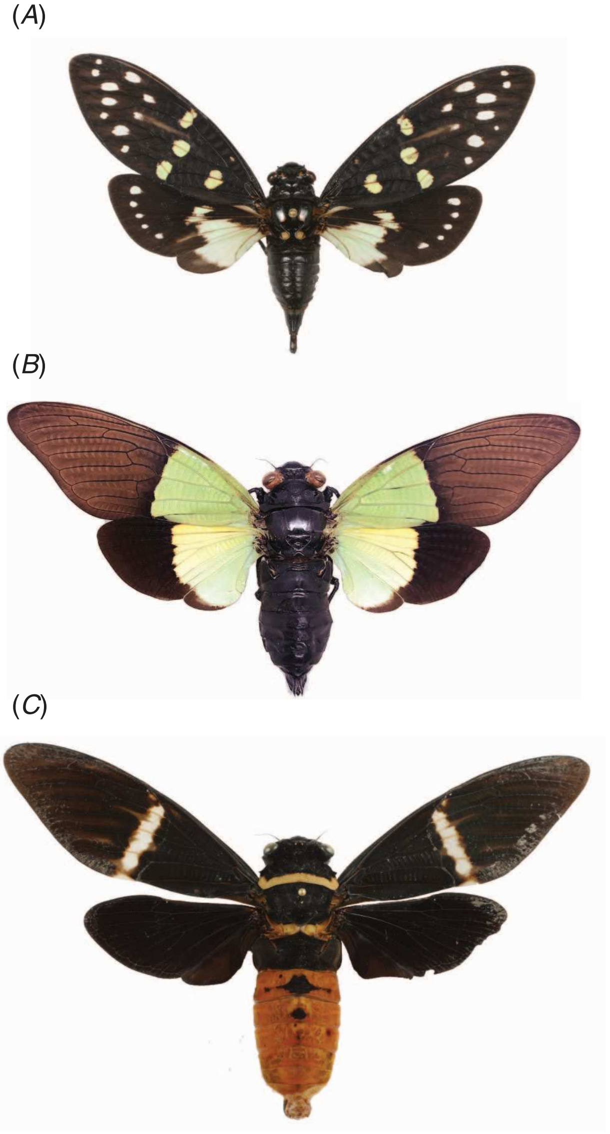
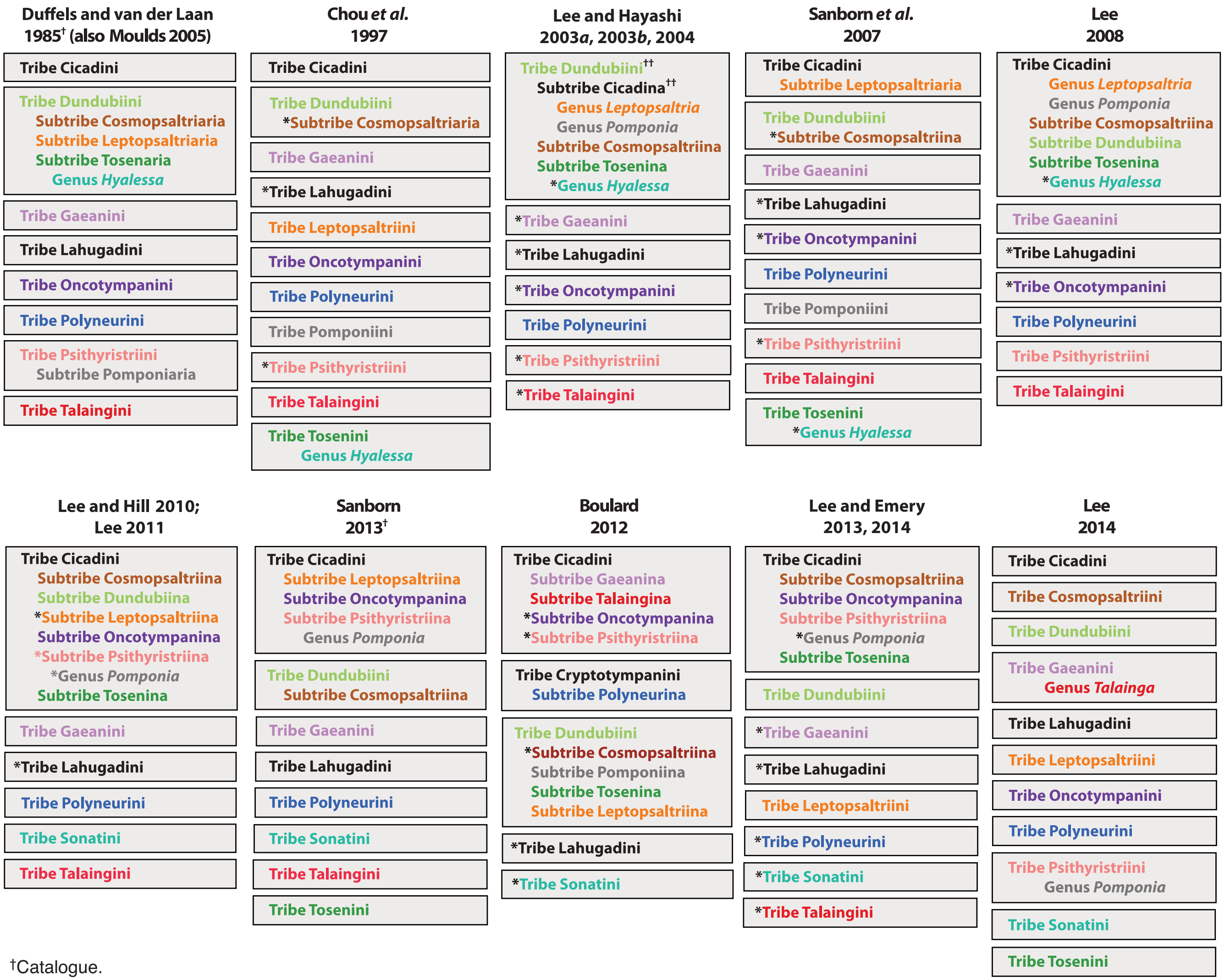


Fig. 1. Three cicadas from the Asian clade illustrating colourful, opaque-winged phenotypes. *A*, *Gaeana maculata* (Drury, 1773). *B*, *Trengganua sibylla* (Stål, 1863). *C*, *Tosena melanopteryx* Kirkaldy, 1909.



†Catalogue.

††Lee and Hayashi (2003*b*) placed Cicadina as a subtribe of Dundubiini but Cicadini has priority.

*Not addressed in the listed publication; shown with status at that time.

Fig. 2. Historical shifts in classification for cicadas in the Asian cicada clade (subfamily Cicadinae), tribe Cicadini and allied tribes. Only names that have been used at tribal rank are shown (or type genera of such names); subtribes are discussed in the text. Where multiple papers are cited, the changes occurred over multiple publications. Cicadmalleini was added in 2013 and is not shown. Sinosenini was classified in subfamily Cicadettinae until 2018 (Marshall *et al*. 2018) and is not shown. See text for authorities. Cited references are: Duffels and van der Laan 1985; Chou *et al*. 1997; Lee and Hayashi 2003*a*, 2003*b*, 2004; Moulds 2005; Sanborn *et al*. 2007; Lee 2008, 2011, 2014; Lee and Hill 2010; Boulard 2012; Lee and Emery 2013, 2014; Sanborn 2013. Figure modified with permission from Marshall *et al*. (2018), *Zootaxa* (https://www.mapress.com/j/zt), copyright Magnolia Press.

period, and a sense of taxonomic uncertainty exists (Marshall *et al*. 2018; Wei *et al*. 2020). In the context of the family phylogeny, the Asian cicada clade contains more tribes than other lineages of similar genetic depth (Marshall *et al*. 2018). Repeated and convergent evolution of characters like wing colouration and venation may have played a role, as has been shown in other cicada groups. For example, Huechysini Distant, 1905 was created for four opaque-winged genera in Cicadettinae Buckton, 1890, but two of them (*Huechys* Amyot & Audinet-Serville, 1843 and *Scieroptera* Stål, 1866) were found by molecular analysis to be distantly related within the mostly hyaline winged tribe Cicadettini Buckton, 1890 (Marshall *et al*. 2016) and Huechysini has been synonymised (Lee *et al*. 2016). Three tribes likely to belong to the Asian cicada clade were initially defined in part by opaque wings, or included only genera with this attribute (Gaeanini Distant, 1905; Polyneurini Amyot & Audinet-Serville, 1843; Tosenini Amyot & Audinet-Serville, 1843), and their definitions have not been revised in recent years. Family group classification in the Asian clade has also been substantially influenced by characters involved in sound production, including loss of timbals in one tribe (Boulard 1975) and these traits are known to have evolved convergently (reviewed in Moulds 2005 and Marshall *et al*. 2018).

Another example of a problematic morphological feature found within the Asian cicada clade is abdominal tubercles, protrusions of unknown function that extend in pairs from one or more abdominal sternites (Fig. 3). Moulton (1923) used

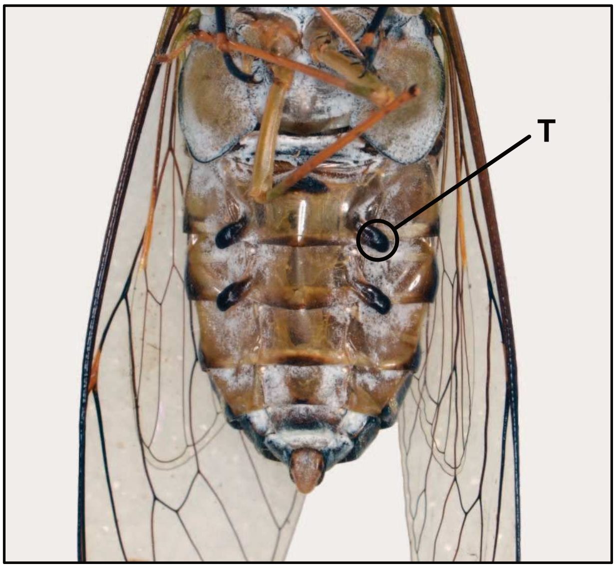


Fig. 3. Ventral view of male *Maua quadrituberculata* (Signoret, 1847) specimen with one of four abdominal tubercles indicated (T).

these to characterise tribe Leptopsaltriini Moulton, 1923 (as Leptopsaltraria). However, Lee (2009*b*) noted taxonomic inconsistency in the presence and number of tubercles, and Lee and Hill (2010) pointed to molecular data suggesting that *Leptosemia* Matsumura, 1917 and *Neocicada* Kato, 1932, which lack tubercles, are embedded within a larger clade of tubercle-bearing genera. However, the study lacked strong genetic support. Currently, many genera without tubercles are included in Leptopsaltriini (Lee and Emery 2013; Marshall *et al*. 2018).

Past sampling of the Asian clade within family-level genetic trees has been limited. The largest study (Marshall *et al*. 2018) sampled 20 genera and lacked two likely member tribes (Tosenini and Cicadmalleini Boulard & Puissant, 2013). Lee and Hill (2010) and Matsuura *et al*. (2018) each sampled only 17 genera; just two opaque winged genera were included. Disproportionately few species have been sampled from the Indian subcontinent, considering that a recent checklist recorded 105 species or subspecies classified in probable tribes of the clade (Price *et al*. 2016).

In this paper, we present a focused molecular phylogenetic analysis of the Asian cicada clade, based on species from 60 of the 88 described ingroup genera (140 of the ~725 spp.) and several undescribed lineages, including the type genera of up to 12 out of 13 tribes and many species from the Indian subcontinent. We explore the taxonomic implications of the tree while examining the phylogenetic utility of key phenotypes. We make some taxonomic changes but leave broader revision to future comparative studies. Because the Marshall *et al*. (2018) analysis showed that Indian lineages are well distributed within the Asian clade, we reconstruct ancestral geographic areas and estimate divergence times in order to test the possibility of an Indian origin for the group.

Methods

Specimen collection and DNA sequencing

Cicada specimens were preserved whole in ethanol at –20 or –80°C or pinned for museum storage after removal of 1–3 legs into ethanol. Occasionally, dried legs were removed from museum specimens. Identification was completed by the authors using published photographs, illustrations, and literature descriptions with assistance from original collectors and other experts (see Acknowledgments). Undescribed taxa were classified to the extent possible. Approximately 140 species or subspecies were sampled from the target group (see Table 1, which includes taxonomic authorities). Five species from the tribes Platypleurini Schmidt, 1918 (*Platypleura* Amyot & Audinet-Serville, 1843; *Yanga* Distant, 1904) and Cryptotympanini Handlirsch, 1925 (*Cryptotympana* Stål, 1861; *Tacua* Amyot & Audinet-Serville, 1843) were used as outgroups, following the genetic tree of Marshall *et al*. (2018). The classification here follows the most recent catalogue (Sanborn 2013) and changes made by subsequent publications, excluding Boulard's (2012, 2013) independent system noted in Fig. 2. The name Platypleurini was recently conserved by conditional reversal of precedence of Hamzini Distant, 1905 (International Commission on Zoological Nomenclature 2020).

Specimens collected by authors from the C. Simon laboratory and some collaborators were assigned an 11-digit voucher code containing two digits for the year, two letters for the country, two letters for the district, three letters for the location, and two digits for the specimen number. Field codes established by collaborators were usually retained. Alcohol-preserved specimens are stored in the C. Simon research collection and some pinned specimens are stored at the University of Connecticut Biodiversity Research Collection. All the recently collected Indian specimens are deposited in the Research Collections of the National Centre for Biological Sciences, India (NCBS) as wet (the entire body preserved in 100% ethanol, stored at –40°C), wet and dry (three legs in 100% ethanol, the remaining specimen pinned dry), and dry specimens (entire body pinned dry). A few Asian pinned voucher specimens are stored in the collections of Y. J. Lee, M. S. Moulds and T.-H. Pham.

DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen Inc., Valencia, CA, USA) or the Nucleospin Tissue kit (Clontech, Mountain View, CA, USA), with a Proteinase K digestion time of ~18 h at 54°C. Standard polymerase chain reaction (PCR) techniques and the Ex Taq kit (Takara Bio Inc., Otsu, Shiga, Japan) or Titanium taq (also Takara Bio) were used to amplify three DNA regions: (1) the 5′ ('Barcoding') region of the mitochondrial cytochrome *c* oxidase subunit I gene (*COI*) was amplified using the primers C1-J-1490 and C1-N-2198 (Folmer *et al*. 1994) with an annealing temperature of 45°C; (2) a central section of the nuclear elongation factor-1 alpha (*EF-1α*) gene was amplified using the primers EF1-PA-f650ambig (Lee and Hill 2010) and EF1-N-1419 (Sueur *et al*. 2007) with an annealing temperature of 45–58°C; and (3) the nuclear acetyltransferase (*ARD1*) gene was amplified using the primers ARD1_1041F and ARD1_1733R (Owen

Table 1. Specimen table

Cicada specimens sequenced, with taxonomic authorities, collection data, GenBank accession codes, and voucher codes. Collectors given just by initials are authors of this article: KH, Kathy B. R. Hill; DM, David C. Marshall; KM, Kiran Marathe; MM, Maxwell S. Moulds; YJL, Young June Lee; THP, Thai-Hong Pham; AM, Alma B. Mohagan; VS, Vivek Sarkar; BP, Benjamin W. Price; JP, J. P. Duffels; MS, Marieke A. Schouten; AB, Arnold J. de Boer; KK, Krushnamegh Kunte; CS, Chris Simon. Other abbreviations are: IRSNB, Royal Belgian Institute of Natural Sciences; KNIC, Korea National Insect Collection. For gene abbreviations see Methods. All dates are >1999

