Insect Systematics and Diversity, (2018) 2(4): 5; 1–27
doi: 10.1093/isd/ixy010
Research

A Comprehensive Phylogeny of Tettigoniidae (Orthoptera: Ensifera) Reveals Extensive Ecomorph Convergence and Widespread Taxonomic Incongruence

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Subject Editor: Alexander Blanke

Received 3 January 2018; Editorial decision 15 June 2018

Abstract

Tettigoniidae (katydids) are a diverse group of insects that are well known for their leaf-like camouflage and acoustic signaling. We present the first comprehensive phylogenetic analysis of katydids based on five molecular markers (18S rDNA, 28S rDNA, cytochrome *c* oxidase II, wingless, and histone 3) for 235 katydid taxa representing the overall diversity of the group. We specifically investigate the monophyly of katydid subfamilies and tribes and elucidate the origins and subsequent dispersal of katydids that has led to their cosmopolitan distribution. Katydids diverged from their ensiferan ancestor in the late Jurassic (~155 MYA) and multiple transoceanic dispersals have resulted in katydids inhabiting nearly every terrestrial biome outside the arctic regions. We find that the subfamilies Zaprochilinae, Saginae, Pterochrozinae, Conocephalinae, Hexacentrinae, Hetrodinae, Austrosaginae, and Lipotactinae are monophyletic while Meconematinae, Listroscelidinae, Tettigoniinae, Pseudophyllinae, Phaneropterinae, Mecopodinae, and Bradyporinae are paraphyletic. This widespread paraphyly is largely due to the convergent evolution of ecomorphs across different continents. Consequently, many of the characters that delineate the subfamilies are convergent, and in many cases biogeography is a better predictor of relationships than taxonomy. We provide a summary of taxonomic changes to better bring katydid taxonomy in line with their phylogeny.

Key words: Molecular phylogeny, Tettigoniidae, Orthoptera, Ensifera, katydid, biogeography, ecomorph, systematics

Tettigoniidae (Insecta: Orthoptera), commonly known as katydids or bush crickets, is a diverse and widespread family with more than 7,500 species found worldwide (Cigliano et al. 2017). Their leaf-like disguises and courtship rituals have made katydids the focus of numerous ecological and physiological studies involving camouflage, acoustic signaling, and sexual selection (Simmons et al. 1993, Simmons and Gwynne 1993, Wedell 1994, Castner 1995, Castner and Nickle 1995a, Nickle and Castner 1995, Simmons 1995, Kasuya and Sato 1998, Lehmann and Lehmann 2000, Gwynne 2001, Rentz et al. 2005, Gao and Kang 2006, Korsunovskaya 2008, Marshall and Hill 2009, Montealegre-Z 2009). Descriptive and revisionary taxonomy within Tettigoniidae is quickly advancing with more than 1,000 new species described since 2010 (Cigliano et al. 2017). However, the lack of a robust phylogenetic hypothesis for Tettigoniidae has made it difficult to place some of these new taxa within recognized groups and has hindered an understanding of patterns of katydid diversity and evolution.

Currently, Tettigoniidae consists of 20 extant subfamilies (Cigliano et al. 2017). Most species are found within five large, cosmopolitan subfamilies (Fig. 1): Conocephalinae (conehead katydids; 1,332 spp.), Tettigoniinae (shieldback katydids; 903 spp.), Phaneropterinae (broad wing katydids; 2,633 spp.), Pseudophyllinae (false-leaf katydids; 982 spp.), and Meconematinae (predatory katydids; 882 spp.). Recent molecular phylogenetic studies have suggested that four of these subfamilies—Phaneropterinae, Tettigoniinae, Meconematinae, and Pseudophyllinae—are not monophyletic (Mugleston et al. 2013, 2016). Indeed, the monophyly of these subfamilies has been questioned by researchers for nearly 100 years beginning with Hebard (1922) who suggested that the lines separating katydid subfamilies were not clearly delineated. More than 4,500 katydid species have been described since Hebard noted the inadequacies of the current composition of the subfamilies. As more species are described, the taxonomy gets even more obfuscated, particularly in groups with widespread distribution. Previous phylogenetic work began to

Version of Record, first published online August 14, 2018 with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

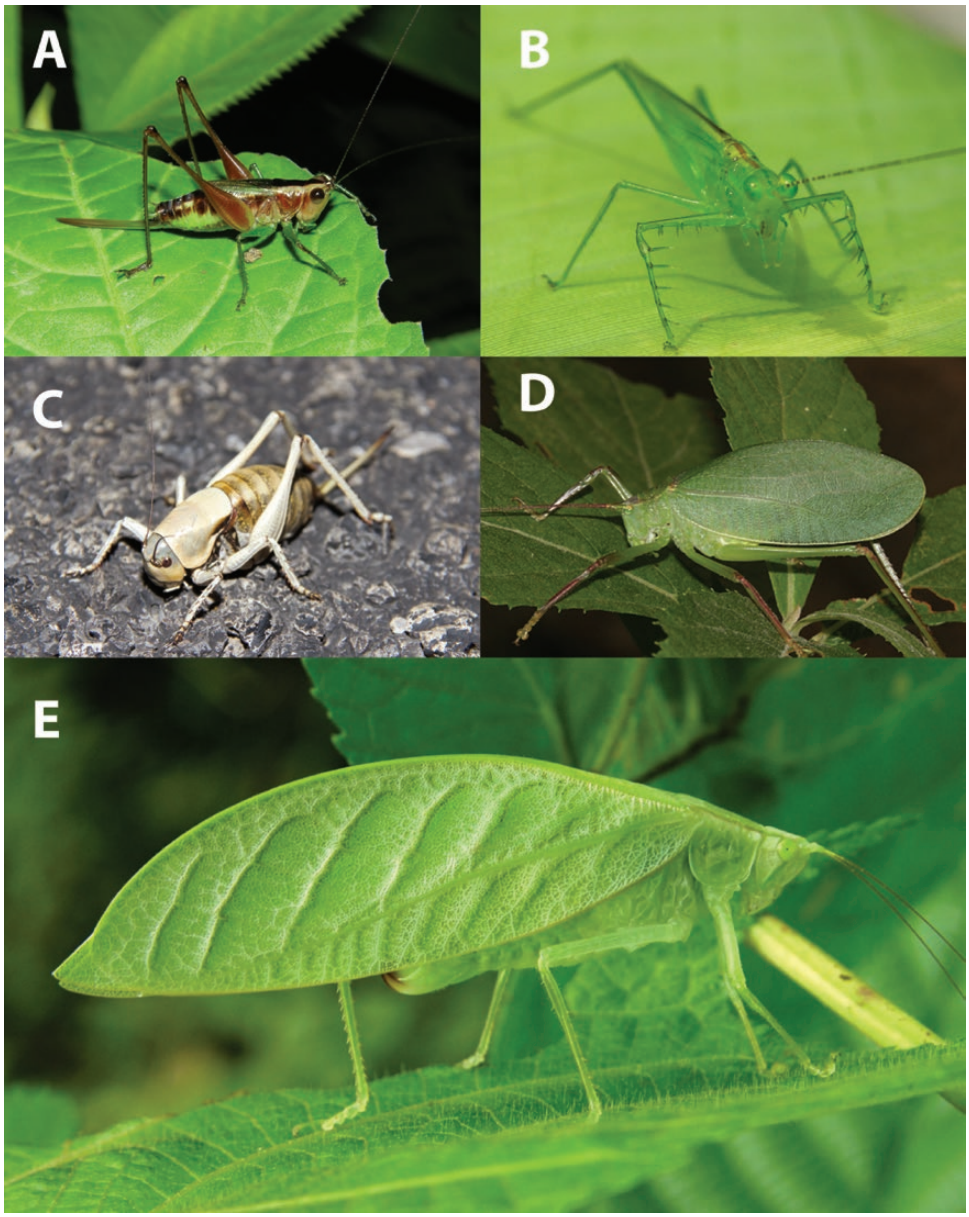

Fig. 1. Five tettigoniid subfamilies contain more than 85% of the described species: Conocephalinae (A; 1,332 spp.), Meconematinae (B; 882 spp.), Tettigoniinae (C; 903 spp.), Pseudophyllinae (D; 982 spp.), and Phaneropterinae (E; 2,633 spp.). Photo credits are as follows: (A, B, and E) Arthur Anker, (C) Joseph Mugleston, (D) Tom Murray.

diagnose which subfamilies needed to be revised (Mugleston et al. 2013), but the katydid tribes have yet to be examined in detail.

Tettigoniidae was originally described under Locustrariae (Latreille 1802). Later Burmeister (1838) grouped tettigoniids with species now placed within Stenopelmatidae and Gryllacrididae. Most of the current subfamilies were originally described as families under Locustodea (Brunner von Wattenwyl 1878), but later renamed as subfamilies under Tettigoniidae when Krauss (1902) described the family. Zeuner (1936) attempted to describe the taxonomic relationships based on wing venation and auditory tracheal morphology, and proposed two major subfamily groups with five subdivisions (Table 1). Subsequent authors largely rejected these subfamily groups, but Rentz (1979) presented a similar overall scheme with his 'primitive' and 'advanced' katydid subfamily distinctions. The relationships among the subfamilies have been based largely on an intuitive evolutionary tree presented by Gorochov (1988). The first approach to resolve the phylogenetic relationships of Tettigoniidae based on modern systematic methods was only recently presented (Mugleston et al. 2013). Using six genes across 135 katydid taxa, the overall relationships within the family began to take shape, but many of the deeper nodes were not well supported leaving relationships between some subfamilies in question. It is clear that the taxonomy for this incredibly diverse insect family is outdated and based largely on convergent, and not phylogenetically informative, characters.

Tettigoniidae represents an ancient group of ensiferan insects with estimates putting the origin of this group in the late Jurassic to the early Cretaceous (Song et al. 2015). Fossil records for Ensifera, the suborder that includes Tettigoniidae among other families, date back to *Raphogla rubra* (Béthoux et al. 2002) (Orthoptera:

Table 1. Zeuner's (1936) higher level classification of Tettigoniidae

Brachycephalia 'Primitive'	Bradyporoids	Bradyporinae
		Hetrodinae
		Acridoxeninae
Dolichocephalia 'Advanced'	Pseudophylloids	Pseudophyllinae
	Tettigonioids	Meconematinae
		Mecopodinae
		Phyllophorinae
		Tettigoniinae
		Saginae
	Conocephaloids	Conocephalinae
		Tympanophorinae
	Phaneropteroids	Phaneropterinae

The terms 'primitive' and 'advanced' were later added by Rentz (1979).

Table 2. Taxonomic distribution of katydid ingroup taxa sampled in this analysis

Subfamily	Tribes sampled	Genera sampled	Total exemplars
Austrosaginae	NA	2 of 5	2
Bradyporinae	2 of 3	2 of 26	2
Conocephalinae	4 of 6	25 of 193	44
Hetrodinae	4 of 5	4 of 14	4
Hexacentrinae	NA	4 of 12	5
Lipotactinae	NA	2 of 2	2
Listroscelidinae	2 of 5	3 of 21	4
Meconematinae	3 of 3	12 of 123	14
Mecopodinae	3 of 6	7 of 54	8
Phaneropterinae	22 of 28		76
Genus groups	11 of 20	66 of 351	
Phasmodinae	NA	1 of 1	1
Phyllophorinae	NA	2 of 12	2
Pseudophyllinae	15 of 19	28 of 240	29
Pterochrozinae	NA	3 of 14	8
Saginae	1	3 of 4	5
Tettigoniinae	8 of 12	22 of 159	26
Tympanophorinae	NA	1 of 2	1
Zaprochilinae	NA	2 of 4	2
Total	64 of 89	189 of 1247	235

Raphoglidae) nearly 250 MYA (Bethoux et al. 2002). Definitive fossils for katydids are known from the Cenozoic (Piton 1940, Sharov 1968, Gorochov 1995a, Storozhenko 1997), but the tempo and timing of katydid evolution has yet to be addressed.

For many katydids, the wings resemble leaves and provide protection from predators (Castner and Nickle 1995b) via crypsis. The independent derivations of leaf-like wings indicate that this particular morphology may be advantageous for arboreal katydids and are likely a result of similar environmental constraints that repeatedly selected for this particular form (Mugleston et al. 2016). It is apparent that the subfamily distinctions are often vague and in many cases are based on similar ecomorphs and not shared derived characters. For example, small, gracile, green or yellow predatory katydids with long legs for grasping insect prey are often placed within the subfamily Meconematinae. While these features probably aid in the predatory habits of these katydids, they are convergent features as Meconematinae is not monophyletic. Additional characters used to identify katydid subfamilies can also be associated with the unique ecology of those katydid lineages including head shape (e.g., Bradyporinae, Hetrodinae, and Conocephalinae) and overall appearance (e.g., Tettigoniinae and Listroscelidinae). The extensive paraphyly within Tettigoniidae (Mugleston et al. 2013, 2016) indicates a critical need to investigate whether the current taxonomy, particularly the taxonomy of widespread and diverse groups, is based on ecomorph convergence rather than phylogenetic history.

The purpose of this paper is to assess the phylogeny of Tettigoniidae using an extensive taxon sampling across five genes. With this phylogeny in place we address the following: 1) do the katydid subfamilies and tribes represent monophyletic groups?; 2) what lineage of katydids is sister to all other katydids?; and 3) do the morphological characters currently used to delineate katydid subfamilies and tribes represent synapomorphies or convergent features of similar ecomorphs?

Materials and Methods

Taxon Sampling

The taxon sampling was designed to best represent the taxonomic and geographic diversity across Tettigoniidae. Katydid subfamilies were sampled relative to the number of species described within (e.g., Phaneropterinae contains ~35% of the known katydid species and represents ~35% of our sampled taxa). Sampling was also focused within widely dispersed taxonomic groups (e.g., Conocephalini) and taxa with noncontiguous distributions or large gaps between species distributions (e.g., Listroscelidinae). Additional sampling among paraphyletic subfamilies and tribes identified from previous work

Table 3. Taxon sampling with subfamily, voucher number (#), locality, and GenBank accession number by gene

Taxon	Sub	Voucher	Locality	18S	28S	COII	H3	WG
Hemisaga sp.	Aust	OR483	Australia	KF570758	KF570896	KF570999	KF571123	KF571257
Pachysaga sp.	Aust	OR484	Australia	KF570757	KF570897	KF571000	KF571124	KF571258
Deracantha sp.	Brad	OR667	Mongolia	–	–	–	KX429887	KX429937
Ephippiger ephippiger	Brad	OR722	Greece	KX446541	KX446592	–	KX446665	KX446706
Acantheremus colwelli	Cono	OR622	Costa Rica	KF570821	KF570917	KF571043	KF571178	KF571312
Austrosalomona sp.	Cono	OR709	Australia	KX446542	KX446593	KX446628	KX446666	KX446707
Belocephalus subapterus	Cono	OR596	SC, United States	KF570797	KF570927	KF571027	KF571153	KF571287
Conocephalus laetus	Cono	OR719	Australia	KX446543	KX446594	KX446629	KX446667	KX446708
Conocephalus saltator	Cono	OR727	Kauai	KX446544	–	–	KX446668	KX446709
Conocephalus sp.	Cono	OR609	South Africa	KF570786	KF570915	KX429847	KF571165	KF571299
Conocephalus sp.	Cono	OR147	South Africa	KX429753	KX429797	KX429848	KX429888	KX429938
Conocephalus sp.	Cono	OR149	Australia	KX429754	KX429798	KX429849	KX429889	KX429939
Conocephalus sp.	Cono	OR548	Namibia	KF570788	KF570936	KF571004	KF571128	KF571262
Conocephalus sp.	Cono	OR556	South Africa	KF570789	KF570937	KF571010	KF571136	KF571270
Conocephalus sp.	Cono	OR599	VA, United States	KF570783	KF570951	KF571029	KF571156	KF571290
Conocephalus sp.	Cono	OR639	India	KF570787	KF570934	KF571058	KF571194	KX446710
Conocephalus sp.	Cono	OR654	Papua New Guinea	KF570785	KF570933	KF571071	KF571207	KF571343
Copiphora hastata	Cono	OR141	Costa Rica	KX429755	KX429799	KX429850	KX429890	KX429940
Copiphora rhinoceros	Cono	OR142	Peru	KF570790	KF570918	KF570977	KF571099	KF571234
Eschatoceras bipunctatus	Cono	OR550	Peru	KF570798	KF570921	KF571006	KF571130	KF571264
Euconocephalus sp.	Cono	OR642	Malaysia	KF570794	KF570926	KF571061	KF571196	KF571331
Euconocephalus sp.	Cono	OR687	Papua New Guinea	KX431992	KX431993	–	KX431994	KX431995
Karniella sp.	Cono	OR740	Rwanda	KX446545	–	KX446630	–	KX446711
Lirometopum coronatum	Cono	OR586	Costa Rica	KF570800	KF570919	KF571017	KF571143	KF571277
Macroxiphus sumatranus	Cono	OR381	Malaysia	KF570803	KF570930	KF570988	KF571110	KF571245
Neoconocephalus triops	Cono	OR595	FL, United States	KF570796	KF570950	KF571026	KF571152	KF571286
Nicsara bifasciata	Cono	OR613	Australia	KF570806	KF570916	KF571035	KF571169	KF571303
Nicsara sp.	Cono	OR558	Australia	KF570802	KF570929	KF571012	KF571138	KF571272
Odontolakis virescens	Cono	OR379	Madagascar	KF570792	KF570932	KF570986	KF571108	KF571243
Orchelimum sp.	Cono	OR030	LA, United States	KF570784	KF570938	KF570959	KF571079	KF571214
Oxylakis sp.	Cono	OR641	Malaysia	KF570799	KF570931	KF571060	KF571443	KX429941
Pseudorhynchus cornutus	Cono	OR655	Papua New Guinea	KF570795	KF570922	KF571072	KF571208	–
Pseudorhynchus hastiferA	Cono	OR557	Zambia	KF570805	KF570925	KF571011	KF571137	KF571271
Pseudorhynchus sp.	Cono	OR717	Australia	KX446546	KX446595	–	KX446669	KX446712
Pseudorhynchus sp.	Cono	OR718	Australia	KX446547	KX446596	KX446631	KX446670	KX446713
Pyrgocorypha sp.	Cono	OR640	India	KF570801	KF570935	KF571059	KF571195	KF571329
Ruspolia consobrina	Cono	OR198	South Africa	KX429756	KX429800	KX429851	KX429891	KX429943
Ruspolia lineosa	Cono	OR380	South Africa	KF570793	KF570923	KF570987	KF571109	KF571244
Ruspolia marshallae	Cono	OR716	Australia	KX446548	KX446597	KX446632	KX446671	KX446714
Ruspolia sp.	Cono	OR555	South Africa	KF570804	KF570924	KX429852	KF571135	KF571269
Sacculiphallus rotundatus	Cono	OR688	Borneo	KX446549	KX446598	KX446633	KX446672	KX446715
Salomona sp.	Cono	OR145	Papua New Guinea	KF570791	KF570928	KF570978	KF571100	KF571235
Salomona sp.	Cono	OR686	Papua New Guinea	KX429757	KX429801	KX429853	KX429892	KX429944
Sphyrometopa femorata	Cono	OR610	Costa Rica	KF570807	KF570920	KX429854	KF571166	KF571300
Sphyrometopa sp.	Cono	OR730	Costa Rica	KX446550	–	–	KX446673	KX446716
Tabangacris albolineata	Cono	OR680	Malaysia	KX429758	KX429802	KX429855	KX429893	–
Unalianus intermedius	Cono	OR739	Vietnam	KX446551	–	KX446634	KX446674	KX446717
Vestria sp.	Cono	OR660	Peru	KX429759	KX429803	–	KX429894	KX429945
Acanthoplus sp.	Het	OR176	Namibia	KF570692	KF570873	KF570979	KF571101	KF571236
Acanthoproctus vittatus	Het	OR091	Zambia	KF570689	KF570870	KF570972	KF571094	KF571229
Enyaliopsis sp.	Het	OR177	Zambia	KF570690	KF570871	KF570980	KF571102	KF571237
Hetrodes sp.	Het	OR554	South Africa	KF570691	KF570872	KF571009	KF571134	KF571268
Aerotegmina kilimandjarica	Hex	OR549	Tanzania	KF570687	KF570904	KF571005	KF571129	KF571263
Glenophisis borneo	Hex	OR638	Malaysia	KF570686	KF570903	KF571057	KF571193	KX429946
Hexacentrus japonicus	Hex	OR382	South Korea	KF570685	–	KF570989	KF571111	KF571246
Hexacentrus mundurra	Hex	OR712	Australia	KX446552	KX446599	KX446635	KX446675	KX446718
Teuthroides mimeticus	Hex	OR656	Papua New Guinea	KF570688	KF570902	KF571073	KF571209	KF571345
Lipotactes maculatus	Lip	OR634	Malaysia	KF570698	KF570876	KF571053	KF571189	KF571323
Mortoniellus ovatus	Lip	OR633	Borneo	KF570697	KF570875	KF571052	KF571188	KF571322
Chlorobalius leucoviridis	List	OR679	Australia	KX429760	KX429804	KX429856	KX429895	KX429947
Neobarrettia sp.	List	OR684	United States	–	–	–	KX429896	KX429949
Neobarrettia sp.	List	OR731	TX, United States	KX446553	–	–	KX446676	KX446719
Requena sp.	List	OR553	Western Australia	KF570696	KF570901	KF571008	KF571133	KF571267
Alloteratura sp.	Mecon	OR636	Malaysia	KF570703	KF570878	KF571055	KF571191	KF571325

