Article

Tackling an intractable problem: Can greater taxon sampling help resolve relationships within the Stenopelmatoidea (Orthoptera: Ensifera)?

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Abstract

The relationships among and within the families that comprise the orthopteran superfamily Stenopelmatoidea (suborder Ensifera) remain poorly understood. We developed a phylogenetic hypothesis based on Bayesian analysis of two nuclear ribosomal and one mitochondrial gene for 118 individuals (84 de novo and 34 from GenBank). These included Gryllacrididae from North, Central, and South America, South Africa and Madagascar, Australia and Papua New Guinea; Stenopelmatidae from North and Central America and South Africa; Anostostomatidae from North and Central America, Papua New Guinea, New Zealand, Australia, and South Africa; members of the Australian endemic *Cooloola* (three species); and a representative of *Lezina* from the Middle East. We also included representatives of all other major ensiferan families: Prophalangopsidae, Rhaphidophoridae, Schizodactylidae, Tettigoniidae, Gryllidae, Gryllotalpidae and Myrmecophilidae and representatives of the suborder Caelifera as outgroups. Bayesian analyses of concatenated sequence data supported a clade of Stenopelmatoidea inclusive of all analyzed members of Gryllacrididae, Stenopelmatidae, Anostostomatidae, *Lezina* and *Cooloola*. We found Gryllacrididae worldwide to be monophyletic, while we did not recover a monophyletic Stenopelmatidae nor Anostostomatidae. Australian *Cooloola* clustered in a clade composed of Australian, New Zealand, and some (but not all) North American Anostostomatidae. *Lezina* was included in a clade of New World Anostostomatidae. Finally, we compiled and compared karyotypes and sound production characteristics for each supported group. Chromosome number, centromere position, drumming, and stridulation differed among some groups, but also show variation within groups. This preliminary trait information may contribute toward future studies of trait evolution. Despite greater taxon sampling within Stenopelmatoidea than previous efforts, some relationships among the families examined continue to remain elusive.

Key words: Anostostomatidae, Gryllacrididae, Stenopelmatidae, *Lezina, Cooloola,* genetic, karyotype, drumming, sound production

Introduction

In the last 20 years, there have been more than 25 papers addressing the higher classification (family level and above) of the Orthoptera. Several schemes have relied almost exclusively on morphological characters (Desutter-Grandcolas, 2003; Gorochov, 2001; Ingrisch & Rentz, 2009; Johns, 1997; Nickle & Naskrecki, 1997; Storozhenko, 1997); or genetics (Bai & Huan, 2012; Fenn *et al.*, 2008; Flook *et al.*, 1999; Ishiwata *et al.*, 2011; Jost & Naskrecki, 2003; Jost & Shaw, 2006; Legendre *et al.*, 2010; Lu & Huang, 2012; Ma & Chen, 2011; Plazzi *et al.*, 2011; Song *et*

al., 2015; Terry & Whiting, 2005; Wang *et al.*, 2011; Wheeler *et al.*, 2001; Yang *et al.*, 2016; Zhang *et al.*, 2013; Zhou *et al.*, 2014; Zhou *et al.*, 2010); or a combination of morphological and behavioral (Gwynne, 1995); or morphological and neurophysiological characters (Strauss, 2017; Strauss & Lakes-Harlan, 2008, 2009; Strauss & Stritih, 2016).

While there is near unanimous agreement (but see Yoshizawa, 2011) that the order Orthoptera is monophyletic, as are the two suborders Caelifera (short antennae grasshoppers and their allies) and Ensifera (long antennae katydids, crickets, and their allies, Fenn *et al.*, 2008; Flook *et al.*, 1999; Jost & Shaw, 2006; Song *et al.*, 2015; but see Wang *et al.*, 2011), higher level relationships within some groups of the Ensifera remain poorly understood (Legendre *et al.*, 2010). For example, the superfamily Stenopelmatoidea [=Gryllacridoidea] includes the families Anostostomatidae, Cooloolidae, Gryllacrididae, and Stenopelmatidae based on Orthoptera Species File (OSF) (Cigliano *et al.*, 2017), yet these families have not always been supported as a monophyletic group on the basis of morphological phylogenetic hypotheses (Ander, 1939; Desutter-Grandcolas, 2003; Gwynne, 1995). Phylogenetic hypotheses based on molecular markers have also varied. While Jost and Shaw (2006) found support for the Stenopelmatoidea (inclusive of the genus *Lezina* Walker) using ribosomal DNA markers, Legendre *et al.* (2010) suggested that clade support was sensitive to character weights employed and the type of analysis (e.g., parsimony versus Bayesian). More recently in an analysis of four nuclear gene regions across many Orthoptera, a Stenopelmatoidea clade was recovered including representatives of Anostostomatidae, *Cooloola* Rentz, Stenopelmatidae and Gryllacrididae, however, with low bootstrap support (Song *et al.*, 2015). None of these previous studies examined very many species within the Stenopelmatoidea that are broadly representative of the extant ranges of these families; therefore, the integrity within families across their global distributions has yet to be examined, as acknowledged by Song *et al.* (2015). One conclusion from all these studies seems widely acknowledged: that the katydid allies, including the Stenopelmatoidea, remain one of the most intractable problems in ensiferan higher taxonomy (Desutter-Grandcolas, 2003; Jost & Shaw, 2006; Legendre *et al.*, 2010).

The importance of a well-supported phylogeny is universally understood, both in terms of tracking patterns of biodiversity and as a framework for understanding adaptation and trait evolution. Phylogenetic signal can be increased by increasing taxon sampling (Hillis, 1996; Rannala *et al.*, 1998) and increasing informative character sampling (Swofford *et al.*, 1996), although the relative influence of these has been debated (Rosenberg & Kumar, 2001; Zwickl & Hillis, 2002). Incomplete taxon sampling may be of greatest concern when relatively few species represent widely distributed groups (Zwickl & Hillis, 2002), as with previous sampling of the Stenopelmatoidea. Poor taxon sampling in previous phylogenetic analyses likely results because at least some of these groups are not well studied and, as a result, their diversity is under represented in the phylogenetic hypothesis. For example, evidence suggests that the North American stenopelmatid Jerusalem crickets are probably comprised of more than 80 species, yet only 36 have been formally described to date (Weissman, 2001b). Furthermore, others have found that definitive morphological characters are sometimes lacking, or homoplastic in origin (Desutter-Grandcolas, 2003; Jost & Shaw, 2006). Molecular markers might be able to resolve some of these relationships, particularly when multiple genes are targeted. Such an approach was shown to be useful in resolving relationships within a subset of the Anostostomatidae (Pratt *et al.*, 2008), the katydid family Tettigoniidae (Mugleston *et al.*, 2013), the crickets *sensu lato* (Chintauan-Marquier *et al.*, 2016), and more broadly across Orthoptera (Song *et al.*, 2015).

Because of these recent results for Anostostomatidae and Tettigoniidae, we wondered if increased sampling at the family level within the Stenopelmatoidea might help resolve these higher-level relationships within this superfamily. Using a combined analysis of nuclear ribosomal and mitochondrial DNA sequence data, we examined the phylogenetic relationships within and among the Stenopelmatoidea, *Lezina*, *Cooloola*, as well as representatives of other ensiferan families including Prophalangopsidae (=Haglidae), Tettigoniidae, Gryllidae, Gryllotalpidae, Myrmecophilidae, Rhaphidophoridae and Schizodactylidae. As we were mainly interested in relationships within the Stenopelmatoidea, we included Stenopelmatidae from North and Central America and South Africa; three species of the Australian endemic cooloola monsters (genus *Cooloola*); Anostostomatidae from North America, South Africa, Australia, New Zealand and Papua New Guinea; and Gryllacrididae from Australia, Papua New Guinea, South Africa, Madagascar, and the Americas. Photographs of some of the unique lineages examined here are presented in Fig. 1. We used the recovered phylogenetic relationships from concatenated Bayesian analyses to assess monophyly at the family level and higher level relationships. In addition to estimating a phylogeny, we summarize known information related to karyotype and song production in these groups. Kevan (1986), Gwynne (1995), Hemp *et al.* (2010), Gómez *et al.* (2012), and Jaiswara *et al.* (2012) all showed the

effectiveness of such an "integrative taxonomic" approach in the Orthoptera, where certain biological characters, along with more traditional morphological characters, are combined into a phylogenetic scheme. While we appreciate that chromosomal characteristics (e.g., chromosome number and centromere position) are presently not utilized in constructing any higher ensiferan phylogeny, we discuss how such data, because of their evolutionarily conservative nature, may contribute to this discussion.

FIGURE 1. Representatives of major groups included in our analysis with emphasis on the Stenopelmatoidea. Panel 1: A. *Comicus* sp. probably *calcaris*. B. *Sia* sp. C. *Stenopelmatopterus politus*. D. *Stenopelmatus* sp. E. *Stenopelmatus* sp. F. *Oryctopus* sp. from India, (not included in analysis). Panel 2: G. *Xanthogryllacris punctipennis*. H. *Penalva flavocalceatus* I. *Cooloola propator* J. *Anabropsis* sp. K. *Lezina concolor*. L. *Cnemotettix bifasciatus*. Photo credits: R. Lakes-Harlan: A; D.B. Weissman: B, C, D, E, J, L; R. Balakrishnan: F; D.C.F. Rentz: G, H, I; G. Wizen: K. Respective family supported by this paper: Schizodactylidae: A. Stenopelmatidae: B, C, D, E, F. Gryllacrididae: G. Anostostomatidae: H, I, J, K, L. The colored boxes around photographs correspond to the same colors denoting families in Figures 2 and 3.
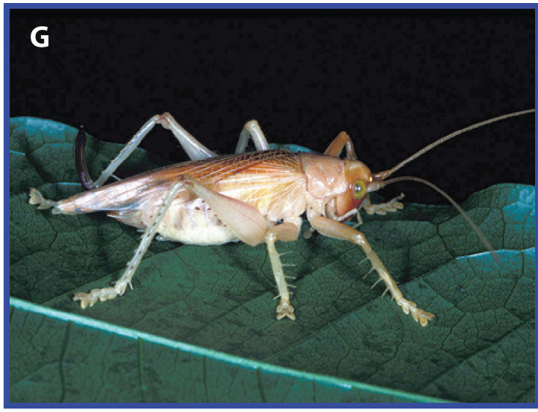
FIGURE 1. (Continued)

Methods

Stenopelmatid, anostostomatid, gryllacridid and rhaphidophorid samples from the Americas were collected and identified by D.B.W., A.G.V and O. Cadena-Castañeda. Australasian gryllacridid, anostostomatid and *Cooloola* individuals were collected and identified by D.C.F.R., G. Monteith, and P.A. Naskrecki. C.S.B. collected and identified African stenopelmatid and anostostomatid representatives. Specimens (Table 1) have been deposited in the Australian National Insect Collection (ANIC: CSIRO, Canberra, Australia); the California Academy of Sciences (CAS: San Francisco, CA, U.S.A.); Queensland Museum (QM: Brisbane, Australia); Stellenbosch University (SU: Stellenbosch, South Africa); and Universidad Distrital Francisco José de Caldas, Colección de Artrópodos y otros Invertebrados (CAUD). Prophalangopsidae voucher specimens are deposited with K.A. Judge at MacEwan University, Edmonton, Alberta, Canada. Collection locality data are listed in Supplement 1. Any undescribed "names" used in this paper are disclaimed as 'not available' as per Article 8.3 of the International

Commission on Zoological Nomenclature (1999). A variety of field collection methods were employed including hand collection, pitfall trapping, oatmeal trails, etc. (see Weissman & Lightfoot, 2007). Whole samples were typically preserved in 75% or 95% ethanol, and 1–2 legs were removed from each individual and preserved in 95% or 100% ethanol for genetic analysis.

Genetic data collection. We stored tissue samples at -80 °C upon arrival in the laboratory. We used DNEASY Tissue Kits (Qiagen, Valencia, CA) to isolate genomic DNA from the femur of each specimen. We amplified segments of three genes: 28S and 18S nuclear Ribosomal RNA Genes, and the mitochondrial Cytochrome Oxidase I Gene (COI). For polymerase chain amplifications, we used the following conditions: 94°C for 2 min; 35 cycles of 94°C for 30 s, 50°C (or 50–47°C step down) for 30 s, and 72°C for 45 s; 72°C for 7 min. Amplification reactions consisted of 2 µl of DNA, 0.5U Taq Polymerase (Qiagen), 1.8mM $MgCl_2$, 0.2 mM each dNTP, and 0.4 mM each primer in 25 µl total volume. We purified PCR products using the QIAquick PCR Purification Kit (Qiagen, Valencia, CA), and sequenced products in both directions using Big Dye Terminator III (Applied Biosystems) and an ABI 3730XL automated sequencer. We used previously published primers for all amplifications: 28s—28Sa 5' GACCCGTCTTGAAACACGGA, 28Sb 5' TCGGAAGGAACCAGCTAC (Whiting *et al.*, 2003); 18S—18S-1F 5' GACGAAAAATAACGATACGGG, 18S-1R CTCAATCTGTCAATCCTTCCA (Pratt *et al.*, 2008); COI—C1-J-2183 5' CAACATTTATTTTGATTTTTTGG, C1-N-2872 ATCARGATARTCTGAGTATCGTCG (Simon *et al.*, 1994).

In addition to generating sequence data from new specimens, we incorporated sequences available from GenBank® (https://www.ncbi.nlm.nih.gov/genbank/) to supplement taxon sampling, particularly in the Australian and New Zealand Anostostomatidae, Tettigoniidae, Gryllidae, Gryllotalpidae and three representatives of the suborder Caelifera used as outgroups (Table 1). Although our sampling was not exhaustive, our goal for taxon sampling within the three major families previously hypothesized to form the Stenopelmatoidea, was to sample representatives from across the geographic distributions of these groups and from multiple subfamilies and genera.