Genus	Species	Authority	Date (D/M/Y)	Location	Lat.	Long.	Collectors	*COI*	*EF-1α*	*ARD1*	Voucher code
Aceropyga	*corynetus corynetus*	Duffels, 1977	29/1/03	Fiji: Viti Levu	–17.441	178.093	KH, DM	MW479513	MT599151	MT599003	03.FJ.WE.NAH.01
Aceropyga	*distans distans*	(Walker, 1858)	26/1/03	Fiji: Viti Levu	–18.077	178.448	KH, DM	GQ527084	MT599150	MT599002	03.FJ.CE.COL.01
Aceropyga	*poecilochlora*	(Walker, 1858)	19/12/07	Vanuatu: Malakula, Dog's Neck	–16.153	167.455	M Espeland, P Ala	MT639352	MT599310	MT599142	Vanuatu.30a
Aetanna	*pallidula*	Lee, 2014	1/5/05	Laos: Luang Namtha Pr.	–	–	Jönsson, Malm, Viklund	MT639333	MT599285	–	Laos30a
Ambragaeana	*ambra*	Chao & Yao, 1985	12/7/07	China: Fenghua, Yunlong Co.	–	–	M Villet	–	MT599289	MT599125	MHV0814
Ayesha	sp.	Distant, 1905	–/9/05	Malaysia	–	–	YJL	GQ527091	MT599179	MT599025	05.MY.SB.KKB.03
Ayuthia	*spectabile* [1]	Distant, 1919	–/4/11	Malaysia: Perak, Tapah Hills	–	–	L Jingke	MT639267	MT599213	MT599058	11.MY.PK.TAP.01
Ayuthia	*spectabile* [2]	Distant, 1919	–/4/11	Malaysia: Perak, Tapah Hills	–	–	L Jingke	MT639268	MT599214	MT599059	11.MY.PK.TAP.02
Balinta	cf. *tenebricosa* [1]	(Distant, 1888)	–/4–5/03	Laos: Mount Pan (Ph.-Pan)	–	–	H Karuba	MT639228	MT599159	MT599011	03.LA.XA.PAN.03
Balinta	cf. *tenebricosa* [2]	(Distant, 1888)	24/5/12	Vietnam: Cuc Phuong NP	20.263	105.702	KH, DM, THP	MT639289	MT599236	MT599081	12.VN.NB.CPS.04
Becquartina	*bleuzeni* [1]	Boulard, 2005	6/5/11	Vietnam: Tam Dao NP	–	–	AB, MS	MT639273	MT599220	MT599065	11.VN.VP.TDP.13
Becquartina	*bleuzeni* [2]	Boulard, 2005	6/5/11	Vietnam: Tam Dao NP	–	–	AB, MS	MT639274	MT599221	MT599066	11.VN.VP.TDP.20
Becquartina	*electa* [1]	(Jacobi, 1902)	18/5/12	Vietnam: Bach Ma NP	16.198	107.861	KH, DM, THP	MT639294	MT599241	MT599086	12.VN.TT.BMT.04
Becquartina	*electa* [2]	(Jacobi, 1902)	12/7/07	China: Fenghua, Yunlong Co.	–	–	M Villet	MT639336	MT599290	MT599126	MHV0816
Cabecita	sp. [1]	Lee, 2014	5–6/6/07	Thailand: Sakon Nakhon Pr.	–	–	W Kongnara	MT639248	MT599192	MT599038	07.TH.SN.PPN.01
Cabecita	sp. [2]	Lee, 2014	2–9/5/07	Thailand: Ubon Ratchathani Pr.	15.456	105.581	S Mingman	MT639249	MT599193	MT599039	07.TH.UR.PTN.01
Calcagninus	*picturatus*	(Distant, 1888)	14/6/12	India: Kerala, Kozhikode	11.333	76.067	BP	MT639322	MT599275	–	NCBS_AC221
Calcagninus	sp. [1]	Distant, 1892	6/6/12	India: Kerala, Thiruvanan.	8.750	77.100	BP	MT639316	MT599268	–	NCBS_AC197
Calcagninus	sp. [2]	Distant, 1892	11/6/12	India: Kerala, Idukki	9.967	77.133	BP	MT639320	MT599273	–	NCBS_AC213
Callogaeana	cf. *guangxiensis* [1]	Chao & Yao, 1985	15/6/08	China: Anhui, Yuexi, Tiantou	–	–	L Jingke	MT639252	–	–	08.CN.AH.TIA.21
Callogaeana	cf. *guangxiensis* [2]	Chao & Yao, 1985	24/5/12	Vietnam: Cuc Phuong NP	20.263	105.702	KH, DM, THP	MT639288	MT599235	MT599080	12.VN.NB.CPS.03
Callogaeana	cf. *guangxiensis* [3]	Chao & Yao, 1985	6/5/11	Vietnam: Tam Dao NP	–	–	AB, MS	MT639276	MT599223	MT599068	11.VN.VP.TDP.23
Champaka	cf. *solivenae*	Lee, 2015	3/5/12	Philippines: Mindanao	8.165	124.933	KH, DM, D Mohagan	MT639283	MT599230	MT599075	12.PH.MN.KGS.10
Champaka	*solivenae*	Lee, 2015	9/7/10	Philippines: Mindanao	7.017	125.233	KH, J Jones, D Mohagan	MT639265	MT599211	MT599056	10.PH.MN.SCI.10
Champaka	*spinosa* [1]	(Fabricius, 1787)	–/7/09	Malaysia: Sarawak	–	–	J Urban	MT639346	MT599300	MT599136	Mulu5.BORa
Champaka	*spinosa* [2]	(Fabricius, 1787)	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639345	MT599299	MT599135	Mulu3.BOR33
Changa	*sita* [1]	(Distant, 1881)	15/5/12	India: Nagaland, Peren District	25.648	93.479	BP	MG953084	MT599264	MT599110	NCBS_AC177
Changa	*sita* [2]	(Distant, 1881)	17/5/12	India: Nagaland, Peren District	25.648	93.479	BP	MT639314	MT599267	MT599113	NCBS_AC183
Cicada	*lodosi*	Boulard, 1979	3/7/11	Turkey: Aydın, Söke, Gülübahçe	37.659	27.296	T Trilar, M Gogala	MT639272	MT599218	MT599063	11.TR.AY.PRI.01
Cicada	*mordoganensis* [1]	Boulard, 1979	12/8/11	Greece: Island Kos, Dykeos Mun.	36.842	27.147	T Trilar, KP Trilar	MT639266	MT599212	MT599057	11.GR.AI.PYL.01
Cicada	*mordoganensis* [2]	Boulard, 1979	24/6/11	Turkey: Aydın, Kuşadasi	37.728	27.309	T Trilar, M Gogala	MT639271	MT599217	MT599062	11.TR.AY.DAV.04
Cicada	*orni* [1]	Linnaeus, 1758	9/7/07	France: Bouches-du-Rhône	43.275	5.700	J Sueur, J Windmill	GQ527099	MT599183	MT599029	07.FR.BD.CLP.06
Cicada	*orni* [2]	Linnaeus, 1758	11/7/03	Croatia: Pirovik, Cela.	–	–	T Trilar, M Gogala	GQ527102	MT599152	MT599004	03.HR.SB.PIR.20
Cicadidae	sp. A	Latreille, 1802	16/5/12	India: Nagaland, Peren District	25.648	93.479	T Karmakar, S Joshi	–	MT599266	MT599112	NCBS_AC180
Cicadidae	sp. B	Latreille, 1802	12/4/13	India: Kerala, Kozhikode	–	–	G Agavekar	MT639349	MT599306	–	NCBS_PT208
Cicadinae	sp. A	Latreille, 1802	4/7/08	China: Guizhou, Doupengshan	26.377	107.474	T Sota	MT639326	MT599279	MT599118	China20080704a
Cicadinae	sp. B	Latreille, 1802	17/5/12	Vietnam: Bach Ma NP	16.220	107.858	KH, DM, THP	MT639292	MT599239	MT599084	12.VN.TT.BMB.03
Cicadinae	sp. C	Latreille, 1802	3/5/12	Philippines: Mindanao	8.165	124.933	KH, DM, D Mohagan	MT639281	MT599228	MT599073	12.PH.MN.KGS.01
Cicadmalleus	*micheli*	Bld. & Puis., 2013	–	Thailand	–	–	S Puissant, M Boulard	MW479512	–	–	Cicadmalleus1
Cosmopsaltria	*capitata*	Distant, 1888	–/1–2/09	PNG: Mount Bosuvai	–6.532	143.110	Bishop Museum	MT639259	MT599204	MT599049	09.PG.SH.NUN.01
Cosmopsaltria	*doryca*	(Boisduval, 1835)	6/2/09	Indonesia: Besum, nr. Genyem	–	–	MS, Mambrasar	MT639258	MT599203	MT599048	09.ID.WP.BES.B
Cosmopsaltria	*gestroei*	(Distant, 1905)	1/2/08	PNG: Morobe, Kamiali	–7.296	157.093	Bishop Museum	MT639253	MT599197	MT599042	08.PG.MR.KAM.01
Cryptotympana	*atrata*	(Fabricius, 1775)	1/7/03	Taiwan: Taoyuan Hsien	–	–	J-H Chen	GQ527122	MT599251	MT599096	03.TW.TY.CHP.24[A]
Diceropyga	*subapicalis*	(Walker, 1870)	9/1/07	Australia: Queensland	–12.715	143.286	KH, DM, MM	MT639239	MT599182	MT599028	07.AU.QL.CLA.04

(*continued next page*)

Table 1. (*continued*)

Genus	Species	Authority	Date (D/M/Y)	Location	Lat.	Long.	Collectors	*COI*	*EF-1α*	*ARD1*	Voucher code
Distantalna	*splendida* [1]	(Distant, 1878)	24/5/12	Vietnam: Cuc Phuong NP	20.263	105.702	KH, DM, THP	MT639287	MT599234	MT599079	12.VN.NB.CPS.02
Distantalna	*splendida* [2]	(Distant, 1878)	25/5/05	Vietnam: Cuc Phuong NP	–	–	THP, AB, MS	MT639328	MT599281	MT599119	CSL30
Dundubia	cf. *hastata*	(Moulton, 1923)	19/10/04	India: Meghalaya, Umpyrsung	25.116	92.359	Svenson	MT639235	MT599171	MT599019	04.IN.ML.UMP.01
Dundubia	cf. *vaginata*	(Fabricius, 1787)	24/4/12	Philippines: Mindanao	6.735	126.142	KH, DM, AM, Catanach	MT639278	MT599225	MT599070	12.PH.MN.HWC.11
Dundubia	sp.	A & A-S, 1843	16/4/12	India: West Bengal, Jalpaiguri	–	–	KK	–	MT599258	MT599103	NCBS_AB706
Dundubia	*spiculata*	Noualhier, 1896	–/9/04	Thailand	–	–	M Boulard	GQ527089	MT599173	–	04.TH.CR.DMK.01
Dundubia	*vaginata* [1]	(Fabricius, 1787)	–/4/03	Malaysia: Sabah	6.006	116.543	T Trilar, KP Trilar	GQ527104	MT599161	MT599013	03.MY.SA.KIN.23
Dundubia	*vaginata* [2]	(Fabricius, 1787)	2/7/10	Philippines: Dinagat, Santiago	10.377	125.635	KH, DM, AM, D Mohagan	MT639262	MT599207	MT599052	10.PH.DI.RED.03
Euterpnosia	*cucphuongensis*	Pham *et al*., 2010	24/5/12	Vietnam: Cuc Phuong NP	20.268	105.630	KH, DM, THP	MT639286	MT599233	MT599078	12.VN.NB.CPP.01
Euterpnosia	*viridifrons*	Matsum., 1917	4/6/03	Taiwan: Taipei Hsien	–	–	J-H Chen	MT639302	MT599249	MT599094	0545
Formosemia	*apicalis*	(Matsum., 1907)	20/10/03	Taiwan: Kaohsiung Hsien.	–	–	J-H Chen	GQ527098	MT599165	–	03.TW.KH.HSI.74
Formotosena	sp. [1]	Kato, 1925	–/5/03	Vietnam: Bach Ma NP	–	–	H Karuba	MT639231	MT599167	MT599015	03.VN.TT.BAC.01
Formotosena	sp. [2]	Kato, 1925	26/5/12	Vietnam: Tam Dao NP	21.444	105.619	KH, DM	MT639297	MT599244	MT599089	12.VN.VC.TDL.01
Gaeana	*cheni*	Chou & Yao, 1985	–/4–5/03	Laos: Mount Pan (Ph.-Pan)	–	–	H Karuba	MT639227	MT599158	MT599010	03.LA.XA.PAN.02
Gaeana	*maculata* [1]	(Drury, 1773)	15/6/08	China: Anhui, Yuexi, Tiantou	–	–	L Jingke	MT639251	MT599196	–	08.CN.AH.TIA.07
Gaeana	*maculata* [2]	(Drury, 1773)	18/4/12	India: West Bengal, Jalpaiguri	–	–	KK	MT639308	MT599257	MT599102	NCBS_AB702
Gaeana	*maculata* [3]	(Drury, 1773)	1/6/12	Vietnam: Vinh Phuc, Me Linh	21.384	105.712	KH, DM, T Du	MT639295	MT599242	MT599087	12.VN.VC.MLI.08
Gaeana	*maculata* [4]	(Drury, 1773)	15/5/12	India: Nagaland, Peren District	25.648	93.479	BP	MT639313	MT599265	MT599111	NCBS_AC179
Galgoria	*herzbergi*	(Schmidt, 1932)	–/4–5/03	Laos: Mount Pan (Ph.-Pan)	–	–	H Karuba	MT639229	MT599160	MT599012	03.LA.XA.PAN.06
gen. nr. *Cicada*	sp.	Latreille, 1802	24/5/12	India: West Bengal, Jalpaiguri	26.650	89.550	T Karmakar	MG953088	–	–	NCBS_AC226
gen. nr. *Tanna*	sp.	Distant, 1905	9/6/12	India: Kerala, Thiruvanan.	8.647	77.167	BP	MG953087	MT599272	MT599115	NCBS_AC211
Graptopsaltria	*bimaculata*	Kato, 1925	–/8–9/03	Japan: Kyushu Island	–	–	S Sick	MT639222	–	–	03.JP.KS.RYA.01
Graptopsaltria	*nigrofuscata*	(Motsch., 1866)	11/8/03	Japan: Tochigi, Ashikaga City	–	–	H Karuba, J Yoshimura	MG953024	MT599156	MT599008	03.JP.YN.MAC.08
Haphsa	*bindusara* [1]	(Distant, 1881)	–/4/03	N. Thailand	–	–	M Boulard	GQ527085	–	–	03.TH.XX.BKW.01
Haphsa	*bindusara* [2]	(Distant, 1881)	–/3/07	Thailand: Chaiyaphum, Tat Ton	–	–	Tawi, Jaruphan, Budsawong	MT639245	MT599189	MT599035	07.TH.CY.TTN.01
Haphsa	*durga*	(Distant, 1881)	–/3/02	N. Thailand	–	–	M Boulard	GQ527078	–	–	02.TH.CR.DMK.01
Haphsa	*karenensis*	Ollenbach, 1929	–/5/03	N. Thailand	–	–	M Boulard	GQ527086	–	–	03.TH.XX.BPK.01
Haphsa	*nicomache*	(Walker, 1850)	15/6/09	Pakistan: Islamabad	–	–	Z Ahmed	MT639260	MT599205	MT599050	09.PK.IS.ISD.01
Haphsa	sp. A	Distant, 1905	29/3/10	Laos: Tha Phabat, near Pakxan	–	–	M Hori	MT639334	MT599286	MT599122	Laos20100329.1
Haphsa	sp. B	Distant, 1905	28/5/12	Vietnam: Tam Dao NP	21.465	105.646	KH, DM	MT639300	MT599247	MT599092	12.VN.VC.TDQ.02
Haphsa	sp. C	Distant, 1905	15/5/12	India: Nagaland, Peren District	25.694	93.532	BP	MG953083	–	MT599108	NCBS_AC165^{B}
Hyalessa	*maculaticollis* [1]	(Motsch., 1866)	–/8/03	Japan: Miuami, Ashikara City	–	–	H Karuba	MT639224	MT599154	MT599006	03.JP.YN.MAC.03
Hyalessa	*maculaticollis* [2]	(Motsch., 1866)	26/7/09	China: Zhejiang, Tianmu Shan	30.325	119.443	KH, DM, J Xiang	MT639255	MT599199	MT599044	09.CN.ZJ.BUD.01
Kalabita	*operculata*	Moulton, 1923	16/3/03	Malaysia: Sabah	6.052	116.591	T Trilar, KP Trilar	MT639230	MT599163	–	03.MY.SA.KMS.01
Kaphsa	nr. *concordia* [1]	Lee, 2012	–/3–4/07	Thailand: Chaiyaphum, Tat Ton	15.941	102.099	Jaruphane, Budsawong	MT639246	MT599190	MT599036	07.TH.CY.TTN.02
Kaphsa	nr. *concordia* [2]	Lee, 2012	–/3/07	Thailand: Chaiyaphum, Tat Ton	15.941	102.099	Jaruphane, Budsawong	MT639247	MT599191	MT599037	07.TH.CY.TTN.03
Kaphsa	sp.	Lee, 2012	14/5/12	India: Nagaland, Peren District	25.694	93.532	BP	MT639311	MT599262	MT599107	NCBS_AC160
Karenia	cf. *ravida* [1]	Distant, 1888	28/8/05	China: Sichuan, Ganzi Pref.	30.496	102.295	D Sikes	MT639236	MT599174	MT599021	05.CN.SC.TGV.01
Karenia	cf. *ravida* [2]	Distant, 1888	28/8/05	China: Sichuan, Ganzi Pref.	30.496	102.295	D Sikes	MT639237	MT599175	MT599022	05.CN.SC.TGV.02
Lahugada	*dohertyi*	(Distant, 1891)	11/5/14	India: West Bengal	–	–	VS	MG953092	MT599308	MT599140	NCBS_PZ564
Leptosemia	*takanonis*	Matsum., 1917	–/7/05	Korea	–	–	YJL	GQ527090	MT599177	–	05.KR.GW.DHM.01
Macrosemia	cf. *pieli*	(Kato, 1938)	23/7/09	China: Zhejiang Pr., MoganShan	30.611	119.848	KH, DM, J Xiang	MT639256	MT599201	MT599046	09.CN.ZJ.MMN.03
Macrosemia	*kareisana* [1]	(Matsum., 1907)	–/8/02	Taiwan	–	–	YJL	GQ527081	MT599147	–	02.TW.NT.STT.01
Macrosemia	*kareisana* [2]	(Matsum., 1907)	14/8/06	Taiwan: Taitung Hsien	–	–	J-H Chen	MT639307	MT599256	MT599101	1112
Macrosemia	*tonkiniana*	(Jacobi, 1905)	–/9/00	Thailand	–	–	M Boulard	GQ527073	–	–	00.TH.CM.CHD.01
Maua	*philippinensis*	Schmidt, 1924	25/4/12	Philippines: Mindanao	6.735	126.141	KH, DM, AM, Catanach	MT639279	MT599226	MT599071	12.PH.MN.HWF.01
Megapomponia	*atrotunicata*	Lee & Sanb., 2010	–/10/07	Cambodia: Ratanakiri, Veunsai	13.983	106.817	S DeGreef, P Naskrecki	MT639240	MT599184	MT599030	07.KH.RT.VNS.01
Megapomponia	*intermedia*	(Distant, 1905)	–/9/02	Thailand	–	–	M Boulard	GQ527077	–	–	02.TH.CM.HNG.02

(*continued next page*)

Table 1. (*continued*)