Table 3. Continued

Taxon	Sub	Voucher	Locality	18S	28S	COII	H3	WG
Arachnoscelis rehni	Mecon	OR582	Costa Rica	KF570695	KF570900	KF571013	KF571139	KF571273
Austrophlugis debaari	Mecon	OR705	Australia	KX446554	KX446600	KX446636	KX446677	KX446720
Chandozhinskia bivittata vietnamica	Mecon	OR735	Vietnam	KX446555	–	KX446637	KX446678	KX446721
Kuzicus megaterminatus	Mecon	OR635	India	KF570701	KF570877	KF571054	KF571190	KF571324
Meconema thalassinum	Mecon	OR685	United States	KX429761	KX429805	–	KX429897	KX429950
Meiophisis micropennis	Mecon	OR657	Papua New Guinea	KF570812	KF570889	KF571074	KF571458	KX429948
Oceaniphisis sp.	Mecon	OR734	French Polynesia	KX446556	–	–	–	KX446722
Phlugiola arborea	Mecon	OR666	Peru	KX429762	KX429806	–	KX429898	KX429951
Phlugis irregularis	Mecon	OR624	Bolivia	KF570755	KF570899	KF571045	KF571179	KF571314
Phlugis sp.	Mecon	OR583	Costa Rica	KF570754	KF570898	KF571014	KF571140	KF571274
Poecilomerus sp.	Mecon	OR608	Madagascar	KF570811	KF570907	KX429857	KF571164	KF571298
Xiphidiopsis lita	Mecon	OR728	Hawaii	KX446557	–	KX446638	KX446679	KX446723
Xiphidiopsis sp.	Mecon	OR637	Malaysia	KF570702	KF570879	KF571056	KF571192	KF571326
Anoedopoda erosa	Mecop	OR600	Cameroon	KF570774	KF570952	KF571030	KF571157	KF571291
Eumecopoda cyrtoscelis	Mecop	OR385	Papua New Guinea	KF570771	KF570912	–	KF571113	KF571248
Mecopoda elongata	Mecop	OR736	Vietnam	KX446558	–	KX446639	KX446680	KX446724
Phrictaeformia insulana	Mecop	OR653	Papua New Guinea	KF570773	KF570908	KF571070	KF571206	KF571342
Phrictaetypus viridis	Mecop	OR393	Papua New Guinea	KF570772	KF570909	KF570997	KF571121	KF571256
Segestidea defoliara gracilis	Mecop	OR137	Papua New Guinea	KX429763	KX429807	KX429858	KX429899	KX429952
Segestidea novaeguineae	Mecop	OR136	Papua New Guinea	KX429764	KX429808	–	KX429900	KX429953
Zitsikama tessellata	Mecop	OR384	South Africa	KF570756	KF570881	KF570990	KF571112	KF571247
Acrometopa macropoda	Phan	OR043	Slovenia	KF570717	KF570853	KF570962	KF571082	KF571217
Acropsis tectiformis	Phan	OR626	Peru	KF570741	KF570834	KF571046	KF571181	KF571315
Aegimia sp.	Phan	OR619	Costa Rica	KF570749	KF570955	KF571040	KF571175	KF571309
Aganacris sp.	Phan	OR084	Bolivia	KF570720	KF570839	KF570971	KF571093	KF571228
Amblycorypha sp.	Phan	OR597	United States	KF570727	KF570842	KX429859	KF571154	KF571288
Anaulacomera sp.	Phan	OR627	Peru	KF570723	KF570841	KF571047	KF571182	KF571316
Anaulacomera sp.	Phan	OR146	Bolivia	KX429765	KX429809	KX429860	KX429901	KX429954
Austrodontura capensis	Phan	OR671	South Africa	KX429766	KX429810	KX429861	KX429902	KX429955
Barbitistes constrictus	Phan	OR077	Germany	–	KX429811	KX429862	KX429903	KX429956
Barbitistes ocskayi	Phan	OR068	Slovenia	–	–	–	KX429904	KX429957
Barbitistes serricauda	Phan	OR069	Germany	KF570742	KF570859	KF570964	KF571084	KF571219
Centrofera bimaculata	Phan	OR696	Brazil	KX446559	KX446601	KX446640	KX446681	KX446725
Ceraia mytra	Phan	OR621	Panama	KF570728	KF570838	KF571042	KF571177	KF571311
Chloroscirtus forceps	Phan	OR617	Costa Rica	KF570729	KF570843	KF571038	KF571173	KF571307
Cnemidophyllum eximium	Phan	OR135	Peru	KX429767	KX429812	KX429863	KX429905	KX429958
Deflorita integra	Phan	OR647	Malaysia	KF570737	KF570847	KF571200	KF571449	KF571336
Dolichocercus sp.	Phan	OR625	Peru	KF570740	KF570855	KX429864	KF571180	KX429960
Ducetia chelocerca	Phan	OR701	South Africa	KX446560	KX446602	KX446641	KX446682	KX446726
Ducetia japonica	Phan	OR644	India	KF570746	KF570862	KF571063	KX429906	KF571333
Ducetia japonica	Phan	OR713	Australia	KX446561	KX446603	KX446642	KX446683	KX446727
Dysmorpha obesa	Phan	OR589	Malaysia	KF570739	KF570868	KF571020	KF571146	KF571280
Dysonia pirani	Phan	OR386	Peru	KF570722	KF570849	KF570991	KF571114	KF571249
Elimaea sp.	Phan	OR681	India	KX429768	KX429813	KX429865	KX429907	KX429961
Enochletica ostentatrix	Phan	OR606	Cameroon	KF570716	KF570857	KF571034	KX429908	KF571296
Euceraia rufovariegata	Phan	OR663	Peru	–	KX429814	–	KX429909	–
Eulioptera reticulata	Phan	OR148	Zambia	KX429769	KX429815	KX429866	KX429910	KX429962
Eurycorypha sp.	Phan	OR672	South Africa	KX429770	KX429816	KX429867	KX429911	KX429963
Hemielimaea sp.	Phan	OR682	Malaysia	KX429771	KX429817	KX429868	KX429912	KX429964
Hemimirollia gracilis	Phan	OR649	Malaysia	KF570736	KF570846	KF571066	KF571202	KF571338
Hemimirollia sp.	Phan	OR646	India	KF570735	KF570845	KF571065	KF571199	KF571335
Hetaira aurigera	Phan	OR695	Peru	KX446572	KX446613	KX446649	KX446692	KX446736
Holochlora sp.	Phan	OR611	India	KF570724	KF570860	–	KF571167	KF571301
Horatosphaga inclusa	Phan	OR700	Ghana	KX446562	KX446604	KX446643	KX446684	KX446728
Horatosphaga sp.	Phan	OR604	Namibia	KF570733	KF570954	KF571033	KF571161	KF571294
Hueikaeana sp.	Phan	OR645	Malaysia	KF570734	KF570861	KF571064	KF571198	KF571334
Hyperphrona irregularis	Phan	OR669	Peru	KX429772	KX429818	–	KX429913	KX429965
Insara elegans	Phan	OR675	AZ, United States	KX429773	KX429819	–	–	KX429966
Insara sp.	Phan	OR616	Costa Rica	KF570744	KF570856	KF571037	KF571172	KF571306
Leptophyes punctatissima	Phan	OR044	Germany	KF570751	KF570851	KF570963	KF571083	KF571218
Letana megastridula	Phan	OR650	India	KF570748	KF570848	KF571067	KF571203	KF571339
Leucopodoptera eumundii	Phan	OR714	Australia	KX446563	KX446605	KX446644	–	KX446729
Microcentrum rhombifolium	Phan	OR033	UT, United States	KX429774	KF570836	KF570960	KF571080	KF571215

Table 3. Continued

Taxon	Sub	Voucher	Locality	18S	28S	COII	H3	WG
Montezumina modesta	Phan	OR683	United States	KX429775	KX429820	KX429869	KX429914	–
Monticolaria sp.	Phan	OR552	Africa	KF570747	KF570854	–	KF571132	KF571266
Morgenia rubricornis	Phan	OR703	Cameroon	KX446564	KX446606	–	KX446685	KX446730
Noia testacea	Phan	OR677	India	KX429776	KX429821	KX429870	KX429915	KX429967
Obolopteryx brevihastata	Phan	OR721	TX, United States	KX446565	KX446607	–	KX446686	KX446731
Orophus tessellatus	Phan	OR697	Costa Rica	KX446566	KX446608	KX446645	KX446687	KX446732
Parapyrrhicia dentipes	Phan	OR670	Madagascar	KX429777	KX429822	KX429871	KX429916	KX429968
Parascudderia setrina	Phan	OR662	Peru	KX429778	KX429823	–	KX429917	KX429969
Phaneroptera falcata	Phan	OR076	Germany	KF570718	KF570864	–	KF571088	KF571223
Phaneroptera gracilis	Phan	OR715	Australia	KX446567	KX446609	KX446646	KX446688	KX446733
Phylloptera sp.	Phan	OR388	Panama	KF570858	KX429824	KF570993	KF571116	KF571251
Plangia graminea	Phan	OR698	South Africa	KX446568	KX446610	–	KX446689	KX446734
Poecilimon ornatus	Phan	OR074	Slovenia	KF570752	KF570852	KF570966	KF571086	KF571221
Polichne argentata	Phan	OR632	Australia	KF570719	KF570865	KF571051	KF571187	KF571321
Polysarcus denticauda	Phan	OR038	Slovenia	KX429779	KX429825	–	KX429918	KX429970
Quiva pulchella	Phan	OR661	Peru	KX429780	KX429826	–	KX429919	KX429971
Rectimarginalis ensis	Phan	OR648	Malaysia	KF570725	KF570850	KF571201	KF571450	KX429972
Scaphura elegans	Phan	OR668	Argentina	KX429781	KX429827	–	KX429920	KX429973
Scudderia furcata	Phan	OR551	LA, United States	KF570753	KF570837	KF571007	KF571131	KF571265
Sinochlora voluptaria	Phan	OR738	Vietnam	KX446569	–	KX446647	KX446690	–
Steirodon sp.	Phan	OR618	Costa Rica	KF570732	KF570840	KF571039	KF571174	KF571308
Stenophyllia modesta	Phan	OR060	Chile	KX446570	KX446611	–	KX429921	KX429974
Stilpnochlora sp.	Phan	OR592	FL, United States	KF570731	KX429828	KF571023	KF571149	KF571283
Sympaestria sp.	Phan	OR678	Malaysia	KX429782	KX429829		KX429922	KX429975
Syntechna tarasca	Phan	OR620	Costa Rica	KF570721	KF570835	KF571041	KF571176	KF571310
Terpnistria sp.	Phan	OR704	Cameroon	KX446571	KX446612	KX446648	KX446691	KX446735
Torbia viridissima	Phan	OR631	Australia	KF570750	KF570866	KF571050	KF571186	KF571320
Trigonocorypha sp.	Phan	OR378	Madagascar	KF570745	KF570844	KF570985	KF571107	KF571242
Trigonocorypha sp.	Phan	OR651	India	KF570726	KF570867	KF571068	KF571204	KF571340
Tylopsis sp.	Phan	OR607	South Africa	KF570738	KF570869	KX429873	KF571163	KF571297
Viadana azteca	Phan	OR729	Guatemala	KX446573	–	–	KX446693	KX446737
Vossia obesa	Phan	OR387	Cameroon	KF570743	KF570863	KF570992	KF571115	KF571250
Weissenbornia sp.	Phan	OR605	Cameroon	KF570730	KX429830	KX429874	KF571162	KF571295
Zeuneria sp.	Phan	OR702	Zambia	KX446574	KX446614	KX446650	KX446694	KX446738
Phasmodes sp.	Phas	OR485	Australia	KF570817	KF570944	KF571001	KF571125	KF571259
Phyllophora sp.	Phyll	OR132	Papua New Guinea	KF570816	KF570911	KF570974	KF571096	KF571231
Sasima sp.	Phyll	OR131	Papua New Guinea	KF570770	KF570910	KF570973	KF571095	KF571230
Acanthodiphrus sp.	Pseud	OR584	Costa Rica	KF570709	KF570830	KF571015	KF571141	KF571275
Acanthoprion suspectum	Pseud	OR676	India	KX429783	KX429831	–	KX429923	KX429976
Acauloplacella sp.	Pseud	OR652	Papua New Guinea	KF570808	KF570883	KF571069	KF571205	KF571341
Acauloplax exigua	Pseud	OR699	Zambia	KX446575	KX446615	KX446651	–	KX446739
Adenes obesus	Pseud	OR392	Ghana	KF570707	KF570823	–	KF571120	KF571255
Adenes obesus	Pseud	OR601	Cameroon	KF570704	KF570953	–	KF571158	KF571292
Balboana tibialis	Pseud	OR389	Costa Rica	KF570712	KF570827	KF570994	KF571117	KF571252
Calamoptera grandis	Pseud	OR585	Costa Rica	KF570710	KF570832	KF571016	KF571142	KF571276
Callimenellus apterus	Pseud	OR140	India	KX429784	KX429832	–	KX429924	KX429977
Championica sp.	Pseud	OR615	Peru	KF570705	KF570831	KF571036	KF571171	KF571305
Cymatomera denticollis	Pseud	OR139	Africa	KF570779	KF570885	KF570976	KF571098	KF571233
Diyllus sp.	Pseud	OR623	Costa Rica	KF570711	KF570828	KF571044	KX429926	KF571313
Goethalsiella tridens	Pseud	OR588	Costa Rica	KF570775	KF570913	KF571019	KF571145	KF571279
Hemigyrus sp.	Pseud	OR737	Vietnam	KX446576	–	KX446652	–	KX446740
Homalaspidia laeta	Pseud	OR694	Peru	KX446577	KX446616	KX446653	–	KX446741
Ischnomela pulchripennis	Pseud	OR614	Costa Rica	KF570776	KF570914	KX429876	KF571170	KF571304
Leptotettix sp.	Pseud	OR665	Peru	KX429785	KX429833	–	–	–
Panoploscelis sp.	Pseud	OR377	Peru	KF570713	KF570826	KF570984	KF571106	KF571241
Parapleminia sp.	Pseud	OR629	Brazil	KF570708	KF570824	KX429877	KF571184	KF571318
Parasimodera saussurei	Pseud	OR673	Madagascar	KX429786	KX429834	KX429875	KX429925	KX429978
Phricta spinosa	Pseud	OR708	Australia	KX446578	KX446617	KX446654	KX446695	KX446742
Phyllozelus infumatus	Pseud	OR643	India	KF570781	KF570888	KF571062	KF571197	KF571332
Pterophylla camellifolia	Pseud	OR658	Kentucky	KF570715	KF570833	KF571210	KF571459	KX429979
Sathrophyllia fuliginosa	Pseud	OR587	India	KF570780	KF570887	KF571018	KF571144	KF571278
Schedocentrus sp.	Pseud	OR630	Peru	KF570714	KF570906	KF571049	KF571185	KF571319
Stenampyx annulicornis	Pseud	OR602	Cameroon	KF570782	KF570886	KF571031	KF571159	KF571293