Phylogenetic Analyses. We created consensus sequences for each individual using sequences generated from both directions. We used Sequencher v. 5.0 (Gene Codes Corporation, MI) to verify and align contigs for each gene region. There were no gaps in COI sequences. We further verified the protein translation using the invertebrate mitochondrial genetic code in MEGA5 (Tamura *et al.*, 2011). There were no stop codons found in the protein alignment and 90% of proteins were conserved across at least 90% of the sequenced taxa. Nuclear ribosomal 18S and 28S sequences were aligned using the E-INS-I strategy in MAFFT Online Version 7 http://mafft.cbrc.jp/alignment/server/ (Katoh & Standley, 2013). We used Gblocks 0.91 (Castresana, 2000) to eliminate poorly aligned and divergent regions of the alignments using the default parameters and allowing gaps within the final blocks. Final aligned and trimmed gene regions were concatenated and we used PartitionFinder 1.11 (Lanfear *et al.*, 2012) to evaluate partitioning of the three genes and three codon positions with the COI gene. We used the BIC criterion to select the best fit partition and molecular models, estimated simultaneously.

To assess phylogenetic relationships, we performed a Bayesian concatenated analysis in MrBayes 3.2 (Ronquist *et al.*, 2012) using the data partitions and models selected with BIC in PartitionFinder. Tree searches consisted of two MCMC analyses for 5×10^6 generations each, sampling every 1000 steps and removing 25% of the initial samples from the posterior. Convergence was assessed with the standard deviation of split frequencies and effective samples sizes and visually examining trace plots in TRACER V1.5 (Nylander *et al.*, 2008). Effective sample sizes for all parameters exceeded 1400 after combining the parameter log files from each run. A 50% majority rule consensus phylogram was compiled with branch support based on posterior probabilities (*Pp*).

Divergence dates were estimated using a Bayesian molecular clock framework implemented in BEAST v1.8.3 (Drummond *et al.*, 2012). We followed the same partitioning strategy and substitution models that were implemented in our previous Bayesian phylogenetic analyses. We compared estimates from two different clock models (relaxed uncorrelated lognormal clock and random local clock), with each implementing different tree priors (yule process and birth-death process) to evaluate the effects on divergence times and support values. For each clock calibration, BEAST analyses consisted of two independent runs each with 50 million generations and samples retained every 1000 generations to verify topology and parameter estimates. We used TRACER (Rambaut *et al.*, 2014) to display results of parameter mixing and effective sample sizes after discarding 25% of the initial samples. We combined and summarized the trees and parameter estimates from the paired runs using LogCombiner v1.8.3 and TreeAnnotator v1.8.3 (Drummond *et al.*, 2012) with posterior probability limit set to 0.5 and mean node heights summarized.

We used three node age priors as calibration points on the tree with normal distributions as follows: (1) at the stem of Caelifera, we used a mean age constraint of 255.7 Ma and standard deviation of 2.5 to produce a 95% prior range between 250.8 Ma and 260.6 Ma consistent with the oldest definitive Caelifera fossil (Riek, 1976; Song *et al.*, 2015), (2) at the stem of Grylloidea (Gryllidae + Myrmecophilidae + Gryllotalpidae), we used a mean age constraint of 231.5 Ma and standard deviation of 1.8 to produce a 95% prior range between 228.0 Ma and 235.0 Ma consistent with the oldest definitive Grylloidea fossil (Heads & Leuzinger, 2011; Song *et al.*, 2015), and (3) at the stem of Stenopelmatoidea, we used a mean age constraint of 235 Ma and standard deviation of 3.9 to produce a 95% prior range between 227.4 Ma and 242.6 Ma consistent with the oldest known Stenopelmatoidea fossil from the Ladinian/Carnian period of the Triassic (Béthoux, 2012).

Cytological and Communication Characters. We determined chromosome counts and centromere position for Stenopelmatidae, *Lezina,* and the anostostomatids *Cnemotettix* Caudell and *Glaphyrosoma* Brunner von Wattenwyl. Squashes were made using testes removed from last instar or recently-molted adult males, incubated in a 0.05% colchicine solution at room temperature for one hour and then fixed in 3 parts 100% ethanol: 1 part glacial acetic acid and stained with aceto-carmine. For other groups for which we did not have appropriate samples, we report karyotype characteristics from the literature. We summarize the number of chromosomes and the position of the centromere (of sex chromosomes and autosomes) for each major clade derived from phylogenetic analyses.

We observed and recorded information on communication (methods described in Weissman, 2001a). We also gathered information from the literature or from our own personal communications. Acoustic communication in the focal groups is performed via drumming and stridulation. Drumming is performed with either the abdomen or hind leg(s) striking the substrate. Stridulation in Ensifera is usually accomplished by rubbing the tegmina together (tegminal stridulation) or rubbing a hind femur against pegs on the side of the abdomen (femoral-abdominal mechanism). Of the examined groups in this study, only the Prophalangopsidae, Tettigoniidae and Grylloidea employ tegminal stridulation.

Results

We gathered sequence data for 84 individuals. These were combined with 34 GenBank sequences for a total dataset consisting of 118 individuals in Gryllacrididae, Anostostomatidae, Stenopelmatidae, *Cooloola*, *Lezina,* Prophalangopsidae, Tettigoniidae, Rhaphidophoridae, Schizodactylidae, Gryllidae, Gryllotalpidae, and the suborder Caelifera (Table 1). After alignment and clipping, our final data matrix consisted of 776 bases of 18S, 311 bases of 28S and 573 bases of COI for a total of 1,660 characters, 489 of which were parsimony informative.

Phylogenetic analyses. The best-fit partitioning scheme selected by PartitionFinder included two partitions. The first partition included 18S, 28S and COI codon positions 1 and 2; SYM+I+G model. The second included COI codon position 3; GTR + G.

Bayesian tree searches of the concatenated dataset performed in MrBayes resulted in generally high posterior probabilities at most nodes (Fig. 2). The base of our tree included three major clades. First, a well-supported Rhaphidophoridae camel or hump-backed cricket clade was recovered with moderate support as sister to the splay-footed cricket family Schizodactylidae (*Comicus* Brunner von Wattenwyl). Second, our analysis grouped the mole cricket family Gryllotalpidae and the ant cricket family Myrmecophilidae with the true cricket family Gryllidae. The third clade contained all other sequenced families. Within this third clade we recovered the families Prophalangopsidae + Tettigoniidae as sister to a well-supported superfamily Stenopelmatoidea. The ambidextrous or hump-winged crickets comprise the superfamily Hagloidea, which contains one living family, the Prophalangopsidae. We have examined all four-extant species (in two genera: *Cyphoderris* Uhler and *Paracyphoderris* Storozhenko) of the subfamily Cyphoderrinae from North America and Asia and find them monophyletic. Additionally, our results show *C. buckelli* Hebard and *C. strepitans* Morris & Gwynne as most closely related to each other than to *C. monstrosa* Uhler, while Kumala *et al.* (2005) showed *C. monstrosa* and *C. strepitans* as most closely related. The katydid family Tettigoniidae is a very diverse family (Mugleston *et al.*, 2013; Song *et al.*, 2015), and here we have only included a few representatives of this group.

TABLE 1. List of all material cited in text, along with GenBank accession numbers (see Supplement 1 for complete specimen collection data). Specimens are arranged alphabetically by family, then by specimen code.

Presently considered in Family	Code (Fig 2)	Species	Year Collected	Country	Repository (see 'Methods')	ID authority	GenBank accession numbers COI	18S	28S
Anostostomatidae	ANOP	*Anostostoma opacum*	2001	Australia	ANIC	D.C.F. Rentz	KY809637	KY809553	KY809469
Anostostomatidae	CNMI	*Cnemotettix miniatus*	2002	USA	CASENT/ 8164850	D.B. Weissman	KY809638	KY809554	KY809470
Anostostomatidae	CNBI	*Cnemotettix bifasciatus?*	2002	USA	CASENT/ 8164851	D.B. Weissman	NA	KY809555	KY809471
Anostostomatidae	COPR	*Cooloola propator*	2006	Australia	QM	G.B. Monteith	KY809661	KY809579	KY809495
Anostostomatidae	COZI	*Cooloola ziljan*	1987	Australia	QM	G.B. Monteith	NA	KY809580	KY809496
Anostostomatidae	COSP	*Cooloola* sp. #1	2010	Australia	QM	G.B. Monteith	KY809662	KY809581	KY809497
Anostostomatidae	F953	*Glaphyrosoma* #5	1999	Mexico	CASENT/ 8164852	D.B. Weissman	KY809654	KY809572	KY809488
Anostostomatidae	F1372	*Glaphyrosoma* #1	2003	Mexico	CASENT/ 8164853	D.B. Weissman	KY809639	KY809556	KY809472
Anostostomatidae	F1792	*Glaphyrosoma* #2	2006	Mexico	CASENT/ 8164855	D.B. Weissman	KY809640	KY809557	KY809473
Anostostomatidae	F2014	*Glaphyrosoma* #3	2008	Mexico	CASENT/ 8164857	D.B. Weissman	KY809641	KY809558	KY809474
Anostostomatidae	F2020	*Glaphyrosoma* #4	2008	Mexico	CASENT/ 8164859	D.B. Weissman	KY809642	KY809559	KY809475
Anostostomatidae	F2022	*Anabropsis* sp.	2008	Mexico	CASENT/ 8164860	D.B. Weissman	KY809643	KY809560	KY809476
Anostostomatidae	F2232	*Anabropsis* sp.	2011	Mexico	CASENT/ 8164862	D.B. Weissman	KY809644	KY809561	KY809477
Anostostomatidae	F2252	*Lezina concolor*	2012	Israel	DS	D. Simon	KY809683	KY809602	KY809518
Anostostomatidae	F2262	*Hemiandrus* sp.$	2008	Australia	QM	G.B. Monteith	NA	KY809562	KY809478
Anostostomatidae	F2264	Genus A$	2008	Australia	QM	G.B. Monteith	KY809645	KY809563	KY809479
Anostostomatidae	F2266	Genus A$	2009	Australia	QM	G.B. Monteith	KY809646	KY809564	KY809480
Anostostomatidae	F2267	Genus B$	2009	Australia	QM	G.B. Monteith	KY809647	KY809565	KY809481
Anostostomatidae	F2326	*Anabropsis* n. sp. 2	2012	Guatemala	CAUD	O. Cadena-Castañeda	KY809648	KY809566	KY809482
Anostostomatidae	F2328	*Anabropsis costaricensis*	2012	Costa Rica	CAUD	O. Cadena-Castañeda	KY809649	KY809567	KY809483
Anostostomatidae	F2329	*Anabropsis marmorata*	2012	Costa Rica	CAUD	O. Cadena-Castañeda	KY809650	KY809568	KY809484
Anostostomatidae	F2330	*New genus "Costa Rica"*	2012	Costa Rica	CAUD	O. Cadena-Castañeda	KY809651	KY809569	KY809485

TABLE 1. (Continued)

Presently considered in Family	Code (Fig 2)	Species	Year Collected	Country	Repository (see 'Methods')	ID authority	GenBank accession numbers		
							COI	**18S**	**28S**
Anostostomatidae	F2331	*Glaphyrosoma "Guatemala"*	2012	Guatemala	CAUD	O. Cadena-Castañeda	KY809652	KY809570	KY809486
Anostostomatidae	F2333	new genus	2006	Colombia	CAUD	O. Cadena-Castañeda	KY809708	KY809571	KY809487
Anostostomatidae	PELA1	*Penalva lateralis* #1	2010	Australia	ANIC	D.C.F. Rentz	KY809655	KY809573	KY809489
Anostostomatidae	PESP	*Penalva* sp.	2010	Australia	ANIC	D.C.F. Rentz	KY809656	KY809574	KY809490
Anostostomatidae	PNG6	? *Penalva*	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809658	KY809576	KY809492
Anostostomatidae	PNG12	? *Penalva*	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809657	KY809575	KY809491
Anostostomatidae	SA6	*Henicus* sp.	2006	South Africa	US	C.S. Bazelet	KY809659	KY809577	KY809493
Anostostomatidae	SA21	*Onosandridus calcaratus*	2006	South Africa	US	C.S. Bazelet	KY809660	KY809578	KY809494
Gryllacrididae	AUSP	*Australogryllacris* sp.	2010	Australia	ANIC	D.C.F. Rentz	KY809663	KY809582	KY809498
Gryllacrididae	BOSP	*Bothrogryllacris* sp.	2010	Australia	ANIC	D.C.F. Rentz	KY809664	KY809583	KY809499
Gryllacrididae	CHS1	*Chauliogryllacris* sp. #1	2010	Australia	ANIC	D.C.F. Rentz	KY809665	KY809584	KY809500
Gryllacrididae	EPSP	*Epacra* sp.	2010	Australia	ANIC	D.C.F. Rentz	KY809666	KY809585	KY809501
Gryllacrididae	F2124	?*Brachybaenus* sp.	2009	Costa Rica	CASENT/ 8164863	D.B. Weissman	KY809667	KY809586	KY809502
Gryllacrididae	F2335	*Brachybaenus* sp. 1	2009	Colombia	CAUD	O. Cadena-Castañeda	KY809668	KY809587	KY809503
Gryllacrididae	PASP	*Paragryllacris* sp.	2010	Australia	ANIC	D.C.F. Rentz	KY809669	KY809588	KY809504
Gryllacrididae	PNG2	? Genus	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809673	KY809592	KY809508
Gryllacrididae	PNG3	? Genus	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809676	KY809595	KY809511
Gryllacrididae	PNG4	? Genus	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809677	KY809596	KY809512
Gryllacrididae	PNG11	? Genus	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809670	KY809589	KY809505
Gryllacrididae	PNG18	? *Nunkeria*	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809671	KY809590	KY809506
Gryllacrididae	PNG19	? Genus	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809672	KY809591	KY809507
Gryllacrididae	PNG22	? Genus	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809674	KY809593	KY809509
Gryllacrididae	PNG28	? Genus	2009	Papua New Guinea	ANIC	D.C.F. Rentz	KY809675	KY809594	KY809510
Gryllacrididae	SA05	? Genus	2006	South Africa	US	C.S. Bazelet	KY809678	KY809597	KY809513