Genus	Species	Authority	Date (D/M/Y)	Location	Lat.	Long.	Collectors	*COI*	*EF-1α*	*ARD1*	Voucher code
Megapomponia	*merula*	(Distant, 1905)	–/10/06	Malaysia: Sarawak, Lambir Hills	4.198	114.042	J Cryan	GQ527097	MT599181	MT599027	06.MY.SK.LAM.20
Meimuna	*gakokizana*	Matsum., 1917	–/8/02	Taiwan	–	–	YJL	GQ527080	MT599146	MT598999	02.TW.NT.PLC.01
Meimuna	*mongolica*	(Distant, 1881)	21/7/09	China: Zhejiang, Hangzhou	30.253	120.131	Z Lei, KH, DM	MT639257	MT599202	MT599047	09.CN.ZJ.WLK.05
Meimuna	*opalifera* [1]	(Walker, 1850)	–/8/03	Japan: Miuami, Ashikara City	–	–	H Karuba	MT639223	MT599153	MT599005	03.JP.YN.MAC.01
Meimuna	*opalifera* [2]	(Walker, 1850)	–/8/04	Korea	–	–	YJL	GQ527088	MT599172	MT599020	04.KR.GG.GNG.01
Meimuna	sp.	Distant, 1905	6/5/11	Vietnam: Tam Dao NP	–	–	AB, MS	MT639275	MT599222	MT599067	11.VN.VP.TDP.22
Meimuna	*tripurasura*	(Distant, 1881)	8/4/13	India: Arunachal Pradesh	–	–	KK	MT639324	MT599277	MT599116	NCBS_AC534
Miniterpnosia	*chorus* [1]	Lee, 2013	–/4–5/03	Laos: Mount Pan (Ph.-Pan)	–	–	H Karuba	MT639226	MT599157	MT599009	03.LA.XA.PAN.01
Miniterpnosia	*chorus* [2]	Lee, 2013	27/5/12	Vietnam: Tam Dao NP	21.451	105.647	KH, DM	MT639296	MT599243	MT599088	12.VN.VC.TDA.03
Neocicada	*chisos*	(Davis, 1916)	29/6/07	USA: Texas, Jeff Davis Co.	30.512	–103.756	KH, DM	GQ527101	MT599195	MT599041	07.US.TX.FDC.01
Neocicada	*h. johannis*	(Walker, 1850)	18/6/05	USA: Florida, Escambia Co.	30.544	–87.351	KH, DM	GQ527093	MT599180	MT599026	05.US.FL.FWC.01
Neocicada	*hieroglyphica*	(Say, 1830)	17/6/11	USA: Oklahoma, Latimer Co.	34.754	–95.068	KH, DM	GQ527093	MT599219	MT599064	11.US.OK.TAW.01
Neoncotympana	*leeseungmoi*	Lee, 2011	3/5/12	Philippines: Mindanao	8.165	124.933	KH, DM, D Mohagan	MT639282	MT599229	MT599074	12.PH.MN.KGS.05
Oncotympana	*averta*	Lee, 2011	9/7/10	Philippines: Mindanao	7.017	125.233	KH, JJ, DM, D Mohagan	MT639264	MT599210	MT599055	10.PH.MN.SCI.01
Oncotympana	cf. *averta*	Lee, 2011	1/5/12	Philippines: Mindanao	8.164	124.933	KH, DM, D Mohagan	MT639280	MT599227	MT599072	12.PH.MN.KGC.01
Oncotympana	*pallidiventris*	(Stål, 1870)	2/7/10	Philippines: Dinagat	10.377	125.635	KH, J Jones, DM, AM	MG953069	MT599208	MT599053	10.PH.DI.RED.04
Orientopsaltria	*agatha*	(Moulton, 1911)	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639343	MT599297	MT599133	Mulu3.BOR08
Orientopsaltria	*ida*	(Moulton, 1911)	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639344	MT599298	MT599134	Mulu3.BOR18
Orientopsaltria	*inermis*	(Stål, 1870)	7/7/10	Philippines: Mindanao	8.251	125.032	KH, J Jones, DM, AM	MT639263	MT599209	MT599054	10.PH.MN.IMP.02
Orientopsaltria	*maculosa*	Duff. & Zaid., 2000	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639339	MT599293	MT599129	Mulu1.BOR13
Paranosia	aff. *andersoni*	(Distant, 1892)	–/3/07	Thailand: Chiang Mai	18.553	98.480	A Areeluck	MT639241	MT599185	MT599031	07.TH.CM.DOI.01
Paratalainga	*yunnanensis*	Chao & Lei, 1992	6/5/11	Vietnam: Vinh Phuc, Tam Dao	–	–	AB, MS	MT639277	MT599224	MT599069	11.VN.VP.TDP.24
Platylomia	aff. *ficulnea*	(Distant, 1892)	21/4/12	India: West Bengal, Jalpaiguri	–	–	KK	MG953080	MT599259	MT599104	NCBS_AB709
Platylomia	*bivocalis*	(Matsum., 1907)	24/5/05	Taiwan: Pingtung Hsien	–	–	J-H Chen	MT639304	MT599253	MT599098	0940
Platylomia	*flavida*	(G-Ménev., 1834)	–/5/05	Malaysia: Perak	–	–	YJL	GQ527092	MT599178	MT599024	05.MY.PK.PRK.01
Platylomia	*malickyi*	Beuk, 1998	–/6/03	Thailand	–	–	M Boulard	GQ527087	MT599164	–	03.TH.XX.HNK.01
Platypleura	*polita*	(Walker, 1850)	12/4/13	India: Kerala, Kozhikode	–	–	G Agavekar	MT639348	MT599305	–	NCBS_PT207
Platypleura	*takasagona*	Matsum., 1917	4/6/03	Taiwan: Taipei Hsien	–	–	J-H Chen	KR674166	MT599250	MT599095	0551
Polyneura	sp.	Westwood, 1840	–/7/05	China: Tibet, LinZhi Fa-Mu-Dui	–	–	L Jingke	MT639351	MT599309	MT599141	Tibet1
Pomponia	*backanensis*	Pham & Yang, 2009	20/5/12	Vietnam: Cuc Phuong NP	20.250	105.714	KH, DM, THP	MT639290	MT599237	MT599082	12.VN.NB.CPV.01
Pomponia	cf. *linearis* [1]	(Walker, 1850)	26/7/09	China: Zhejiang, Tianmu Shan	30.325	119.443	KH, DM, J Xiang	MG953066	MT599200	MT599045	09.CN.ZJ.BUD.03
Pomponia	cf. *linearis* [2]	(Walker, 1850)	18/5/12	Vietnam: Bach Ma NP	16.196	107.862	KH, DM, THP	MT639293	MT599240	MT599085	12.VN.TT.BME.01
Pomponia	*linearis* cx.	(Walker, 1850)	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639341	MT599295	MT599131	Mulu1.BORa
Pomponia	sp. A [1]	Stål, 1866	26/5/03	India: Kerala, Wayanad	–	–	G Svenson	MT639234	MT599170	MT599018	04.IN.KL.WAY.01
Pomponia	sp. A [2]	Stål, 1866	6/6/12	India: Kerala, Thiruvanan.	8.750	77.100	BP	MT639318	MT599270	–	NCBS_AC201
Pomponia	sp. A [3]	Stål, 1866	11/6/12	India: Kerala, Idukki	9.967	77.133	BP	MT639321	MT599274	–	NCBS_AC217
Pomponia	sp. A [4]	Stål, 1866	26/5/12	India; West Bengal, Jalpaiguri	26.650	89.550	T Karmakar	MT639323	MT599276	–	NCBS_AC222
Pomponia	sp. A [5]	Stål, 1866	9/6/13	India; Karnataka, Shimoga	–	–	KK	MT639350	MT599307	–	NCBS_PT501
Pomponia	sp. B	Stål, 1866	15/5/12	India: Nagaland, Peren District	25.648	93.479	BP	MT639312	MT599263	MT599109	NCBS_AC174
Pomponia	*yayeyamana*	Kato, 1933	–/8/02	Taiwan	–	–	KNIC	GQ527079	MT599145	–	02.TW.KH.SNP.01
Psithyristria	*grandis*	Lee & Hill, 2010	–/6/07	Philippines: E Luzon	–	–	IRSNB	GQ527112	MT599304	MT599139	Psith15
Psithyristria	*nodinervis*	Stål, 1870	–/6/07	Philippines: E Luzon	–	–	IRSNB	GQ527120	MT599303	–	Psith8
Psithyristria	*peculiaris*	Lee & Hill, 2010	–/6/07	Philippines: E Luzon	–	–	IRSNB	GQ527106	MT599302	MT599138	Psith1
Purana	*capricornis*	Kos & Gog., 2000	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639338	MT599292	MT599128	Mulu1.BOR03
Purana	cf. *barbosae*	(Distant, 1889)	19/4/12	Philippines: Mindanao, Bukidnon	7.879	125.064	KH, DM, T Catanach	MT639284	MT599231	MT599076	12.PH.MN.MUS.01
Purana	cf. *carmente* [1]	(Walker, 1850)	–/6/07	Thailand: Chaiyaphum	15.671	101.449	K Sa-nog, B Adnafai	MT639244	MT599188	MT599034	07.TH.CY.PHN.02
Purana	cf. *carmente* [2]	(Walker, 1850)	–/5/12	Indonesia: West Java, Ciamis	–7.144	108.230	M Hori	MT639331	MT599283	MT599120	Indonesia201205.1
Purana	cf. *morrisi* [1]	(Distant, 1892)	8/6/12	India: Kerala, Thiruvanan.	8.682	77.139	BP	MT639319	–	MT599114	NCBS_AC203
Purana	cf. *morrisi* [2]	(Distant, 1892)	6/6/12	India: Kerala, Thiruvanan.	8.750	77.100	BP	MT639315	–	–	NCBS_AC196

(*continued next page*)

Table 1. (*continued*)

Genus	Species	Authority	Date (D/M/Y)	Location	Lat.	Long.	Collectors	*COI*	*EF-1α*	*ARD1*	Voucher code
Purana	cf. *morrisi* [3]	(Distant, 1892)	6/6/12	India: Kerala, Thiruvanan.	8.750	77.100	BP	MT639317	MT599269	–	NCBS_AC200
Purana	cf. *morrisi* [4]	(Distant, 1892)	8/6/12	India: Kerala, Thiruvanan.	8.682	77.139	BP	–	MT599271	–	NCBS_AC204
Purana	cf. *parvituberculata*	Kos & Gog., 2000	6/6/10	Vietnam: Vinh Phuc, Me Linh	–	–	THP, AB, MS	MT639329	MT599282	–	CSL35
Purana	*crassinotata*	Lee, 2015	29/6/10	Philippines: Camiguin, Sagay	9.167	124.729	KH, J Jones, D Mohagan	MT639261	MT599206	MT599051	10.PH.CG.MTC.01
Purana	*pryeri*	(Distant, 1881)	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639337	MT599291	MT599127	Mulu1.BOR02
Purana	sp. B	Distant, 1905	26/5/12	Vietnam: Tam Dao NP	21.444	105.619	KH, DM	MT639298	MT599245	MT599090	12.VN.VC.TDL.09
Purana	sp. C	Distant, 1905	24/10/05	India: Maharashtra, Sindhudurg	15.933	73.942	J Cryan	MT639238	MT599176	MT599023	05.IN.MH.AMW.01
Purana	*trui*	Pham *et al*., 2012	17/5/12	Vietnam: Bach Ma NP	16.220	107.858	KH, DM, THP	MT639291	MT599238	MT599083	12.VN.TT.BMB.01
Rustia	*dentivitta*	(Walker, 1862)	–/6/07	Thailand: Chaiyaphum	15.671	101.449	K Sa-nog, B Adnafai	MT639243	MT599187	MT599033	07.TH.CY.PHN.01
Semia	sp.	Matsum., 1917	23/5/12	Vietnam: Cuc Phuong NP	20.360	105.599	KH, DM, THP	MT639285	MT599232	MT599077	12.VN.NB.CPO.01
Semia	*watanabei* [1]	(Matsum., 1907)	–/8/02	Taiwan	–	–	YJL	GQ527083	MT599149	MT599001	02.TW.TT.GUT.01
Semia	*watanabei* [2]	(Matsum., 1907)	27/5/04	Taiwan: Pingtung Hsien	–	–	J-H Chen	MT639303	MT599252	MT599097	0774
Sinotympana	*incomparabilis* [1]	Lee, 2009	11/5/04	China: Guangdong	–	–	P Grootaert	MT639232	MT599168	MT599016	04.CN.GD.NKS.01
Sinotympana	*incomparabilis* [2]	Lee, 2009	11/5/04	China: Guangdong	–	–	P Grootaert	MT639233	MT599169	MT599017	04.CN.GD.NKS.02
Sulphogaeana	*sulphurea*	(Westwd., 1839)	5/10/12	India: Nagaland, Kohima	25.618	93.954	BP	MT639310	MT599261	MT599106	NCBS_AC158
Tacua	*speciosa*	(Illiger, 1800)	3/4/03	Malaysia: Sabah	6.006	116.543	T Trilar, KP Trilar	KR674150	MT599162	MT599014	03.MY.SA.KIN.24
Taiwanosemia	*hoppoensis*	(Matsum., 1907)	–/8/02	Taiwan	–	–	YJL	GQ527082	MT599148	MT599000	02.TW.TN.CHS.01
Talainga	*chinensis*	Distant, 1900	2/5/04	Vietnam: Tam Dao NP	–	–	THP, AB, MS	MT639327	MT599280	–	CSL26
Talainga	*chinensis*	Distant, 1900	1/5/11	Vietnam: Ha Giang, nr Dang Van	–	–	M Hori	MT639353	MT599311	MT599143	Vietnam20110501a.1
Tanna	*infuscata*	Lee & Haya., 2004	18/6/05	Taiwan: Taitung Hsien	–	–	J-H Chen	MT639306	MT599255	MT599100	0968
Tanna	*japonensis* [1]	(Distant, 1892)	–/8/02	Japan	–	–	YJL	GQ527076	MT599144	–	02.JP.HG.ROK.01
Tanna	*japonensis* [2]	(Distant, 1892)	–/8/03	Japan: Miuami, Ashikara City	–	–	H Karuba	MT639225	MT599155	MT599007	03.JP.YN.MAC.05
Tanna	*kimtaewooi*	Lee, 2010	27/5/12	Vietnam: Tam Dao NP	21.453	105.636	KH, DM	MT639299	MT599246	MT599091	12.VN.VC.TDM.01
Tanna	*sozanensis*	Kato, 1926	4/6/03	Taiwan: Taipei Hsien	–	–	J-H Chen	GQ527094	MT599166	–	03.TW.TP.UCH.41
Terpnosia	aff. *mesonotalis*	Distant, 1917	30/4/05	Laos: Luang Namtha Prov.	21.152	101.355	Jönsson, Malm, Viklund	MT639332	MT599284	MT599121	Laos29a
Terpnosia	cf. *graecina*	(Distant, 1889)	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639342	MT599296	MT599132	Mulu1.BORb
Terpnosia	cf. *maculipes*	(Walker, 1850)	–/3/07	Thailand: Chiang Mai	18.553	98.480	A Areeluck	MT639242	MT599186	MT599032	07.TH.CM.DOI.02
Terpnosia	cf. *mawi*	Distant, 1909	28/5/12	Vietnam: Tam Dao NP	21.465	105.646	KH, DM	MT639301	MT599248	MT599093	12.VN.VC.TDQ.03
Terpnosia	*collina*	(Distant, 1888)	5/10/12	India: Nagaland, Kohima	25.618	93.954	BP	MT639309	MT599260	MT599105	NCBS_AC155
Terpnosia	*mawi*	Distant, 1909	30/6/06	China: Jiangxi, Wugongshan	27.463	114.158	T Sota	MT639325	MT599278	MT599117	China20060630b
Tosena	*melanopteryx* [1]	Kirkaldy, 1909	3/7/03	Vietnam: Tam Dao NP	–	–	THP, AB, MS	MT639330	–	–	CSL36
Tosena	*melanopteryx* [2]	Kirkaldy, 1909	–/10/08	Thailand: Chanthaburi	12.817	102.117	Suthida, Charoenchai	MT639254	MT599198	MT599043	08.TH.CT.KKT.01
Trengganua	*sibylla* [1]	(Stål, 1863)	–/4/11	Malaysia: Perak	–	–	L Jingke	MT639269	MT599215	MT599060	11.MY.PK.TAP.03
Trengganua	*sibylla* [2]	(Stål, 1863)	–/4/11	Malaysia: Perak	–	–	L Jingke	MT639270	MT599216	MT599061	11.MY.PK.TAP.04
Unipomponia	*decem* [1]	(Walker, 1857)	–/1/09	Malaysia: Sarawak	–	–	J Urban	MT639340	MT599294	MT599130	Mulu1.BOR34
Unipomponia	*decem* [2]	(Walker, 1857)	16/1/09	Malaysia	–	–	J Urban	MT639347	MT599301	MT599137	MuluParkBr.1
Vittagaeana **n.**	*paviei* **comb. n.**	(Westwd., 1842)	2/4/10	Laos: Bolikhamxay, Pakxan	–	–	M Hori	MT639335	MT599287	MT599123	Laos20100402a
Yanga	*heathi*	(Distant, 1899)	–/11/08	Madagascar: Toliara Pr.	–25.006	46.303	J Cryan	KR674245	MT599288	MT599124	MadLoc6.1
Yezoterpnosia	sp.	Matsum., 1917	–/5–6/07	Thailand: Nakhon Nayok	–	–	P Sandao	MT639250	MT599194	MT599040	07.TN.NN.KHA.01
Yezoterpnosia	*vacua*	(Olivier, 1790)	21/5/05	Japan: Hiroshima Pref., Miyoshi	–	–	J-H Chen	MT639305	MT599254	MT599099	0945

[A] 03.TW.TY.CHP.24 was listed with code 0624 in Marshall *et al*. (2018).

[B] NCBS_AC165 was listed as *Meimuna* sp. in Marshall *et al*. (2018).

et al. 2015), using a touchdown procedure with annealing temperature 45–55°C. Touchdown was occasionally used for *COI* and *EF-1α*, commonly with longer extension times. In some cases, modified primers were used as listed in Marshall *et al*. (2018). DNA extracted from dried specimens was often difficult to amplify, especially for the nuclear gene regions, and in some cases PCR products were further amplified in a second reaction. PCR products were cleaned with Clontech Extract II kits (Clontech, Mountain View, CA, USA) or ExoSAP-IT (USB Corp., Cleveland, OH, USA).

Cleaned PCR products were Sanger sequenced using Big Dye (ver. 1.1, Applied Biosystems, Foster City, CA, USA) at 1/8- to 1/4-scale reaction volume with BDX64 (MCLAB, San Francisco, CA, USA) and the BDX64 protocol, and then sequenced on an ABI 3100 or 3130*xl* capillary sequencer. For some specimens, a modified protocol used 0.25 µL of BigDye (ver. 1.1, Applied Biosystems), 0.75 µL of BDX64 (MCLAB, South San Francisco, CA, USA), 1.5 µL of BigDye 5× buffer, 0.7 µL of 2-µM primer stock, 2.2 µL of H_2O, 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 s, 50°C for 15 s, and 60°C for 2.5 min; (3) hold at 60°C for 5 min. Sequencing products were cleaned by Sephadex (Millipore) filtration. The Indian samples were extracted and amplified in the Kunte Laboratory, and sequenced in the NCBS Sequencing Facility, usually following the protocols described above.

Sequences were analysed using ABI PRISM SEQUENCING ANALYSIS (ver. 3.7, Applied Biosystems) and manually aligned and edited in SEQUENCHER (ver. 3.1, Gene Codes Corp., Ann Arbor, MI, USA) or Mesquite (ver. 3.5, W. P. Maddison and D. R. Maddison, see http://mesquiteproject.org, accessed 5 February 2021). All segments were initially sequenced only in one direction. If reads were unclear, the gene was resequenced, usually in the reverse direction. Heterozygous sites in nuclear-gene sequences were coded using IUPAC (International Union of Pure and Applied Chemistry) ambiguity codes. During alignment of the mitochondrial sequences, chromatograms were checked for double-peaked signals that may indicate 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 suspected nuclear copy. In a limited number of these cases, amplified products were cloned with TOPO TA cloning kits, with the original PCR amplifications repeated with PrimeSTAR HS DNA polymerase (Takara) or another high-fidelity taq. Codon translation was used to confirm the absence of stop codons in coding regions. An unalignable UTR segment was removed for *Yanga heathi* (Distant, 1899). The Indian work was completed in the Kunte Laboratory and at the NCBS Sequencing Facility, using the DNA extraction, amplification and sequencing methods just described. *COI* sequence from *Cicadmalleus* Boulard & Puissant, 2013 became available at a late stage from an anchored phylogenomic analysis (see Acknowledgments).

A maximum likelihood tree was generated in RAxML (ver. 7.4.2, see https://github.com/stamatak/standard-RAxML; Stamatakis 2006) using the rapid bootstrap option and the GTR+Γ model for each aligned amplicon, to check for implausible exact or nearly exact matches that could be caused by specimen contamination, sample mix-up, or mislabelling. Finally, taxon duplicates were removed to create a trimmed data matrix for the main analysis and figures. Because taxon duplicates were often taken from different locations and could represent distinct taxa, the full dataset was also analysed using the Bayesian methods below and the resulting tree is available in Fig. S1 of the Supplementary material.

Phylogenetic analysis

Partitioning schemes and MrBayes-available substitution models for data subsets were selected using the ‘greedy’ search algorithm (Lanfear *et al*. 2012) and the BIC criterion in PartitionFinder (ver. 2.1.1, see http://www.robertlanfear.com/partitionfinder/; Guindon *et al*. 2010; Lanfear *et al*. 2016) with Python (ver. 2.7, Python Software Foundation, see http://www.python.org/psf, accessed 6 February 2021) with 13 potential subsets including individual codon positions of protein-coding data (with each gene separately treated) and the *18S* ribosomal data.