Table 3. Continued

Taxon	Sub	Voucher	Locality	18S	28S	COII	H3	WG
Teleutias sp.	Pseud	OR391	Peru	KF570815	KF570829	KF570996	KF571119	KF571254
Xiphophyllum sp.	Pseud	OR628	Bolivia	KF570706	KF570825	KF571048	KF571183	KF571317
Zabalius ophthalmicus	Pseud	OR138	Africa	KF570778	KF570884	KF570975	KF571097	KF571232
Mimetica incisa	Pter	OR706	South America	KX446579	KX446618	–	KX446696	KX446743
Mimetica tuberata	Pter	OR612	Costa Rica	KF570694	KF570945	–	KF571168	KF571302
Roxelana crassicornis	Pter	OR690	Peru	KX446581	KX446620	KX446656	KX446697	KX446745
Typophyllum abruptum	Pter	OR692	Peru	KX446582	KX446621	KX446657	–	KX446746
Typophyllum lacinipenne	Pter	OR691	Peru	KX446583	KX446622	KX446658	KX446698	KX446747
Typophyllum mortuifolium	Pter	OR693	Peru	KX446584	KX446623	KX446659	KX446699	KX446748
Typophyllum sp.	Pter	OR196	Peru	KF570693	KF570946	KF570981	KF571103	KF571238
Typophyllum sp.	Pter	OR689	Peru	KX446580	KX446619	KX446655	–	KX446744
Clonia sp.	Sagi	OR201	South Africa	KF570699	KF570880	KF570983	KF571105	KF571240
Peringueyella sp.	Sagi	OR199	South Africa	KF570810	KF570905	KF570982	KF571104	KF571239
Saga campbelli	Sagi	OR726	Greece	KX446585		–	–	KX446749
Saga natoliae	Sagi	OR725	Greece	KX446586	–	KX446660	KX446700	KX446750
Saga sp.	Sagi	OR732	Syria	KX446587	–	KX446661	KX446701	KX446751
Anabrus sp.	Tett	OR034	NV, United States	KF570763	KF570890	KF570961	KF571081	KF571216
Alfredectes sp.	Tett	OR603	South Africa	KF570809	KF570874	KF571032	KF571160	–
Ateloplus coconino	Tett	OR674	AZ, United States	KX429787	KX429835	KX429878	KX429927	KX429980
Atlanticus sp.	Tett	OR598	FL, United States	KF570761	KX429836	KF571028	KF571155	KF571289
Bicolorana kraussi	Tett	OR080	Slovenia	KX429788	KX429837	KX429879	KX429928	KX429981
Capnobotes sp.	Tett	OR591	UT, United States	KF570759	KX429838	KF571022	KF571148	KF571282
Decticus verrucivorus	Tett	OR039	Slovenia	KX429789	KX429839	–	KX429929	–
Eobiana japonica	Tett	OR590	Japan	KF570760	KF570895	KF571021	KF571147	KF571281
Eremopedes ephippiata	Tett	OR723	AZ, United States	KX446588	KX446624	–	KX446702	–
Eupholidoptera chabrieri	Tett	OR042	Slovenia	KX429790	KX429840	KX429880	KX429930	KX429982
Metrioptera brachyptera	Tett	OR070	Germany	KX429796	–	KX429881	KX429931	KX429983
Pachytrachis gracilis	Tett	OR081	Slovenia	KF570769	KF570892	KF570968	KF571090	KF571225
Pachytrachis sp.	Tett	OR045	Slovenia	KX429791	KX429841	KX429882	KX429932	KX429984
Pediodectes sp.	Tett	OR659	Texas	KF570766	KF570939	KF571075	KF571211	KF571348
Pholidoptera littoralis	Tett	OR041	Slovenia	KX429792	KX429842	KX429883	KX429933	KX429985
Pholidoptera griseoaptera	Tett	OR079	Germany	KF570767	KF570893	KF570967	KF571089	KF571224
Plagiostira albonotata	Tett	OR594	UT, United States	KF570768	KF570894	KF571025	KF571151	KF571285
Platycleis affinis	Tett	OR071	Slovenia	KF570764	KF570891	KF570965	KF571085	KF571220
Platydecticus sp.	Tett	OR664	Chile	KX429793	KX429843	–	–	–
Rhachidorus blackdownensis	Tett	OR711	Australia	KX446589	KX446625	KX446662	KX446703	KX446752
Rhachidorus sp.	Tett	OR710	Australia	KX446590	KX446626	KX446663	KX446704	KX446753
Roeseliana roeselii	Tett	OR046	Germany		–	KX429884	KX429934	KX429986
Sepiana sepium	Tett	OR072	Slovenia	KX429794	KX429844	KX429885	KX429935	KX429987
Steiroxys trilineata	Tett	OR593	WA, United States	KF570762	KX429845	KF571024	KF571150	KF571284
Tettigonia cantans	Tett	OR075	Germany	KF570765	–	–	KF571087	KF571222
Tettigonia viridissima	Tett	OR040	Germany	KX429795	KX429846	KX429886	KX429936	KX429988
Tympanophora sp.	Tymp	OR486	Australia	KF570777	KF570947	KF571002	KF571126	KF571260
Kawanaphila sp.	Zap	OR487	Australia	KF570700	KF570882	KF571003	KF571127	KF571261
Zaprochilus sp.	Zap	OR707	Australia	KX446591	KX446627	KX446664	KX446705	KX446754

Outgroups	Family	Voucher	Locality	18S	28S	COII	H3	WG
Camptonotus carolinensis	Gryllacrididae	OR024	NC, United States	KF570818	KF570941	KF570958	KF571078	KF571213
Capnogryllacris sp.	Gryllacrididae	OR390	Malaysia	KF570819	KF570942	KF570995	KF571118	KF571253
Cyphoderris monstrosa	Prophalangopsidae	OR021	Canada	KF570814	KF570943	KF570957	KF571077	KF571212
Troglophilus neglectus	Rhaphidophoridae	OR083	Slovenia	KF570820	KF570948	KF570970	KF571092	KF571227
Stenopelmatus fuscus	Stenopelmatidae	OR014	UT, United States	KF570813	KF570940	KF570956	KF571076	–

Subfamilies are abbreviated as follows: (Aust) Austrosaginae, (Brad) Bradyporinae, (Cono) Conocephalinae, (Het) Hetrodinae, (Hex) Hexacentrinae, (Lip) Lipotactinae, (List) Listroscelidinae, (Mecon) Meconematinae, (Mecop) Mecopodinae, (Phan) Phaneropterinae, (Phas) Phasmodinae, (Phyll) Phyllophorinae, (Pseu) Pseudophyllinae, (Pter) Pterochrozinae, (Sagi) Saginae, (Tett) Tettigoniinae, (Tymp) Tympanophorinae, (Zap) Zaprochilinae. Dashes indicate missing sequence data.

(Mugleston et al. 2013, 2016) was conducted to further refine our understanding of these problematic groups. Katydid exemplars were selected from 18 of the 20 extant subfamilies (90%), 64 of the 89 tribes (72%), and 189 of 1247 genera (15%) (Table 2). The total ingroup sample consisted of 235 katydid species, including 50 taxa unique to this study (Table 3). We were unable to sample two small subfamilies. The first, Acridoxeninae (one sp.), has been posited to represent an ancient divergence from the rest of the Tettigoniidae (Rentz 1979). This monotypic subfamily is restricted to tropical West Africa and we were unable to obtain specimens suitable for DNA extraction. The second is Microtettigoniinae (seven spp.), a subfamily of diminutive katydids that are thought to represent a more recent divergence,

and their absence is not critical to understanding the deeper nodes in our tree. Outgroup taxa from three superfamilies (Stenopelmatoidea, Hagloidea, and Rhaphidophoroidea) that are hypothesized to be closely related to Tettigoniidae (Song et al. 2015) were included. Specimen vouchers are deposited in the Insect Genomics Collection, M.L. Bean Museum, Brigham Young University.

DNA Extraction and Sequencing

Muscle tissue (~25 mg) was extracted from the mesothoracic (larger specimens) or metathoracic (smaller individuals) femora of voucher katydids. DNA extractions were conducted using Qiagen DNeasy Blood and Tissue kit (Valencia, CA) following the protocol supplied by the manufacturer. Five loci (two ribosomal DNA, one mitochondrial, and two nuclear protein-coding) commonly used in insect phylogenetic studies were used for this analysis (Colgan et al. 1998, Whiting 2002, Svenson and Whiting 2004, Buckman et al. 2013, Mugleston et al. 2013). The five loci include 28S ribosomal subunit (28S rDNA, 2.2 kb), 18S ribosomal subunit (18S rDNA, 1.9 kb), cytochrome *c* oxidase subunit II (COII, 650 bp), histone 3 (H3, 375 bp), and wingless (WG, 450 bp). Genes were sequenced and amplified using oligonucleotide primers from Integrated DNA Technologies (San Diego, CA). PCR protocols were previously developed for H3 (Colgan et al. 1998), 28S rDNA (Whiting 2002, Mugleston et al. 2013), 18S rDNA (Whiting 2002), WG (Wild and Maddison 2008), and COII (Svenson and Whiting 2004, 2009) (Table 4). PCRs for ribosomal genes were conducted after replacing 1.25 µl of water with DMSO. All reactions were run on GeneAmp PCR system 9700 (Applied Biosystems, Foster City, CA). PCR product was inspected with 2% agarose gel electrophoresis using ethidium bromide to confirm amplification and test for contamination. Products were cleaned with PrepEase purification plates (USB Corporation, Cleveland, OH)

Table 4. PCR protocols with primers used in this study

Primers	Sequence 5=>3	Annealing (°C)	Elongation (s)
18S rDNA			
18S 1F	TACCTGGTTGATCCTGCCAGTAG	52°	105 s
18S bi	GAGTCTCGTTCGTTATCGGA		
18S b5.0[a]	TAACCGCAACAACTTTAAT		
18S a0.7	ATTAAAGTTGTTGCGGTT	46°	105 s
18S 9R	GATCCTTCCGCAGGTTCACCTAC		
18S a2.0[a]	ATGGTTGCAAAGCTGAAAC		
28S rDNA			
28S Tetrd1a	CGAGCGAACAGGGAAGAGCC	54°	120 s
28S rD5B	CCACAGCGCCAGTTCTGATTA		
28S 3b[a]	CCYTGAACGGTTTCACGTACT		
28S 3a[a]	AGTACGTGAAACCGTTCAGG		
28S B[a]	TCGGAAGGAACCAGCTAC		
28S A	GACCCGTCTTGAAGCACG	54°	120 s
28S Tet7b1	CTCTCCCGGATTTTCAAGGTC		
28S Tet4.7[a]	CCGGTCAAGCGAATGATTAGA		
COII			
COII F-lue	TCTAATATGGCAGATTAGTGC	52°	75 s
COII R-lys	GAGACCAGTACTTGCTTTCAGTCATC		
COII 2a1[b]	ATAGAKCWTCYCCHTTAATAGAACA	52°	75 s
CPOO 9b1[b]	GTACTTGCTTTCAGTCATCTWATG		
Histone 3			
H3 AF	ATGGCTCGTACCAAGCAGACV	50°	45 s
H3 AR	ATATCCTTRGGCATRATRGTG		
Wingless			
WG 550F	ATGCGTCAGGARTGYAARTGY	50°	45 s
WG ABRZ	CACTTNACYTCRCARCACCAR		
WG 578F2[c]	TGCACNGTGAARACYTCGTGG	50°	45 s
WG ABR2[c]	ACYTCGCAGCACCARTGGAA		

Primer sources referenced in the text.
[a]Internal primers used for sequencing only.
[b]Second primer set used if the previous set was unsuccessful in amplifying desired sequence.
[c]Nested PCR with only the nested primers used for sequencing.

Table 5. Fossil calibration points used in this study

Family	Subfamily	Species	Age (MYA)	Reference
Raphoglidae		*Raphogla rubra*	251–260.4	Bethoux et al. (2002)
Gryllacrididae	Zeuneropterinae	*Zeuneroptera scotica*	56–65	Sharov (1968)
Tettigoniidae	Tettigoniinae	*Decticus* sp.	23.1–33.9	Zeuner (1939)
Tettigoniidae	Conocephalinae	*Orchelimum placidum*	33.9–38	Scudder (1890)
Tettigoniidae	Lipotactinae	*Eomortoniellus*	33.9–37.2	Zeuner (1939)

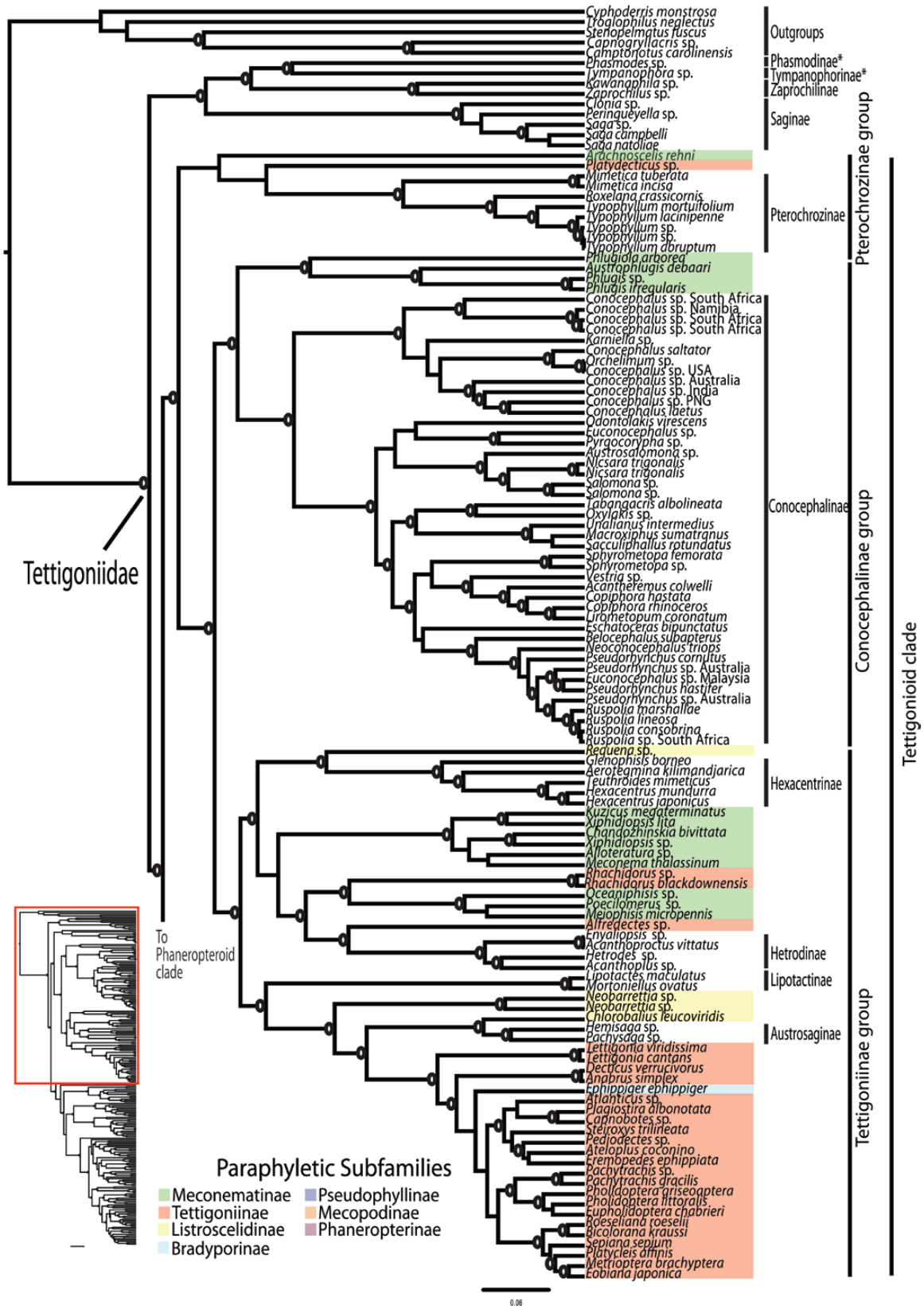

Fig. 2. BEAST tree (log likelihood score of –1.133E5) consisting of 235 ingroup taxa (partial). Posterior probabilities over 90 are marked with a circle at the node. Colored boxes around terminals indicate paraphyletic subfamilies. Vertical lines with the accompanying name denote monophyletic groups. Asterisks (*) denote subfamilies represented by only a single exemplar in this study. Subfamilies, subfamily groups, and Tettigonioid or Phaneropteroid clades are marked to the right of the tree.

following the manufacturer's instructions. Products were sequenced with BigDye chain terminating chemistry and fractioned on an ABI3730xl (Applied Biosystems) at the Brigham Young University DNA Sequencing Center (Provo, UT).

Alignment

Contigs were concatenated and edited using Geneious v6.1.5 (Kearse et al. 2012). Primer regions were trimmed from the ends of the concatenated sequences. Protein-coding sequences were

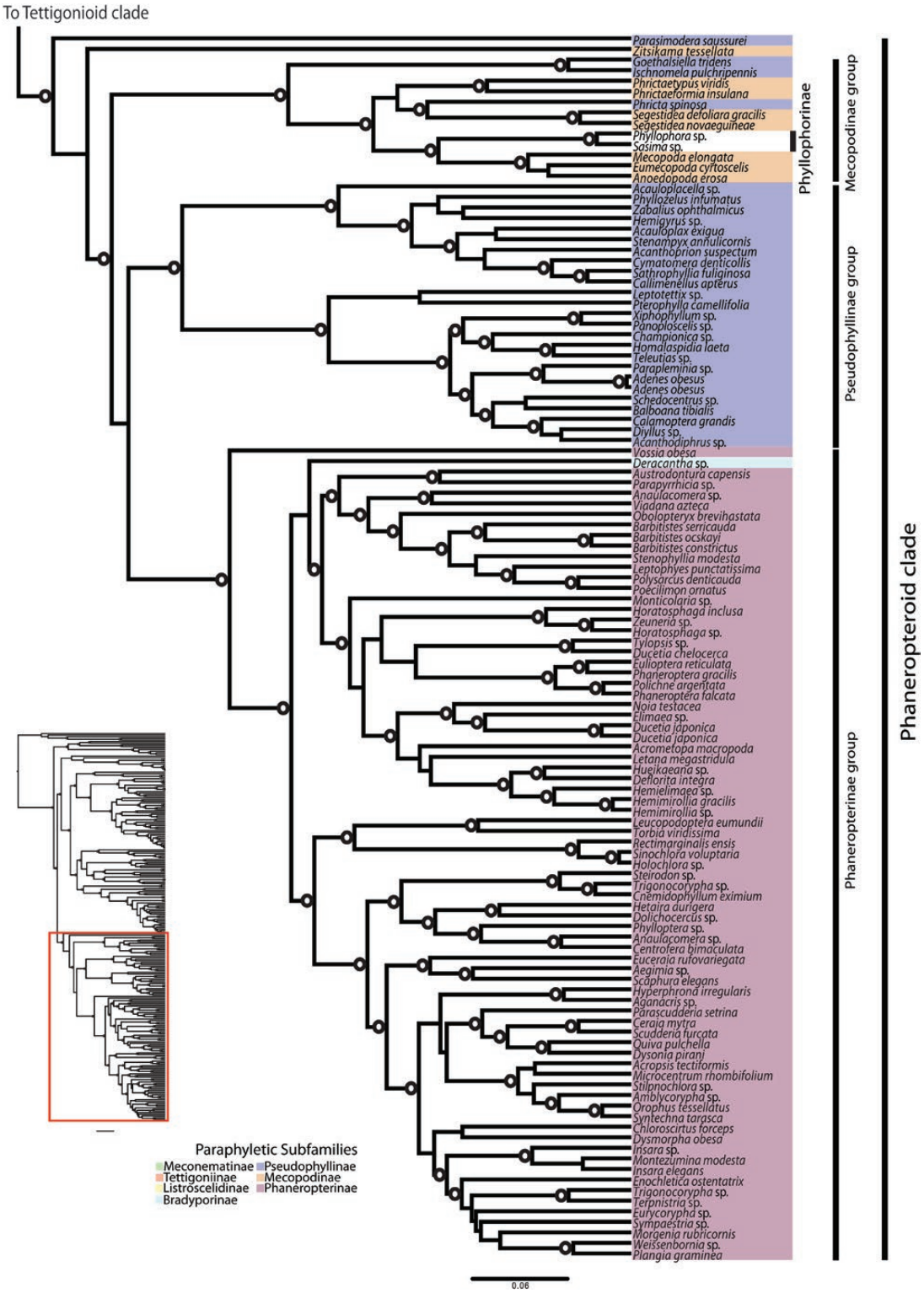

Fig. 3. BEAST tree (log likelihood score of –1.133E5) consisting of 235 ingroup taxa (continued). Posterior probabilities over 90 are marked with a circle at the node. Colored boxes around terminals indicate paraphyletic subfamilies. Vertical lines with the accompanying name denote monophyletic groups. Asterisks (*) denote subfamilies represented by only a single exemplar in this study. Subfamilies, subfamily groups, and Tettigonioid or Phaneropteroid clades are marked to the right of the tree.