TABLE 1. (Continued)

Presently considered in Family	Code (Fig 2)	Species	Year Collected	Country	Repository (see 'Methods')	ID authority	GenBank accession numbers		
							COI	18S	28S
Prophalangopsidae	F2255	*Cyphoderris strepitans*	2009	USA	Illinois State U.	S.K. Sakaluk	KY809679	KY809598	KY809514
Prophalangopsidae	F2285	*Cyphoderris monstrosa*	2012	Canada	KAJ	K.A. Judge	KY809680	KY809599	KY809515
Prophalangopsidae	F2289	*Cyphoderris buckelli*	2012	Canada	KAJ	K.A. Judge	KY809681	KY809600	KY809516
Prophalangopsidae	PAER	*Paracyphoderris erebeus*	2011	Russia	US	S.Y. Storozhenko	KY809682	KY809601	KY809517
Rhaphidophoridae	F2283	*Pristoceuthophilus sp.*	2012	USA	CASENT/8164864	D.B. Weissman	KY809684	KY809603	KY809519
Rhaphidophoridae	F2284	*Pristoceuthophilus sp.*	2012	USA	CASENT/8164865	D.B. Weissman	KY809685	KY809604	KY809520
Schizodactylidae	F2273	*Comicus prob. calcaris*	2010	Namibia	Univ. Giessen	R. Lakes-Harlan	KY809686	KY809605	KY809521
Stenopelmatidae	F73	*Stenopelmatopterus sartorianus*	1995	Costa Rica	CASENT/8164866	D.B. Weissman	KY809713	KY809633	KY809549
Stenopelmatidae	F150	*Stenopelmatus monahansensis*	1995	USA	CASENT/8164867	D.B. Weissman	KY809691	KY809610	KY809526
Stenopelmatidae	F402	*Stenopelmatus sp. #1*	1996	Honduras	CASENT/8164869	D.B. Weissman	KY809709	KY809628	KY809544
Stenopelmatidae	F437	*Stenopelmatus sp. #2*	1996	Honduras	CASENT/8164870	D.B. Weissman	KY809710	KY809629	KY809545
Stenopelmatidae	F470	*Stenopelmatus sp. #4*	1996	Honduras	CASENT/8164872	D.B. Weissman	NA	KY809630	KY809546
Stenopelmatidae	F533	*Ammopelmatus muwu*	1996	USA	CASENT/8164873	D.B. Weissman	KY809711	KY809631	KY809547
Stenopelmatidae	F638	*Stenopelmatus "La Rumorosa"*	1998	Mexico	CASENT/8164874	D.B. Weissman	KY809712	KY809632	KY809548
Stenopelmatidae	F987	*Stenopelmatus navajo*	1999	USA	CASENT/8164876	D.B. Weissman	KY809714	KY809634	KY809550
Stenopelmatidae	F1105	*Stenopelmatus "Lamphere Dunes"*	2000	USA	CASENT/8164878	D.B. Weissman	KY809687	KY809606	KY809522
Stenopelmatidae	F1134	*Stenopelmatus nigrocapitatus*	2001	USA	CASENT/8164879	D.B. Weissman	KY809688	KY809607	KY809523
Stenopelmatidae	F1143	*Stenopelmatus "Catalina Island"*	2001	USA	CASENT/8164880	D.B. Weissman	KY809689	KY809608	KY809524
Stenopelmatidae	F1400	*Stenopelmatus "Fairview"*	2003	USA	CASENT/8164882	D.B. Weissman	KY809690	KY809609	KY809525
Stenopelmatidae	F1669	*Ammopelmatus kelsoensis*	2005	USA	CASENT/8164884	D.B. Weissman	KY809692	KY809611	KY809527
Stenopelmatidae	F1689	*Stenopelmatus "Vandenburg"*	2004	USA	CASENT/8164885	D.B. Weissman	KY809693	KY809612	KY809528
Stenopelmatidae	F1769	*Stenopelmatopterus politus*	2006	Mexico	CASENT/8164886	D.B. Weissman	KY809694	KY809613	KY809529

TABLE 1. (Continued)

Presently considered in Family	Code (Fig 2)	Species	Year Collected	Country	Repository (see 'Methods')	ID authority	COI	18S	28S
							GenBank accession numbers		
Stenopelmatidae	F1771	*Stenopelmatus* small black #2	2006	Mexico	CASENT/8164887	D.B. Weissman	KY809695	KY809614	KY809530
Stenopelmatidae	F1774	*Stenopelmatus piceiventris*	2006	Mexico	CASENT/8164889	D.B. Weissman	KY809696	KY809615	KY809531
Stenopelmatidae	F1919	*Viscainopelmatus davewarneri*	2007	Mexico	CASENT/8164895	D.B. Weissman	KY809697	KY809616	KY809532
Stenopelmatidae	F2004	*Stenopelmatus* sp. #3	1995	Honduras	CASENT/8164896	D.B. Weissman	KY809698	KY809617	KY809533
Stenopelmatidae	F2011	*Stenopelmatus typhlops*	2008	Mexico	CASENT/8164897	D.B. Weissman	KY809699	KY809618	KY809534
Stenopelmatidae	F2031	*Stenopelmatus talpa*	2008	Mexico	CASENT/8164898	D.B. Weissman	KY809700	KY809619	KY809535
Stenopelmatidae	F2120	*Ammopelmatus* "clarki"	2009	Mexico	CASENT/8164900	D.B. Weissman	KY809701	KY809620	KY809536
Stenopelmatidae	F2152	*Stenopelmatus* small black #3	2009	Mexico	CASENT/8164902	D.B. Weissman	KY809702	KY809621	KY809537
Stenopelmatidae	F2172	*Stenopelmatus ?sallei*	1973	Mexico	CASENT/8164903	D.B. Weissman	KY809703	KY809622	KY809538
Stenopelmatidae	F2180	*Stenopelmatus piceiventris*	2007	Mexico	CASENT/8164904	D.B. Weissman	KY809704	KY809623	KY809539
Stenopelmatidae	F2182	*Stenopelmatus* small black #4	2007	Mexico	CASENT/8164906	D.B. Weissman	KY809705	KY809624	KY809540
Stenopelmatidae	F2245	*Sia* sp. #1	2011	South Africa	CASENT/8164908	D.B. Weissman	KY809706	KY809625	KY809541
Stenopelmatidae	F2281	*Sia* sp. #2	2011	South Africa	CASENT/8164910	C.S. Bazelet	KY809707	KY809626	KY809542
Stenopelmatidae	F2332	*Stenopelmatus* sp.	2012	Guatemala	CAUD	O. Cadena-Castañeda	KY809653	KY809627	KY809543
Stenopelmatidae	SA1	*Sia* sp.	2008	South Africa	US	C.S. Bazelet	KY809715	KY809635	KY809551
Stenopelmatidae	SMM1	*Stenopelmatus* "mahogani"	2001	USA	CASENT/8164911	A.G. Vandergast	KY809716	KY809636	KY809552

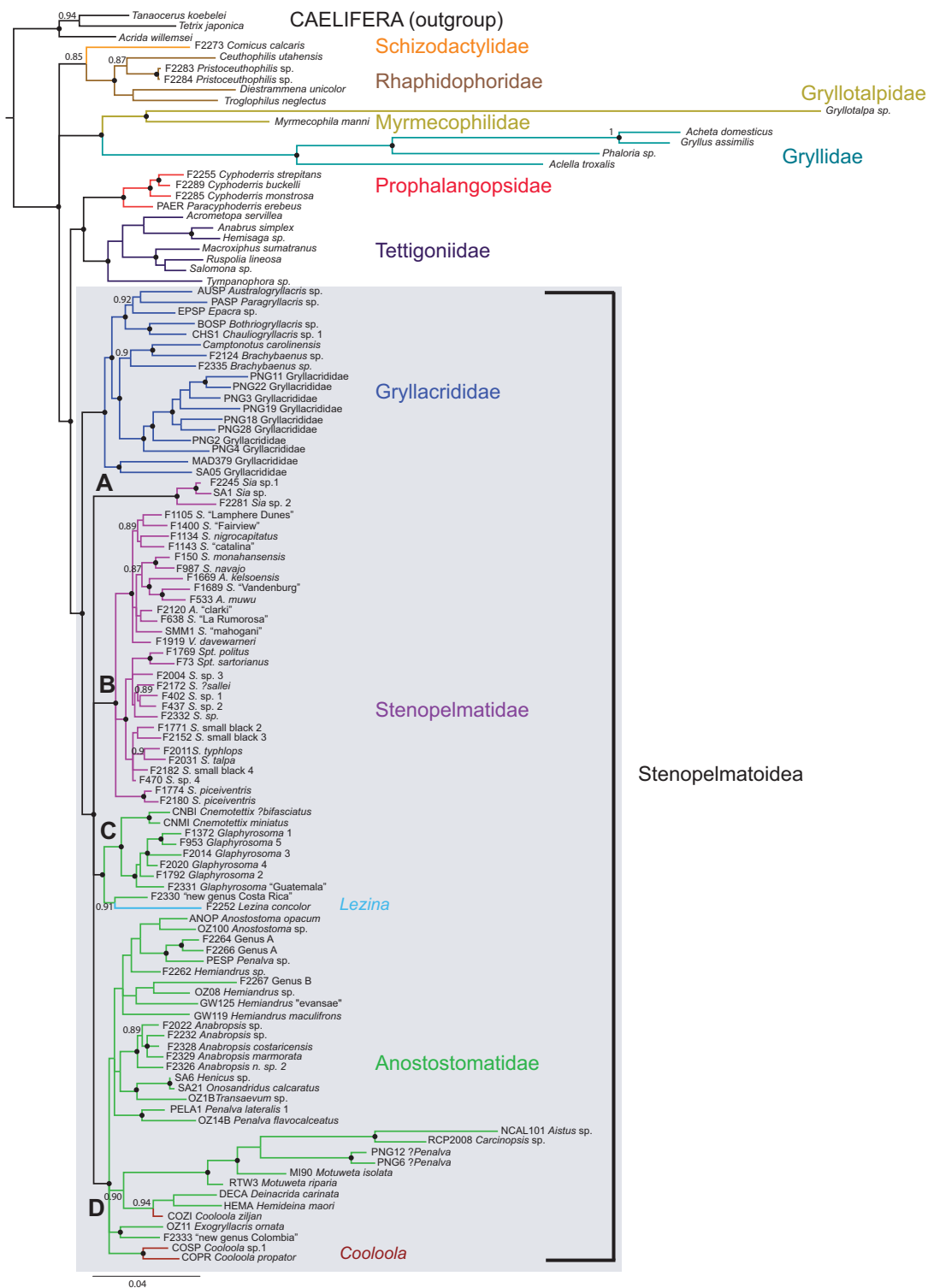$ See Monteith and Field, 2001

Data from GenBank

Family	Isolate	Species	Country	Reference	COI	18S	28S
Anostostomatidae	NCAL101	*Aistus* sp.	New Calendonia	1	EU676752	EU676734	EU676695
Anostostomatidae	OZ100	*Anostostoma* sp.	Australia	1	EU676762	EU676731	EU676706
Anostostomatidae	RCP2008	*Carcinopsis* sp.	New Calendonia	1	EU676751	EU676733	EU676696

TABLE 1. (Continued)

Family	Code	Species	Source	Locality	Ref			
Anostostomatidae	DECA	Deinacrida carinata		New Zealand	1	EU676684	EU676711	EU676737
Anostostomatidae	OZ11	Exogryllacris ornata		Australia	1	EU676703	EU676727	EU676758
Anostostomatidae	HEMA	Hemideina maori		New Zealand	1	EU676685	EU676708	EU676736
Anostostomatidae	GW119	Hemiandrus maculifrons		New Zealand	1	EU676691	EU676717	EU676770
Anostostomatidae	OZ08	Hemiandrus sp.		Australia	1	EU676697	EU676725	EU676756
Anostostomatidae	GW125	Hemiandrus "evansae"		New Zealand	1	EU676694	EU676719	EU676795
Anostostomatidae	MI90	Motuweta isolata		New Zealand	1	EU676689	EU676720	EU676748
Anostostomatidae	RTW3	Motuweta riparia		New Zealand	1	EU676687	EU676721	EU676750
Anostostomatidae	OZ14B	Penalva flavocalceata		Australia	1	EU676704	EU676728	EU676759
Anostostomatidae	OZ1B	Transaevum sp.		Australia	1	EU676699	EU676723	EU676754
Gryllacrididae	MAD379	Gryllacrididae sp.		Madagascar	1	EU676683	EU676735	EU676764
Gryllacrididae	BYU ACOR024	Camptonotus carolinensis	BYU	USA	2	AY521808	AY521876	
Rhaphidophoridae	BYU ACOR017	Ceuthophilis utahensis	BYU	USA	2	AY521800	AY521870	
Rhaphidophoridae	OR083	Troglophilus neglectus	BYU	Not provided	3	KF570948	KF570820	
Rhaphidophoridae	OR418	Diestrammena unicolor	BYU	Not provided	3	KM853396	KM853293	
Myrmecophilidae	OR022	Myrmecophila manni	BYU	Not provided	3	KM853517	KM853173	NC011301*
Gryllidae	OR429	Acheta domesticus	BYU	Not provided	3	KM853392	KM853300	
Gryllidae	OR443	Aclella troxalis	BYU	Not provided	3	KM853386	KM853306	
Gryllidae	OR016	Gryllus assimilis	BYU	Not provided	3	KM853519	KM853171	
Gryllidae	OR447	Phaloria sp.	BYU	Not provided	3	KM853385	KM853307	
Gryllotalpidae	OR050	Gryllotalpa sp.	BYU	Not provided	3	KM853513	KM853176	
Tettigoniidae	OR486	Tympanophora sp.	BYU	Not provided	4	KF570947.1	KF570777.1	
Tettigoniidae	OR381	Macroxiphus sumatranus	BYU	Not provided	4	KF570930.	KF570803.1	
Tettigoniidae	OR380	Ruspolia lineosa	BYU	Not provided	4	KF570923.1	KF570793.1	
Tettigoniidae	OR145	Salomona sp.	BYU	Not provided	4	KF570928.1	KF570791.1	
Tettigoniidae	OR483	Hemisaga sp.	BYU	Not provided	4	KF570896.1	KF570758.1	
Tettigoniidae	OR034	Anabrus simplex	BYU	Not provided	4	KF570890.1	KF570763.1	NC009967*
Tettigoniidae	OR043	Acrometopa servillea	BYU	Not provided	4	KF570853.1	KF570717.1	
Caelifera	OR559	Tanaocerus koebelei	BYU	Not provided	3	KM853350	KM853342	
Caelifera	OR257	Tetrix japonica	BYU	Not provided	3	KM853473	KM853217	NC018543**
Caelifera	OR059	Acrida willemsei	BYU	Not provided	3	KM853512	KM853177	NC011303*