Bayesian and maximum likelihood (ML) phylogenetic trees for the combined genetic dataset were estimated using MrBayes (ver. 3.2.6, see https://github.com/NBISweden/MrBayes/; Ronquist *et al*. 2012) and GARLI 2.0 (ver. 2.0.1019 and ver. 2.01.1067, see https://code.google.com/archive/p/garli/; Zwickl 2006). Computational resources were provided by the CIPRES Science Gateway (ver. 3.3, see http://www.phylo.org/; Miller *et al*. 2010) and the Computational Biology Core at the University of Connecticut. For the MrBayes analysis, model settings were assigned following the partition scheme and substitution models shown in the Results and Discussion section, 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 during model selection, and a default exponential branch length prior with a mean of 0.1 substitutions per 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 3×10^8 generations, terminating when the average standard deviation of split frequencies dropped below 0.005 (*stoprule = yes*, *stopval = 0.005*, with *diagnfreq = 30,000*) with the default burn-in 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 postburn-in parameter effective sample sizes were checked using Tracer (ver. 1.7.1, A. Rambaut and A. J. Drummond, see http://tree.bio.ed.ac.uk/software/tracer/, accessed 3 December 2019) and confirmed above 200. The dataset file with the complete final model is available as Supplementary material.

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 of 10 heuristic search replicates, 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. All other settings were left as shown in default form. For each of 200 bootstrap replicates used to assess branch support, 10 heuristic searches were completed under the above settings. The resulting ML bootstrap values were mapped onto the MrBayes consensus tree along with the Bayesian posterior probabilities.

Morphological examination

Pinned cicada specimens lodged in the collections of C. Simon, M. S. Moulds, Y. J. Lee, T.-H. Pham, V. Sarkar, and the National Centre for Biological Sciences, India (NCBS) were examined to test taxonomic implications of the molecular phylogeny and to inform ancestral character states mapping, as explained below. Literature information was used when male specimens were not available. Images of type specimens were obtained from depositories when necessary to confirm uncertain identifications. Male genitalia were dissected from relaxed specimens and cleared through 10% KOH, using procedures in Moulds (2012). Specimens were examined with Wild stereomicroscopes. Morphological terminology follows Moulds (2005).

Ancestral character states for opaque wings and abdominal tubercles

The MrBayes phylogram (see Results) and Mesquite (ver. 3.6, see http://mesquiteproject.org) were used to reconstruct maximum likelihood ancestral character states for wing colouration and abdominal tubercles. For wing morphology, all ingroup taxa were coded as State 0 (entirely or mostly hyaline wings, including species with colour-tinted but still transparent wings) or 1 (entirely or mostly opaque wings). *Ayuthia spectabile* Distant, 1919, which has most of the forewing hyaline and most of the hindwing opaque-white, was scored as uncertain. *Talainga* Distant, 1890, *Paratalainga* He, 1984, and *Graptopsaltria* Stål, 1866, which have some partly clear cells but most wing surface opaque, were scored as State 1. The taxa from Clade F on Fig. 5 (see Results) were coded for the presence or absence of pairs of abdominal tubercles on one or more sternites and this character was reconstructed on just the section of the tree for that clade, minus *Cicadmalleus* and taxa for which only female morphology is known to us. (These features are distinct from the epipleural extensions observed in species such as *Euterpnosia cucphuongensis* Pham, Ta & Yang, 2010, which were not considered here.) Maximum likelihood ancestral states under the supplied MkV model (1 transition rate) were reconstructed for each node in the analyses. In order to estimate the minimum number of origins required in each case, the two characters were also traced under the criterion of maximum parsimony.

Biogeographic analysis

Likelihood-based estimates of ancestral ranges for the ingroup taxa were calculated using the dispersal–extinction–cladogenesis model (Ree and Smith 2008) in Lagrange (ver. 20130526, R. H. Ree, see http://www.reelab.net/lagrange/configurator/index, accessed 3 June 2018; Ree and Smith 2008) and the MrBayes phylogram. The MrBayes ingroup tree was first converted to a chronogram using r8s (ver. 1.81, see https://sourceforge.net/projects/r8s/; Sanderson 2002) under the penalised likelihood criterion and a smoothing parameter determined from cross-validation analysis, after polytomies were randomly resolved using Mesquite (ver. 3.5, see http://mesquiteproject.org) and three zero-length branches were converted to a minimal length of 0.001 substitutions per site. Areas were coded as follows: Asia (including Europe and north Africa), Australasia (including eastern Indonesia, New Guinea, Wallacea, Oceania), India (for southern India only, south of 17° latitude), and North America. The principal purpose of the coding scheme – and the separate coding of the southern Indian subcontinent – was to identify, if present, patterns consistent with ancestry in southern India *v.* patterns consistent with Asian ancestry. Distributions including up to two areas were allowed, and no time constraints were incorporated. Because the relationship of the ingroup clade to other world Cicadinae is unresolved within a large, global polytomy (see Marshall *et al.* 2018), the analysis was conducted with the ingroup taxa alone. Python scripts for Lagrange were assembled using an online configurator tool.

Divergence-time analysis

Divergence times were estimated for the cicada ingroup tree using BEAST (ver. 2.5.2, see http://www.beast2.org/) and its accompanying utility BEAUti (ver. 2.5.2, see https://beast.community/beauti; Bouckaert *et al*. 2019). The outgroup lineages were excluded because of the long ingroup stem combined with the small outgroup. A recent review (Moulds 2018) listed five fossil Cicadidae that we were able to assign to specific ingroup clades (Table 2). For each, the youngest age of the corresponding geological stratum was applied as a minimum-age constraint in a uniform prior distribution. For all constraints, the maximum age was set to 150 Ma, following Marshall *et al*. (2016) who used the fossil-calibrated Insecta tree in Misof *et al*. (2014) to arrive at this value as an estimate for the Cercopidae – Cicadoidea divergence date. Two calibration methods were used, one with each fossil applied to the most recent common ancestor (MRCA) of the group in question, and another with the fossil applied to the origin of the stem supporting the group (by selecting *use originate* in the prior panel for the fossil). The latter option allows for the possibility that diagnostic traits for a genus appeared along the stem lineage supporting the extant members of the clade. Fossil calibration groups were constrained to be monophyletic. Justifications for the fossil calibration points are as follows:

Meimuna protopalifera Fujiyama, 1969. This taxon was originally placed in *Meimuna* Distant, 1905, but Moulds (2018) noted that species in *Haphsa* Distant, 1905 cannot

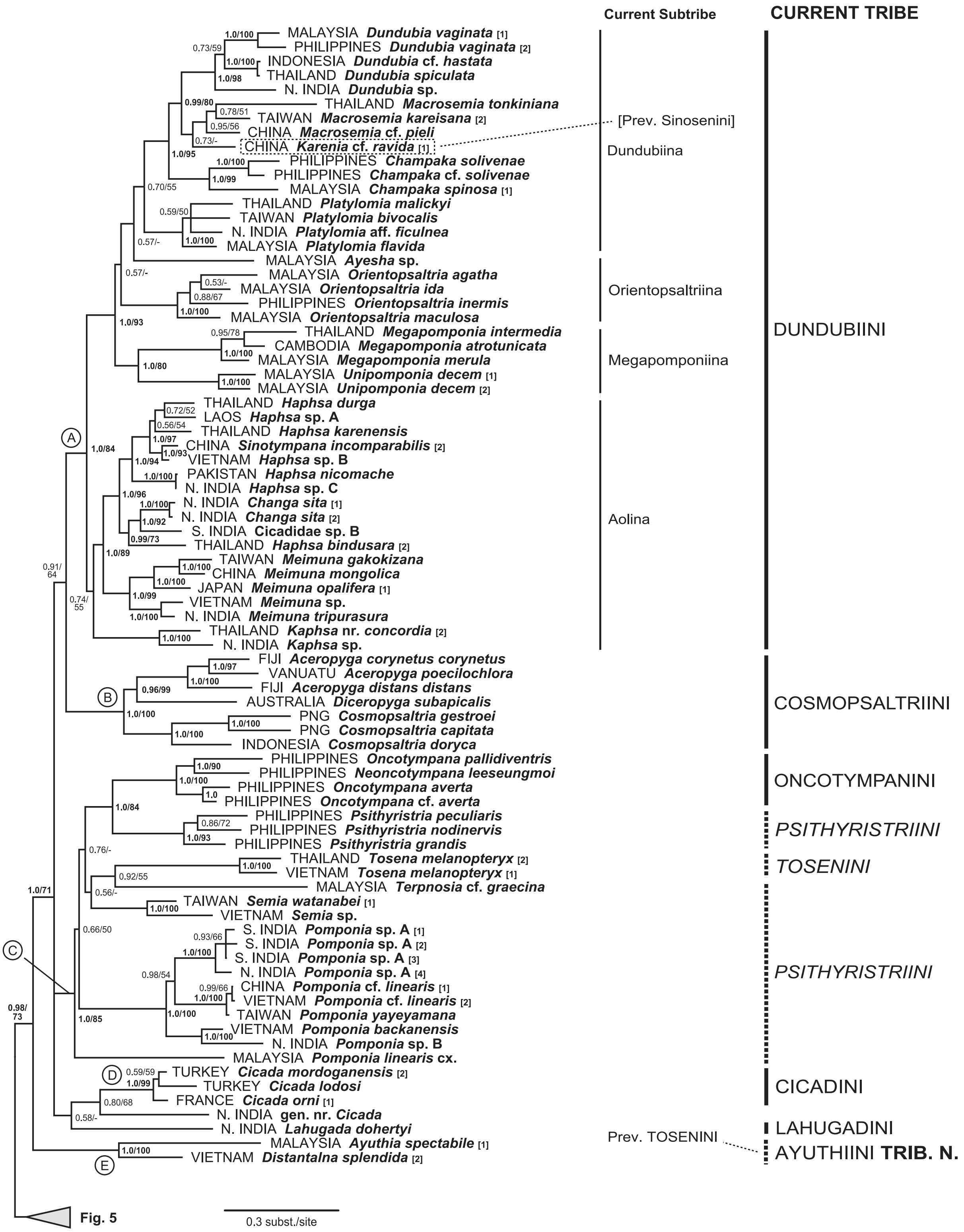


Fig. 4. Molecular phylogeny of Asian cicada tribes related to Cicadini. Upper half of tree, with Bayesian posterior probabilities and maximum likelihood bootstrap support values shown for branches. Bold values indicate strong support. Current tribe and subtribe classification is shown, with italicised names and dotted lines indicating conflicts between tree and classification. Circled letters refer to clades discussed in the text. Subscript values in brackets are specimen numbers for taxon duplicates.

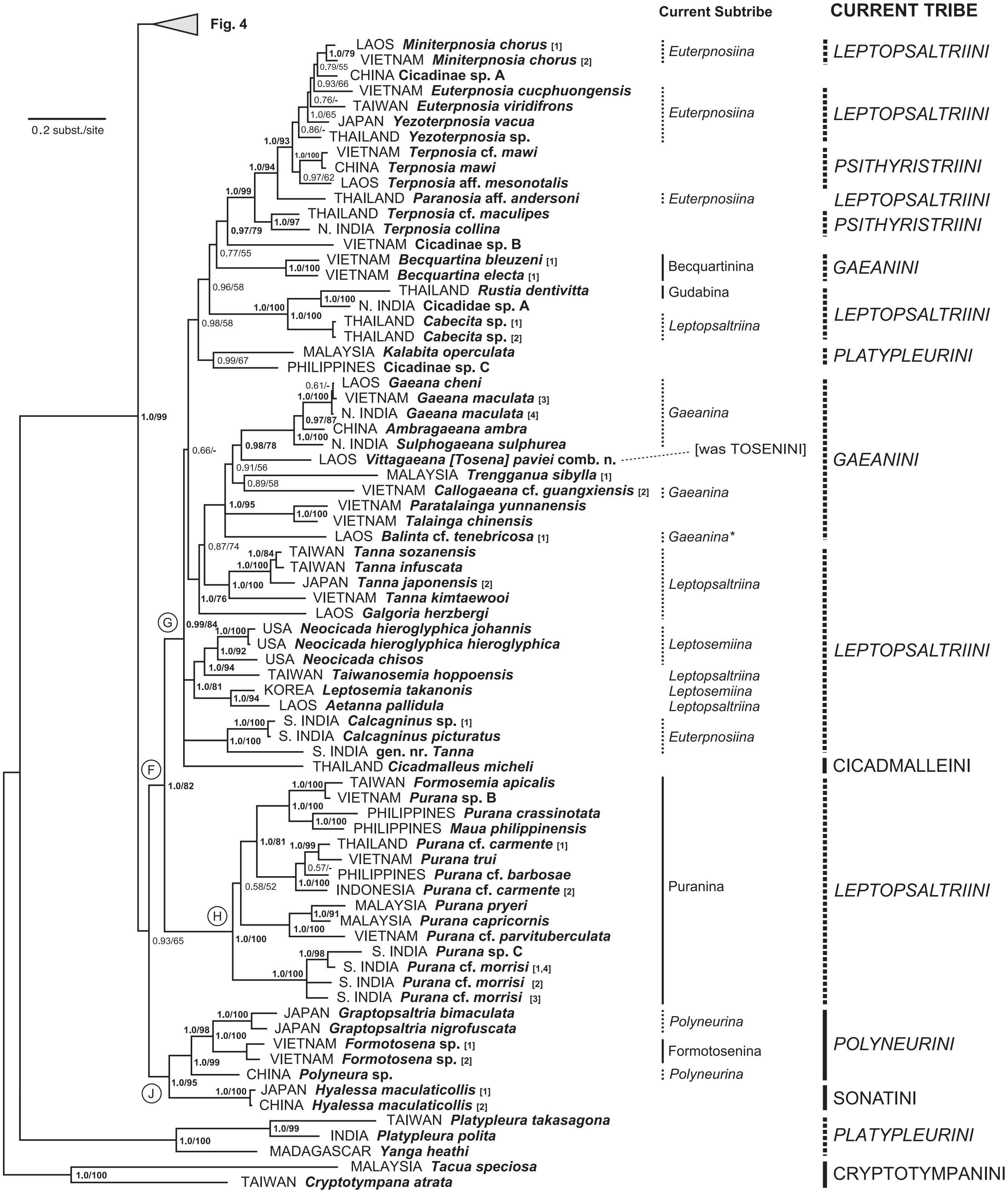


Fig. 5. Molecular phylogeny of Asian cicada tribes related to Cicadini. Lower half of tree, with Bayesian posterior probabilities and maximum likelihood bootstrap support values shown for branches. Bold values indicate strong support. Current tribe and subtribe classification is shown, with italicised names and dotted lines indicating conflicts between tree and classification. Circled letters refer to clades discussed in the text. Subscript values in brackets are specimen numbers for taxon duplicates. The asterisk (*) denotes that *Balinta* Distant, 1905 is placed in a monotypic subtribe in Boulard's (2012, 2013) system.

Table 2. Fossil calibrations used in the divergence-time analysis
The underlined youngest age of the geological stratum was used to constrain the minimum age of each cicada clade. See Moulds (2018) for details

Taxon	Tribe	Age (Ma)
Cicada sp. aff. *orni* Linnaeus, 1758	Cicadini	3.6–2.6
Graptopsaltria inaba Fujiyama, 1982	Polyneurini	11.6–5.3
Meimuna protopalifera Fujiyama, 1969	Dundubiini	23–16
Tanyocicada lapidescens (Zhang, 1989)	Leptopsaltriini	16.0–11.6
Yezoterpnosia sp. aff. *vacua* (Olivier, 1790)	Leptopsaltriini	11.6–5.3

be excluded. We applied the fossil calibration to the branch supporting the clade containing *Meimuna* and *Haphsa*. The much younger *Meimuna* sp. fossil (Fujiyama 1982) adds no further information.

Tanyocicada lapidescens (Zhang, 1989). Moulds (2018) agreed with Zhang's (1989) comparison of this fossil to *Oncotympana* [now *Hyalessa*] *melanoptera* (Distant, 1904). However, several differences were recognised later, and Moulds (2020) established a new genus, *Tanyocicada*. Moulds noted similarities to genera including *Tanna* Distant, 1905, *Purana* Distant, 1905, *Maua* Distant, 1905, *Leptosemia*, and *Dundubia* Amyot & Audinet-Serville, 1843, but the small size of the fossil cicada suggests a genus related to current Leptopsaltriini, a tribe with representatives scattered across Clade F in Fig. 5 (see Results). We applied the fossil calibration to the branch supporting this group, which contains all of the Leptopsaltriini.

Graptopsaltria inaba Fujiyama, 1982. The fossil is a complete forewing, and both Fujiyama (1982) and Moulds (2018) confirm its placement in *Graptopsaltria* Stål, 1866 although it differs from the extant Japanese species. We applied this fossil to the branch supporting the two *Graptopsaltria* in the tree. The much younger congeneric fossil *Graptopsaltria* aff. *nigrofuscata* (Motschulsky, 1866) (see Moulds 2018) would be applied to the same branch.

Yezoterpnosia sp. aff. *vacua* (Olivier, 1790). Kinugasa and Miyatake (1979) identified this as an unknown species affiliated with *Yezoterpnosia vacua*, but they considered only extant Japanese taxa, a decision that may be unwarranted given its Miocene age. From comparison with illustrations of wings in sources such as Chou *et al*. (1997) and the Moulds collection, we find that similarity is greatest for the clade containing *Miniterpnosia* Lee, 2013, *Euterpnosia* Matsumura, 1917, and *Yezoterpnosia* Matsumura, 1917, so we applied the fossil constraint to the branch supporting this clade.

Cicada sp. aff. *orni* Linnaeus, 1758. Moulds (2018) noted that the characters of this fossil described by Wagner (1967) do not allow discrimination among the currently defined *Cicada* Linnaeus, 1758 species. We assigned this taxon to the stem supporting the *Cicada orni* complex. The lineage leading to *Lahugada* Distant, 1905 can be excluded because of differences in the relative sizes of the apical and ulnar areas.

The fossil calibrations constrain only the minimum age of the tree. To further constrain the maximum age, a relaxed molecular clock prior on branch rates (*ucld.mean*) was introduced for the *COI* partition, based on estimates from the literature (see Marshall *et al*. 2016). The midpoint of this range is close to the Brower (1994) *COI* clock rate for insects of 2.3% pairwise corrected divergence per million years (Ma) (0.0115 substitutions per site per million years, substitutions site^{-1} Ma^{-1}), whereas the upper end is close to the *COI* rate of 0.035 substitutions site^{-1} Ma^{-1} estimated by Papadopoulou *et al*. (2010). *COI* was modelled as a whole-gene subset in the BEAST analysis, with the remaining sites partitioned as in the Bayesian phylogenetic analysis.