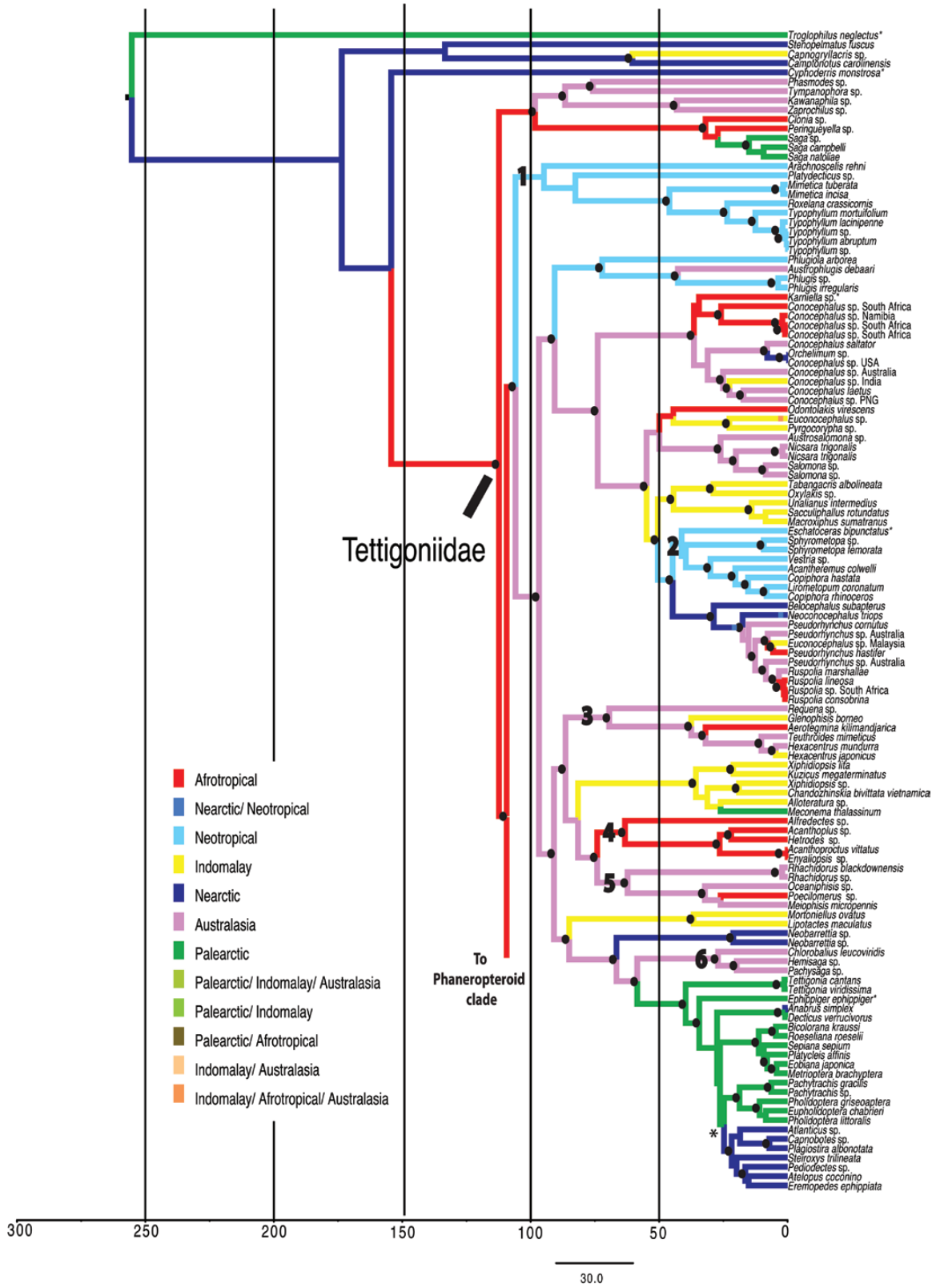

Fig. 4. BEAST tree consisting of 235 ingroup taxa (partial). Posterior probabilities over 90 are marked with a circle at the node. Asterisks denote taxa that were recovered in a different position than in the phylogenetic analysis (Figs. 2 and 3). Colored branches indicate the biogeographic region. Vertical lines are based on fossil calibrations with each line indicating 50 million years.

translated to amino acid sequences using MEGA v5 (Kumar et al. 2008). Edited sequences were submitted to GenBank (Table 3). Once the proper reading frame was established, sequences were aligned using the MUSCLE plugin under the default parameters found in MEGA (Kumar et al. 2008). Aligned amino acid sequences were then back translated into nucleotide sequences and these were exported

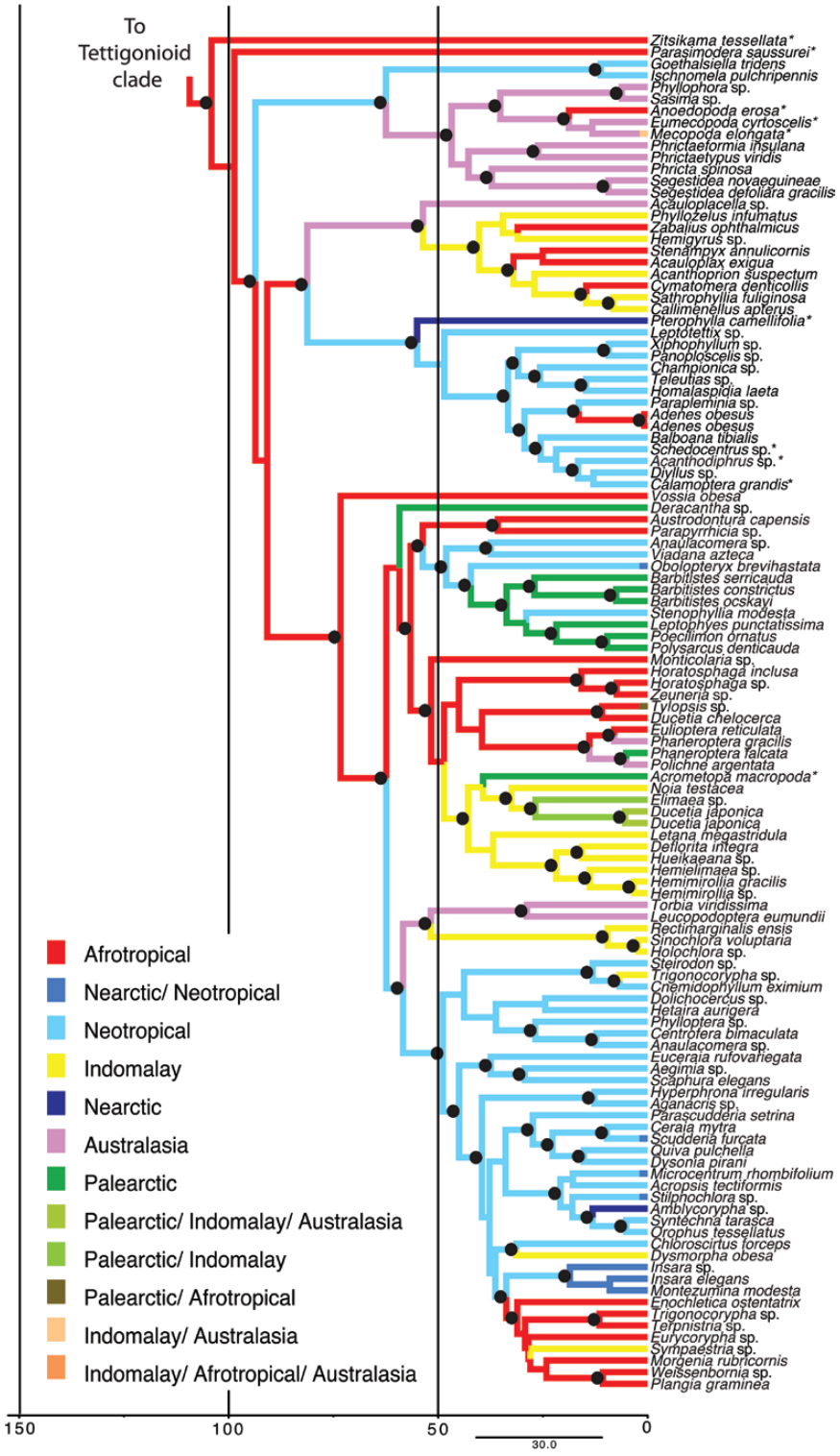

Fig. 5. BEAST tree consisting of 235 ingroup taxa (continued). Posterior probabilities over 90 are marked with a circle at the node. Asterisks denote taxa that were recovered in a different position than in the phylogenetic analysis (Figs. 2 and 3). Colored branches indicate the biogeographic region. Vertical lines are based on fossil calibrations with each line indicating 50 million years.

for further analysis. 28S rDNA and 18S rDNA were aligned using MAFFT v6 (Katoh et al. 2005) under the E-INS-I algorithm with the default settings. E-INS-I was developed to handle data with intermixed conserved and nonconserved regions (Katoh et al. 2005).

Phylogenetic Analysis

Phylogenetic analyses were conducted using BEAST v1.8 (Drummond et al. 2012). Data were partitioned using PartitionFinder v1.1 (Lanfear et al. 2012) and by gene for the analysis. When data were

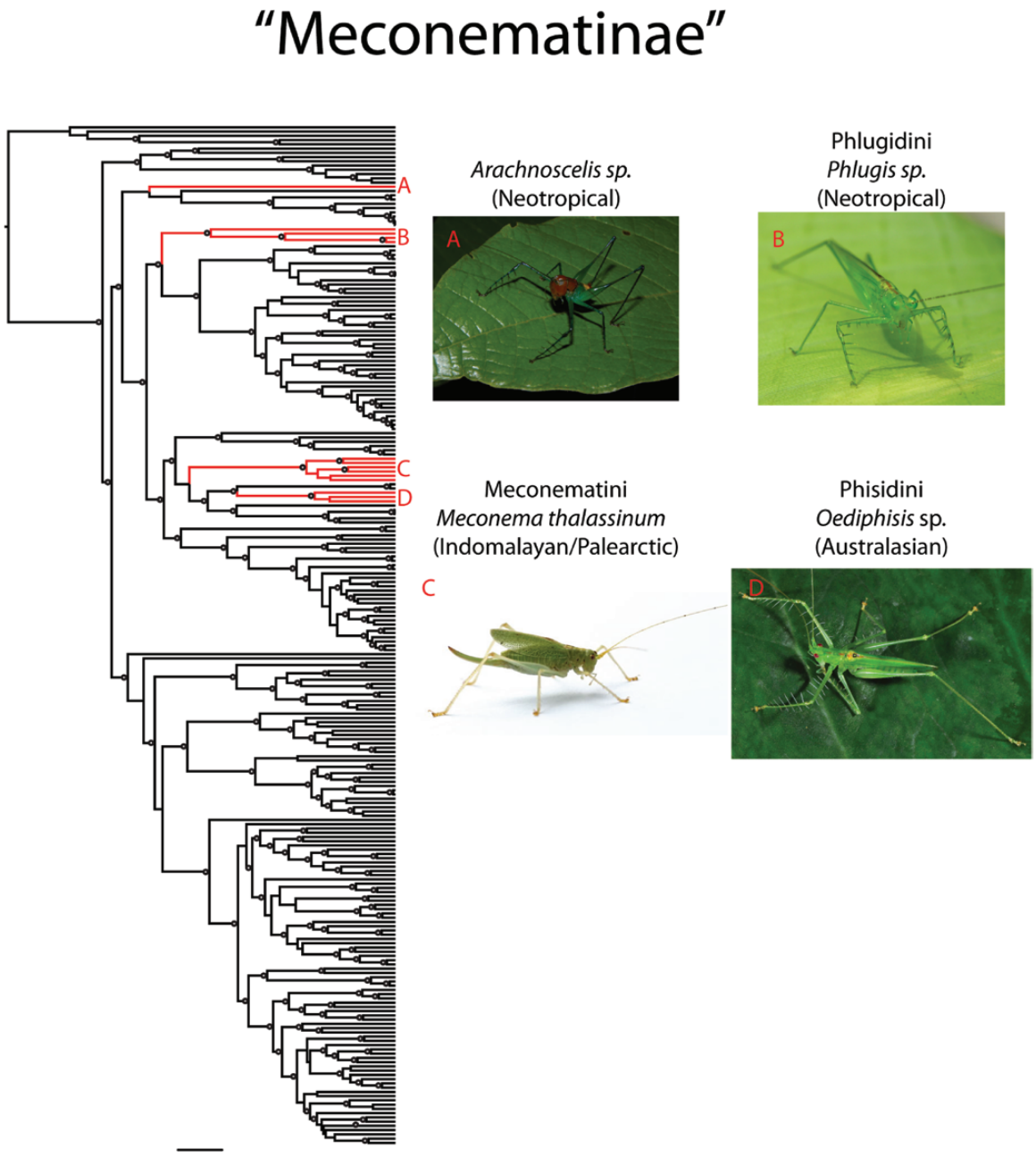

Fig. 6. Convergent gracile predatory ecomorphs. Meconematinae is paraphyletic and recovered in four positions across the Tettigoniidae phylogeny. Though similar in form, each is only distantly related. (A) *Arachnoscelis* (Karny, 1911) (Neotropical) is sister to the Neotropical Pterochrozinae group. (B) Phlugidini is sister to the cosmopolitan Conocephalinae. (C) The Indomalayan and Palearctic Meconematini is sister to a diverse clade of Afrotropical and Australasian katydids. (D) Phisidini (Australasian) is sister to the Australian shieldback katydids. Posterior probabilities over 90 are marked with a circle at the node. Photo credits are as follows: (A) Reinaldo Aguilar, (B and D) Arthur Anker, (C) Brandon Woo.

partitioned via PartitionFinder, BEAST did not reach stationarity so the partition by gene data set was used. BEAUTI v1.8 (Drummond et al. 2012) was used to build the necessary .xml files for the BEAST run. Parameters of the run included a lognormal relaxed clock with the tree prior set to Yule process. A starting tree was generated from RAxML (Stamatakis 2006) partitioning the data by gene. Three independent BEAST runs at 40 × 10^7 sampling every 40,000 generations were conducted using the BYU super computing resources (https://marylou.buy.edu/). Log files were inspected in Tracer v1.5 (Rambaut and Drummond 2003) to determine whether length of the runs was sufficient to reach stationarity, determine the log likelihood score for the runs, and determine whether the estimated sample sizes (ESS) were sufficient for the analysis. Tree files from the independent runs were combined using LogCombiner v1.8 (Drummond et al. 2012) with a resampling frequency of every 120K generations to get the ~10,000 data points as recommended by the developers. Twenty-five percent of each tree file was removed as burn-in. TreeAnnotator v1.8 (Drummond et al. 2012) was used to find the best tree within the sample trees.