1. Pratt *et al.*, 2008, 2. Terry & Whiting, 2005, 3. Song *et al.*, 2015, 4. Mugleston *et al.*, 2013, *Fenn *et al.*, 2008; ** Xiao *et al.*, 2012

0.94 *Tanaocerus koebelei*
Tetrix japonica
Acrida willemsei
F2273 *Comicus calcaris* — Schizodactylidae
0.85
0.87 *Ceuthophilis utahensis*
F2283 *Pristoceuthophilis* sp.
F2284 *Pristoceuthophilis* sp.
Diestrammena unicolor — Rhaphidophoridae
Troglophilus neglectus
Gryllotalpa sp. — Gryllotalpidae
Myrmecophila manni — Myrmecophilidae
Acheta domesticus
1 *Gryllus assimilis*
Phaloria sp.
Aclella troxalis — Gryllidae
F2255 *Cyphoderris strepitans*
F2289 *Cyphoderris buckelli*
F2285 *Cyphoderris monstrosa*
PAER *Paracyphoderris erebeus* — Prophalangopsidae
Acrometopa servillea
Anabrus simplex
Hemisaga sp.
Macroxiphus sumatranus
Ruspolia lineosa — Tettigoniidae
Salomona sp.
Tympanophora sp.

AUSP *Australogryllacris* sp.
0.92 PASP *Paragryllacris* sp.
EPSP *Epacra* sp.
BOSP *Bothriogryllacris* sp.
CHS1 *Chauliogryllacris* sp. 1
Camptonotus carolinensis
0.9 F2124 *Brachybaenus* sp.
F2335 *Brachybaenus* sp.
PNG11 Gryllacrididae
PNG22 Gryllacrididae — Gryllacrididae
PNG3 Gryllacrididae
PNG19 Gryllacrididae
PNG18 Gryllacrididae
PNG28 Gryllacrididae
PNG2 Gryllacrididae
PNG4 Gryllacrididae
MAD379 Gryllacrididae
SA05 Gryllacrididae

A
F2245 *Sia* sp.1
SA1 *Sia* sp.
F2281 *Sia* sp. 2
0.89 F1105 *S.* "Lamphere Dunes"
F1400 *S.* "Fairview"
F1134 *S. nigrocapitatus*
F1143 *S.* "catalina"
F150 *S. monahansensis*
0.87 F987 *S. navajo*
F1669 *A. kelsoensis*
F1689 *S.* "Vandenburg"
F533 *A. muwu*
F2120 *A.* "clarki"
F638 *S.* "La Rumorosa"
SMM1 *S.* "mahogani"
F1919 *V. davewarneri*
F1769 *Spt. politus*
F73 *Spt. sartorianus*
F2004 *S.* sp. 3
0.89 F2172 *S.* ?*sallei*
F402 *S.* sp. 1
F437 *S.* sp. 2
F2332 *S.* sp.
F1771 *S.* small black 2
F2152 *S.* small black 3
0.9 F2011 *S. typhlops*
F2031 *S. talpa*
F2182 *S.* small black 4
F470 *S.* sp. 4
F1774 *S. piceiventris*
F2180 *S. piceiventris* — Stenopelmatidae

B

C
CNBI *Cnemotettix* ?*bifasciatus*
CNMI *Cnemotettix miniatus*
F1372 *Glaphyrosoma* 1
F953 *Glaphyrosoma* 5
F2014 *Glaphyrosoma* 3
F2020 *Glaphyrosoma* 4
F1792 *Glaphyrosoma* 2
F2331 *Glaphyrosoma* "Guatemala"
F2330 "new genus Costa Rica"
0.91 F2252 *Lezina concolor* — *Lezina*

ANOP *Anostostoma opacum*
OZ100 *Anostostoma* sp.
F2264 Genus A
F2266 Genus A
PESP *Penalva* sp.
F2262 *Hemiandrus* sp.
F2267 Genus B
OZ08 *Hemiandrus* sp.
GW125 *Hemiandrus* "evansae"
GW119 *Hemiandrus maculifrons*
0.89 F2022 *Anabropsis* sp.
F2232 *Anabropsis* sp.
F2328 *Anabropsis costaricensis*
F2329 *Anabropsis marmorata*
F2326 *Anabropsis* n. sp. 2
SA6 *Henicus* sp.
SA21 *Onosandrus calcaratus*
OZ1B *Transaevum* sp.
PELA1 *Penalva lateralis* 1
OZ14B *Penalva flavocalceatus* — Anostostomatidae
NCAL101 *Aistus* sp.
RCP2008 *Carcinopsis* sp.
PNG12 ?*Penalva*
PNG6 ?*Penalva*
MI90 *Motuweta isolata*
RTW3 *Motuweta riparia*
DECA *Deinacrida carinata*
HEMA *Hemideina maori*
COZI *Cooloola ziljan*
OZ11 *Exogryllacris ornata*
F2333 "new genus Colombia"
COSP *Cooloola* sp.1
COPR *Cooloola propator* — *Cooloola*

D 0.90 0.94

Stenopelmatoidea

0.04

FIGURE 2. Majority rule Bayesian concatenated gene tree. Black dots demarcate nodes with posterior probability values > 0.95. Colored clades represent currently defined families and the Stenopelmatoidea clade is highlighted in a grey box.

The well supported Stenopelmatoidea superfamily is comprised of Gryllacrididae, and a well-supported clade containing Stenopelmatidae plus Anostostomatidae (inclusive of both *Lezina* and *Cooloola*). The raspy or leaf-rolling cricket family Gryllacrididae, united by their ability to produce silk (Morton & Rentz, 1983; Walker *et al.*,

2012), formed a well-supported clade. While taxon sampling within this clade is far from complete, representatives were included from Australia, Papua New Guinea, South Africa, Madagascar, and South, Central and North America. Furthermore, subclades within this group appear to be regionally defined with samples collected in the Americas, Papua New Guinea, Africa, and Australia each comprising well supported subclades ($Pp \geq 0.90$ for regional subclades).

The final clade is comprised of two Stenopelmatidae clades (Clades A and B, Fig. 2) and two Anostostomatidae clades (Clades C and D, Fig. 2), however the relationships among these clades were unresolved. Clade A contained all representatives of the South African Jerusalem cricket genus, *Sia* Giebel (subfamily Siinae) that were included in our analyses. Clade B contained the New World Jerusalem crickets (subfamily Stenopelmatinae). The third clade (C) included *Lezina*, a new anostostomatid genus from Costa Rica (personal communication, O. Cadena-Castañeda, 2013) and the New World anostostomatid genera *Glaphyrosoma* and *Cnemotettix*, both currently placed in the tribe Glaphyrosomini Rentz and Weissman (1973).

Clade D contained most of the analyzed Anostostomatidae and was inclusive of *Cooloola*. This clade contained a diverse array of genera from different parts of the globe, and relationships within this clade were generally not well-resolved. One moderately supported subclade ($Pp = 0.9$) clustered New Zealand giant weta *Deinacrida* White and ground weta *Hemideina* Walker, both currently placed in the subfamily Deinacridinae (Johns, 1997), with a subclade of more highly divergent taxa which included two New Zealand tusked weta *Motuweta* Johns, the New Caledonia genera *Aistus* Brunner von Wattenwyl and *Carcinopsis* Brunner von Wattenwyl (sequence data from Pratt *et al.*, 2008), and our newly examined Papua New Guinea anostostomatids. Pratt *et al.* (2008) suggested that high levels of divergence in these New Zealand and New Caledonia taxa were indicative of elevated substitution rates, and that this group was likely derived from a common Australian ancestor on the basis of regional biogeography and lineage dating. Results from our additional sampling indicate a close phylogenetic relationship between these taxa on the islands of New Zealand, New Caledonia, and Papua New Guinea.

Notably, we did not recover *Cooloola* as a monophyletic group in Clade D. *Cooloola ziljan* Rentz was placed as sister to *Deinacrida* and *Hemideina* ($Pp = 0.94$). The two remaining *Cooloola* species (*C.* n.sp. "Mt Moffatt" and *C. propator* Rentz) formed a separate monophyletic clade ($Pp > 0.95$).

Lineage Dating. Our recovered lineage dating tree (Fig. 3) supported a very similar topology to the MrBayes consensus tree. One exception was the placement of Schizodactylidae (genus *Comicus*) as sister to the clade containing Stenopelmatoidea, Tettigoniidae and Prophalangopsidae. In the MrBayes analysis the Schizodactylidae were recovered as sister to Rhaphidophoridae, albeit with moderate support ($Pp = 0.85$). The dated tree also provided further resolution within Stenopelmatidae and Anostostomatidae clades. Stenopelmatidae Clades A and B were supported as sister to Anostostomatidae Clade C ($Pp = 0.86$), and all of these as sister to Anostostomatidae Clade D ($Pp = 0.99$). Median clade dates of the two major clades in the Stenopelmatoidea fell in late Triassic and Jurassic, although with wide credible intervals (Stenopelmatidae + Anostostomatidae 209 MYA, 95% CIs 180—260 MYA; Gryllacrididae 184 MYA, 95% CIs 150—275 MYA). Major clades within Stenopelmatidae + Anostostomatidae also overlapped temporally (Stenopelmatidae Clades A + B + Anostostomatidae Clade C median age = 186 MYA; 95% CIs 150–220 MYA; Anostostomatidae Clade D 179 MYA; 95% CIs 130—270 MYA). Biogeographically, this corresponds to a period of major global tectonic and geological changes (Scotese, 1992). The supercontinent of Pangea began to break apart in the Middle Jurassic. In the Late Jurassic, the Central Atlantic Ocean was a narrow ocean that separated Africa from eastern North America and Eastern and Western Gondwana had begun to separate. The fragmentation of Gondwana continued through the Cretaceous and into the Paleogene (150—30 MYA), roughly contemporaneous with dated nodes within Gryllacrididae, Stenopelmatidae and Anostostomatidae clades (Fig. 3, Ali & Aitchison, 2008; Gibbons *et al.*, 2013; Scotese, 1992).

Cytology and Sound Production. Cytological and communication characteristics are summarized in Table 2, with details of taxa examined and literature sources cited in Supplements 2 and 3. We did not note any obvious patterns in chromosome counts (Table 2, S2) among different clades as these varied extensively within each clade. In contrast, the position of the centromere (middle of the chromosome [= metacentric or submetacentric] vs. end of the chromosome [= rod-shaped or telocentric or acrocentric, depending on author]) presented a distinct pattern: all examined Stenopelmatoidea (Gryllacrididae, Anostostomatidae, Stenopelmatidae, *Cooloola,* and *Lezina*), plus the Rhaphidophoridae and Prophalangopsidae always have the X chromosome, and usually some autosomes, metacentric in nature. For other groups genetically examined in Fig. 2, Tettigoniidae (katydids, bush crickets),

Gryllotalpidae (mole crickets), and Gryllidae (true crickets) are known to contain taxa with all chromosomes, including the X, rod shaped while there are other species that have a mixture of rod and metacentric elements (Hewitt, 1979; White, 1973). To date no Myrmecophilidae (ant cricket) has been karyotyped. In contrast to the groups listed above, *Schizodactylus* Brulle, in the Schizodactylidae, is unique among the examined superfamilies in having only rod-shaped autosomes and sex chromosomes, although only one taxon has been reported on.

Mechanisms of sound production (Table 2, S3) also varied extensively among families, and there are no obvious phylogenetic consistencies in sound production at this level. We do note two patterns that highlight differences among the distinct Anostostomatidae and Stenopelmatidae lineages. First, adult anostostomatid males of all examined (Fig. 2) Clade C *Cnemotettix* and *Glaphyrosoma* species have been observed to drum using one rear leg at a time (Weissman, 2001a, and unpublished), a mechanism not noted in any other Anostostomatidae. Second, while adults of both sexes of New World Stenopelmatinae Jerusalem crickets (Fig. 2, Clade B) have been found to produce abdominal drumming (Weissman, 2001a), no drumming was detected in any Clade A South African Jerusalem crickets (Weissman & Bazelet, 2013). While the above cytological and sound production information is not exhaustive, we present it so others can add more examples and promote future studies into these features for integrative taxonomy. Our list will also serve to correct several omissions presented under stridulation type in Gwynne's (1995) Fig. 3.