The final analyses used a Yule tree prior, log-normal relaxed-clock branch rate priors, and uniform prior distributions for all parameters except the *COI* rate mean. *Automatic set clock rate* and *automatic set fix mean substitution rate flag* were deselected. In the Site Model panel, *Fix mean substitution rate* was not selected and *substitution rate* was not estimated. Four-category gamma distributions were used, and empirical base frequencies were selected for *COI* because Marshall *et al*. (2016) found that estimating base frequencies with *COI* in a cicada tribe of similar depth allowed Bayesian chains to estimate implausibly high levels of *COI* substitution. Base frequencies were estimated for all other partitions (following the PartitionFinder output). The clock and substitution model parameters were unlinked across subsets, whereas the tree parameters were linked. The XML files from the BEAST analyses are available as supplementary material. BEAST analyses were run until the effective sample sizes (estimated in Tracer) for divergence times and other parameters were mostly >200 after a 10% burn-in. TreeAnnotator (ver. 2.5.0, part of the BEAST package) was used to calculate the maximum clade credibility tree with mean node heights.

To visualise the temporal pattern of diversification within the tree, a lineage-through-time (LTT) plot was calculated in R (ver. 3.4.2, R Foundation for Statistical Computing, Vienna, Austria, see http:/www.R-project.org, accessed 6 February 2021) from the BEAST crown-group-calibrated chronogram using the 'ape' package (Analyses of Phylogenetics and Evolution, ver. 4.1, see http://ape-package.ird.fr/; Paradis *et al*. 2004). The number of lineages was plotted as log-transformed values.

Results and discussion

Genetic data and model selection

The final alignment for 181 specimens contained 2575 sites – 648 bp from *COI*, 685 bp from *ARD1*, and 1242 bp from *EF-1α* (~500 bp of the latter due to rare long insertions). Twenty-seven conspecific sequences were removed to create a trimmed 155-specimen dataset. In total, 68% of the data matrix was applicable and not missing (*COI* 97%, *ARD1* 76%, *EF-1α* 49%), as calculated by Mesquite (ver. 3.6, see http://mesquiteproject.org). GenBank numbers are found in Table 1.

With the outgroup taxa removed, the number of parsimony-informative sites was 308/648 for *COI*, 222/685 for *ARD1*, and 309/1242 for *EF-1α* for a total of 839. Ingroup pairwise uncorrected distances approached 20% for *COI* (with most distances spanning the root node at ~16%), 10% for *ARD1*, and

12% for *EF-1α*. PartitionFinder suggested an eight-subset scheme as follows: mtDNA 1st position: GTR+I+G; mtDNA 2nd position: HKY+I+G; mtDNA 3rd position: HKY+G; *EF-1α* 1st position plus *ARD1* UTR: HKY+G; *ARD1* 3rd position: HKY+G; *EF-1α* 2nd position JC+I; other nuclear coding JC+I, *EF-1α* intron GTR+G.

Phylogenetic analysis results and taxonomic implications

The MrBayes analysis based on the trimmed dataset finished at 36.3 million generations. All chains swapped regularly with chains of adjoining temperatures. The harmonic mean scores after burn-in were –39031.57 and –39042.98 (total –39042.28), with all potential scale reduction factors within 0.001 of 1.0. The Garli maximum likelihood analysis concluded at 110 000 generations with a score of –38830.0258, yielding a similar tree that differed in topology from the 50% majority-rule MrBayes tree only at weakly supported nodes (not shown). The MrBayes tree is displayed in Fig. 4 and 5 with posterior probabilities and ML bootstrap scores for each branch. The tree shows a moderately balanced internal structure with diversification along most major ingroup lineages. Support values are poor for some short branches but many clades are moderately to well supported with >0.95 posterior probability and >70% bootstrap values. Congeneric ingroup samples form monophyletic clades supported by the genetic data except for *Euterpnosia* Matsumura, 1917, *Haphsa*, *Oncotympana* Stål, 1870, *Pomponia* Stål, 1866, *Purana*, *Terpnosia* Distant, 1892, *Tosena* Amyot & Audinet-Serville, 1843, and *Yezoterpnosia* Matsumura, 1917 (although not necessarily with the type species sampled).

Fig. 4 and 5 also show the current subtribe and tribe classification for the Asian cicada clade. Some sections of the molecular tree closely match the current classification, whereas others do not. We examine each section of the tree below and discuss the taxonomic implications of the results. In some cases, we propose new taxonomic changes or groups as detailed in the Taxonomy section that follows.

Dundubiini + Cosmopsaltriini (Clades A and B, Fig. 4)

Tribes Dundubiini Distant, 1905 and Cosmopsaltriini Kato, 1932, containing genera from east Asia, Australasia, India, and Oceania, have undergone more detailed systematic analysis than many other groups in the Asian clade (e.g. Duffels 1988; Beuk 2002; Duffels and Turner 2002; Lee and Hayashi 2003*a*, 2003*b*, 2004; Lee 2014; Lee and Emery 2014), including molecular analysis (Lee and Hill 2010, Matsuura *et al*. 2018). Both tribes and their subtribe structure are reasonably well supported on the genetic tree as Clades A and B (Fig. 4). *Platylomia* Stål, 1870 is only weakly supported as belonging to Dundubiina, and the relationships of the dundubiine subtribes remain uncertain. Lee (2010*b*) removed *Champaka* Distant, 1905 from synonymy with *Platylomia* (see Beuk 2002) and placed it in Dundubiina, a decision which is supported here. *Platylomia* is the type genus of Platylomiini Metcalf, 1955, an unavailable *nomen nudum* under Articles 13.1 and 13.2.1 of the 'Code of Zoological Nomenclature' (International Commission on Zoological Nomenclature 1999) (see Duffels 1977, p. 23).

Subtribe Megapomponiina Lee, 2014 was established for *Megapomponia* Boulard, 2005, later with the addition of *Unipomponia* Lee, 2014, and these changes are concordant with the genetic tree (Fig. 4, Clade A) (Lee and Emery 2014). These genera differ from most Dundubiina and Orientopsaltriina Lee, 2014 in having short opercula. *Megapomponia* (then part of the genus *Pomponia*) was correctly associated with the genera from Dundubiina and Orientopsaltriina by Beuk (2002, his fig. 38) despite this difference, because of the partial sclerotisation of the dorsal part of the pygofer (see below). The placement of *Ayesha* Distant, 1905 in Orientopsaltriina (Lee and Emery 2014) is neither clearly supported nor contradicted by the genetic data.

The one tribe-level misclassification apparent within Clade A is *Karenia* Distant, 1888. Tribe Sinosenini Boulard, 1975 was named for this genus, then in Cicadettinae, due to the absence of timbals and associated differences in sound-associated morphology. However, these attributes are now understood to change convergently in cicada evolution (Moulds 2005), and Sinosenini was moved to Cicadinae following family-level genetic results (Marshall *et al*. 2018) confirmed by morphological data (Li *et al*. 2015; Wang *et al*. 2018). Although an association with Dundubiini was noted, the tribe was left in place pending additional study. With Dundubiini now extensively sampled, the evidence for synonymy of Dundubiini and Sinosenini is strong (mitogenome data further confirms the association, C. Wei, pers. comm.). We have also confirmed that *Karenia* possesses a completely unsclerotised dorsal pygofer

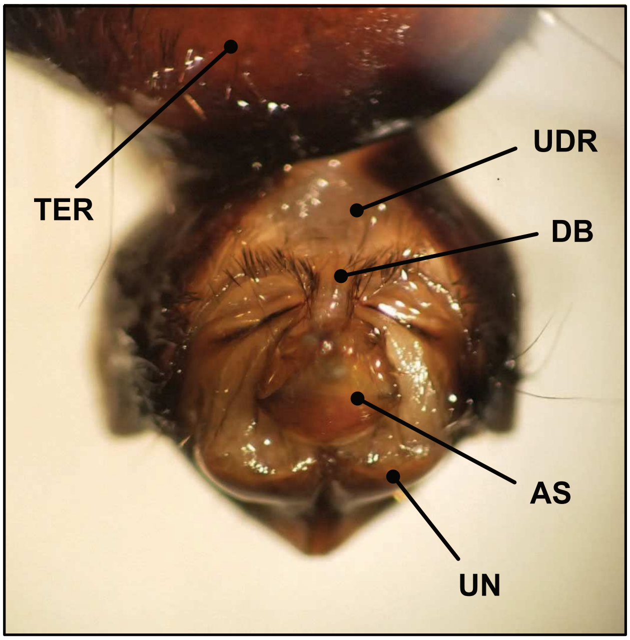


Fig. 6. Posterior view of pygofer of *Karenia* cf. *ravida* showing unsclerotised dorsal region (UDR) diagnostic for Dundubiini. Other labelled structures: AS, anal style; DB, dorsal beak, TER, tergite VIII; UN, uncus.

(Fig. 6), identified by Beuk (2002) as diagnostic for Dundubiini (see below). Within Dundubiini, the genetic evidence places *Karenia* with genera from subtribe Dundubiina, and this is supported by the presence of a clear basal lobe on the pygofer (Wei *et al*. 2009; Pham and Yang 2012), which distinguishes Dundubiina according to Lee and Emery (2014). However, some *Orientopsaltria* Kato, 1944 illustrated by Duffels and Zaidi (2000) possess this feature as well, including *Orientopsaltria agatha* (Moulton, 1911) found in the genetic tree apart from the Dundubiina genera. Wang *et al*. (2018) presented a tree based on antennal morphology which suggested that *Karenia* is closer to *Meimuna* than to *Dundubia*, but the relationship was not well supported. On balance, we recognise Sinosenini Boulard, 1975 **syn. nov.** as synonymous with Dundubiina Distant, 1905.

The lower section of the Dundubiini clade (A) on the genetic tree corresponds to subtribe Aolina Boulard, 2012, here represented by *Changa* Lee, 2016, *Haphsa*, *Kaphsa* Lee, 2012, *Sinotympana* Lee, 2009, and notably *Meimuna*. Beuk (2002) identified the heterogeneous nature of *Meimuna* at the time of his work and, following his cladistic results, transferred *Meimuna* out of Dundubiina to Cosmopsaltriina, then the sister clade of the subtribe. Later, Aolina was created by Boulard (2012) (not Boulard (2013), which also states ‘new subtribe’) for genus *Aola* Distant, 1905 (currently synonymised with *Haphsa*), and later several genera were transferred to this subtribe by Lee and Emery (2014) including *Sinosemia* Matsumura, 1927, *Meimuna*, *Sinotympana*, *Haphsa*, and *Kaphsa*. These latter changes agree with our results, although *Kaphsa* is only weakly supported as the earliest split within the group.

Within Aolina, genus *Meimuna* is monophyletic but not *Haphsa*, within which *Sinotympana* and *Changa* are nested (Fig. 4) with good support. *Haphsa bindusara* (Distant, 1881), type species of the *Haphsa* synonym *Aola* (see Lee 2008), is separated from congeneric samples and the *Haphsa* type, *H. nicomache* (Walker, 1850), by genus *Changa*. Boulard (2012, 2013) continues to use *Aola* and has added new species to the genus. Lee (2009*a*) described *Sinotympana* while noting a likely close relationship to *Haphsa* based mainly on shapes of the male operculum and abdomen (see also Pham *et al*. 2019). Lee (2016) compared *Changa* mainly with *Khimbya* Distant, 1905 but also attempted to distinguish *Changa* from *Haphsa* mainly by its comparatively long male abdomen, distinctly slender body shape, and a difference in the shape of the uncus. Further morphological study comparing all of the *Haphsa* species to *Changa* and *Sinotympana* will be needed to resolve the conflict between the tree and the current taxonomy.

Tribe Cosmopsaltriini (Fig. 4, Clade B), here represented by the type genus plus the well-studied genera *Aceropyga* Duffels, 1977 and *Diceropyga* Stål, 1870, is weakly supported as the sister clade to tribe Dundubiini, with monophyletic genera and relationships matching those found in Duffels and Turner (2002) using morphology, as well as the taxon–area cladogram of Duffels (1986, 1993). De Boer and Duffels (1996) suggested *Meimuna* to be the sister group of what we are calling the Cosmopsaltriini, but the genetic tree does not support this unless the remaining dundubiines are included with *Meimuna*. Unfortunately, we could not include *Moana* Myers, 1928, another genus that has undergone divergent morphological evolution related to acoustic behaviour, to test Duffels (1993) proposal that this interesting genus belongs in Cosmopsaltriini.

Beuk’s (2002) morphological study of Dundubiini + Cosmopsaltriini

Beuk (2002) completed a morphological cladistic analysis of the dundubiine and cosmopsaltriine genera then grouped as subtribes of Dundubiini. Fig. 7 compares the well supported relationships among these taxa (or their corresponding representatives) from Beuk’s morphological analysis and the genetic tree (Fig. 4, 5). There are many differences, especially the close relationship of *Macrosemia* Kato, 1925 and *Dundubia* in the genetic study. *Macrosemia* has historically been confused with *Platylomia* but *Macrosemia* and *Dundubia* are well supported as sister genera in the tree and separated from *Platylomia* by species currently classified in the genus *Champaka*. The two analyses also differ on the branching order of the two outgroups (*Cicada* and *Purana*). Two areas of agreement are (1) the earlier divergences of Cosmopsaltriini, *Meimuna*, *Haphsa*, and *Changa* and (2) the distal clade containing the remaining ingroup genera. The latter clade was supported in Beuk’s study by one of three synapomorphies reconstructed for multigeneric clades, a completely unsclerotised dorsal pygofer. Two other synapomorphies, which supported the branch containing *Meimuna* + Cosmopsaltriini in the morphological tree, both involve the shape of the uncus and were not confirmed by the genetic data.

Oncotympanini + Psithyristriini (part) + Tosenini (part) (Clade C, Fig. 4)

The remaining large clade (Clade C) in the upper half of the tree contains tribe Oncotympanini Ishihara, 1961 and a taxonomically incoherent assemblage from Psithyristriini Distant, 1905 and Tosenini Amyot & Audinet-Serville, 1843, both of which also appear in well supported positions in the lower half of the tree (Fig. 5). *Psithyristria* Stål, 1870, with its remarkable wing-vein evolution (see Lee and Hill 2010), is a distinctive genus so we are confident that the tribe Psithyristriini is represented here although not by the type (*P. specularis* Stål, 1870). The *Psithyristria* species are well supported as monophyletic and related to *Oncotympana* and tribe Oncotympanini (as redefined by Lee 2011), a relationship that has not been previously suggested although both are from the Philippines. The well supported position of *Neoncotympana leeseungmoi* Lee, 2011 between the sampled *Oncotympana* species shows that *Oncotympana* may not be monophyletic. *Neoncotympana* Lee, 2011 is distinguished by several divergent features including a much narrower head and swollen postclypeus (Lee 2011).

Aside from *Semia* Matsumura, 1917, the remaining genera and tribes in Clade C, *Terpnosia* (Psithyristriini) and *Tosena* (Tosenini), appear to be in need of revision. *Tosena melanopteryx* Kirkaldy, 1909 closely resembles the type of *Tosena* (*Tosena fasciata* Fabricius, 1787), so this lineage is

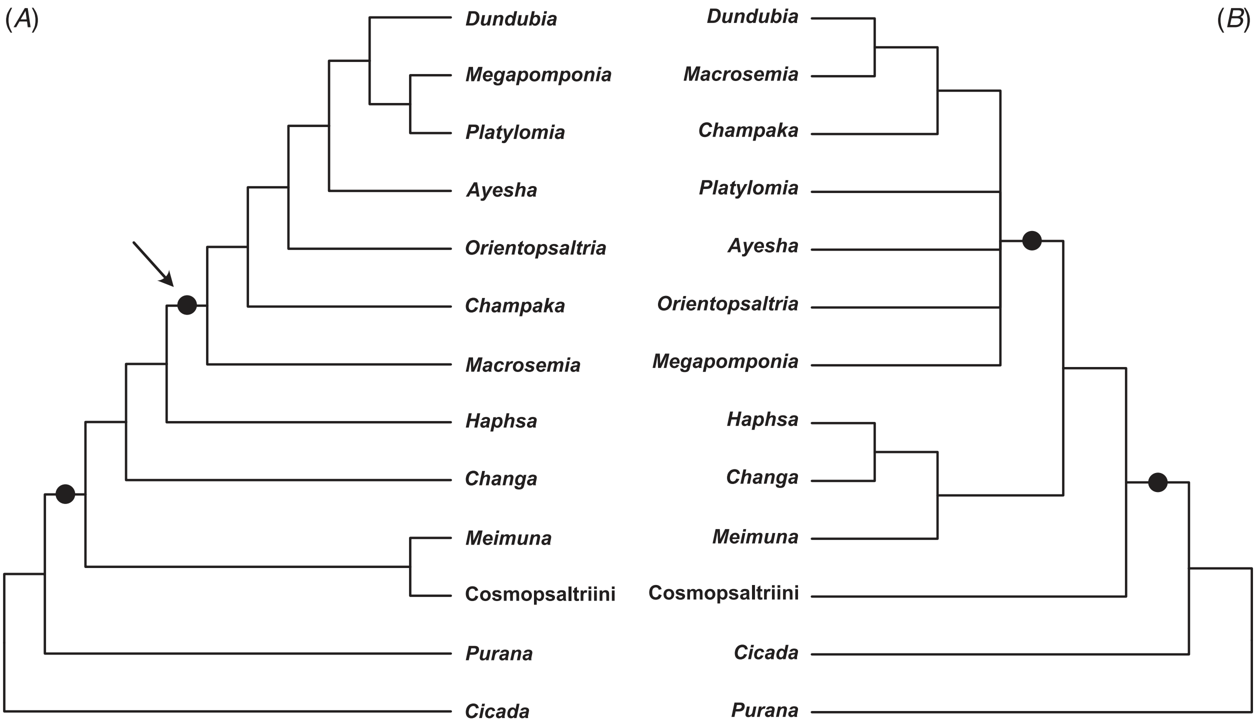


Fig. 7. Comparison of (*A*) morphological cladogram of Dundubiini from Beuk (2002, his fig. 39) and (*B*) the corresponding taxa from the genetic tree (Fig. 4, 5), showing only strongly supported relationships for the latter. The morphological analysis was rooted on *Cicada* and *Purana*, with *Cicada* viewed as more distantly related. Taxa are given with their current generic classification. Black dots indicate nodes in agreement between the analyses. Arrow indicates the origin of a reconstructed synapomorphy in the Beuk study – the complete sclerotisation of the dorsal section of the pygofer. *Meimuna* in both trees contains *Meimuna* s. str. and the species proposed as 'new genus A' by Beuk, as sister lineages.

likely to represent true Tosenini (see also discussion below on *Vittagaeana paviei* **comb. nov.**). Tosenini is one of the oldest family groups in Cicadidae, with priority over Psithyristriini and Oncotympanini. The original description of Tosenini emphasised leather-like wings and included many opaque-winged genera that have since been removed (e.g. *Huechys* Amyot & Audinet-Serville, 1843 and *Mogannia* Amyot & Audinet-Serville, 1843 from Cicadettinae, and *Gaeana* Amyot and Audinet-Serville, 1843 discussed below). In the genetic tree, *Tosena melanopteryx* is well separated from *Distantalna splendida* (Distant, 1878), recently removed from *Tosena* by Boulard (2009) but left in Tosenini, and from *Trengganua sibylla* Stål, 1863 (also classified in Tosenini) which falls close to *Gaeana* in the lower half of the tree (Fig. 5).