Divergence Time Estimates

Divergence time estimates were made using BEAST v1.8 (Drummond and Rambaut 2007, Drummond et al. 2012). Parameters, programs, and methods for verifying stationarity are identical to those

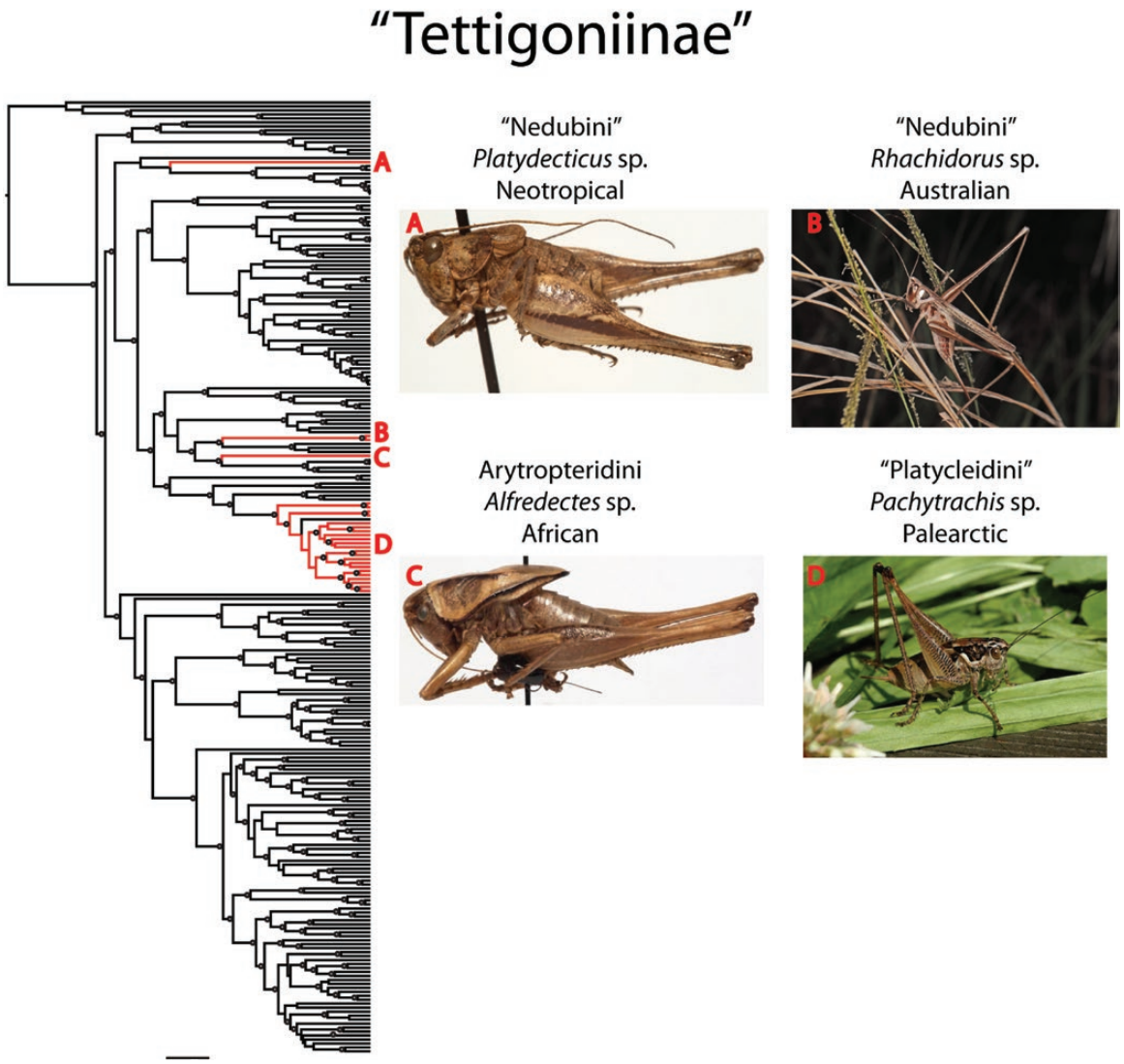

Fig. 7. Convergent shieldback ecomorphs. Tettigoniinae is recovered in four locations across the phylogeny. For most (A–C) the sister lineage is found in the same biogeographic region. The similarity in form is apparent though they are only distantly related. (A) *Platydecticus* (Chopard, 1951) is part of the Neotropical Pterochrozinae group. (B) *Rhachidorus* (Herman, 1874) is sister to the Australasian Phisidini. (C) The African tribe Arytropteridini is sister to the African Hetrodinae. (D) The northern hemisphere shieldbacks form a large group that diverged more recently from the rest of the Tettigoniinae group. Posterior probabilities over 90 are marked with a circle at the node. Photo credits are as follows: (A and C) Orthoptera species file online, (B) David Rentz, (D) Blaž Šegula.

described above with the following exceptions: the tree prior was set to Yule process and lognormal for fossil calibration points. Monophyly was constrained for subfamilies with fossil calibrations (Table 5). One calibration point, *Eomortoniellus* sp., was used for the subfamily Lipotactinae. Currently, *Eomortoniellus* (Zeuner, 1936) is listed under Tympanophorinae (Cigliano et al. 2017). Lipotactinae was originally described as a tribe (Lipotactini) within Tympanophorinae. When Lipotactinae was elevated to a subfamily (Ingrisch 1995), only the extant genera were addressed. More recently, the extinct fauna were described as belonging to the tribe Lipotactini (=Lipotactinae) Gorochov (2010). Three independent runs for 35 × 10^7 generations and sampling every 35K generations were conducted. After the analyses reached stationarity, the treefiles were combined as above with 10% removed as burn-in. The tree was then imported to Adobe Illustrator CS5 v15.0 for editing.

Biogeography

To investigate the biogeographic origins of the major katydid clades, the ancestral ranges were inferred using BioGeoBEARS in R (Matzke 2014). The script provided by the developers allows probabilistic models of biogeography to be compared statistically using the likelihood ratio test. BioGeoBEARS includes a variable (+J) to account for the possibility of founder effect in the separate clades. Geographic areas were designated as in Cox (2001).

Zoobank Registration

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:087BB8D2-AA12-4E6B-915E-DA8E77707041.

Results

Alignment

The concatenated and aligned data set is 5,398 bp. Protein-coding genes were aligned unambiguously once the reading frames were established. An indel within WG resulted in a 3-bp gap in the

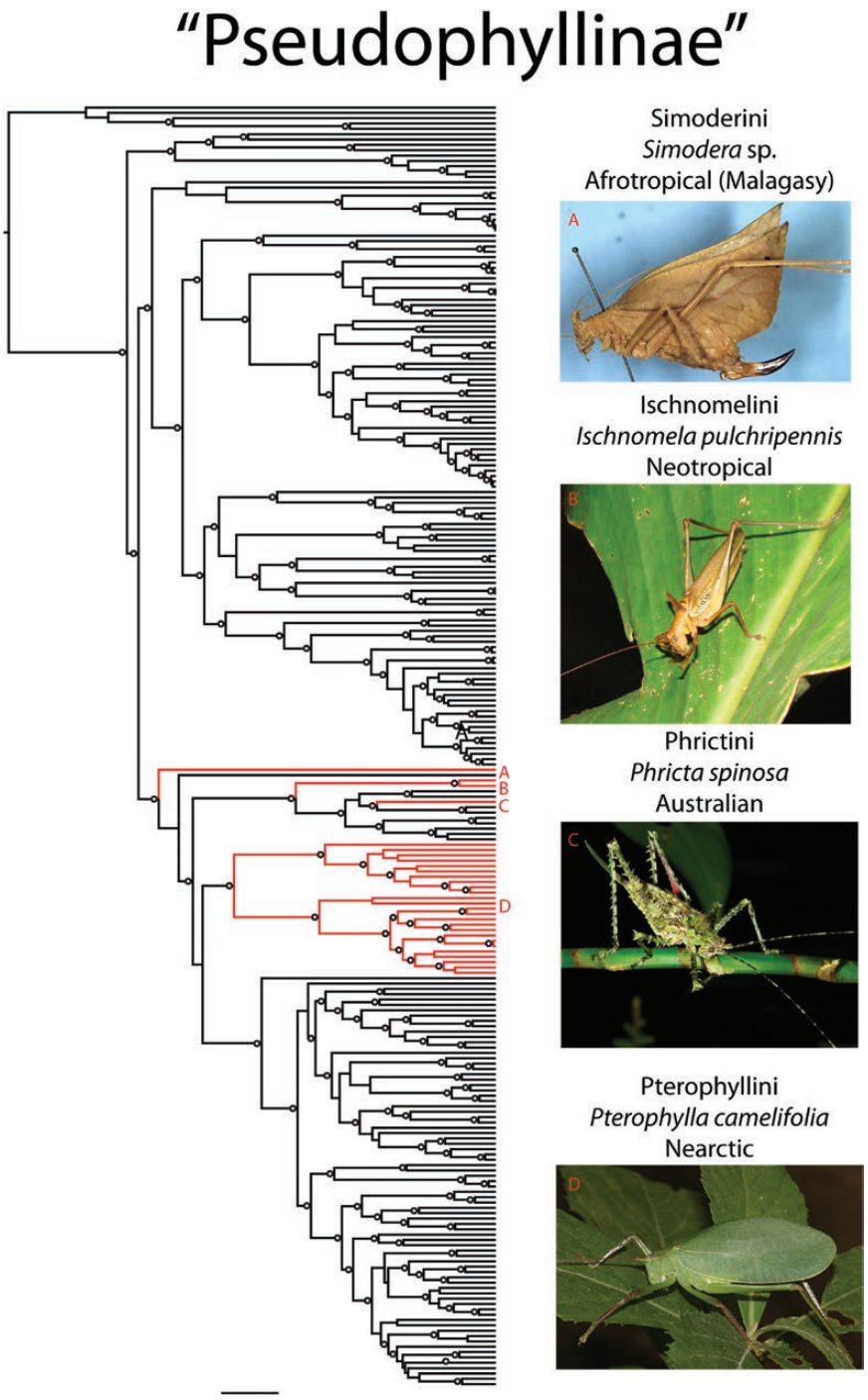

Fig. 8. Convergence in the false-leaf katydids (Pseudophyllinae). Four distinct and distantly related lineages are currently described under Pseudophyllinae. (A) Simoderini is an Afrotropical (Malagasy) tribe that resulted from an early divergence from the remaining Phaneropteroid clade. (B) Ischnomelini is a New World tribe of false-leaf katydids that are recovered as sister to the remaining katydids in the Mecopodinae group. (C) The Australian *Phricta* (Redtenbacher, 1892) is nested within the Australasian mecopodine tribe Sexavaini. (D) The remaining katydids make up the Pseudophyllinae group. Posterior probabilities over 90 are marked with a circle at the node. Photo credits are as follows: (A) Orthoptera species file online, (B) Joseph Mugleston, (C) Neil Hewett, (D) Tom Murray.

alignment of all sampled taxa except the outgroup Rhaphidophoridae. In three taxa, *Vestria* sp. (Stål, 1874) (Conocephalinae), *Phlugis irregularis* (Brunner, 1915) (Phlugidini), and *Phlugis* sp. (Stål, 1861) (Phlugidini), the gap was an additional 3 bp (total of 6 bp). Alignments of 18S rDNA and 28S rDNA contained conserved and variable regions. These variable regions were included in the analysis as they have been shown to have no significant affect on the final topology (Mugleston et al. 2013, 2016).

Phylogenetic Analysis

The optimal tree from the BEAST analysis (log likelihood –1.133E5) is shown in Figs. 2 and 3. Our topology is largely congruent with that of earlier analyses (Mugleston et al. 2013, 2016), but provides greater detail into the phylogenetic relationships of the tribes and subfamilies of Tettigoniidae. We found Tettigoniidae to be monophyletic, and the sister relationship between Tettigoniidae and the outgroup taxa is in line with the findings of Song et al.

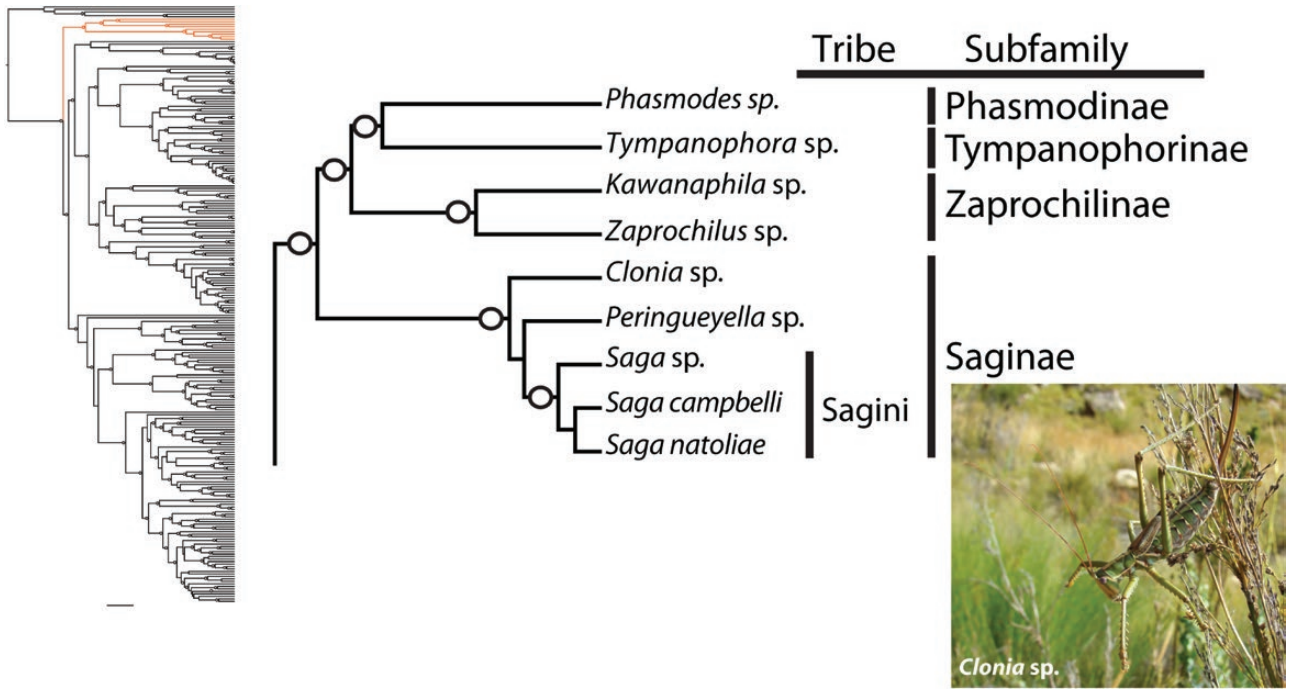

Fig. 9. Three Australian endemic subfamilies and the Afrotropical/Palearctic Saginae form a sister clade to the remaining Tettigoniidae. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credit: Joseph Mugleston.

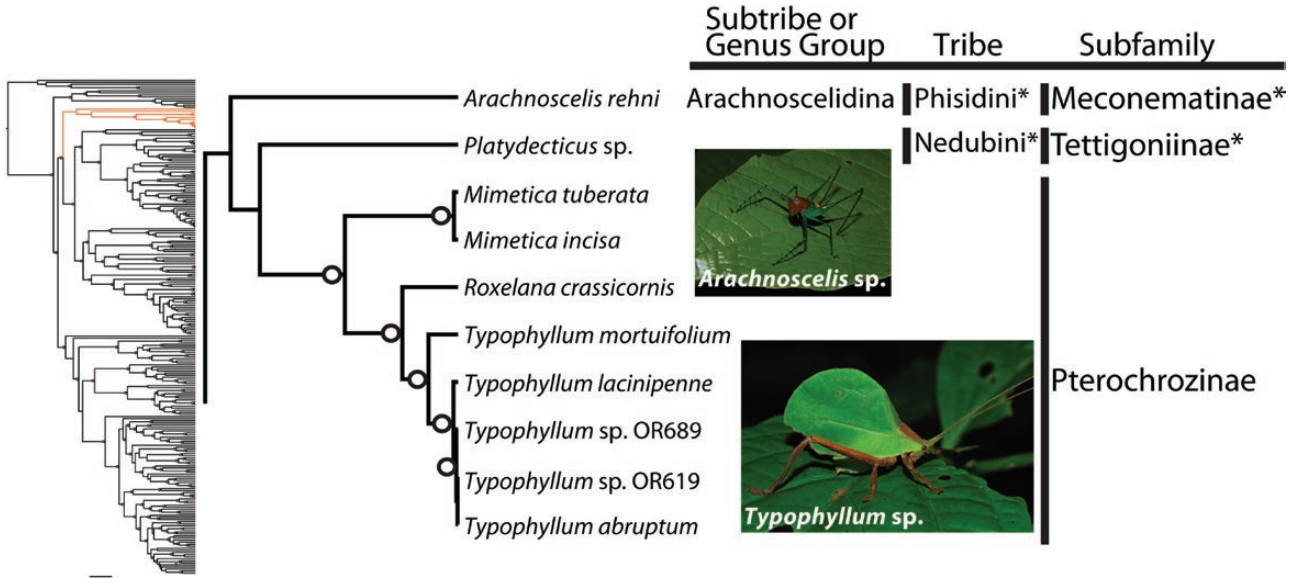

Fig. 10. Pterochrozinae group. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credits are as follows: (*Arachnoscelis* sp.) (Karny, 1911) Reinaldo Aguilar, (*Typophyllum* sp.) (Serville, 1838) Arthur Anker.

(2015) with Tettigoniidae + (((Gryllacrididae + Stenopelmatidae) + Rhaphidophoridae) + Prophalangopsidae).

Topological Congruence With Taxonomy

As in our earlier studies (Mugleston et al. 2013, 2016), the majority of katydid species are contained within two large clades: the Tettigonioid clade (Fig. 2) and Phaneropteroid clade (Fig. 3). Sister to these two clades is a smaller group containing four small subfamilies. The Tettigonioid clade has three major subclades, the Pterochrozinae group, Conocephalinae group, and Tettigoniinae group. The Pterochrozinae group forms the sister group to the remaining Tettigonioid clade (Conocephalinae group + Tettigoniinae group). Within the Tettigonioid clade the subfamilies Pterochrozinae, Conocephalinae, Hexacentrinae, Hetrodinae, Austrosaginae, and Lipotactinae are monophyletic. Paraphyletic subfamilies within the Tettigonioid clade include Meconematinae, Listroscelidinae, Tettigoniinae, and Bradyporinae. Within the Phaneropteroid clade are three additional subfamily groups including the Mecopodinae group,

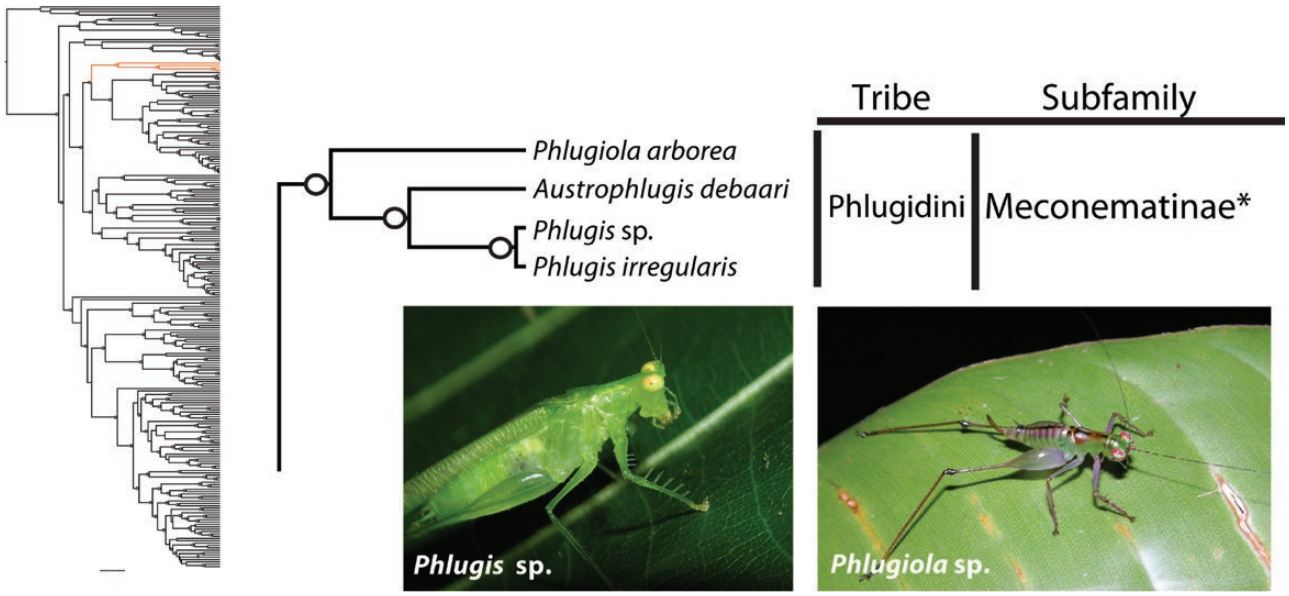

Fig. 11. Conocephalinae group: Phlugidini. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credit: Arthur Anker.