Discussion

Previous phylogenetic studies of Orthoptera have called for additional taxa sampling, use of additional informative genetic markers, and integration of molecular, morphological, behavioral and ecological data to better resolve relationships among major lineages, particularly within the Stenopelmatoidea (Jost & Shaw, 2006; Legendre *et al.*, 2010; Mugleston *et al.*, 2013; Song *et al.*, 2015). With our geographically diverse genetic sampling within the three largest families, we provide several novel contributions towards the understanding of relationships within this group. First, we recovered a highly-supported superfamily Stenopelmatoidea clade containing representatives of Gryllacrididae, Anostostomatidae, Stenopelmatidae, *Lezina* and *Cooloola*. Second, we recovered a monophyletic Gryllacrididae, similar to others (Chintauan-Marquier *et al.*, 2016; Jost & Shaw, 2006; Legendre *et al.*, 2010; Mugleston *et al.*, 2013; Song *et al.*, 2015) but with greater geographical and taxon sampling. Third, we could not recover a monophyletic Anostostomatidae nor Stenopelmatidae, echoing previous suggestions that these groups require taxonomic revision (Legendre *et al.*, 2010). Fourth, we place *Cooloola* as paraphyletic within Anostostomatidae. Fifth, we find support grouping Old World *Lezina* with New World Glaphyrosomini, the latter absent from previous analyses. Sixth, our dated tree suggests clade ages for major lineages within the Stenopelmatoidea in the late Triassic and Jurassic, during which the break-up of the supercontinent of Pangea and the formation of Gondwana occurred (Ali & Aitchison, 2008; Gibbons *et al.*, 2013; Scotese, 1992). This is compelling, as these major lineages, (Gryllacrididae, Anostostomatidae + Stenopelmatidae) have mainly Gondwanan distributions (Cigliano *et al.*, 2017).

Anostostomatidae. The family Anostostomatidae was separated from Stenopelmatidae by Johns (1997) based on diagnostic morphological features of the fastigium, coxae, foretibia, metasternum, and hind femur. However, Johns (1997) also expressed doubt as to the monophyly of his newly erected family. We recovered two Anostostomatidae clades, including *Lezina* and *Cooloola.* One was inclusive of two New World genera, *Cnemotettix* (2 species sequenced) and *Glaphyrosoma* (5 species sequenced), a representative of a new genus from Costa Rica (O. Cadena-Castañeda, in prep), and our sequenced representative of *Lezina*. The second clade is comprised of all other anostostomatids sampled. Previously, *Cnemotettix* and *Glaphyrosoma* were placed in their own tribe Glaphyrosomini (Rentz & Weissman, 1973), subfamily unknown. Further, Weissman (2001a, Table 19.1) documents that adult males of both genera drum using one rear leg at a time, a trait not noted in other Anostostomatidae, including the New World genus *Anabropsis.* Thus, our genetic (Fig. 2) and other evidence argue against placing the tribe Glaphysosomini in the same subfamily (Anabropsinae) as *Anabropsis*, an action supported by Johns & Hemp (2015) but considered "problematic" by Gorochov & Cadena-Castañeda (2016).
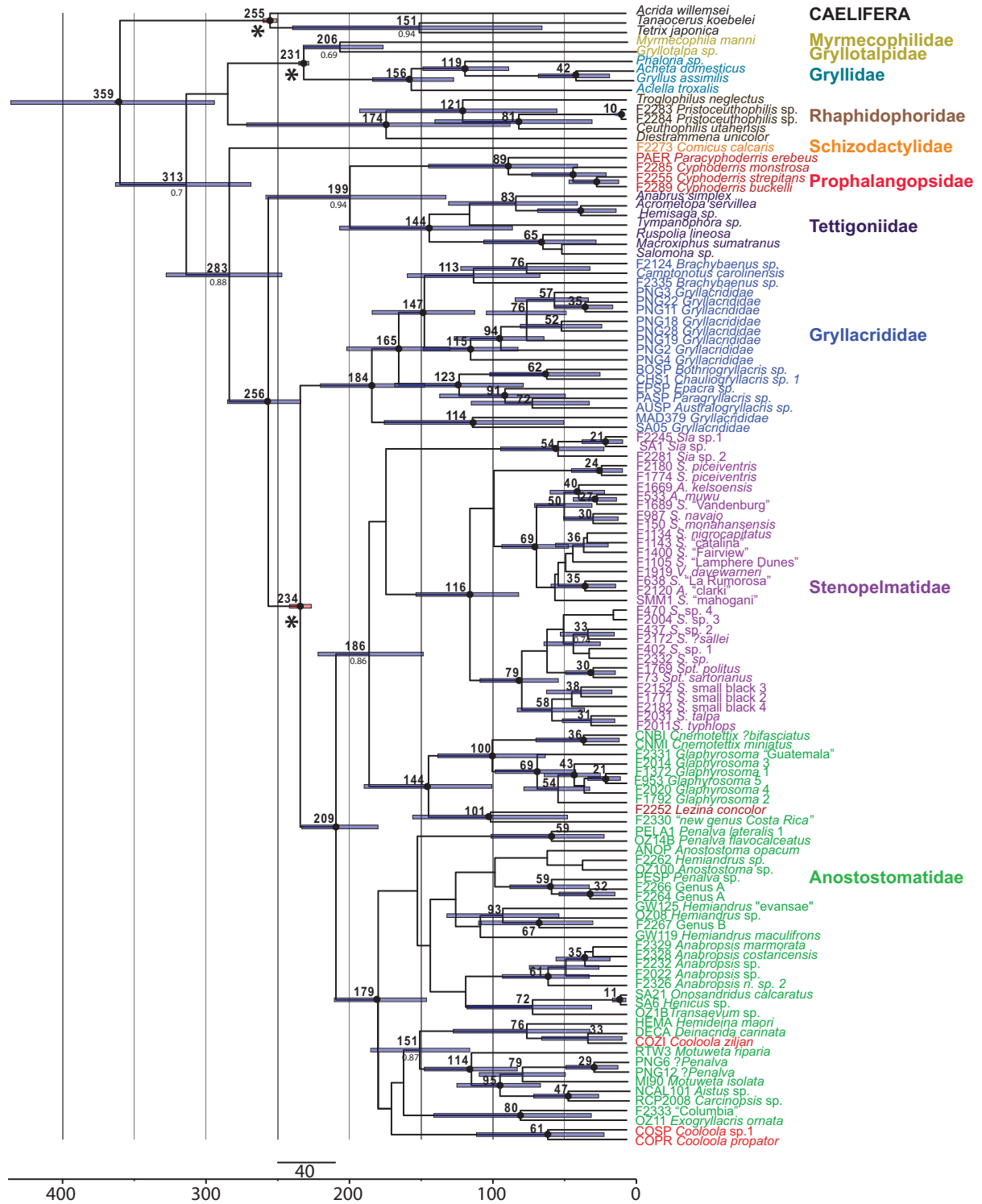
FIGURE 3. Bayesian chronogram estimated in Beast. Clade posterior probabilities > 0.95 are denoted with a black dot. Estimated ages for the most recent common ancestors of clades are indicated at the top left of nodes. Blue bars represent 95% credible intervals around node ages. Asterisks indicate the three nodes that were calibrated using published fossil ages (see methods).

TABLE 2. List of character states summarized by major clades within this paper.

| CLADE | NOMENCLATURE | | CYTOLOGY | | | COMMUNICATION | |
	Higher Taxon Name	Genus Name	2n♂ Number	X Chromosome	Autosome	Drumming*	Stridulation**
	Schizodactylidae	*Comicus*	unknown	unknown	unknown	N	FAS
		Schizodactylus	14	telocentric	all telocentric	N	FAS
	Rhaphidophoridae	several	17–57	metacentric	some metacentric	AD, HLD, T	N
	Gryllotalpidae	*Gryllotalpa*	12–23	most metacentric	most metacentric	N	TS
	Myrmecophilidae		unknown	unknown	unknown	N	N
	Gryllidae	several	7–29	some metacentric	some metacentric	AD, T	TS
	Prophalangopsidae	*Cyphoderris*	27	metacentric	most metacentric	N	TS
	Tettigoniidae	many	12–68	metacentric and telocentric	metacentric and telocentric	AD, HLD	TS, FAS, CS
	Gryllacrididae	several	11–31	metacentric	some metacentric	AD, HLD	FAS
A	Siinae	*Sia*	unknown	unknown	unknown	N	FAS
B	Stenopelmatinae	several	19–27	metacentric	some metacentric	AD	FAS
C	Anostostomatidae	*Lezina*	29	metacentric	some metacentric	N	FAS
C	Anostostomatinae	*Glaphyrosoma*	28, 29	metacentric	some metacentric	HLD	N
C	Anostostomatinae	*Cnemotettix*	25, 27	metacentric	some metacentric	HLD	N
D	Anostostomatinae	*Anostostoma*, *Henicus*	21	metacentric	some metacentric	AD	FAS, MS
D	Anostostomatinae	*Anabropsis*	15	metacentric	some metacentric	N	N
D	Deinacridinae	*Hemideina* & *Deinacrida*	11–29	metacentric	some metacentric	N	FAS, T, TTS
D	Anostostomatidae	*Cooloola*	21	metacentric	some metacentric	N	N

*Types of Drumming: AD = abdominal drumming, HLD = hind leg drumming where the whole rear leg(s) moves up and down but only the tibia actually contacts the substrate, T = tremulation where the abdomen vibrates up and down but does not strike the substrate, N = none recorded.

**Types of Stridulation: TS = tegminal stridulation, FAS = femoral-abdominal stridulation, CS = coxae stridulation, MS = mandibular stridulation, TTS = tergo-tergal stridulation, N = none recorded.

Lezina. The sand obligate genus *Lezina* is comprised of 12 described species (Cigliano *et al.*, 2017) from southwestern Asia and northern Africa. In previous phylogenetic analyses (28S, 18S, and 12S sequence data), *Lezina* has alternately been placed in the family Stenopelmatidae by Flook *et al.* (1999), the subfamily Lezininae in the superfamily Stenopelmatoidea by Jost & Shaw (2006, using sequence data generated by Flook *et al.*, 1999), and clustered with weta in the family Anostostomatidae by Legendre *et al.* (2010, also using sequences from Flook *et al.*, 1999). Desutter-Grandcolas (2003) found *Lezina* always groups with Tettigoniidae, but noted 16 of 85 characters in her data matrix could not be defined. The OSF (Cigliano *et al.*, 2017) places *Lezina* in the subfamily Lezininae in the family Gryllacrididae. We support *Lezina*, within the Stenopelmatoidea, in Anostostomatidae (Clade C) sister to the tribe Glaphyrosomini. This position is supported by Gorochov and Cadena-Castañeda (2016), who note the absence, in both latter groups, of "…subapical spines on the dorsal surface of fore tibia and of a feather-like relief on the outer surface of hind femur." While sound production in *Lezina* is different from that observed with the Glaphyrosomini (see S3), silk production has been documented in both: for *Cnemotettix* by Rentz & Weissman (1973) and for *Lezina* by G. Wizen (pers. comm. to D.B.W., October, 2013). Silk in *Cnemotettix* is used to line burrows in sandy habitats or to stitch together vegetation to form protective daytime retreats (Rentz & Weissman, 1973). Interestingly, we have been unable to document silk production in *Glaphyrosoma.* Gryllacridids are the only other orthopterans known to produce silk, which they also use to line or cover burrows (Morton & Rentz, 1983; Walker *et al.*, 2012). Determination of the molecular structure of silk proteins may provide insight into whether silk production in these groups is ancestral or arose independently in multiple lineages (Craig, 1997; Sutherland *et al.*, 2010; Walker *et al.*, 2012). Additionally, *Lezina* has a metacentric X and several large, metacentric autosomes (see Fig. S2–4) consistent with other anostostomatids.

Cooloola. Previous authors have described these anomalous Australian, endemic, fossorial orthopteroids, based on morphology, as a subfamily (Cooloolinae) in Anostostomatidae (Gorochov, 2001); as a subfamily in Stenopelmatidae (Johns, 1997; Desutter-Grandcolas, 2003); and as a family, the Cooloolidae, in Rentz (1999), Gwynne (1995), Nickle & Naskrecki (1997), and the OSF (Cigliano *et al.*, 2017). Ingrisch and Rentz (2009) erroneously placed *Cooloola* in the Gryllacrididae, when they intended to treat it as an anostostomatid (S. Ingrisch, pers. comm. to D.B.W., 2012). Most recently the molecular analysis of Song *et al.* (2015) supported *Cooloola* as an errant genus within Anostostomatidae, however their analysis only included a single representative of the genus. Here, using three species, we recovered *Cooloola* as a polyphyletic lineage within the larger Anostostomatidae Clade D. However, it may also be important to note that only two of the three gene regions (18S and 28S) could be amplified from *C. ziljan* Rentz for which we had access to an older preserved sample but not fresh material. Polyphyly within *Cooloola* appears to hinge on variable positions within the 28S gene; 18S was identical across all *Cooloola* sampled. Given this, it is possible that this finding of a polyphyletic *Cooloola* reflects shared ancestral polymorphism within the 28S gene and that further genetic sampling within this group could reveal a more cohesive genetic lineage. Given ongoing morphological work by D.C.F.R. (in prep), subfamily status for *Cooloola* within Anostostomatidae, or even family status as a "divergent lineage sister to Anostostomatidae" (H. Song, personal communication to D.B.W., 2017) may gain future support. However, currently, we do not find molecular support for family status.

Stenopelmatidae Jerusalem crickets. We also recovered two separate clades of Jerusalem crickets (Stenopelmatidae) in our analyses that are comprised of geographically distinguishable South African (subfamily Siinae) and North and Central American representatives (subfamily Stenopelmatinae). These Jerusalem cricket subfamilies are also distinguishable by differences in acoustical signaling. While New World Stenopelmatinae produce abdominal drumming (Weissman, 2001a), such has not been detected in Siinae (Weissman & Bazelet, 2013). Femoral-abdominal stridulation has been observed in both subfamilies, although it is rare in New World stenopelmatids (Weissman, 2001a).

Several potentially important voids remain in our taxon sampling of the Anostostomatidae and Stenopelmatidae. Most notably many South American Anostostomatidae (e.g. *Cratomelus* Blanchard, *Leiomelus* Ander, *Dolichochaeta* Philippi) have not been sampled, nor have southeast Asian Anostostomatidae (e.g. *Paterdecolyus* Griffini), and representatives of the remaining extant Stenopelmatidae subfamily Oryctopinae. The latter are restricted to India and Sri Lanka (Cigliano *et al.*, 2017) and could not be obtained for this study. Inclusion of these groups may help to further resolve the distributional extents of the major anostostomatid and stenopelmatid clades detected here, and the relationships among them. Overall, our results warrant taxonomic changes in Anostostomatidae and Stenopelmatidae at the family and subfamily level classification, however we think these should wait until more sampling and morphological analysis have been completed.