Tosena melanopteryx was proposed by Kirkaldy (1909) as a replacement name for *Cicada* (*Tosena*) *melanoptera* White, 1846, a primary homonym of *Cicada melanoptera* Gmelin, 1789. Boulard (2005) suggested retaining *melanoptera* because White originally placed *melanoptera* in subgenus *Tosena*, but ICZN Article 57.4 (International Commission on Zoological Nomenclature 1999) states that subgeneric names are not relevant for homonymy, which is determined by the combination of generic name and species epithet. The replacement name has been used by Naruse and Tagaki (1977) and Chou *et al*. (1997).

Genus *Terpnosia* was considered by Lee (2012) who questioned some of the species currently placed there as well as in *Pomponia* (see photographs in Lee 2012). Two species from this genus did not group together in an earlier mitochondrial phylogeny (Łukasik *et al*. 2019). The types of both genera come from Java, and we have no specimens from that locality. It is possible that all specimens of *Pomponia* and *Terpnosia* we have sampled will be found not to be congeneric with the type species. Nevertheless, we suspect that true *Terpnosia* and *Pomponia* will fall within Clade C. *Terpnosia graecina* Distant 1889, suggested by Lee (2012) to be a true *Terpnosia* (and currently classified in Psithyristriini), probably falls within this large clade. Lee and Hill (2010) synonymised Terpnosiina with Leptopsaltriina based on morphological characteristics of species of *Terpnosia* that are now known not to be true *Terpnosia* (Lee 2012). Lee (2012) later removed Terpnosiina from synonymy with Leptopsaltriina and synonymised it with Psithyristriina. This decision is concordant with the genetic tree if *Terpnosia* cf. *graecina* Distant, 1889 (from Borneo) eventually proves to be a true *Terpnosia* (keeping in mind that the genus *Leptopsaltria* was not sampled, as discussed below).

Cicadini (Clade D)

The name Cicadini Latreille, 1802 has been applied to radically different assemblages of genera (Fig. 2; see also Wang *et al*. 2017). At the time of Metcalf's (1963) and Duffels and van der Laan's (1985) catalogues, the group included

Cicada, *Leptosemia*, *Neocicada*, *Onomacritus* Distant, 1912, and genera since moved to other tribes (Tamasini Moulds, 2005 and Cicadatrini Distant, 1905, the latter now in Cicadettinae). Lee and Hill (2010) removed the remaining distantly related taxa but included most of the genera in the upper half of the genetic tree plus Leptopsaltriini (see Fig. 5), and this was followed by Sanborn (2013) with the addition of subtribe Gudabina Lee, 2013 (see also Marathe *et al*. 2018). Since that time many of these decisions have been reversed (Lee and Emery 2013, 2014; Lee 2014) and only genus *Cicada* remains. Boulard (2013) has maintained a somewhat different classification. No well-supported close relatives of *Cicada* were found in our analysis, although there is a suggestion of a relationship to tribe Lahugadini Distant, 1905 and an undescribed genus from India.

Ayuthia + Distantalna (Clade E, Fig. 4)

Distantalna and *Ayuthia* Distant, 1919, both classified in Tosenini before this study, form Clade E in Fig. 4 and are well separated from the clade likely to contain the *Tosena* type (Clade C), as noted above. The two species representing these genera superficially appear dissimilar, with *Ayuthia* having the basal half of the forewings white and *Distantalna* having the wings opaque black. Although Lee (2014) has suggested that *Ayuthia* may be misplaced in Tosenini, the classification of *Distantalna* has not been previously questioned. Guided in part by the genetic depth of this clade and differences in tribal-level attributes, we have erected a group Ayuthiini **trib. nov.** to include *Ayuthia* (Ayuthiina, **subtrib. nov.**) and *Distantalna* (Distantalnina, **subtrib. nov.**) (see Taxonomy below).

Gaeanini + Tosenini (part) + Psithyristriini (part) + Leptopsaltriini (Fig. 5, Clade F)

The lower section of the genetic tree (Fig. 5) is dominated by a large, well supported, taxonomically incoherent clade (F) containing cicadas from five different tribes, including two tribes defined in part by opaque wings. Unfortunately, we did not sample the type genus *Leptopsaltria* Stål, 1866 of Leptopsaltriini, so we cannot be sure of the position of the tribe. A close relationship of *Leptopsaltria* to *Tanna* is suggested by the external morphology of the *Leptopsaltria* type *Cicada tuberosa* Signoret, 1847 as illustrated in Distant (1889) and Kato (1932), so we believe it likely that true *Leptopsaltria* will fall within this larger clade. There is clearly confusion with both the tribe and subtribe levels of the presumed Leptopsaltriini clade in the tree, with species from Leptopsaltriina Moulton, 1923, Leptosemiina Lee, 2013, and Euterpnosiina Lee, 2013 strongly conflicting with well supported nodes (see Lee and Emery 2013). Puranina Lee, 2013 is monophyletic, with *Purana* clearly grouped with *Formosemia* Matsumura, 1917 and *Maua*, albeit not the type, *M. quadrituberculata* (Signoret, 1847), which was not sampled. The *Terpnosia* species in this clade are among those identified by Lee (2012) as likely requiring reassignment. The significance of the character of abdominal tubercles for this section of the tree is discussed below under 'Ancestral character-state reconstruction'.

The cicadas of tribe Gaeanini are recognised in part by their opaque black forewings, and *Talainga* and its former opaque-winged tribe were recently moved into Gaeanini by Lee (2014), in a move that is supported here. However, the Gaeanini genera in the genetic tree (see Clade G) are split by several taxa, including *Vittagaeana paviei* **comb. nov.** (in *Tosena* and Tosenini before this study), which is well separated from the other sampled *Tosena* species (found in Clade C, Fig. 4). *Vittagaeana paviei* **comb. nov.** was originally described in genus *Gaeana* (Noualhier, 1896) and later moved to *Tosena* by Moulton (1923), but we believe that true *Tosena* are represented in the genetic tree by *Tosena melanopteryx* (Fig. 1*C*, 4 Clade C), which closely resembles the type *Tosena fasciata*. Stoll's (1788) figure shows that *Tosena fasciata* possesses a pale pronotal collar, a brown abdomen, black hindwings, and a transverse pale forewing stripe that terminates at the radial cell. These features are also found in *Tosena albata* Distant, 1878, *Tosena depicta* Distant, 1888, and *Tosena mearesiana* (Westwood, 1842) (except the latter is missing the forewing stripe). In contrast, *Vittagaeana paviei* **comb. nov.** and *Vittagaeana dives* **comb. nov.** (Westwood, 1842) (Fig. 8*A*, *B*; see also Boulard 2003) have a fully black prothorax, a black abdomen, hindwings with black colouration limited to the distal portion, and a transverse forewing stripe that crosses the entire wing. Furthermore, the uncus of *Tosena melanopteryx*, illustrated in Pham (2012), is short and slightly divided apically like that of *Tosena fasciata* (shown in Hayashi 1978), whereas the uncus in *Vittagaeana* **gen. nov.** is large and dominated by a nearly undivided median lobe (Fig. 8*C*, *D*). The complete description and diagnosis of *Vittagaeana* **gen. nov.** is found below in the Taxonomy section.

With the description of the new gaeanine genus *Vittagaeana* **gen. nov.**, the composition of tribe Gaeanini would agree with the genetic tree after the removal of *Becquartina* Kato, 1940 (subtribe Becquartinina Boulard, 2005), which is well supported in the upper part of Clade G (Fig. 5) and appears to be misplaced in Gaeanini, in part due to its opaque wing phenotype (see below under 'Ancestral character-state reconstruction'). However, redefining Gaeanini would require distinguishing one or more new tribes containing the other Leptopsaltriini and misclassified Psithyristriini lineages. A new status for Gaeanini as a subtribe within Leptopsaltriini may also be warranted, but such changes will require more detailed morphological analysis.

Coherence within the lower half of the genetic tree (Fig. 5) is better at the generic level except for the *Terpnosia* and *Tosena* problems discussed above. *Formosemia* and *Maua philippinensis* Schmidt, 1924 are nested within *Purana* (see Clade H), suggesting that the latter genus may require further division. Duffels (2009) raised concerns about the monophyly of *Maua*.

The most extremely misclassified taxon is *Kalabita* Moulton, 1923 (Fig. 5, Clade G) which was placed in the Platypleurini, a tribe with no other known representatives in the Asian cicada clade. Moulton (1923) originally placed *Kalabita* in Dundubiaria, so a connection to the Asian clade was evident then, and we have been unable to determine how

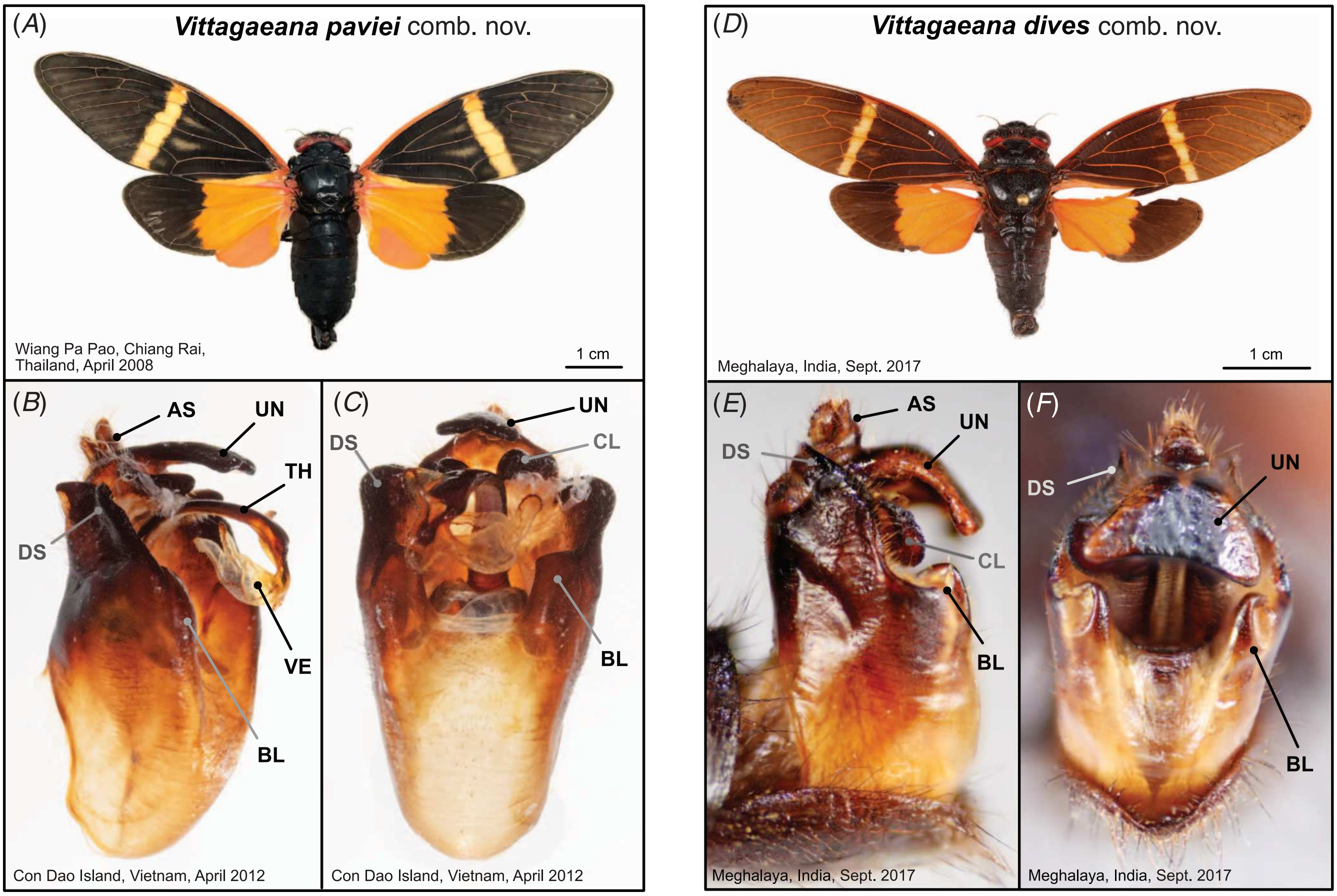


Fig. 8. Former *Tosena* species now constituting *Vittagaeana* **gen. nov.** *A*, *B*, *C*, *Vittagaeana paviei* **comb. nov.** dorsal habitus, lateral pygofer, and ventral pygofer. *D*, *E*, *F*, *Vittagaeana dives* **comb. nov.** dorsal habitus, lateral pygofer, and ventral pygofer. Labelled structures: AS, anal style; BL, basal lobe; CL, clasping lobe; DS, distal shoulder; TH, theca; UN, uncus; VE, vesica. Photo credits: *A*: Y. J. Lee; *B*, *C*: D. Rentz; *D, E, F*: V. Sarkar.

the genus became listed under Platypleurini in Metcalf's (1963) catalogue. Platypleurini was named by Schmidt (1918) without distinguishing characters. Kato (1932) focused on expanded forewing costal margins and lateral extensions of the pronotal collar when classifying genera in the Platypleurini, and *Kalabita* possesses weak versions of both features. However, *Kalabita* lacks the broad and compressed head + thorax, strongly ampliate pronotal collar lateral margins, and prostrate foreleg primary spine mentioned by Moulds (2005) in a partial diagnosis, as well as the leather-like and opaque tegmina that characterise many platypleurine genera. We found that the dorsal surface of the pygofer is only weakly sclerotised, a less prominent version of the dundubiine pygofer discussed above. We have observed this in other genera from Asian clade, including *Vittagaeana* **gen. nov.** We move *Kalabita* into Leptopsaltriini, without subtribe assignment because the tribe requires revision.

A last taxon of interest is *Cicadmalleus* (Fig. 5, Clade G) and its monogeneric tribe Cicadmalleini, characterised by an unusual 'hammer-head' morphology. With only female specimens available in their first study, Boulard and Puissant (2013) placed *Cicadmalleus* in a new subtribe within Cicadettini, subfamily Cicadettinae. Upon examining males they reassigned the group to Cicadinae at tribal level and proposed a relationship to Leptopsaltriini (Boulard and Puissant 2016), which is consistent with the genetic results. Although *Cicadmalleus* was well supported as belonging to Clade G, its position within the clade was unstable because only *COI* was available, and this reduced the support values for other relationships without changing the consensus topology. The supports shown within Clade G are from a separate analysis excluding the genus.

Boulard and Puissant (2013) originally used an incorrect root (Cicadmalleu-) when naming subtribe 'Cicadmalleuina' in Cicadettini. In 2016, they acknowledged this error and offered the correctly formed name Cicadmalleini at tribe level. Under the 'Code of Zoological Nomenclature' (International Commission on Zoological Nomenclature 1999), whether this name supplants the original spelling depends on how the original action is characterised. Correction is mandated in case of *lapsus calami* or inadvertent error (Article 32.5.1) and misspelling of the generic name (32.5.3.3). Preservation is called for if incorrect Latinisation or the use of an incorrect connecting vowel is the cause (32.5.1). Under a more radical interpretation, the 2013 name is unavailable because it is not formed from the stem of an available name (11.7.1.1) and it is not in prevailing usage (29.5). (Only one additional paper has used the incorrectly spelled name.) Because evidence exists in Boulard and Puissant (2013) for an inadvertent misspelling of the stem (bold-faced text showing both a correctly identified stem and later a correct family group suffix on p. 4) we apply 32.5.1 and use the corrected name Cicadmalleini Boulard & Puissant, 2013.

Polyneurini + Sonatini

The last clade (Clade J) in the lower half of Fig. 5 contains species in Polyneurini and Sonatini Lee, 2010, well supported as sister tribes. Polyneurini was erected for *Polyneura* Westwood, 1840 and *Cystosoma* Westwood, 1842, and later other disparate genera with similarly complex reticulate wing venation, but *Cystosoma* was eventually removed as this feature was found to evolve repeatedly and convergently within Cicadidae (Moulds 2005). *Formotosena* Kato, 1925 and *Graptopsaltria*, which have more typical wing venation for cicadas, were placed in Polyneurini because of genitalic attributes (Hayashi 1978), and this is supported by the genetic data. However, subtribe Polyneurina is divided by subtribe Formotosenina Boulard, 2008 in the tree. The deep position of *Hyalessa maculaticollis* (Motschulsky, 1866), sister to Polyneurini, supports the erection of tribe Sonatini to accommodate this species, then in genus *Sonata* (Lee 2011). The type of *Hyalessa* (*H. ronshana* China, 1925) was not sequenced, but the congeneric status of *Hyalessa maculaticollis* is uncontroversial (see Wang *et al*. 2014; Puissant and Lee 2016).

Ancestral character-state reconstruction

Maximum likelihood reconstruction of ancestral character states for wing colouration finds that the ingroup common ancestor was probably hyaline-winged (proportional likelihood 0.99558959) and that opaque wings have appeared up to five times (Fig. 9). No appreciable probability of the opaque-wing state appears for any nodes below the most recent common ancestors of the five coloured-wing clades, except for the common ancestor of Sonatini + Polyneurini, which has a proportional likelihood of 0.085 for opaque wings. Reconstruction under maximum parsimony also suggests five origins (not shown).

Character-state reconstructions are dependent on taxon sampling, which is further limited by extinction. The positions of *Tosena melanopteryx* and *Distantalna splendida*, separated from most of the other opaque-winged genera by several well supported branches (Fig. 9), give reason to doubt the utility of this character above the generic level. *Becquartina* is a similar case although the branch supports in the tree do not conclusively rule out an association with Gaeanini so further study is needed.

For the character of abdominal tubercles, reconstruction under maximum likelihood suggests as many as eight origins (Fig. 10). However, both states have high probabilities at several nodes, and key branches are weakly supported. Under maximum parsimony, the simplest possible solution finds one gain at the ancestor and five losses (the true Gaeanini, *Neocicada*, *Kalabita*, *Leptosemia takanonis* Matsumura, 1917, and the large distal clade containing *Becquartina*, *Yezoterpnosia*, *Miniterpnosia*, etc.). Absence of tubercles in *Neocicada* and *Leptosemia* led Lee and Hill (2010) to question the utility of the trait.

The most probable origins (under the ML model) of the opaque wing and abdominal tubercle phenotypes are plotted on Fig. 11, which summarises the phylogenetic results from Fig. 4 and 5 and includes dorsal images of representative genera to illustrate variation in wing morphology.

Geography and timing of diversification

The reconstruction of ancestral geographic ranges for the Asian cicada tree is shown in Fig. 12 and 13. East Asian taxa are well distributed across the tree, with representatives in most major clades. Indian taxa are also present throughout the tree, although species with ranges reaching to South India are limited to four clades – the *Calcagninus* Distant, 1892 group, a *Purana* subclade, one undescribed species within *Haphsa*, and one taxon within *Pomponia*. Taxa from Oceania are limited to one well supported clade (Cosmopsaltriini, Fig. 12).