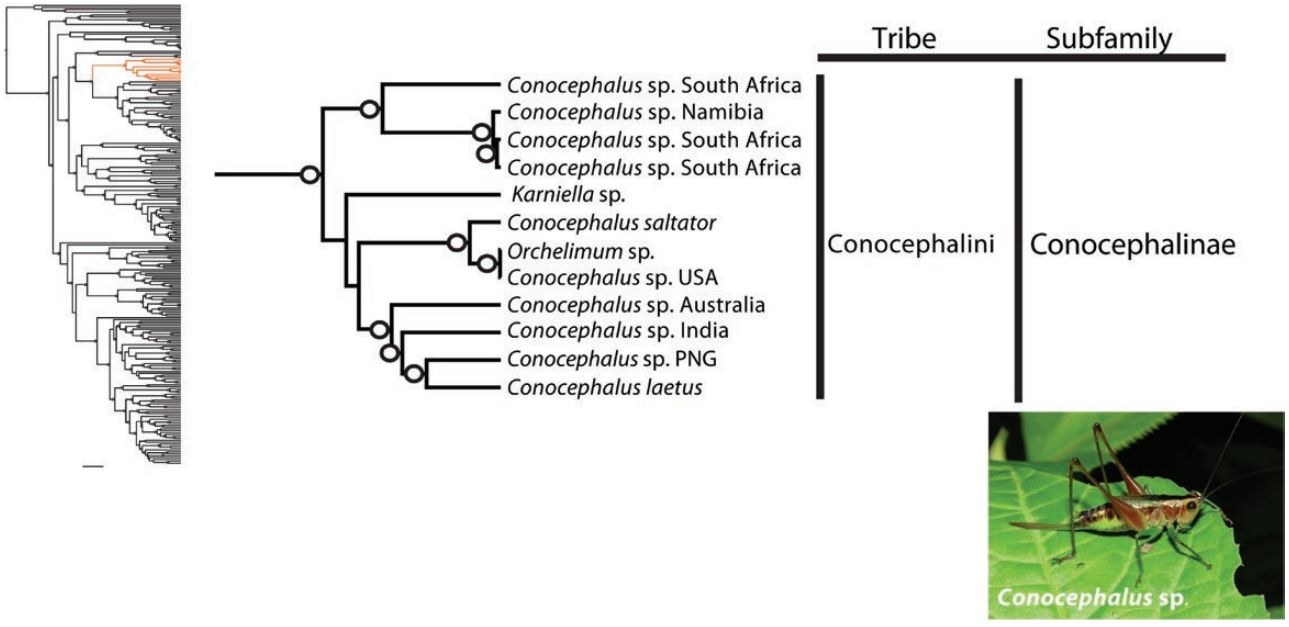

Fig. 12. Conocephalinae group: Conocephalini (Conocephalinae). Posterior probability values over 90 are marked with a circle at the node. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Photo credit: Arthur Anker.

Pseudophyllinae group, and Phaneropterinae group. The Mecopodinae group is sister to Phaneropterinae group + Pseudophyllinae group. Within the Phaneropteroid clade only Phyllophorinae is recovered as monophyletic. Mecopodinae, Phaneropterinae, and Pseudophyllinae are all paraphyletic. Details of relationships within each of these clades are described in the sections below.

Divergence Time Estimates

The topology of the time-calibrated tree (Figs. 4 and 5) is largely congruent with the topology presented in Figs. 2 and 3, except for the positions of a small number of ingroup taxa and one apical clade (indicated by asterisks in Figs. 4 and 5). The positions of these taxa were not well supported in previous analyses, and the differing placement of these taxa on the time-calibrated tree does not affect overall statements of monophyly or biogeography within the subfamilies, subfamily groups, or subclades. The most notable differences are in relationships among the outgroup taxa. This is likely due to the forced monophyly of the ingroup in the time-calibrated tree, the under sampling of outgroup taxa, and the fact that the divergence estimate required a different model. Bayarealike+J model (LnL = −335.9) was selected for biogeographic range indicating long-range dispersal has played an important role in the biogeographical history of Tettigoniidae.

Divergence estimates place the origin of tettigoniids in the late Jurassic around 155 MYA, a date that is congruent with earlier estimates (Song et al. 2015). The earliest divergence between

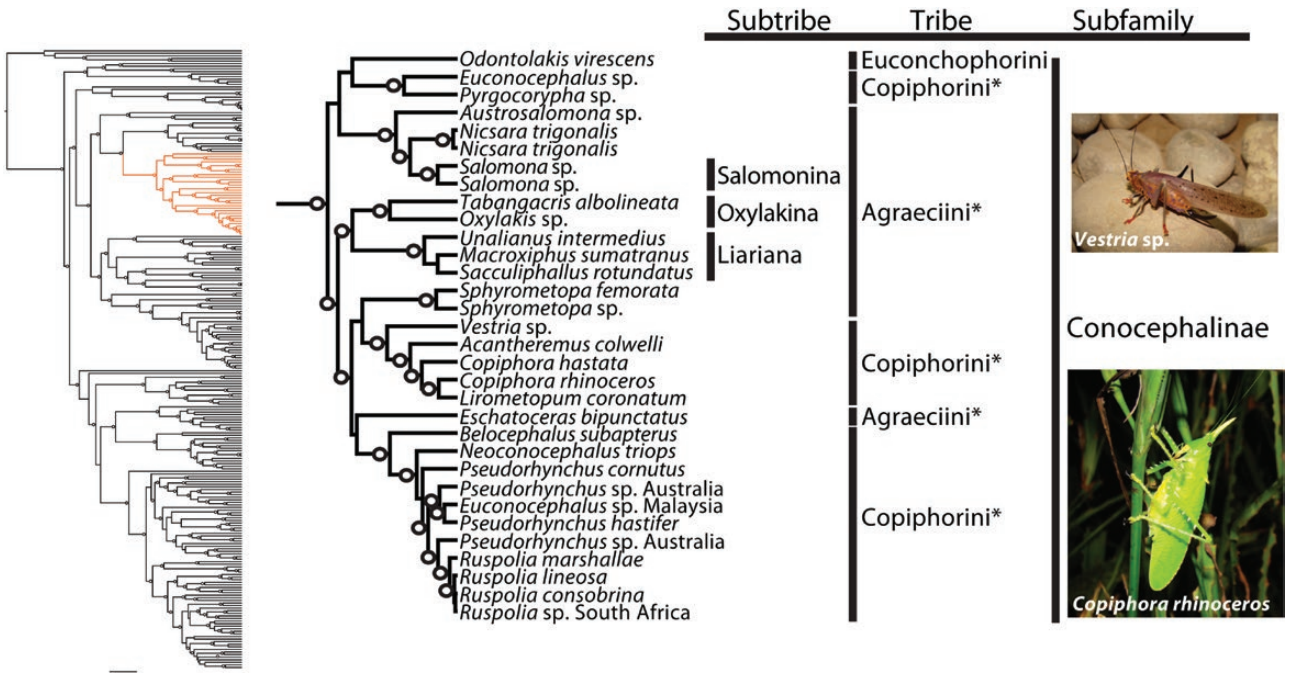

Fig. 13. Conocephalinae group: Euconchophorini, Agraeciini, and Copiphorini. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credit: Joseph Mugleston.

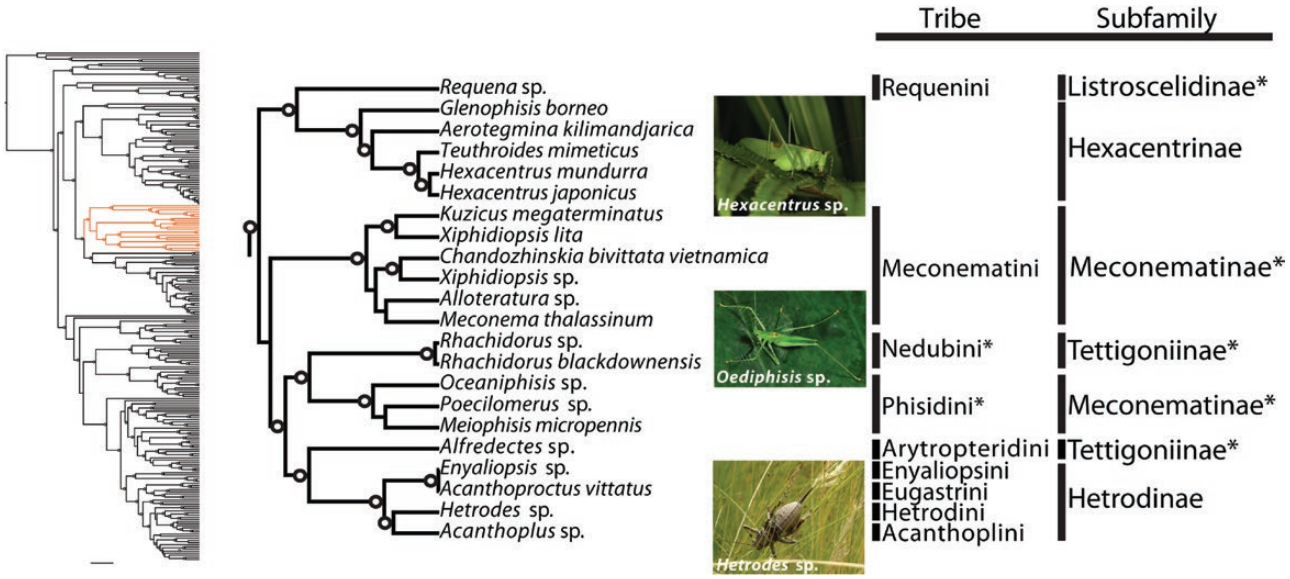

Fig. 14. Tettigoniinae group: Requenini, Hexacentrinae, Meconematini, Australian Nedubini, Phisidini (*sans Arachnoscelis*), Arytropteridini, and Hetrodinae. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credits are as follows: (*Hexacentrus* sp.) (Serville, 1831) Hojun Song, (*Oediphisis* sp.) (Jin, 1992) Arthur Anker, (*Hetrodes* sp.) (Fischer von Waldheim, 1833) Joseph Mugleston.

katydid lineages occurred around 115 MYA with the Tettigonioid and Phaneropteroid clades diverging around 110 MYA. The six subfamily groups were present by 90 MYA. Early katydid lineages show a widespread occurrence in the Afrotropical, Neotropical, and Australasian regions. The southern distribution along with the estimated divergence times of the major katydid lineages (following the break up of Gondwanaland) imply repeated intercontinental invasions while the southern continents were still within relative close proximity. Earliest dispersal into the Holarctic (Palearctic + Nearctic) regions did not occur until around 60 MYA with two New World lineages that gave rise to *Neobarrettia* spp. (Rehn, 1901) and *Pterophylla camellifolia* (Fabricius, 1775). Since 60 MYA the landmasses have been near their current position indicating repeated intercontinental dispersals leading to the now global distribution of katydids.

Taxonomy and Biogeography

Many katydid subclades are more congruent with biogeography than the current taxonomy as seen by mapping the biogeographic regions onto the tree topology. For example, the Pterochrozinae

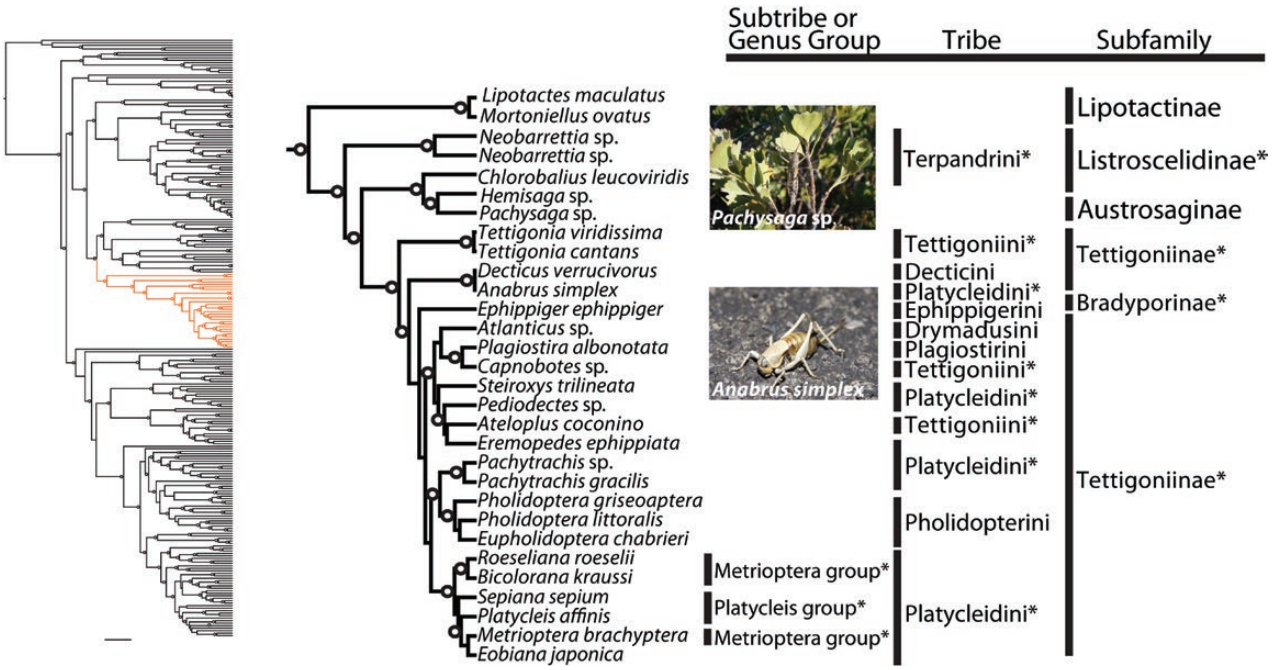

Fig. 15. Tettigoniinae group: Terpandrini, Austrosaginae, and Holarctic Tettigoniinae. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credit: Joseph Mugleston.

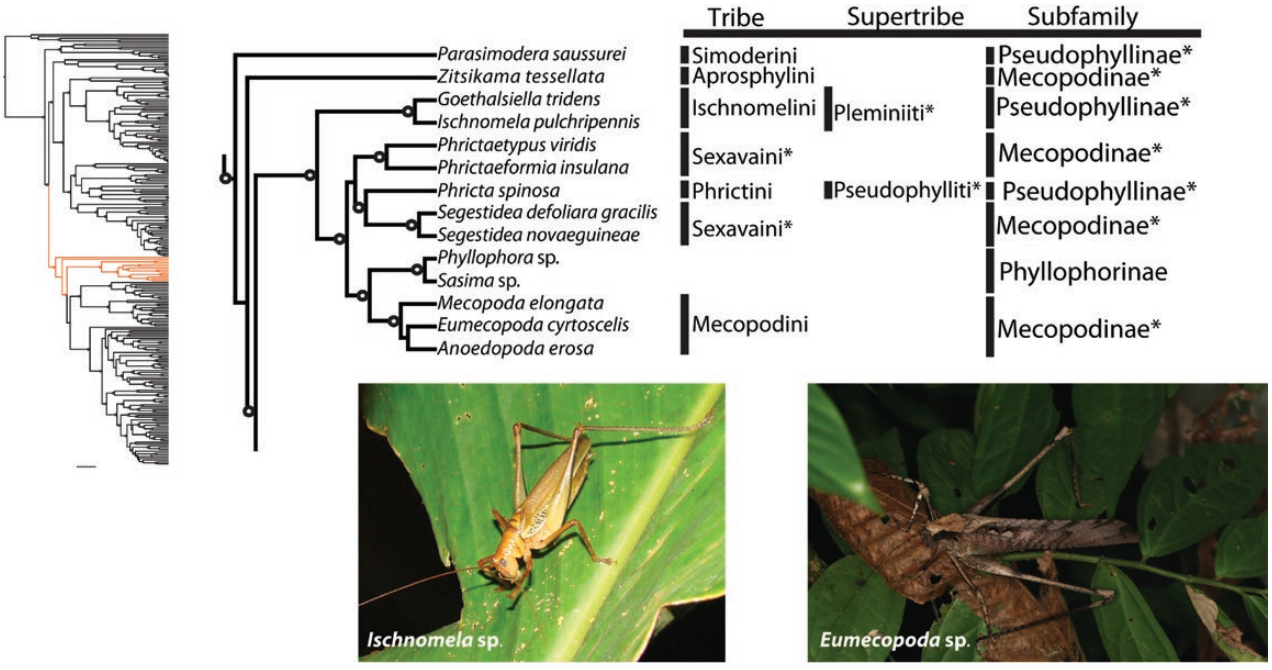

Fig. 16. Early Phaneropteroid clade lineages and Mecopodinae group. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credits are as follows: (*Ischnomela* sp.) (Stål, 1873) Joseph Mugleston, (*Eumecopoda* sp.) (Hebard, 1922) Hojun Song.

group includes *Arachnoscelis* (Karny, 1911) (traditionally part of Meconematinae), *Platydecticus* (Chopard, 1951) (traditionally part of Tettigoniinae), and the monophyletic Pterochrozinae (Fig. 4; Node 1). Although taxonomically distant, these closely related lineages are all found in the Neotropics. Additional examples of clades that share a common geographic range but show relationships contrary to current taxonomy are Copiphorini and Agraeciini (Conocephalinae) in the Neotropics (Fig. 4; Node 2), Hexacentrinae + *Requena* (Walker, 1869) (traditionally a genus within Listroscelidinae) both originate in the Australasian region (Fig. 4; Node 3), *Alfredectes* sp. (Rentz, 1988) (currently a genus in Tettigoniinae) + Hetrodinae in Africa (Fig. 4; Node 4), and *Rhachidorus* sp. (Herman, 1874) (currently a genus in Tettigoniinae) + Phisidini (traditionally considered Meconematinae) in the Australasian region (Fig. 4; Node 5), and *Chlorobalius* (Tepper, 1896) (traditionally considered a genus in Listroscelidinae) + Austrosaginae in Australia (Fig. 4; Node 6).