Schizodactylidae. The taxonomic placement of Schizodactylidae remains ambiguous in our study as well as previous efforts. Our MrBayes concatenated trees support a relationship between representatives of the families Rhaphidophoridae (camel and humped-back crickets) and Schizodactylidae (splay-footed crickets), the latter composed of two genera placed in the superfamily Schizodactyloidea in OSF (Cigliano *et al.*, 2017). However, we alternatively recovered our representative of Schizodactylidae (genus *Comicus*) as sister to the Stenopelmatoidea + Prophalangopsidae + Tettigoniidae in the lineage dating analysis. Elsewhere, the splay-footed crickets were treated as closest to Gryllacrididae by Gorochov (1995); as a sister-group, with Rhaphidophoridae to Grylloidea-Gryllotalpidae by Desutter-Grandcolas (2003); and sister to Raphidophoroidea + Hagloidea + Stenopelmatoidea + Tettigonioidea (Song *et al.*, 2015). Surprisingly, in Chintauan-Marquier *et al.* (2016), analysis of three nuclear and three mitochondrial gene regions showed the two splay-footed genera to be polyphyletic. What was not discussed by previous authorities is that McClung & Asana (1933) karyotyped the second genus in the family (*Schizodactylus* Brullé, from India) and found a reduced chromosome number when compared with Stenopelmatoidea, and, most importantly, that all chromosomes, including the X, were rod-shaped in character, indicating an end-located centromere.

The presence of metacentric autosomes, with a centromere positioned more toward the middle of the chromosome, and a metacentric (or sub-metacentric) sex chromosome in the males of Stenopelmatoidea (including *Lezina* and *Cooloola*), Prophalangopsidae, and Rhaphidophoridae is a consistent and apparently plesiomorphic character. We predict that the one remaining Stenopelmatidae clade in Fig. 1 that has not been karyotyped, the southern African Jerusalem crickets *Sia* (Clade A) will have both metacentric autosomes and a metacentric X chromosome. We also predict that the stenopelmatid genus *Oryctopus* Brunner von Wattenwyl (subfamily Oryctopinae)*,* from India, will be cytologically similar, if it is, in fact, phylogenetically related to the other Stenopelmatidae.

On the other hand, *Schizodactylus* shows little cytological resemblance to the above groups, especially with reference to autosomal and X chromosome centromere positions. But they are more similar cytologically to some in the superfamily Grylloidea (Gryllotalpidae: mole crickets, and Gryllidae: true crickets), in which some, but not all, species contain only rod-shaped chromosomes (Hewitt, 1979; White, 1973). This relationship is also seen on morphological grounds by Desutter-Grandcolas (2003), and on genetic grounds by Jost and Shaw (2006), and Legendre *et al.* (2010). Ingrisch and Rentz (2009) and Song *et al.* (2015) assigned superfamily status to this group—the Schizodactyloidea. Also, Heads and Leuzinger (2011) likewise believe that "morphological and molecular support for the Schizodactylidae-Grylloidea sister-group relationship is compelling." As S. Heads writes (pers. comm. to D.B.W., 2013): "Since the Schizodactylidae are monobasic, in a phylogenetic sense the family and superfamily are equivalent (i.e. Schizodactylidae = Schizodactyloidea). Also, placing them in their own superfamily has some taxonomic advantages in equating their rank with the sister-group Grylloidea and also serves as a place to put any additional schizodactyloid taxa that may turn up in the future (these would probably be fossil taxa)."

Relationships among other recovered clades. With the exception of Stenopelmatidae and Anostostomatidae, all other orthopteran families for which multiple representatives were included in this study were recovered as monophyletic. We recovered Stenopelmatoidea as most closely related to a highly-supported clade of Prophalangopsidae and Tettigoniidae. The recovered sister relationship of Prophalangopsidae and Tettigoniidae is intriguing. A recent genetic analysis of Tettigoniidae placed Nearctic Nedubini as basal to all other katydids (Cole & Chiang, 2016). Within the Nearctic Nedubini, in which males have symmetrically developed tegmina and files, the ratio of right tegmen over left is almost exactly 50:50 with fixed overlap in any given male. Thus, Cole and Chiang (2016) hypothesized that the Nedubini may be a transitional state between the Prophalangopsidae, which are fully ambidextrous in any given male, and the remaining Tettigoniidae, which have the tegminal overlap fixed as left over right. Our analysis also supported a close relationship between Gryllotalpidae, Myrmecophilidae and Gryllidae, a relationship supported in a more comprehensive taxon set of Grylloidea (Chintauan-Marquier *et al.*, 2016).

Some of the deeper nodes within our tree were weakly supported. This is not an uncommon result in higher level phylogenies of the Orthoptera and other insects (Legendre *et al.*, 2010; Whitfield & Kjer, 2008). Lack of resolution likely reflects a dearth of informative characters in the markers used, and suggests that more genetic data are needed (Legendre *et al.*, 2010). Short basal branch lengths may also reflect a rapid and ancient evolutionary radiation, in which case, further resolution may prove difficult (Lee *et al.*, 2013; Whitfield & Kjer, 2008; Whitfield

& Lockhart, 2007). High throughput sequencing approaches (e.g., targeted enrichment, RADseq), could provide the level of data needed to address whether short branch lengths reflect lack of appropriate data, rapid diversification, or both (Fenn *et al.*, 2008; Townsend *et al.*, 2011; Trautwein *et al.*, 2012; Whitfield & Kjer, 2008). Legendre *et al.* (2010) also called for integration of molecular, morphological, behavioral and ecological data. The information on karyotype and sound production reported here may provide useful characters in subsequent integrated analyses.

Note on two identification errors found in GenBank deposited sequences. Utilizing published sequence data from previous studies can be useful to increase taxon sampling, particularly when specimens are difficult to obtain, such as with the Stenopelmatoidea. However, errors in taxonomic information in GenBank and other sequence databases may lead to erroneous conclusions about phylogenetic relationships in subsequent analyses. Therefore, we wish to correct two misidentifications listed in Pratt *et al.* (2008) from specimens sent by D.B.W. to S.A. Trewick. The locality for *Stenopelmatus* sp. "F79" is listed in Pratt *et al.* (2008) as South Africa when, in fact, it is from Riverside Co., California (only the stenopelmatid genus *Sia* occurs in South Africa). "F234," a *Cnemotettix* silk-spinning cricket from Monterey, California, is incorrectly listed in Pratt *et al.* (2008) and associated GenBank records as *Stenopelmatus* sp. from South Africa. We have analyzed the GenBank sequences deposited for these two specimens with our dataset (analysis not shown), and verified D.B.W.'s identifications. Both of these samples were used by Pratt *et al.* (2008) as outgroups, and neither appears to affect their conclusions. But without a source citation, errors can unknowingly be repeated by future researchers. We were able to discover these errors (verified by S.A. Trewick to D.B.W. pers. comm., 2012) because the original specimen codes of D.B.W. were included in Pratt *et al.* (2008). This example illustrates that depositing sequenced specimens in appropriate museum collections and including specimen identification information is critical, especially when working with poorly described faunas, such as many tropical orthopteroid groups. For instance, there are no generic keys to the Papua New Guinea gryllacridids or anostostomatids and the western U.S. may have 70+ undescribed species of *Stenopelmatus* Burmeister Jerusalem crickets (Weissman *et al.*, in prep.). For example, *Stenopelmatus fuscus* Haldeman, was originally described from Santa Fe, New Mexico, and its distribution is limited from north-central New Mexico to northeastern Arizona (D.B.W., unpubl.). Unfortunately the distribution of this taxon is frequently and incorrectly cited (for example Evans, 2008) to include almost all of the western U.S.

Conclusions

The phylogenetic relationships among and within the families comprising the Stenopelmatoidea have proven difficult to resolve and have varied widely in both molecular and morphological analyses. This may partially result because the diversity within at least some of these groups remains under described and thus under sampled. This situation is in addition to, and maybe because of, the difficulties in adequately sampling these largely nocturnal, ground dwelling, non-singing, secretive insects. Here we provide greater taxon sampling within the three (Anostostomatidae, Gryllacrididae and Stenopelmatidae) most widely distributed families within the Stenopelmatoidea but find strong support for monophyly in just one (Gryllacrididae). Greater taxon sampling also uncovered a previously unrecognized relationship between Middle Eastern *Lezina* and the New World tribe Glaphyrosomini. However, despite the addition of taxa, some relationships among the families comprising the katydid allies still remain elusive. The inclusion of many additional independent loci may be needed to better resolve relationships among Stenopelmatidae and Anostostomatidae lineages as well as more generally within Ensifera.

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Data Accessibility. All sequence data generated for this study are publicly available from GenBank (https://www.ncbi.nlm.nih.gov/genbank/); accession numbers KY809469-KY809716.

References

Ali, J.R. & Aitchison, J.C. (2008) Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth-Science Reviews*, 88, 145–166. https://doi.org/10.1016/j.earscirev.2008.01.007

Ander, K. (1939) Vergleichend-anatomische und phylogenetishe studien über die Ensifera (Saltatoria). *Opuscula Entomologica Supplementum*, 2, 1–306.

Bai, J. & Huan, Y. (2012) The molecular phylogenetic analysis of some species of orthoptera based on mitochonrial ND2 gene (in Chinese, English abstract). *Chinese Journal of Zoology*, 47, 1–10.

Béthoux, O. (2012) King crickets, raspy crickets and weta, their wings, their fossil relatives. *Journal of Orthoptera Research*, 21, 179–225. https://doi.org/10.1665/034.021.0206

Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17, 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Chintauan-Marquier, I.C., Legendre, F., Hugel, S., Robillard, T., Grandcolas, P., Nel, A., Zuccon, D. & Desutter-Grandcolas, L. (2016) Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. *Cladistics*, 32, 54–81. https://doi.org/10.1111/cla.12114

Cigliano, M.M., Braun, H., Eades, D.C. & Otte, D. (2017) Orthoptera Species File. Version 5.0. Available from: http://Orthoptera.SpeciesFile.org. (accessed 1 March 2017)

Cole, J.A. & Chiang, B.H. (2016) The Nearctic Nedubini: the most basal lineage of katydids is resolved among the paraphyletic "Tettigoniinae"(Orthoptera: Tettigoniidae). *Annals of the Entomological Society of America*, 109, 652–662. https://doi.org/10.1093/aesa/saw030

Craig, C.L. (1997) Evolution of arthropod silks. *Annual Review of Entomology*, 42, 231–267. https://doi.org/10.1146/annurev.ento.42.1.231

Desutter-Grandcolas, L. (2003) Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta*, 32, 525–561. https://doi.org/10.1046/j.1463-6409.2003.00142.x

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29, 1969–1973. https://doi.org/10.1093/molbev/mss075

Evans, A.V. (2008) *Field Guide to Insects & Spiders & Related Species of North America*. Sterling Publishing Co., Inc., New York, 496 pp.

Fenn, J.D., Song, H., Cameron, S.L. & Whiting, M.F. (2008) A preliminary mitochondrial genome phylogeny of Orthoptera (Insecta) and approaches to maximizing phylogenetic signal found within mitochondrial genome data. *Molecular Phylogenetics and Evolution*, 49, 59–68. https://doi.org/10.1016/j.ympev.2008.07.004

Flook, P.K., Klee, S. & Rowell, C.H.F. (1999) Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, insecta) and implications for their higher systematics. *Systematic Biology*, 48, 233–253. https://doi.org/10.1080/106351599260274

Gibbons, A.D., Whittaker, J.M. & Müller, R.D. (2013) The breakup of East Gondwana: assimilating constraints from Cretaceous ocean basins around India into a best-fit tectonic model. *Journal of Geophysical Research: Solid Earth*, 118, 808–822. https://doi.org/10.1002/jgrb.50079

Gomez, R.A., Lightfoot, D.C. & Miller, K.B. (2012) A phylogenetic review of the North American band-winged grasshopper genus, *Encoptolophus* Scudder with description of *Nebulatettix* gen.n. (Orthoptera: Acrididae: Oedipodinae). *Insect

Systematics & Evolution, 43, 371–374.
https://doi.org/10.1163/1876312X-04303001

Gorochov, A.V. (1995) System and evolution of the suborder Ensifera (Orthoptera). Parts 1 and 2. *Trudy Zoologicheskogo Instituta Rossijskoj Akademii Nauk*, 260, 1–213. (In Russian).

Gorochov, A.V. (2001) The higher classification, phylogeny and evolution of the superfamily Stenopelmatoidea. *In:* Field, L.H. (Ed.), *The Biology of Wetas*, *King Crickets*, *and Their Allies*. CAB International, New York, pp. 1–33.
https://doi.org/10.1079/9780851994086.0003

Gorochov, A.V. & Cadena-Castañeda, O.J. (2016) New and little known Stenopelmatoidea (Orthoptera: Ensifera) from America. *Zoosystematica Rossica*, 25, 98–143.

Gwynne, D.T. (1995) Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research*, 4, 203–218.
https://doi.org/10.2307/3503478

Heads, S.W. & Leuzinger, L. (2011) On the placement of the Cretaceous orthopteran *Brauckmannia groeningae* from Brazil, with notes on the relationships of Schizodactylidae (Orthoptera, Ensifera). *Zookeys*, 77, 17–30.
https://doi.org/10.3897/zookeys.77.769

Hemp, C., Heller, K.G., Kehl, S., Warchalowska-Sliwa, E., Wagele, J.W. & Hemp, A. (2010) The Phlesirtes complex (Orthoptera, Tettigoniidae, Conocephalinae, Conocephalini) reviewed: integrating morphological, molecular, chromosomal and bioacoustic data. *Systematic Entomology*, 35, 554–580.
https://doi.org/10.1111/j.1365-3113.2009.00512.x

Hewitt, G.M. (1979) Grasshoppers and crickets. *In:* John, B. (Ed.), *Animal Cytogenetics*. Gebrüder Borntraeger, Berlin, pp. 1–170.