The Lagrange results indicate that Asian + Indian ancestry is most likely for the lower half of the tree (Fig. 13) and Asian ancestry is most probable for the upper half (Fig. 12) (final –lnL = 46.14, dispersal = 0.001156, extinction = 4.285e-09). In both cases, an alternative ancestral area solution is found with a probability within 2 points of the most likely solution, Asia alone for the lower half and Asia + Australasia for the upper half. A South Indian taxon related to *Haphsa* is estimated to have entered India from Asia, whereas other South Indian groups (*Calcagninus* and the Indian *Purana* subclade) either arrived in the same manner or (less likely) trace their geography to an Indian ancestor for the group. *Neocicada* is estimated to have entered North America from East Asia.

With the fossils constraining the applicable crown nodes, BEAST estimates the age of the most recent common ancestor (MRCA) of the ingroup taxa to be 38 Ma (95% highest posterior density, or HPD, interval 28–50 Ma) (Fig. 14*A*), in the Middle Eocene to Early Oligocene Epochs depending on prior belief in the *COI* rate. With the fossils instead constraining the origins of the stems supporting their clades, a younger mean ingroup age of 31 Ma is estimated, extending to the Oligocene–Miocene transition (23–41 Ma). Posterior age estimates of the fossil calibrated nodes show that the minimum ages of some fossils sometimes conflict with the molecular clock prior (Fig. 14*B*, *C*) (e.g. *Meimuna protopalifera* in both analyses). As expected from this, when the fossil calibrations are removed, a younger mean age of 20 Ma (95% HPD is estimated for the tree, dating the radiation to the late Oligocene or Miocene (not shown)). The final trees estimated in BEAST differ from those estimated by MrBayes and Garli only at poorly supported nodes. An early Miocene age was found for the Asian clade by Price *et al*. (2019), as an outgroup for analysis of tribe Platypleurini. However, their study used fewer fossil calibrations. With the uncertainty in the clock and fossil calibrations and the seemingly low level of

Fig. 9. Reconstruction of maximum likelihood ancestral character-states on the MrBayes phylogeny (Fig. 4, 5), for the trait of opaque wings. The tree has been trimmed to contain one exemplar per genus for monophyletic genera. Proportion of black and white colour at nodes indicates proportional likelihood of the two states. Five origins of opaque-wing morphology are suggested, although topological uncertainty is not taken into account. Strongly supported branches from the MrBayes tree are indicated with stars. Solution –log-likelihood = 20.97929271; Mk1 rate = 0.31128549.

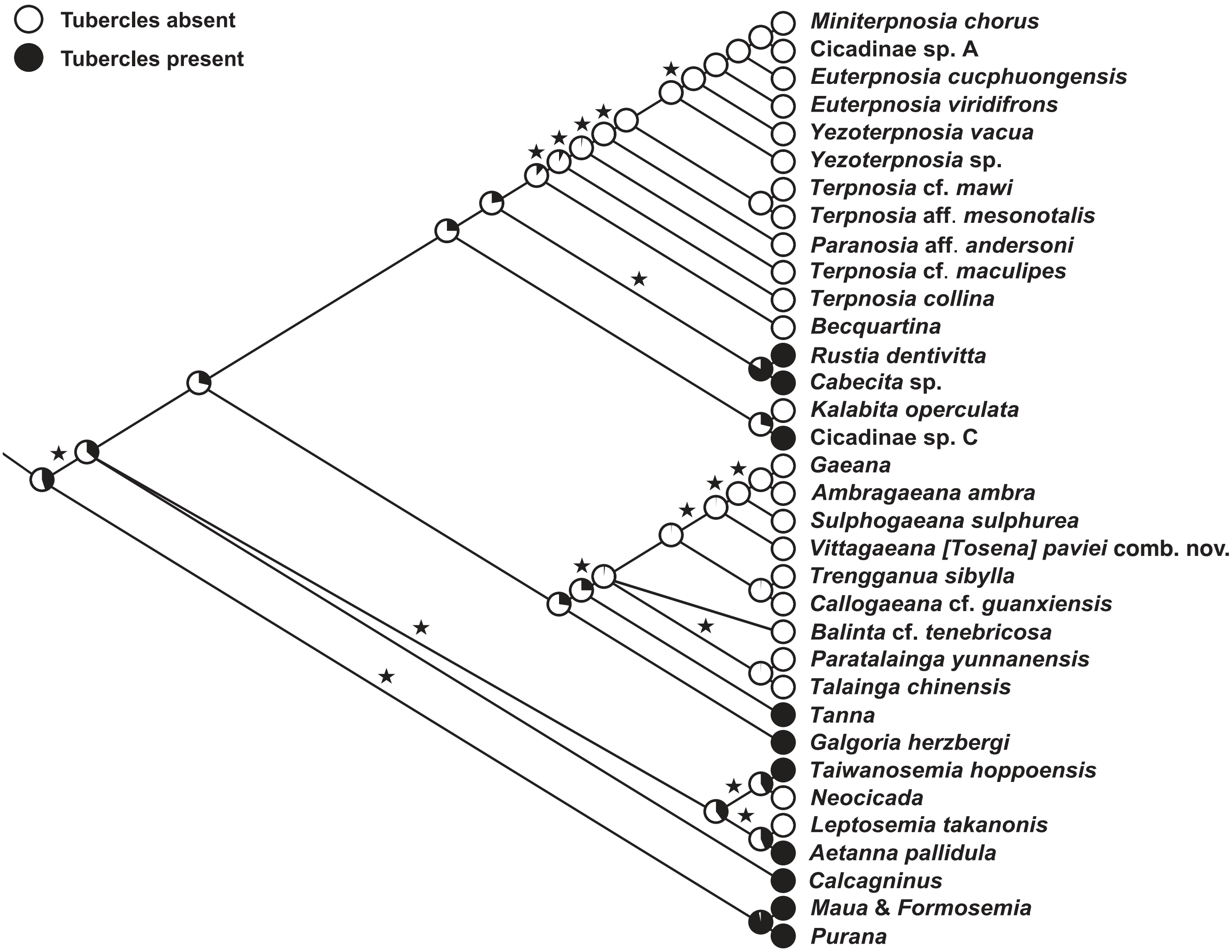


Fig. 10. Reconstruction of maximum likelihood ancestral character-states on Clade F of the MrBayes phylogeny (see Fig. 5), for the trait of abdominal tubercles. The tree has been trimmed to contain one exemplar per genus for monophyletic genera. Proportion of black and white colour at nodes indicates proportional likelihood of the two states. Gray terminals indicate uncertain character states. Topological uncertainty is not taken into account. Strongly supported branches from the MrBayes tree are indicated with stars. Solution –log-likelihood = 17.58150273; Mk1 rate = 0.01818047.

phylogenetic signal for mitochondrial branch lengths in datasets of this sort (Marshall *et al*. 2016), there remains a large degree of uncertainty in the age estimates.

Although the divergence time estimates are uncertain, our analyses suggest that the Asian clade did not diverge long before the collision of India with Asia (50–35 Ma: Karanth 2006; Aitchison *et al*. 2007; Ali and Aitchison 2008). This conclusion is further supported by the fact that two of the four earliest diverging branches in the tree were estimated to have an Asian-only ancestral range (Fig. 12, 13). The sister-lineage in one case was estimated to have had an Indian + Asian ancestral range, so dispersal between India and Asia may have been occurring at early stages of the radiation.

The lineage-through-time plot shows approximately steady diversification for the deeper half of the tree (Fig. 14*D*), with the rate slowing to the present (the latter perhaps caused by lack of sampling of closely related species). There are no relict early diverging lineages in the tree or long, deep internal branches, and few monotypic lineages diverge even from the middle depth of the tree (only *Ayuthia*, *Distantalna*, and *Lahugada*, with one extant species each) (Fig. 14*A*). In contrast to this pattern, in family level analyses the Asian clade is supported by a branch about equal in length to the depth of the ingroup (Marshall *et al*. 2018), suggesting that the diversification of this group was preceded by a long episode without speciation or an episode of phylogenetically correlated extinction (or genetic substitution occurred in an extremely non-clocklike manner). Taxon sampling seems unlikely to explain this pattern given the large number of genera (and regions) sampled here and at the family level.

Conclusions and future directions

The Asian cicada clade has evolved with a steady pattern of diversification mainly during the middle to late Cenozoic Era. Speciation and extinction have left few long branches

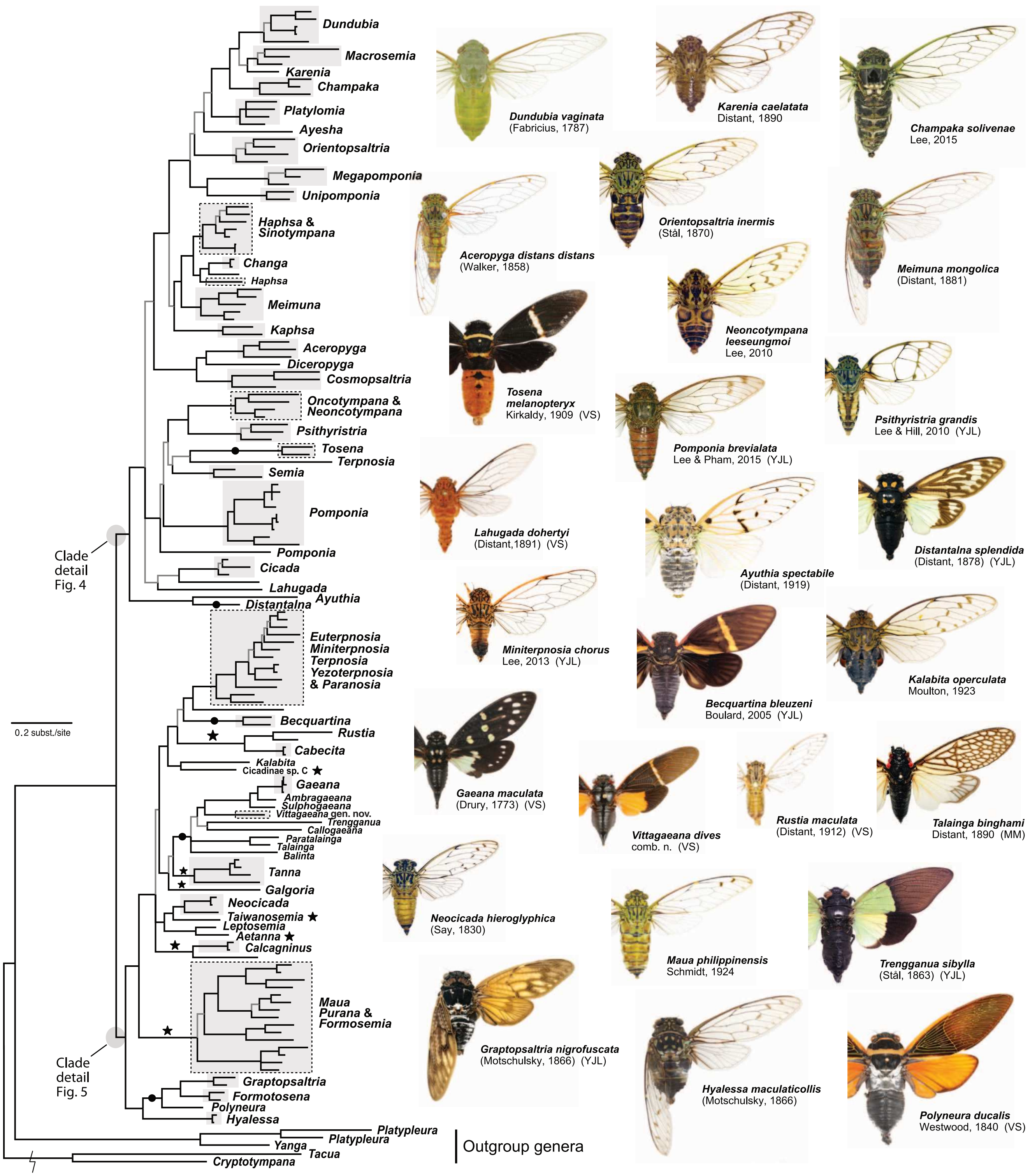


Fig. 11. Asian cicadas related to Cicadini. Summary of molecular tree with labelled genera and representative photographs illustrating morphological forms found in the clade, especially variations in wing colour, pattern, and venation. Solid circles mark potential reconstructed (maximum likelihood) origins of opaque-winged phenotypes (Fig. 9). Stars indicate reconstructed potential origins of abdominal tubercles (Fig. 10). For maximum parsimony solutions see the text. Dotted lines around boxes indicate genus-level taxonomy in conflict with the tree. Gray branches indicate poor support. Detailed phylogenetic results and branch supports are shown in Fig. 4 and 5 as indicated. 0.2 substitutions site^{-1} have been removed from outgroup branch. Initials after taxon authorships indicate photo credit.

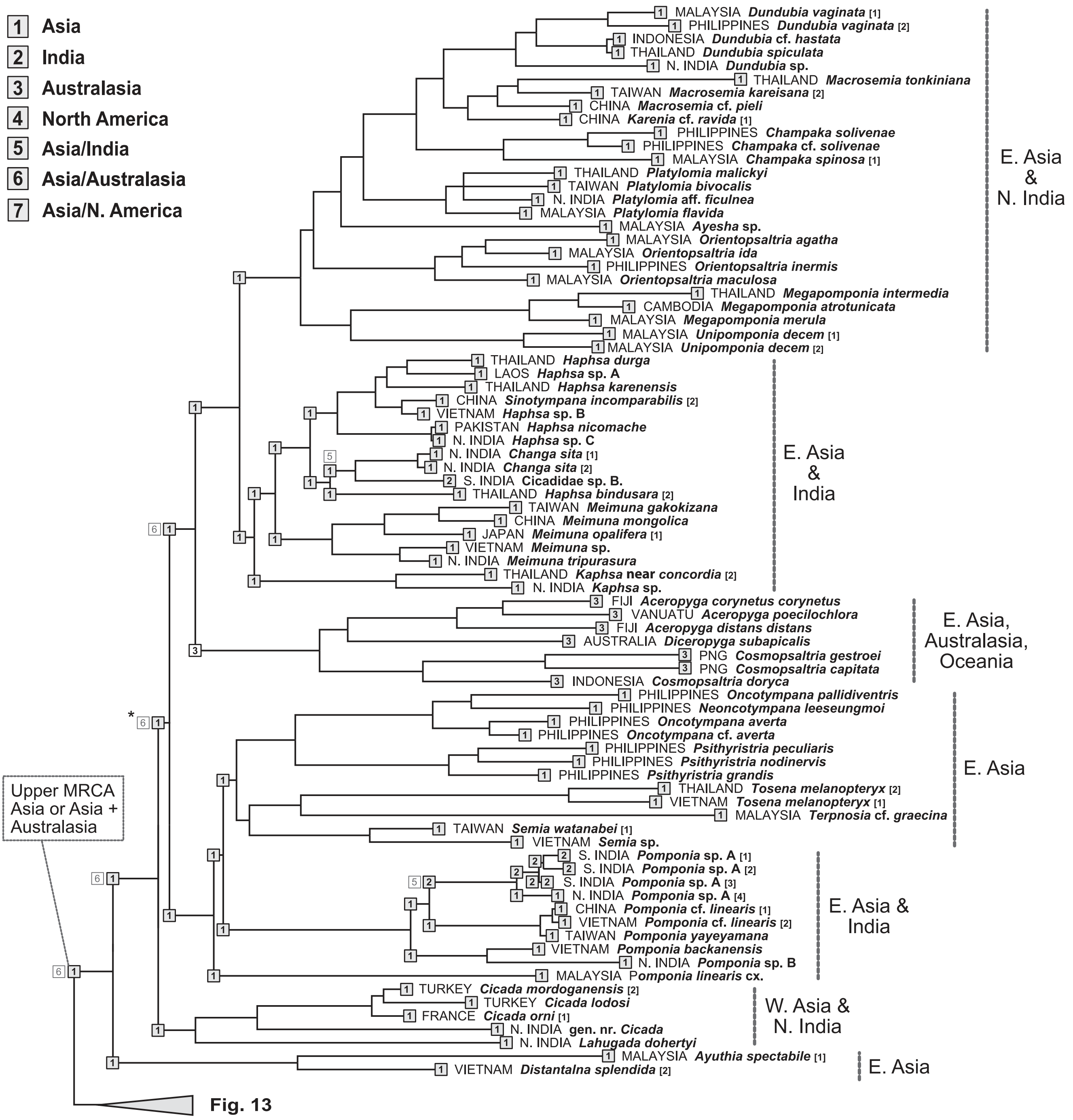


Fig. 12. Lagrange DEC reconstruction of ancestral geographic areas, upper half of tree. Subscript values in brackets are specimen numbers for taxon duplicates. Asterisk indicates arbitrarily resolved node.

where diagnostic morphological differences could accumulate – a challenging situation for taxonomists. At the same time, divergent forms like opaque wings have evolved repeatedly or evolved and then sporadically disappeared. This has created taxonomic confusion when these features have been used to define subtribes and tribes. Morphological characters based on the sound-producing apparatus, already known to be problematic (Duffels 1993; Moulds 2005; Sanborn *et al*. 2016; Marshall *et al*. 2018), have also frequently been used. Refining the higher classification of the Asian Cicadidae clade may prove challenging for these reasons. In addition to a few taxonomic rearrangements, we have added one new genus and three family level groups, but we leave further revision until more exhaustive morphological study is possible. New family

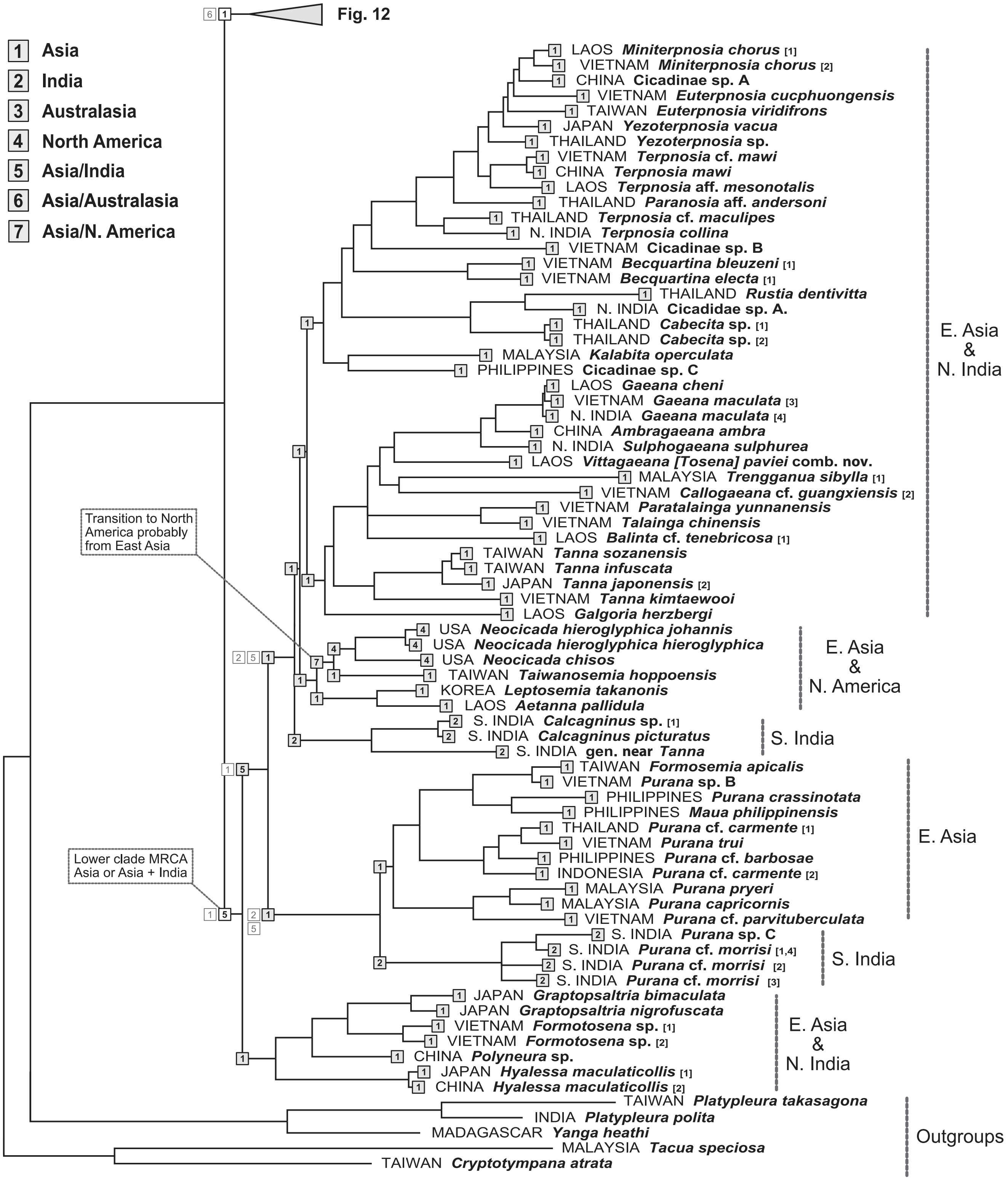


Fig. 13. Lagrange DEC reconstruction of ancestral geographic areas, lower half of tree. Subscript values in brackets are specimen numbers for taxon duplicates.