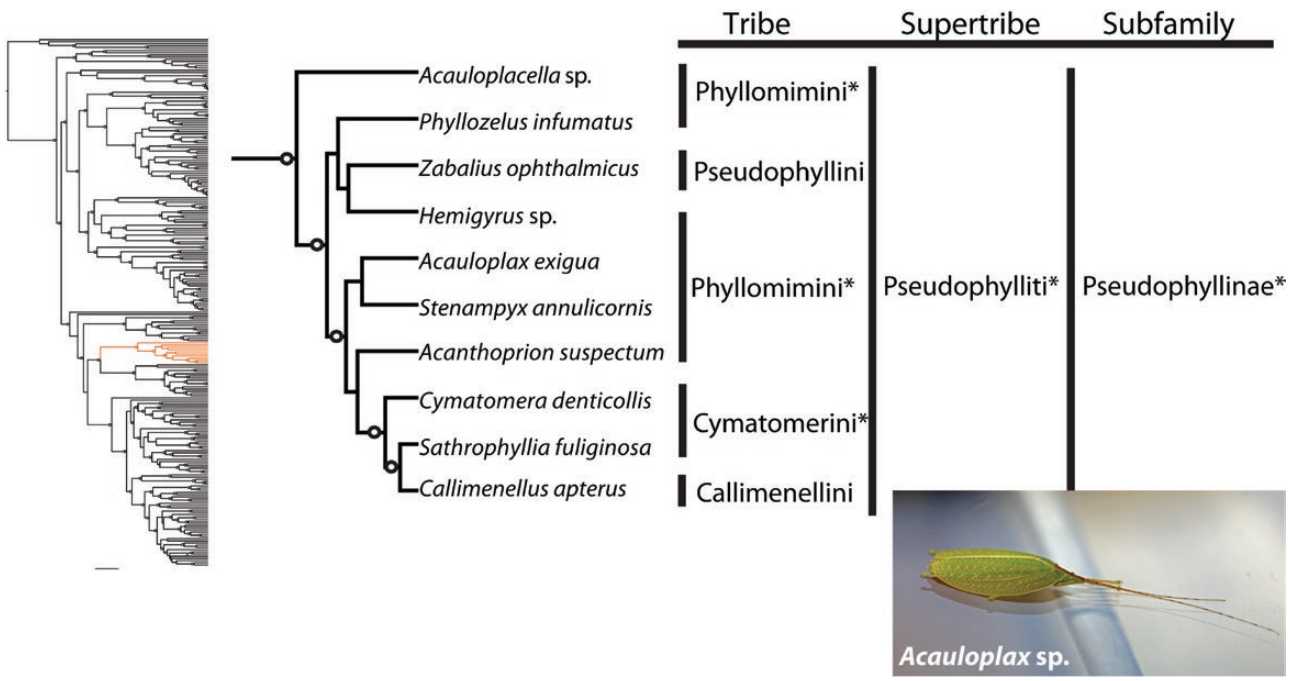

Fig. 17. Pseudophyllinae group: supertribe 'Pseudophylliti'. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credit: Nigel Voaden.

Subfamilies and tribes with broad distributions were largely found to be paraphyletic. Meconematinae is split between four clades within the Tettigonioid clade (Fig. 6). *Arachnoscelis* is found within to the Neotropical Pterochrozinae group and not within the Phisidini as suggested by its current taxonomic placement in that tribe. Phlugidini, a Neotropical and Australasian tribe of Meconematinae is sister to Conocephalinae. The remaining two tribes currently described under Meconematinae are found in the Tettigoniinae group. Phisidini (excluding *Arachnoscelis*) is sister to the African clade (Hetrodinae + *Alfredectes* sp.). Meconematini, the Indomalayan/Palearctic tribe, is sister to (Hetrodinae + *Arytropteris* [Herman, 1874]) + Phisidini. A similar trend is seen in the shieldback katydid subfamily Tettigoniinae (Fig. 7). Holarctic shieldback katydids sampled in this study all fall within an apical clade of the Tettigonioids. However, three taxa from the southern hemisphere, *Alfredectes*, *Rhachidorus*, and *Platydecticus*, are sister to subfamilies that are geographically close to each lineage and not the larger Holarctic Tettigoniinae. The phaneropteroid subfamily Pseudophyllinae (Fig. 8) was recovered as paraphyletic due to lineages that diverged early from the rest of the Phaneropteroid clade (*Simodera* sp.) (Karsch, 1891) and three lineages currently considered part of Pseudophyllinae, but present within the Mecopodinae group as discussed below. In contrast to these trends, the large (~1,300 species), cosmopolitan subfamily Conocephalinae is monophyletic, although the tribes Copiphorini and Agraeciini are paraphyletic. Most the Copiphorini and Agraeciini are grouped by biogeographic region except for the slender, grass-like conehead clade containing *Ruspolia* (Schulthess, 1898), *Neoconocephalus* (Karny, 1907), *Pseudorhynchus* (Serville, 1838), etc. which are found nearly worldwide and discussed in more detail below.

Discussion

Katydid Basal Relationships

Previous works have been uncertain as to how the katydid lineages are related. Zeuner's (1936) basal Brachycephalia (Table 1) share characters thought to be plesiomorphic including a globose head, a protrusion (fastigium) of the forehead (vertex), and antennae that insert below the ventral margin of the eyes. Rentz (1979) presented a comparable division with his 'primitive' and 'advanced' katydids using similar characters to Zeuner's Brachycephalia and Dolichocephalia, respectively. Gorochov (1988) presented yet another hypothesis in his cladogram with (((Mecopodinae + Phyllophorinae) + Pseudophyllinae) + Phaneropterinae) as sister to the remaining Tettigoniidae. Recently, it was proposed that Nearctic Nedubini (Tettigoniinae) is sister to all other katydids (Cole and Chiang 2016) with the ambidextrous wings, pronotum, and feeding habits unifying this early split from the rest of the other lineages. Nedubini is present in this analysis, but only South American and Australian lineages that are nested within the Tettigonioid clade and not sister to all other Tettigoniidae. Our earlier investigations presented Pterochrozinae as the sister lineage to all remaining katydids (Mugleston et al. 2013) though these results were not well supported. A subsequent and larger analysis sampling a greater diversity of Tettigoniidae (Mugleston et al. 2016) found a clade comprised of the three Australian endemics and Saginae (((Phasmodinae + Tympanophorinae) + Zaprochilinae) + Saginae) as sister to the remaining katydids.

In this study, the clade consisting of three small (38 spp.) Australian subfamilies (Zaprochilinae, Tympanophorinae, and Phasmodinae) and Saginae is again recovered as sister to all the remaining katydids (Fig. 9). The Australian subfamilies include Tympanophorinae (balloon wing predatory katydids) and two subfamilies of the stick-like, nectar and pollen feeders (Phasmodinae and Zaprochilinae).

Saginae is supported as a monophyletic subfamily. Its position relative to the other katydids was uncertain in our prior analyses (Mugleston et al. 2013) but the additional taxa in this analysis provides support for Saginae diverging relatively early and being sister to the three Australian endemic subfamilies.

Tettigonioid Clade

This large clade was recovered in similar form to previous analyses (Mugleston et al. 2013, 2016). Leaf-like wings are largely absent from this clade with a few noteworthy exceptions including the

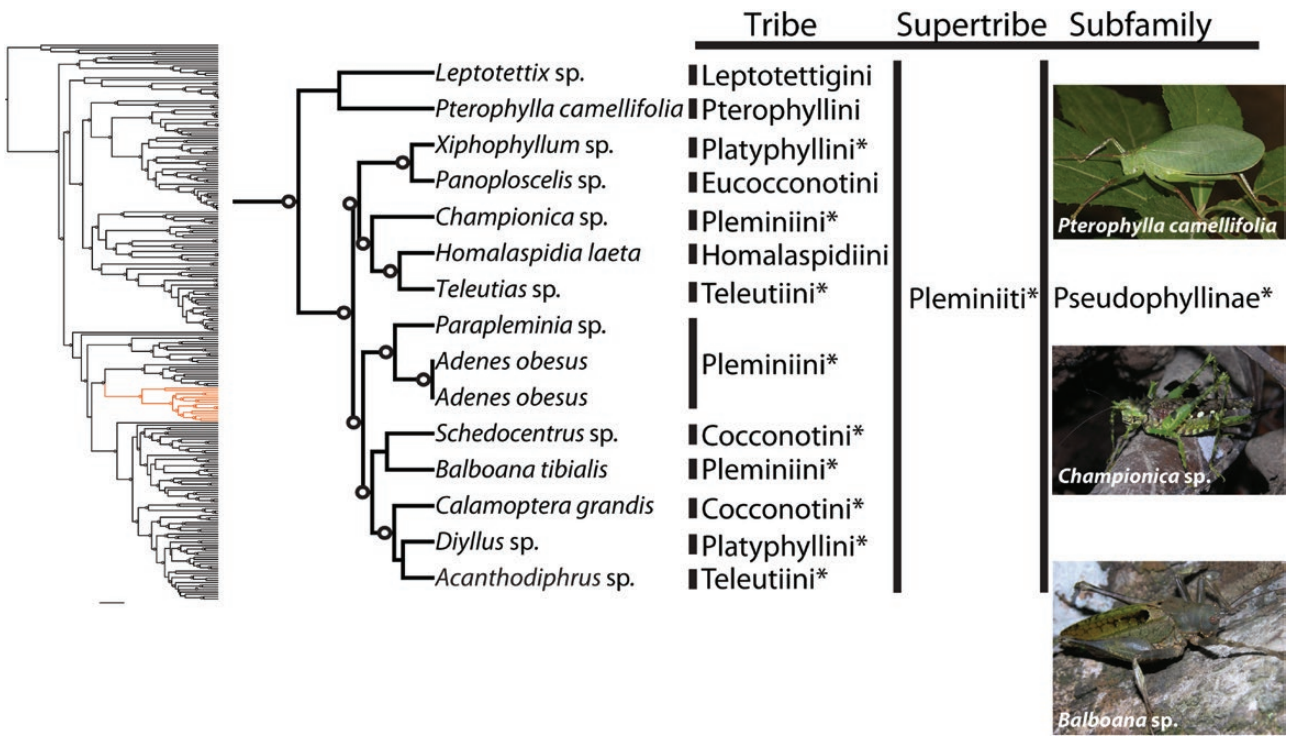

Fig. 18. Pseudophylline group: supertribe 'Pleminiiti'. Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credits are as follows: (*Pterophylla camellifolia* (Fabricius, 1775)) Tom Murray, (*Championica* sp. (Saussure & Pictet, 1898) and *Balboana* sp.(Uvarov, 1939)) Arthur Anker.

Pterochrozinae and a few lineages of tropical Conocephalinae and Hexacentrinae. The Tettigonioid clade derives from an Afrotropical ancestor with an early (110 MYA) divergence that coincides with the split of Gondwanaland. The early split in this clade gave rise to the Pterochrozinae group, and an Australasian lineage that eventually gave rise to the Conocephalinae group + Tettigoniinae group. Ten subfamilies are contained within this clade. Of these 10, only six are monophyletic: Pterochrozinae, Conocephalinae, Hexacentrinae, Hetrodinae, Lipotactinae, and Austrosaginae.

Pterochrozinae Group

The earliest divergence in the Tettigonioid clade gave rise to the Pterochrozinae group (Fig. 10). Pterochrozinae was recently elevated from a tribe within Pseudophyllinae to a subfamily (Braun 2015) based on the results of Mugleston et al. (2013) where it was made evident Pterochrozinae was not closely related to the other pseudophyllines. The impressive leaf-like disguises of Pterochrozinae have made them the quintessential example of katydid crypsis. Pterochrozinae split from their most recent non-leaf-like ancestor roughly 80 MYA. The diversification of this group coincides with the rapid diversification of angiosperms (Magallón and Castillo 2009) which may have contributed to the Neotropical radiation of these leaf-like katydids. The positions of *Platydecticus* and *Arachnoscelis* as sister to the Pterochrozinae are not well supported (pp 0.86 and 0.74, respectively). The taxonomic position of *Arachnoscelis* has been questioned in the past. Gorochov (1995b) thought this genus would be best placed within the Phisidini though others have proposed this genus being part of the 'catch-all' subfamily Listroscelidinae (Rentz 2001, Fialho et al. 2014). The authors' earlier phylogenetic work placed this subfamily as sister to the Neotropical tribe Phlugidini (Mugleston et al. 2013) and these results were the basis for Cadena-Castañeda and García (2014) proposing *Arachnoscelis* to be separate from the other Meconematinae and possibly along with Phlugidini a separate subfamily from the remaining Meconematinae. Our results place *Arachnoscelis* as a sister lineage to the Neotropical Pterochrozinae group and it seems apparent that this genus is not closely related to others currently described under Meconematinae or Listroscelidinae. Another taxon in the Pterochrozinae group is the shieldback genus *Platydecticus*. Under the current taxonomy, this genus of WG diminutive shieldback katydid is within the Tettigoniinae tribe Nedubini. Our results further support the arguments against including *Platydecticus* within Tettigoniinae (Rentz 1979, Cole and Chiang 2016).

Conocephalinae Group

As in our prior work (Mugleston et al. 2013, 2016), the well-supported Conocephalinae group contains the primarily New World tribe Phlugidini (currently seen as a tribe in Meconematinae) and the monophyletic subfamily Conocephalinae. This group diverged from the sister Tettigoniinae group about 95 MYA. By 85 MYA, the ancestor to the Phlugidini dispersed to the New World and eventually gave rise to that clade. The Conocephalinae are Australasian in origin, but have had numerous oceanic dispersals giving this large subfamily its current cosmopolitan distribution.

Phlugidini

Phlugidini is monophyletic and sister to the conehead katydids (Conocephalinae; Fig. 11). Phlugidini in this analysis includes the diminutive *Phlugiola arborea* (Nickle, 2002) which was recovered as the sister lineage to the Old World *Austrophlugis* (Rentz, 2001) + the New World *Phlugis*. This relationship implies a more recent dispersal back to Australia. Similarities between the other Meconematinae

Fig. 19. Phaneropterinae group (partial). Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credits are as follows: (*Barbitistes ocskayi*) (Charpentier, 1850) Orthoptera species file online and (*Phaneroptera* sp. (Serville, 1831)) Arthur Anker.

tribes and Phlugidini are apparently convergent and may be linked to the constraints that led to the independent derivations of these small, agile predatory katydids. The paraphyly of Meconematinae was presented in earlier studies (Mugleston et al. 2013, 2016) supporting Phlugidini being separate from Meconematinae and warranting the potential elevation of Phlugidini from a tribe within the Meconematinae to its own subfamily. Further work to revise Conocephalinae may allude to characters that link Phlugidini as an aberrant form of Conocephalinae as has been suggested (Cadena-Castañeda and García 2014).

Conocephalinae

The conehead katydids (Conocephalinae), so named for the hypognathous faces giving the head a cone-like appearance, form a large and diverse lineage that is well supported as a monophyletic group. This subfamily is further split into two subclades. The first subclade (Fig. 12) consists of the monophyletic tribe Conocephalini (meadow katydids). In agreement with our prior work (Mugleston et al. 2013, 2016), the Agraeciini and Copiphorini tribes (Fig. 13) are paraphyletic. The monophyly of these tribes has been a difficult topic for more than a century, as the characters that separate the tribes are not clear. Caudell (1911) following Redtenbacher (1891) separated the two by the fastigium (point) of the vertex being noticeably narrower than the first antennal segment (Agraeciini) rather than wider than the first segment (Copiphorini). The difficulty of placing taxa within these similar tribes was recognized early on (Caudell 1918, Zeuner 1936). Walker and Gurney (1972) provided a table with five characters used to differentiate the two tribes, but four of the five characters included the qualifiers 'usually', 'seldom', or 'often'. One character on Walker and Gurney's table was fixed in both tribes: the ventral tooth of the vertex. The lack of characters to distinguish the two tribes has led to a number of taxa being difficult to place. For example, *Sphyrometopa* (Carl, 1908) has a broad fastigium typical of Copiphorini, but a curved ovipositor and no tooth on the ventral surface of the vertex. The latter set of characters has led to *Sphyrometopa* being placed within Agraeciini, although our results show it is more closely related to the Neotropical *Copiphora* (Serville, 1831). Overall, the differences between these tribes are limited to a minor difference in the projection from the vertex and this does not appear to be phylogenetically informative. From our results it is clear in some cases biogeographic regions are a better indicator of relationships within this conehead subclade (e.g., Indomalayan Agraeciini, Australasian Agraeciini, and Neotropical Agraeciini + Copiphorini). An obvious exception to this is the clade of slender Copiphorini (*Neoconocephalus*, *Euconocephalus* (Karny, 1907), *Ruspolia*, *Belocephalus* (Scudder, 1875), *Pseudorhynchus*, etc.). These katydids are widespread and represent multiple oversea dispersals leading to their current worldwide distribution. The overlap in morphology between the two tribes has made the differences between them difficult to ascertain. The single character used to distinguish the tribes is not useful, and there appears to be no real support or justification for the continued use of both tribes Agraeciini and Copiphorini. To alleviate further confusion, Copiphorini should no longer be viewed as a valid tribe and the species currently within this tribe should be placed within Agraeciini, the senior listing.

Tettigoniinae Group

The remaining subfamilies in the Tettigonioid clade are found within the Tettigoniinae group. This group includes taxa currently listed under the subfamilies Listroscelidinae, Hetrodinae, Hexacentrinae, Meconematinae, Tettigoniinae, Lipotactinae, Bradyporinae, and Austrosaginae. The Tettigoniinae group can be further divided

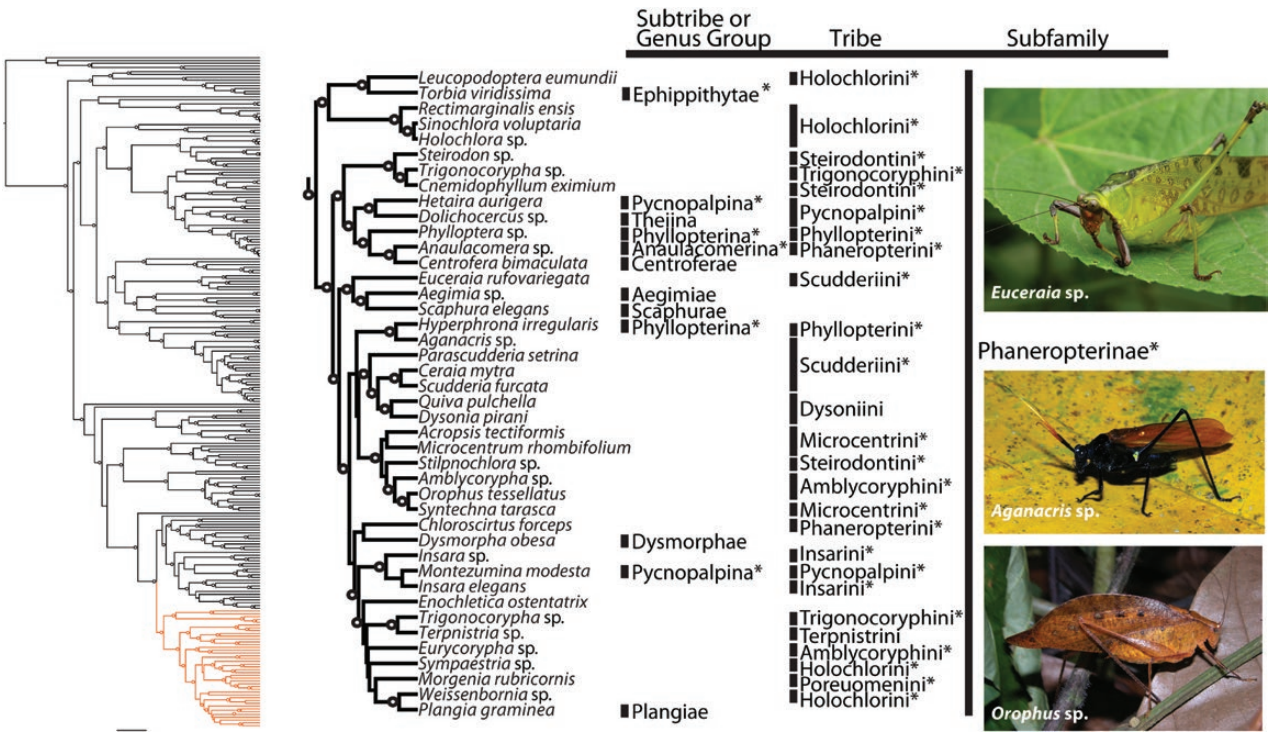

Fig. 20. Phaneropterinae group (continued). Vertical bars indicate subtribes, tribes, and subfamilies. Paraphyletic groups are marked with an asterisk. Posterior probability values over 90 are marked with a circle at the node. Photo credit: Arthur Anker.

into two subclades. The first subclade (Fig. 14) is composed of Australian and African lineages currently listed under Tettigoniinae, Hexacentrinae, and Hetrodinae, the Meconematinae tribes Phisidini and Meconematini, and the Listroscelidinae tribe Requenini. Sister to this cohort of smaller subfamilies and tribes are the Holarctic shieldback katydids (Tettigoniinae) and their closely related lineages (Austrosaginae, Lipotactinae, the Bradyporinae tribe Ephippigerini, and the Listroscelidinae tribe Terpandrini). The relationships between the smaller subfamilies and the Tettigoniinae have long been debated with current subfamilies being viewed as tribes within other subfamilies and various sister relationships as discussed below.