Hillis, D.M. (1996) Inferring complex phylogenies. *Nature*, 383, 130–131.
https://doi.org/10.1038/383130a0

Ingrisch, S. & Rentz, D.C.F. (2009) Orthoptera. *In:* Resh, V. & Carde, R. (Eds.), *Encyclopedia of Insects*. *2nd Edition*. Elsevier, San Diego, California, pp. 732–743.
https://doi.org/10.1016/b978-0-12-374144-8.00196-x

International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature. 4th Edition*. The Natural History Museum, London, 306 pp.

Ishiwata, K., Sasaki, G., Ogawa, J., Miyata, T. & Su, Z.H. (2011) Phylogenetic relationships among insect orders based on three nuclear protein-coding gene sequences. *Molecular Phylogenetics and Evolution*, 58, 169–180.
https://doi.org/10.1016/j.ympev.2010.11.001

Jaiswara, R., Balakrishnan, R., Robillard, T., Rao, K., Cruaud, C. & Desutter-Grandcolas, L. (2012) Testing concordance in species boundaries using acoustic, morphological, and molecular data in the field cricket genus *Itaropsis* (Orthoptera: Grylloidea, Gryllidae: Gryllinae). *Zoological Journal of the Linnean Society*, 164, 285–303.
https://doi.org/10.1111/j.1096-3642.2011.00769.x

Johns, P.M. (1997) The Gondwanaland weta: family Anostostomatidae (formerly in Stenopelmatidae, Henicidae or Mimnermidae): nomenclatural problems, world checklist, new genera and species. *Journal of Orthoptera Research*, 6, 125–138. https://doi.org/10.2307/3503546

Johns, P.M. & Hemp, C. (2015) Redescription of *Libanasa brachyura* Karny, 1928. (Orthoptera: Anostostomatidae:? Lutosinae) from Tanzania and problems at the subfamily level. *Zootaxa*, 3946 (1), 113–124.
https://doi.org/10.11646/zootaxa.3946.1.5

Jost, M.C. & Naskrecki, P. (2003) Phylogeny and evolution of acoustic communication in Orthoptera. *Entomologische Abhandlungen*, 61, 142–143.

Jost, M.C. & Shaw, K.L. (2006) Phylogeny of Ensifera (Hexapoda : Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution*, 38, 510–530.
https://doi.org/10.1016/j.ympev.2005.10.004

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30, 772–780.
https://doi.org/10.1093/molbev/mst010

Kevan, D.K.M. (1986) A rationale for the classification of orthopteroid insects—the saltatorial orthopteroids or grigs—one order or two? *In*: Nickle, D.A. (Ed.), *Proceedings 4th Triennial Meeting*, *Pan American Acridological Society*. Pan American Acridological Society, Detroit, Michigan, pp. 49–67.

Kumala, M., McLennan, D., Brooks, D. & Mason, A. (2005) Phylogenetic relationships within hump-winged grigs, Cyphoderris (Insecta, Orthoptera, Tettigonioidea, Haglidae). *Canadian Journal of Zoology*, 83, 1003–1011.
https://doi.org/10.1139/z05-086

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

Lee, M.S., Soubrier, J. & Edgecombe, G.D. (2013) Rates of phenotypic and genomic evolution during the Cambrian explosion. *Current Biology*, 23, 1889–1895.
https://doi.org/10.1016/j.cub.2013.07.055

Legendre, F., Robillard, T., Song, H., Whiting, M.F. & Desutter-Grandcolas, L. (2010) One hundred years of instability in ensiferan relationships. *Systematic Entomology*, 35, 475–488.
https://doi.org/10.1111/j.1365-3113.2009.00519.x

Lu, H.-J. & Huang, Y. (2012) Phylogenetic relationship among some groups of orthopteran based on complete sequences of the mitochondrial COI gene. *Zoological Research*, 33, 319–328.
https://doi.org/10.3724/SP.J.1141.2012.03319

Ma, T.-T. & Chen, G. (2011) Study on phylogenesis of Orthoptera inferred from mtDNA (in Chinese with English abstract) *Journal of Jilin Agricultural University*, 3 (33), 494–497.

McClung, C.E. & Asana, J.J. (1933) The chromosomes of *Schizodactylus monstrosus*. *Journal of Morphology*, 55, 185–191.
https://doi.org/10.1002/jmor.1050550111

Morton, S.R. & Rentz, D.C.F. (1983) Ecology and taxonomy of fossorial, granivorous gryllacridids (Orthoptera: Gryllacridae) from arid central Australia. *Australian Journal of Zoology*, 31, 557–579.
https://doi.org/10.1071/ZO9830557

Mugleston, J.D., Song, H. & Whiting, M.F. (2013) A century of paraphyly: A molecular phylogeny of katydids (Orthoptera: Tettigoniidae) supports multiple origins of leaf-like wings. *Molecular Phylogenetics and Evolution*, 69, 1120–1134.
https://doi.org/10.1016/j.ympev.2013.07.014

Nickle, D.A. & Naskrecki, P.A. (1997) Recent developments in the systematics of Tettigoniidae and Gryllidae. *In:* Gangwere, S.K., Muralirangan, M.C. & Muraliramgan, M. (Eds.), *Bionomics of Grasshoppers, Katydids, and Their Kin*. CAB International, New York, pp. 41–58.

Nylander, J., Wilgenbusch, J., Warren, D. & Swofford, D. (2008) AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics*, 24, 581–583.
https://doi.org/10.1093/bioinformatics/btm388

Plazzi, F., Ricci, A. & Passamonti, M. (2011) The mitochondrial genome of *Bacillus* stick insects (Phasmatodea) and the phylogeny of orthopteroid insects. *Molecular Phylogenetics and Evolution*, 58, 304–316.
https://doi.org/10.1016/j.ympev.2010.12.005

Pratt, R.C., Morgan-Richards, M. & Trewick, S.A. (2008) Diversification of New Zealand weta (Orthoptera : Ensifera : Anostostomatidae) and their relationships in Australasia. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 363, 3427–3437.
https://doi.org/10.1098/rstb.2008.0112

Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer v1. 6. Available from http://beast.bio.ed.ac.uk/Tracer. (accessed 6 June 2017)

Rannala, B., Huelsenbeck, J.P., Yang, Z. & Nielsen, R. (1998) Taxon sampling and the accuracy of large phylogenies. *Systematic Biology*, 47, 702–710.
https://doi.org/10.1080/106351598260680

Rentz, D.C.F. (1999) Pearson's Monster, a New Species of Cooloola Rentz from Queensland (Orthoptera: Cooloolidae). *Journal of Orthoptera Research*, 8, 25–32.
https://doi.org/10.2307/3503421

Rentz, D.C.F. & Weissman, D.B. (1973) The origins and affinities of the Orthoptera of the Channel Islands and adjacent mainland California. Part I. The genus *Cnemotettix*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 125, 89–120.

Riek, E.F. (1976) New Upper Permian insects from Natal, South Africa. *Annals of the Natal Museum*, 22, 755–789.

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

Rosenberg, M.S. & Kumar, S. (2001) Incomplete taxon sampling is not a problem for phylogenetic inference. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 10751–10756.
https://doi.org/10.1073/pnas.191248498

Scotese, C.R. (1992) Paleogeographic atlas. *In*: *PALEOMAP Project*. Department of Geology, U. of Texas at Arlington. [atlas]

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

Song, H., Amédégnato, C., Cigliano, M.M., Desutter-Grandcolas, L., Heads, S.W., Huang, Y., Otte, D. & Whiting, M.F. (2015) 300 million years of diversification: elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics*, 31, 621–651.
https://doi.org/10.1111/cla.12116

Storozhenko, S.Y. (1997) Fossil history and phylogeny of orthopteroid insects. *In:* Gangwere, S.K., Muralirangan, M.C. & Muralirangan, M. (Eds.), *The Bionomics of Grasshoppers, Katydids and Their Kin*. CAB International, New York, pp. 59–82.

Strauss, J. (2017) The scolopidial accessory organ in the Jerusalem cricket (Orthoptera: Stenopelmatidae). *Arthropod Structure*

& *Development*, 46, 171–177.

    http://dx.doi.org/10.1016/j.asd.2016.12.001

Strauss, J. & Lakes-Harlan, R. (2008) Neuroanatomy of the complex tibial organ of Stenopelmatus (Orthoptera : Ensifera : Stenopelmatidae). *Journal of Comparative Neurology*, 511, 81–91.

    https://doi.org/10.1002/cne.21836

Strauss, J. & Lakes-Harlan, R. (2009) The evolutionary origin of auditory receptors in Tettigonioidea: the complex tibial organ of Schizodactylidae. *Naturwissenschaften*, 96, 143-146.

    https://doi.org/10.1007/s00114-008-0450-4

Strauss, J. & Stritih, N. (2016) The accessory organ, a scolopidial sensory organ, in the cave cricket Troglophilus neglectus (Orthoptera: Ensifera: Rhaphidophoridae). *Acta Zoologica*, 97, 187–195.

    https://doi.org/10.1111/azo.12116

Sutherland, T.D., Young, J.H., Weisman, S., Hayashi, C.Y. & Merritt, D.J. (2010) Insect silk: one name, many materials. *Annual Review of Entomology*, 55, 171–188.

    https://doi.org/10.1146/annurev-ento-112408-085401

Swofford, D.L., Olsen, G.J., Waddell, P.J. & Hillis, D.M. (1996) Phylogenetic inference. *In:* Hillis, D.M., Moritz, C. & Mable, B.K. (Eds.), *Molecular Systematics*. Sinauer Associates, Sunderland, Massachusetts, pp. 407–543.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739.

    https://doi.org/10.1093/molbev/msr121

Terry, M.D. & Whiting, M.F. (2005) Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics*, 21, 240–257.

    https://doi.org/10.1111/j.1096-0031.2005.00062.x

Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Sites, J.W., Kuczynski, C.A., Wiens, J.J. & Reeder, T.W. (2011) Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Molecular Phylogenetics and Evolution*, 61, 363–380.

    https://doi.org/10.1016/j.ympev.2011.07.008

Trautwein, M.D., Wiegmann, B.M., Beutel, R., Kjer, K.M. & Yeates, D.K. (2012) Advances in Insect Phylogeny at the Dawn of the Postgenomic Era. *In:* Berenbaum, M.R. (Ed.), *Annual Review of Entomology*, 57, 449–468.

    https://doi.org/10.1146/annurev-ento-120710-100538

Walker, A.A., Weisman, S., Church, J.S., Merritt, D.J., Mudie, S.T. & Sutherland, T.D. (2012) Silk from Crickets: A New Twist on Spinning. *Plos One*, 7, e30408.

    https://doi.org/10.1371/journal.pone.0030408

Wang, X., Zhou, Z., Huang, Y. & Shi, F. (2011) The phylogenetic relationships of higher Orthopteran categories inferred from 18S rRNA gene sequences. *Acta Zootax Sinica*, 36, 139–150.

Weissman, D.B. (2001a) Communication and reproductive behaviour in North American Jerusalem crickets (*Stenopelmatus*) (Orthoptera: Stenopelmatidae). *In:* Field, L.H. (Ed.), *The Biology of Wetas, King Crickets and Their Allies*. CABI Publications, New York, pp. 351–375.

    https://doi.org/10.1079/9780851994086.0351

Weissman, D.B. (2001b) North and Central America Jerusalem crickets (Orthoptera: Stenopelmatidae): taxonomy, distribution, life cycle, ecology and related biolgy of the American species. *In:* Field, L.H. (Ed.), *The Biology of Wetas, King Crickets and Their Allies*. CABI Publications, New York, New York, pp. 57–72.

    https://doi.org/10.1079/9780851994086.0057

Weissman, D.B. & Bazelet, C.S. (2013) Notes on southern Africa Jerusalem crickets (Orthoptera: Stenopelmatidae: *Sia*). *Zootaxa*, 3616 (1), 49–60.

    https://doi.org/10.11646/zootaxa.3616.1.4

Weissman, D.B. & Lightfoot, D.C. (2007) Techniques for the field capture and captive rearing of North American Jerusalem crickets (Orthoptera: Stenopelmatinae). *In: Invertebrates in Captivity Conference*. Sonoran Arthropod Studies Institute, Tucson, pp. 22–29.

Wheeler, W.C., Whiting, M., Wheeler, Q.D. & Carpenter, J.M. (2001) The phylogeny of the extant hexapod orders. *Cladistics*, 17, 113–169.

    https://doi.org/10.1111/j.1096-0031.2001.tb00115.x

White, M.J.D. (1973) *Animal Cytology and Evolution*. Cambridge University Press, New York, 961 pp.

Whitfield, J.B. & Kjer, K.M. (2008) Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annual Review of Entomology*, 53, 449–472.

    https://doi.org/10.1146/annurev.ento.53.103106.093304

Whitfield, J.B. & Lockhart, P.J. (2007) Deciphering ancient rapid radiations. *Trends in Ecology & Evolution*, 22, 258–265.

    https://doi.org/10.1016/j.tree.2007.01.012

Whiting, M.F., Bradler, S. & Maxwell, T. (2003) Loss and recovery of wings in stick insects. *Nature*, 421, 264–267.

    https://doi.org/10.1038/nature01313

Yang, J., Ren, Q. & Huang, Y. (2016) Complete mitochondrial genomes of three crickets (Orthoptera: Gryllidae) and

comparative analyses within Ensifera mitogenomes. *Zootaxa*, 4092 (4), 529–547.
https://doi.org/10.11646/zootaxa.4092.4.4

Yoshizawa, K. (2011) Monophyletic Polyneoptera recovered by wing base structure. *Systematic Entomology*, 36, 377–394.
https://doi.org/10.1111/j.1365-3113.2011.00572.x

Zhang, H.-L., Huang, Y., Lin, L.-L., Wang, X.-Y. & Zheng, Z.-M. (2013) The phylogeny of the Orthoptera (Insecta) as deduced from mitogenomic gene sequences. *Zoological Studies*, 52, 37.
https://doi.org/10.1186/1810-522X-52-37

Zhou, Z.J, Shi, F. & Zhao, L. (2014) The first mitochondrial genome for the superfamily Hagloidea and implications for its systematic status in Ensifera. *PLoS ONE*, 9, e86027.
https://doi.org/10.1371/journal.pone.0086027

Zhou, Z.J., Ye, H.Y., Huang, Y.A. & Shi, F.M. (2010) The phylogeny of Orthoptera inferred from mtDNA and description of Elimaea cheni (Tettigoniidae: Phaneropterinae) mitogenome. *Journal of Genetics and Genomics*, 37, 315–324.
https://doi.org/10.1016/S1673-8527(09)60049-7

Zwickl, D.J. & Hillis, D.M. (2002) Increased taxon sampling greatly reduces phylogenetic error. *Systematic Biology*, 51, 588–598.
https://doi.org/10.1080/10635150290102339

SUPPLEMENT 1. Complete collection data for specimens first analyzed here. Specimens are presented in the same order as they appear in Table 1.