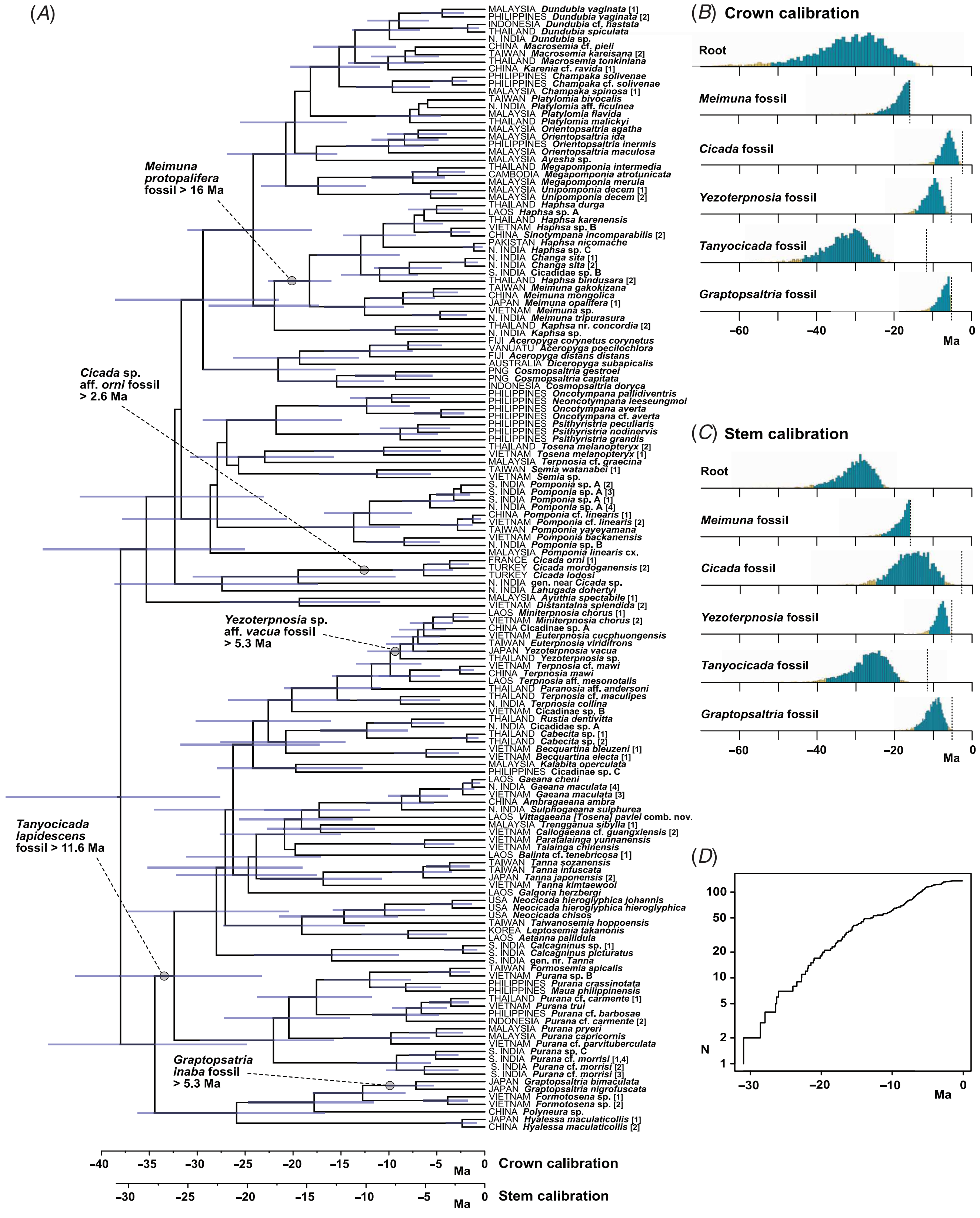


Fig. 14. BEAST divergence time analysis results. *A*, Maximum clade credibility chronogram, with mean node heights and bars indicating 95% HPD intervals, from the analysis with fossils assigned to crown group nodes as indicated. Time scale is also shown for the analysis with fossils assigned to stem origins. *B*, Posterior root and fossil age estimates for the crown-group-calibrated analysis. *C*, Posterior root and fossil age estimates for the stem-origin-calibrated analysis. *D*, Lineage-through-time plot for the chronogram in *A* with *N* (number of lineages) visualised on a log scale, for the stem-origin-calibrated analysis. Ma, Mega-annum.

level trees based on anchored phylogenomic data are in progress that will resolve the branching pattern among some cicadine clades in greater detail. One alternative approach to the existing arrangement could be to seek a combination of attributes to define the entire Asian clade as one tribe, which is supported by a long branch and therefore might be easily diagnosed. The genetic depth of this clade is comparable to that of several current cicadid tribes (Marshall *et al*. 2018).

Problems in defining higher level taxa are found elsewhere in the Cicadidae. As more cicadas are studied globally, exceptions are being found for diagnostic attributes. The uncus and claspers (genitalic characters of the male 10th abdominal segment) play an important role in current Cicadidae classification. Specifically, well developed claspers have been used to identify the Cicadettinae, yet some Dundubiini have similar structures of uncertain homology. Sanborn *et al*. (2020) proposed that the definitions of uncus and claspers might be refined by examining their position of origin (anterior *v*. posterior) (see also Ruschel and Campos 2019), but careful comparative work, perhaps facilitated by the phylogeny presented here, will be needed to establish this. In addition, a large retractable median uncus has been regarded as diagnostic for Cicadinae, but an exception was recently recognised in the genus *Dimissalna* Boulard, 2007 (see Puissant and Sueur 2011), which has a large, retractable uncus but is clearly part of Cicadettinae (Marshall *et al*. 2018; see also Sanborn *et al*. 2020). Furthermore, higher cicada taxonomy suffers from a lack of diagnostic features for female specimens. Cicada taxonomy may not stabilise until additional characters are added to the toolkit. Recent studies offer hope for such advances (e.g. antennal morphology: Wang *et al*. 2018; Malpighian tubules: Li *et al*. 2015; ovipositor morphology: Zhong *et al*. 2017; sperm morphology: Chawanji *et al*. 2006; Cui and Wei 2018).

Taxonomy

Family **CICADIDAE** Latreille
Subfamily **CICADINAE** Latreille
Tribe **AYUTHIINI** Moulds, Lee & Marshall, **trib. nov.**

ZooBank registration: urn:lsid:zoobank.org:act:B86823BC-F98F-47A6-8CC1-75F37D32315C

Type genus: *Ayuthia* Distant, 1919, by the present designation.

Included genera: *Ayuthia* Distant, 1919; *Distantalna* Boulard, 2009.

Diagnosis

Head with distance between supra-antennal plate and eye about equal to length of supra-antennal plate. Postclypeus barely protruding anteriorly; rounded in both lateral and ventral profile; postclypial ridges ill-defined and without transverse grooves. Pronotal collar with lateral margins weakly developed; lateral tooth present. Forewing semiopaque to nodal line or slightly beyond; veins C and R+Sc close together; vein RA_1 close to subcosta (Sc) for its length; distance between veins M and CuA at the basal cell not much shorter than between veins M and R+Sc, distinctly greater than half the gap between M and R+Sc; vein CuA_1 divided by crossvein so that proximal portion longest (in most individuals). Hindwing semiopaque except for apical area; anal lobe broad with vein 3A long and strongly curved at distal end. Foreleg femoral primary spine erect and hindcoxae lacking a large inner protuberance. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity, not meeting. Male abdominal tergites with sides straight or 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; sternites not translucent. Timbals extended below wing bases. Timbal covers not tightly closing tympanal cavity, reaching or nearly reaching metathorax, upper margin reduced at its base, lower margin reduced or fully developed.

Pygofer dorsal beak present on a lightly sclerotised part of pygofer; upper lobe absent; basal lobe moderately to well developed, tight against pygofer margin. Uncus not deeply bifurcate medially, restraining aedeagus in a ventral groove edged either side by a linear, sclerotised ridge. Theca basally turned through 90°, the basal plate turned at its base through 90° to face away from the thecal shaft and distally with a pair of long spreading arms joined by weak sclerotisation between them; basal plate with ventral rib completely fused. Pseudoparameres absent.

Distinguishing features

Distinguished from all other tribes in having, in combination, forewing basal cell tending rounded (rather than long and thin), forewings semiopaque and tending coriaceous to nodal line or a little beyond, hindwings similarly semiopaque except near apex, and male timbal covers that do not tightly close the timbal cavity and do not have their upper margin reduced at its base. The male genitalia have an undivided uncus (not deeply bifurcate medially) that restrains the aedeagus in a ventral groove edged either side by a linear, sclerotised ridge, a theca turned through 90° basally, and a basal plate also turned at its base through 90° so that it faces away from the thecal shaft.

Salvazana Distant, 1913 (currently in tribe Cryptotympanini) is similar to the Ayuthiini **trib. nov.** but differs significantly in the complete development of its male timbal covers that tightly close the timbal cavity, and in the male genitalia that, unlike the Ayuthiini, have the uncus developed only as a pair of long lateral lobes and the basal plate undivided.

Ayuthia and *Distantalna* were previously included in the tribe Tosenini. The Tosenini differ from the Ayuthiini **trib. nov.** in having weakly sclerotised abdominal sternites, a wide pronotal collar between lateral angles and very different male genitalia. The male genitalia of Tosenini differ from those of Ayuthiini in having a pair of auxiliary lobes between the basal lobes, a complex uncus with a developed median lobe and large lateral lobes that carry a large complex ventral lobe, and a theca turned through some 270° basally.

Subtribe **AYUTHIINA** Moulds, Lee & Marshall, **subtrib. nov.**

ZooBank registration: urn:lsid:zoobank.org:act:6037C970-35DA-46FE-A6DE-F8E9E478F208

Type genus: *Ayuthia* Distant, 1919.

Included genera: *Ayuthia*, monotypic.

Diagnosis

(In addition to the characters listed for Ayuthiini **trib. nov.**) Head including eyes narrower than mesonotum. Lateral margin of pronotal collar multitoothed. Ulnar cell 2 longer than apical cell 3. Nodal line crossing CuA after it forks (crossing CuA_1 then following CuA_2). Timbal covers with their lower margin reduced, extending vertically from auditory capsule before turning anteriorly. Distal shoulder of male pygofer very much developed and acutely protruding.

Subtribe **DISTANTALNINA** Moulds, Lee & Marshall, **subtrib. nov.**

ZooBank registration: urn:lsid:zoobank.org:act:E5DD9A10-C889-42DB-8870-128F510888AA

Type genus: *Distantalna* Boulard, 2009.

Included genera: *Distantalna*, monotypic.

Diagnosis

(In addition to the characters listed for Ayuthiini **trib. nov.**) Head including eyes wider than mesonotum. Lateral margin of pronotal collar with a prominent acute tooth. Ulnar cell 2 shorter than apical cell 3. Nodal line crossing CuA before it forks (crossing CuA then following CuA_2). Timbal covers with their lower margin fully developed, extending anteriorly from auditory capsule. Distal shoulder of male pygofer broadly rounded.

Tribe **GAEANINI** Distant

Genus ***Vittagaeana*** Moulds, Sarkar, Lee & Marshall, **gen. nov.**

ZooBank registration: urn:lsid:zoobank.org:act:558A10CC-BD3E-4B9B-AFF5-C4DB232904E1

Type species: *Gaeana paviei* Noualhier, 1896, by the present designation. This species is designated as the type species because it has a wider distribution and is more common than its congener.

Included species: *Vittagaeana paviei* (Noualhier, 1896) **comb. nov.**, *Vittagaeana dives* (Westwood, 1842) **comb. nov.**

Diagnosis

Head (Fig. 8*A*) including eyes about as wide as lateral margins of pronotal collar; eyes large, together measuring almost equal to the width between them; supra-antennal plate almost reaching eye; postclypeus bulbous, broadly rounded transversely and in lateral profile. *Thorax*: pronotal collar width at dorsal midline narrow; paranota marginally ampliate, mid lateral tooth absent or ill-defined; cruciform elevation with its dome wider than long; epimeral lobe reaching operculum. *Forewings* opaque, with 8 apical cells; apical cell 8 more than half as long as CuP+1A, usually around two thirds as long; basal cell broad, rectangular and tending to be rounded towards the apex; veins M and CuA closely separated at basal cell, the distance between them the shortest section of arculus; costal vein (C) no higher than R+Sc; vein CuA weakly bowed so that cubital cell no larger than medial cell; vein CuA_1 divided by crossvein m-cu so that proximal portion longest (equal in some specimens); wing outer margin developed from apex to M_4, reduced thereafter to be almost contiguous with ambient vein throughout most of its length. *Hindwings* with 6 apical cells; width of 1st cubital cell at distal end shorter than that of 2nd cubital cell; anal lobe broad with vein 3A strongly curved at its distal end, separated from wing margin. *Foreleg* femoral primary spine erect. Hindleg meracanthus lanceolate. *Male opercula* reaching distal margin of tympanal cavity, widely separated. *Male abdomen* in cross-section with sides of tergites straight or weakly convex; epipleurites reflexed ventrally from junction with tergites; tergites 2 and 3 not enlarged; sternites IV–VII convex in cross-section, weakly sclerotised; sternites without tubercles. Timbal covers present, flat, fully rounded dorsally and extending to metathorax but not tightly closed, lower margin raised above level of auditory capsule, not reaching operculum. Timbal strongly ribbed but without prominent intermediate short ribs; in lateral view timbals extended below wing bases.

Male genitalia

Pygofer (Fig. 8*B*, *C*) with distal shoulders pointed; upper lobes absent; basal lobes undivided, medium-sized, partly hidden in lateral view; dorsal beak present, small or ill-defined, on a lightly chitinised pygofer apex. Uncus undivided and dominated by median lobe; median lobe flat, broad; lateroventral margins strongly developed as clasping lobes holding aedeagus. Aedeagus with basal plate in lateral view sharply angled through 90° or more, in dorsal view apical arms long, base short; basal portion of basal plate directed upwards against thecal shaft; ventral rib completely fused with basal plate, large; junction between theca and basal plate rigid, without a 'hinge'; thecal shaft straight basally, otherwise curved through 180° over its length; pseudoparameres absent; thecal subapical cerci absent; flabellum absent; conjunctival claws absent; vesica not retractable.

Distinguishing features

Differs from all other genera in having, in combination, fore- and hindwings entirely opaque, forewing with 8 apical cells, forewing veins M and CuA joining the basal cell separately but close together (the distance between them the shortest section of arculus), the lateral margin of the pronotal collar not ampliate, and timbal covers that reach the anterior margin of the timbal cavity.

Vittagaeana **gen. nov.** differs from *Tosena* in having the supra-antennal plate large and almost reaching the eye (well separated from eye in *Tosena*), the lateral margin of the pronotal collar not ampliate and lacking a lateral tooth (ampliate with tooth in *Tosena*), the posterior pronotal collar very narrow, its median length less than one-fifth the median length of the inner area of pronotum (about one-third or longer in *Tosena*), forewing vein CuA_2 straight (strongly curved in *Tosena*), forewing crossvein r distant from base of RA_2 (very close in *Tosena*), and the male theca with a non-retractable vesica rather than retractable.

Vittagaeana **gen. nov.** is closely allied to genera in the Gaeanini (see phylogenetic discussion below). It differs from other genera in that tribe by having the male timbal covers reaching the metathorax and completely closing the timbal cavity. It differs from *Ambragaeana* Chou & Yao, 1985 in lacking an upper pygofer lobe and from *Trengganua* Moulton, 1923 in lacking well developed uncal lateral lobes.

The two *Vittagaeana* **gen. nov.** species are sometimes confused (Boulard 2003, 2008). *Vittagaeana paviei* is larger and can be identified by a head with red that extends forward around the eyes (does not surround the eyes in *V. dives*) (Fig. 8*A, D*). In most *Vittagaeana paviei* specimens, the forewing stripe is broader and covers the apical portion of the medial cell (apical portion exposed in *V. dives*). For male specimens, the much narrower and straighter uncus distinguishes *V. paviei*, compared to the broad uncus that is bent beyond 45° in *V. dives* (Fig. 8*E, F*).

Phylogenetic relationships

The two *Vittagaeana* **gen. nov.** species have long been considered as belonging to the genus *Tosena* and consequently included in the tribe Tosenini. However, the molecular analysis places the type species in a group of genera currently in the tribe Gaeanini, distant from the true Tosenini. This relationship is also supported by the morphology, especially the non-retractable vesica in the male genitalia and the strongly developed lateroventral margins of the uncus formed as lobes for holding the aedeagus. We transfer *Vittagaeana* to the tribe Gaeanini, without subtribe assignment because the gaeanine subtribes require reassessment.

Etymology

From the Latin *vitta*, meaning ribbon, band, stripe, and referring to the transverse pale medial band on the forewing, and *-gaeana* a traditional ending for allied species. Feminine.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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