Requenini, Hexacentrinae, Meconematini, Nedubini, Phisidini, Arytropteridini, and Hetrodinae

This large and taxonomically jumbled subclade contains taxa currently described under five subfamilies (Fig. 14). An early split in this subclade gave rise to the monophyletic Hexacentrinae and the Australian tribe Requenini. The relationship of *Requena* and other katydids has been contested with Rentz (2001) including Requenini as a tribe within Listroscelidinae—a position that it holds today. This position was questioned by Gorochov (2007) who concluded the placement of this tribe is unclear. Additional work is required to determine whether Requenini is an aberrant tribe within Hexacentrinae, or a unique subfamily sister to the Hexacentrinae. However, it is evident that Requenini is neither Conocephalinae nor is it closely related to other taxa currently described as Listroscelidinae and should not be included in either. In agreement with prior analyses, Hexacentrinae was supported as monophyletic. The position of Hexacentrinae has been disputed in the past with some placing this subfamily as a tribe within Conocephalinae (Gorochov 1995a), or Listroscelidinae (Rentz 1996, 2001). Recently, attention has shifted to the relationship between this subfamily and the other katydids. Gorochov (2007) posited a sister relationship between Hexacentrinae and Conocephalinae though our results do not support this. The monophyly of the remaining Tettigoniinae group is largely congruent with biogeography. For instance, Meconematini has an Indomalayan and Palearctic distribution. This tribe was thought to be closely related to Phisidini based on stridulatory structure (Gorochov 2007) but the two tribes were not found to be sister. Instead, the Australasian and Malagasy Phisidini is sister to the Australian shieldback katydids *Rhachidorus*. The tribes within Meconematinae do not form a monophyletic group and represent at least three distinct lineages that have converged to similar morphologies. Meconematinae is paraphyletic and should no longer be considered a valid group in current taxonomy. The remaining lineages in this clade comprise the African Hetrodinae and their sister taxon, the African shieldback tribe Arytropteridini. Currently, Arytropteridini is considered a tribe in Tettigoniinae, but these results put the tribe as a separate subfamily, or an aberrant lineage of Hetrodinae. Arytropteridini and *Rhachidorus* (traditionally considered lineage of the tribe Nedubini) further support the earlier claim that the southern hemisphere Tettigoniinae represent convergent ecomorphs with the Holarctic shieldback katydids or represent a relict form shared with the other species traditionally considered Tettigoniinae. Further investigation into the lineages of the paraphyletic Nedubini is necessary to determine how these taxa are related. In light of the findings here, and in Cole and Chiang (2016), it is apparent that Nedubini is not a monophyletic tribe and the taxa currently described within this tribe should not be included within Tettigoniinae.

Lipotactinae, Terpandrini, Austrosaginae, and Holarctic Tettigoniinae

Lipotactinae is monophyletic and sister to *Neobarrettia* + ((Austrosaginae + Chlorobalius) + Holarctic Tettigoniinae) (Fig. 15). Lipotactinae was originally described within Tympanophorinae (Zeuner 1936) but elevated to a subfamily by Ingrisch (1995) due to

Table 6. Taxonomic changes recommended in this study.

Necessary changes to paraphyletic subfamilies:
- Meconematinae should no longer be used
- Listroscelidinae should no longer be used
- Mecopodinae should no longer be used unless changes are made to exclude Aprosphylini and include the tribes Ischnomelini and Phrictini (formerly Pseudophyllinae) and the subfamily Phyllophorinae
- Pseudophyllinae should no longer be used unless Simoderini, Phrictini, and Ischnomelini are removed
- Tettigoniinae should only include the Holarctic shield back tribes and Ephippigerini (formerly Bradyporinae).
- Phaneropterinae should include Zichyini (formerly Bradyporinae)

Paraphyletic tribes and genus groups that should no longer be used unless further revised
- Nedubini
- Copiphorini
- Agraeciini
- Terpandrini
- Tettigoniini
- Platycleidini
- Sexavaini
- Phyllomimini
- Cymatomerini
- Platyphyllini
- Pleminiini
- Cocconotini
- Anaulacomerina
- Teleutiini
- Phaneropterini
- Odonturini
- Barbitistini
- Acrometopini
- Poreuomenini
- Ducetiini
- Ephippithytae
- Elimaeini
- Mirolliini
- Holochlorini
- Steirodontini
- Trigonocoryphini
- Pycnopalpini
- Pycnopalpina
- Phyllopterini
- Phyllopterina
- Sudderiini
- Microcentrini
- Amblycoryphini
- Insarini
- Terpnistrini

Necessary changes to the recently named supertribes:
- Pseudophylliti
  - o Remove genera within Phrictini
- Pleminiiti
  - o Remove genera within Ischnomelini

Genera rearranged as a result of this study
Arachnoscelis should no longer be included within Phisidini

differences in thoracic sterna, thoracic auditory spiracle, compressed tibia, etc. While emphasis was placed on the extant taxa when these subfamilies were divided, the fossil katydids were not addressed, leaving *Eomortoniellus* spp. under Tympanophorinae instead of moving them along with their modern counterparts *Lipotactes* (Brunner von Wattenwyl, 1898) to Lipotactinae. Gorochov referred to Lipotactinae as a tribe (presumably under Tympanophorinae) and included *Eomortoniellus* with the other Lipotactinae (Gorochov 2010). Tympanophorinae and Lipotactinae are not closely related and similarity between these two groups is likely due to ecomorphic convergence as in the other distantly related katydid subfamilies. Listroscelidinae was shown to be paraphyletic (Mugleston et al. 2013) and the distantly related taxa (*Meiophisis* (Jin, 1992) and *Arachnoscelis*) have since been removed from Listroscelidinae. However, with our additional sampling, the 'taxonomic dump' of Listroscelidinae was again verified (Mugleston et al. 2016). In addition to the Requenini mentioned above, samples from North American and Australian taxa within the tribe Terpandrini were included in this study. Australian *Chlorobalius* are sister to Australian Austrosaginae and not North American *Neobarrettia*. Terpandrini historically has been included in both Saginae (Gorochov 2007) and Listroscelidinae (Rentz 2001, Naskrecki and Rentz 2010, Fialho et al. 2014). Likewise, Austrosaginae genera were also included within Saginae and only elevated to subfamily rank in the last few decades (Rentz 1993). Austrosaginae, Saginae, and the taxa previously described under the paraphyletic Listroscelidinae are all predatory katydids with similar habitus. The taxonomic confusion is another apparent case where convergence in ecomorphs has led to invalid taxonomic groupings. Saginae is only a distant relative to the Austrosaginae and species traditionally described under Listroscelidinae. Additionally, Listroscelidinae are more closely related to biogeographically close taxa in separate subfamilies than to other Listroscelidinae once again verifying that this subfamily does not represent a monophyletic group and should no longer be considered valid.

The nominate subfamily Tettigoniinae is paraphyletic as it is currently defined. The Holarctic Tettigoniinae is not a monophyletic group because the Bradyporinae genus *Ephippiger* sp. (Berthold, 1827) is nested within this group. As with the other large katydid subfamilies, widespread tribes are not monophyletic and similar morphology may have more to do with similarity in habitat and independent selective pressures than with phylogeny. Two relatively recent dispersals to Nearctic regions occurred. The first gave rise to *Anabrus simplex* (Haldeman, 1852), the Mormon cricket. The second is a more recent transition that gave rise to the more apical North American shieldbacks. Tettigoniinae are largely recognized by features associated with spines, plantula, and ovipositor but the characters that are used to define this group do not account for the various southern hemisphere taxa that are currently described as Tettigoniinae but only distantly related. If Tettigoniinae is to continue being used, it should only include the Holarctic taxa + *Ephippiger* sp. and exclude the taxa currently described in the tribe Nedubini.

Phaneropteroid Clade

The Phaneropteroid clade was originally presented as Clade B in Mugleston et al. (2013). Heller et al. (2014) recommended reinstating the family Phaneropteridae to include Mecopodinae, Pseudophyllinae, Phyllophorinae, and Phaneropterinae. Braun (2015) and Song et al. (2015) noted the problems with the changes and Braun (2015) changed Phaneropteridae to the unofficial listing of a subfamily group. We refer to the four subfamilies, Pseudophyllinae, Mecopodinae, Phyllophorinae, and Phaneropterinae (with Zichyini) as the Phaneropteroid clade to avoid further confusion with use of Phaneropteridae, and pending the much-needed revisions of the Tettigoniidae subfamilies. The Phaneropteroid clade is most frequently associated with the leaf-like disguises, as many lineages have independently derived the leaf-like form (Mugleston et al. 2016). Mecopodinae and Pseudophyllinae are both widespread, primarily tropical, and paraphyletic. Phaneropterinae (>2,600 species) is not monophyletic due to the tribe Zichyini (currently considered in Bradyporinae) nested within this widespread and highly diverse clade.

Two early splits within the Phaneropteroid clade gave rise to *Simodera* (Simoderini) and *Zitsikama* (Péringuey, 1916) (Aprosphylini). Originally *Simodera* was described as a mecopodine (Karsch 1891) but later moved to Pseudophyllinae (Kirby 1906). Only a single Simoderini was included in this analysis but the current results support removing this tribe from Pseudophyllinae. Likewise, the relict *Zitsikama* is separate from the remaining Mecopodinae and warrants removal from this subfamily.

Mecopodinae Group

Mecopodinae, Phyllophorinae, and two New World taxa currently listed under Pseudophyllinae (*Goethalsiella* (Hebard, 1927) and *Ischnomela* (Stål, 1873)) form a clade sister to the remaining Phaneropteroid clade (Fig. 16). *Goethalsiella* and *Ischnomela* (Ischnomelini) are sister to the remaining Mecopodinae group and their position away from the remaining Neotropical Pseudophyllinae brings further question to the validity of the characters used to define the false-leaf katydids and the continued use of Pseudophyllinae. The Australian *Phricta spinosa* (Redtenbacher, 1892) is nested within the mecopodine tribe Sexavaini. This genus was originally included within Mecopodinae (Kirby 1906) but later moved to Pseudophyllinae in the tribe Phrictini based on adult specimens sharing more characters with Pseudophyllinae including strongly marginated antennae and a thoracic auditory spiracle that is small, uncovered, and inconspicuous (Rentz et al. 2005). However, Rentz et al. (2005) did recognize that some characters resembled Mecopodinae including the open tibial auditory tympanum and they mentioned further work was necessary. The well-supported position nested in Sexavaini indicates *Phricta* should be within the tribe Sexavaini and not remain in Pseudophyllinae. The subfamily Phyllophorinae is also nested within the Mecopodinae group. Phyllophorines are unique in that males lack the stridulatory regions responsible for the katydid 'song'. In addition to lack of wing stridulation, this subfamily is also identified by the large dentate or crenulate margins of the pronotum (Rentz 1979). It is evident, however, that this monophyletic subfamily is nested within the Mecopodinae group and may require further revision as future work revises the taxonomy of this group.

Pseudophyllinae Group

Pseudophyllinae (false-leaf katydids) under its current definition contains nearly 1,000 described species. Most species within this subfamily are placed in one of two supertribes: Pleminiiti and Pseudophylliti. Taxa currently considered within this subfamily are found primarily in the Old World and New World tropics with a few found in the Holarctic region. False-leaf katydids are generally recognized by the strong margins around the antennae and the small, exposed thoracic auditory spiracle. However, the auditory spiracle was shown to be convergent (Mugleston et al. 2013) and has resulted in the subfamily Pterochrozinae being removed from within Pseudophyllinae.

The remaining taxa, which have been traditionally assigned to Pseudophyllinae, are confined to two clades. One clade is predominantly Old World katydids (Fig. 17) that show multiple dispersals to Africa from an Indomalayan ancestor. The two tribes with more than a single exemplar, Cymatomerini (bark-mimicking katydids) and Phyllomimini, were found to be paraphyletic. Pseudophylliti is currently paraphyletic and should not continue to be used unless the genus *Phricta* is removed from this superfamily.

The second clade in the Pseudophyllinae group contains primarily New World taxa with the exception of the African genus *Adenes* (Karsch, 1891) (Fig. 18). Transoceanic dispersal to Africa from a Neotropical ancestor is evident from the African lineage being a more recent split in this clade. The genera in this clade are currently placed in the supertribe Pleminiiti, but Pleminiiti is paraphyletic due to *Goethalsiella* sp. and *Ischnomela* sp. recovered as sister to the rest of the Mecopodinae group (Fig. 16) as described above. If Pleminiiti continues to be used, *Goethalsiella* and *Ischnomela* should not be included in this group.

Phaneropterinae Group

Nearly 35% of all katydid diversity is currently described under Phaneropterinae (Figs. 19 and 20). The monophyly of this subfamily has been supported in previous analyses (Mugleston et al. 2013, 2016) but questioned due to *Deracantha* (Fischer von Waldheim, 1833) (currently Bradyporinae) nested within (Mugleston et al. 2016). Characters unifying Phaneropterinae typically include the globose head, unarmed prothoracic sternum, short and upturned ovipositor, and hindwings (if present) extending past the tegmina posteriorly. Lineages in this clade are distributed worldwide and in each continent (except Antarctica), can be found in various biomes, and inhabit a variety of niches within each region. Within this clade, most genera are divided among 32 tribes. Many of these tribes are also widely distributed and paraphyletic. From earlier studies it is apparent that convergent ecomorphs due to similar habitats are a common trend in this clade as seen by the five derivations of leaf-like tegmina in the tropical lineages (Mugleston et al. 2016). As with the other katydid subfamilies, many of the Phaneropterinae tribes were described more than a century ago and the lines between the tribes have been blurred as more species have been identified resulting in nearly every phaneropterine tribe including two or more exemplars found to be paraphyletic. The one exception is the Dysoniini, a small tribe of fungus mimics found in the Neotropics. Unlike many of the other subclades, biogeographic regions do not seem to provide much insight into the relationships of this widespread group and may be in part due to the more recent split of the diverse phaneropterine subclade (~75 MYA), multiple transoceanic dispersals, and rapid subsequent radiation.

Conclusion

Tettigoniidae diverged from the remaining ensiferan families in the late Jurassic (~155 MYA), which coincides with the splitting of Gondwanaland into the current southern continents. The cosmopolitan distribution of Tettigoniidae is due in part

to the early movement between continents while landmasses were still relatively close, and continued transoceanic dispersal as the continents moved to their current position. A small clade of three Australian endemic subfamilies (Phasmodinae, Tympanophorinae, and Zaprochilinae) and the Saginae form a sister relationship with the remaining Tettigoniidae. However, additional sampling, particularly of Nearctic lineages traditionally described under Tettigoniinae, is necessary to better understand the early patterns of diversification within this family. Many of the smaller or endemic katydid subfamilies are monophyletic. In contrast, most of the larger or widespread subfamilies (e.g., Tettigoniinae, Meconematinae, Pseudophyllinae, and Listroscelidinae) are paraphyletic. Conocephalinae is the exception as a large, diverse, and widespread monophyletic subfamily. However, the two large conocephaline tribes, Agraeciini and Copiphorini, are paraphyletic and share a similar pattern of paraphyly with the large and widespread katydid subfamilies. Phylogenetic relationships are typically better predicted by biogeographic region than traditional taxonomy. This is likely due to widespread ecomorph convergence that has occurred during the diversification and radiation of katydids. This morphological convergence that has confused taxonomists is likely due to comparable selective pressures. As a result, the vague subfamily distinctions are largely based on convergent ecomorphs and not phylogenetically informative characters. This result has been recognized in other groups, including Phasmatodea (Buckley et al. 2009), Orthoptera (Rhaphidophoridae) (Allegrucci et al. 2010) Mantodea (Svenson and Whiting 2009, Svenson and Rodrigues 2017), and *Anolis* lizards (Losos et al. 1998).

Katydid taxonomy is in need of major higher-level taxonomic revisions to address the rampant convergence that has muddied the current taxonomy. This work recommends a few obvious changes in taxonomy to better represent the evolutionary relationships of these insects (Table 6). Further work is necessary to define these groups and provide operational morphological characters to better differentiate clades with convergent ecomorphs. This study improves our knowledge of the relationships within Tettigoniidae and provides the first comprehensive analysis of the origins and biogeography of katydids. The difficulty in delineating katydid subfamilies was addressed and we temporarily erected unofficial names for the major clades (Tettigonioid and Phaneropteroid clades) and subfamily groups to serve as placeholders pending further work including the revisions of the subfamilies and the paraphyletic tribes within. It is a major challenge to try to bring order to an incredibly diverse group with such rampant convergence in body forms. Our hope is that this work will form the scaffold upon which future phylogenetic research and taxonomic revision can be based to gain a greater understanding of one of the most remarkable diversification events in all of evolution.

Acknowledgments

This research was funded in part by NSF Grant DEB-0816962 to H.S. and M.F.W. Additional funding was provided by NSF Doctoral Dissertation Improvement Grant DEB-1210899 and Brigham Young University Graduate Student Fellowship Award to J.M. Appreciation is due to Gavin Svenson, Heath Ogden, Alison Whiting, Kelly Miller, Stephen Cameron, Rebecca Buckman, James Leavitt, Nathan Mahler, Dana Jensen, K. Jarvis, Michael Terry, James Robertson, Amy Ames, Katharina Dittmar-De La Cruz, Johnny Osborne, Sven Bradler, John C. Abbott, Kathy Hill, and Taewoo Kim for their help in acquiring the specimens used in this study. We also thank the three anonymous reviewers who offered insightful recommendations to improve this work.

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