Specimen codes	Collection data
ANOP	Australia, New South Wales, Bawley Point. ?2002. S35° 30' E150° 24'. DCF Rentz
CNMI	USA, CA, Los Angeles Co., Santa Catalina Island, array CAT-8. 28-ii-2002. N33.37804° W118.40788°. AG Vandergast
CNBI	USA, CA, San Bernardino Co., Silverwood State Park, array SIL-13. x-2000. N34.27269° W117.29306°. AG Vandergast
COPR	Australia, Queensland, Cooloola National Park. 2006. S26° E153.1°. M. deBaar
COZI	Australia, Queensland, Nolan's Pocket, South Kolan, 21 km SW Bundaberg. xi-1987. S24.9795° E152.168°. R. Jansen
COSP	Australia, Queensland, Carnarvon National Park, Mt. Moffatt near Marlong Arch (MM2P). 13-xi-2010. 714m. 25.018°S 147.895°E. N. Starick
F953	Mexico, Tamaulipes, 10 km N Altamira on road to Lomas del Real. 8-vi-1999. 0'. DB Weissman, VF Lee. S99-47
F1372	Mexico, Nuevo Leon, Hwy 61 8.1 km S Hwy 58 at km 182. 20-ix-2003. 6020'. DB Weissman, DC Lightfoot S03-108
F1792	Mexico, Veracruz, Metlac Canyon of Rio Metlac. 20-vi-2006. 2080'. DB Weissman, DC Lightfoot. S06-39
F2014	Mexico, Michoacan, Hwy 15 libre 40 km E Morelia at km sign 205. 1-vi-2008. 7790'. DB Weissman, DC Lightfoot. S08-33
F2020	Mexico, Hidalgo, Hwy 85 1.5 km N Maguey Verde at km sign 142.8. 3-vi-2008. 7270'. DB Weissman, DC Lightfoot. S08-38
F2022	Mexico, Hidalgo, Hwy 85 17 km S Jacala at km sign 163.5. 3-vi-2008. 6430'. DB Weissman, DC Lightfoot. S08-39
F2232	Mexico, Michoacan, Hwy 37 (road to Uruapan) 4.4 km S intersection with Hwy 15 libre at km post 4.4. 29-vi-2011. 6800'. N19° 48' 58.1", W102° 01' 41.8". DB Weissman, DW Weissman. S11-61
F2252	Israel, Negev Desert, Meshash Sands between Beer Sheva and Dimona, 12-iv-2012. D. Simon.
F2262	Australia,Queensland, Lamington National Park, 10-26-ix-2008. S28.193° E153.128°. G.B. Monteith, F. Turco
F2264	same as F2262
F2266	Australia, Queensland, Lamb Range, 6.6 km NNE Tinaroo Falls, 16-24-xi-2009, 1191m. S17.108°, E145.569°. G.B. Monteith, F. Turco
F2267	Australia, Queensland, North Queensland Boulder Cave State Park, Mt. Bartle Frere, 1.2 km E Bobbin Falls, 18-xi-2009. 842m. S17.379°, E145.785°. G.B. Monteith, F. Turco
F2326	Guatemala, San Marcos, 1600m. 22-v-2012
F2328	Costa Rica, Cartago, Reserva Indigena Bajo Chiripo. 1280m. 24-iv-2012
F2329	Costa Rica, Limon, Turrialba Volcan, 655m. 23-iv-2012
F2330	Costa Rica, Alajuela, Manuel Antonio Brenes Reserve. 760m. 26-iv-2012
F2331	Guatemala, Huehuetenango, Barillas, San Ramon, near Rio Bravo. 550m. 18-v-2012
F2333	Colombia, Guavuare, San Jose del Guaviare. ix-2006.
PELA1	Australia, Queensland, Kuranda. 16-31-vi-2010. 335m. S16.48° E145.38°. DCF Rentz
PESP	same as PELA1
PNG6	Papua New Guinea, Western Province, Muller Range, Gugusu, 3-ix-2009. 515m. S5°43'45.3" E142°15'47.8". P Naskrecki, DCF Rentz
PNG12	Papua New Guinea, Western Province, Muller Range, Sawetau. 11-17-ix-2009. 1550-1700m. S5° 39'23.7" E142°18'16.5"E. P Naskrecki, DCF Rentz
SA6	South Africa, Western cape, Jonkershoek Nature Reserve, vi-2006. S33.98411°, E18.94884°. E. Bredenhand

Specimen codes	Collection data
SA21	South Africa, Western Cape, Jonkershoek Nature Reserve, vi-2006. S33.97170°, E18.94277°. E. Bredenhand
AUSP	Australia, Queensland, Kuranda. 16-31-iii-2010. 335m. S16.48° E145.38°. DCF Rentz
BOSP	same as AUSP
CHS1	same as AUSP
EPSP	Australia, Queensland, Mt. Spurgeon, 18 km W Mossman, "Cooper's Camp". 12-13-vi-2010. 1118m. S16° 16' 34.72" E145° 11' 33.55". DCF Rentz
F2124	Costa Rica, Puntarenes, Monteverde. 21-vii-2009. 5000' DB Weissman. S09-99
F2335	Colombia, Choco, Capurgana. Xi-2009
PASP	Australia, Queensland, Kuranda. 16-31-iii-2010. 335m. S16.48° E145.38°. DCF Rentz
PNG2	Papua New Guinea, Western Province, Muller Range, Gugusu, 3-ix-2009. 515m. S5°43'45.3" E142°15'47.8". P Naskrecki, DCF Rentz
PNG3	same as PNG2
PNG4	same as PNG2
PNG11	Papau New Guinea, East New Britain, Nakanai Mts., Lamas. 3/iv/2009. 200m. S5°36'50.7' E151°24'28'. P Naskrecki
PNG18	Papua New Guinea, Western Province, Muller Range, Gugusu, 3-ix-2009. 515m. S5°43'45.3" E142°15'47.8". P Naskrecki, DCF Rentz
PNG19	Papua New Guinea, Western Province, Muller Range, Sawetau. 11-17-ix-2009. 1550-1700m. S5° 39'23.7" E142°18'16.5"E. P Naskrecki, DCF Rentz
PNG22	Papua New Guinea, Western Province, Muller Range, Gugusu, 3-ix-2009. 515m. S5°43'45.3" E142°15'47.8". PNaskrecki, DCF Rentz
PNG28	Papua New Guinea, Eastern Highlands Province, Mt Gahavisuka Provincial Park, nr IBR shelter huts. 30-iv to 1-v-2009. 2311m. S6°0'51.8" E145°24'46.9" P Naskrecki.
SA05	South Africa, Western Cape, Jonkershoek Nature Reserve, vi-2006. S33.98442°, E18.94903°. E. Bredenhand
F2255	USA, Wyoming, Grand Teton National Park, Lower Deadman's Bar, v-2009. 43.759193°, -110.623709°. S.K. Sakaluk
F2285	Canada, British Columbia, Monck Provincial Park, 2012. K.A. Judge
F2289	Canada, British Columbia, Rock Creek, 2012. K.A. Judge
PAER	Russia, Khabarovskii krai, Byreyinskii Nature Reserve, Dusse-Alin Mts., upper stream of Bureya River. 1160-1200 m. 27-29-vi-2011. N52° 01', E135° 05'. E.S. Koshkin
F2283	USA, CA, Santa Clara Co., Los Gatos, Francis Oaks Way, 28-vi-2012. DB Weissman
F2284	same as F2283
F2273	Nimibia, Namib Desert, Gunsbewys Farm. 26-v-2010. R. Lakes-Harlan.
F73	Costa Rica, Puntarenes, Monteverde. 16-vi-1995. 5000' DB Weissman. S95-48
F150	USA, Texas, Ward Co., Monahans Sandhills State Park. 21-vii-1995. DB Weissman. S95-59
F402	Honduras, Cortes, Cusuco National Park. 5-xii-1996. 4900'. DB Weissman. S96-101
F437	Honduras, Ocotepeque, RB Guisayote 20 km E Nueva Ocotepeque. 7-xii-1996. 6720'. DB Weissman. S96-103
F470	Honduras, Francisco Morazan, El Uyuco Biological Reserve. 11-xii-1996. 5200-5500'. DB Weissman. S96-106
F533	USA, CA, Santa Barbara Co., Point Conception. 20-xii-1996. DB Weissman. S96-123
F638	Mexico, Baja California Norte, La Rumorosa. 13-iii-1998. 4460'. DB Weissman, VF Lee. S98-11

Specimen codes	Collection data
F987	USA, AZ, Coconino Co., Moenkopi Dunes 3.1 m SE Tuba City. 7-ix-1999. 4680'. DB Weissman, DC Lightfoot. S99-111
F1105	USA, CA, Humboldt Co., Lamphere Dunes. 1-x-2000. P. Haggart. S00-61
F1134	USA, CA, Kings Co., Tar Canyon. 26-ii-2001. 1040'. DB Weissman, VF Lee. S01-14
F1143	USA, CA, Los Angeles Co., Santa Catalina Island, Toyon Bay, 26-iv-2001. A.W. Weissman. S01-23
F1400	USA, CA, San Benito Co., Lone Tree Road 6.5 m SE Fairview Road. 21-iii-2003. 1480' DB Weissman. S03-8
F1669	USA, CA, San Bernardino Co., Kelso Dunes, 27-ii-2005. 2480'. DB Weissman, VF Lee. S05-16
F1689	USA, CA, Santa Barbara Co., Vandenberg Air Force Base, Bear Creek. 18-x-2004. 418'. A. Abela. S04-147
F1769	Mexico, Veracruz, Metlac Canyon of Rio Metlac. 20-vi-2006. 2080'. DB Weissman, DC Lightfoot. S06-39
F1771	Mexico, Hidalgo, Zimapan. 23-vi-2006. 5600' DB Weissman, DC Lightfoot. S06-50
F1774	Mexico, Oaxaca, Hwy 175 at km sign post 129.2. 19-vi-2006. 9020'. DB Weissman, DC Lightfoot. S06-36
F1919	Mexico, Baja California Norte, sand dunes n of Guerrero Negro. 31-iii-2007. M.v. Dam
F2004	Honduras, Yoro, Pico Pijol, nr. Linda Vista. 17-29-vi-1995. 1400-1800m, G.P. Bruyea, D.C. Hawks
F2011	Mexico, Hidalgo, Hwy 105 6 km N Zacualtipam at km post sign 103.5. 4-vi-2008. 7020'. DB Weissman, DC Lightfoot. S08-44
F2031	Mexico, Hidalgo, Hwy 85 17 km S Jacala at km sign 163.5. 3-vi-2008. 6430'. DB Weissman, DC Lightfoot. S08-39
F2120	Mexico, Baja California Norte, El Berrendo. 16-v-2009. 2100'. N30° 33.103 W115° 08.102 DB Weissman, W.H. Clark. S09-15
F2152	Mexico, Coahuila, Huachichal. 19-ix-2008. 2163' M.v. Dam. S09-156
F2172	Mexico, Chiapas, Cerro Tres Picos. 3-iii-1973. 1500-1800m. D.E. Breedlove
F2180	Mexico, Oaxaca, Cerro Iquana. 4-viii-2007. 7500'. N16° 14' 47" W97° 01' 52" M.v. Dam
F2182	Mexico, Jalisco, Nevado de Colima. 28-vii-2007. N19° 36' 43" W103° 34' 21" M.v. Dam
F2245	South Africa, Western Cape, Jonkersshoek Nature Reserve 1.3 km from entrance kiosk, 15-viii-2011, 680'. DB Weissman, CS Bazelet. S11-81
F2281	South Africa, Western Cape, CederbergNature Reserve, Wolfberg Cracks, 4-i-2011. P Naskrecki, CS Bazelet
SA1	South Africa, Western Cape, Groot Winterhoek Nature Reserve. 28-xi-2008. S32.99885° E19.06147°. CS Bazelet
SMM1	USA, CA, Los Angeles Co., Santa Monica Mountain's National Recreational Area, array SMM-14. vi-2001. N34.16584° W118.79206°. AG Vandergast

SUPPLEMENT 2. Cytological Information

As early as 1963, Lewis and John argued for an evolutionary distinction between the "exophenotype" (obvious and external features) and the "endophenotype" (microscopic and internal features). While both impact fitness, the former primarily relates to differential viability of living individuals while the latter relates to differential fecundity or fertility of the next generation. As John (1981) well stated: "Thus hybridity may lead to vigor (exophenotypic effect) but also to sexual sterility (endophenotypic effect)." But (endophenotypic) karyotypes can also be important phylogenetic characters because they may be more evolutionary conservative, especially for the X chromosome (John & Rentz, 1987), and thus better reflect phylogeny, than (exophenotypic) morphological characters (see, for example, Murphy *et al.*, 2004). As an orthopteran example, White (1973) and Weissman and Rentz (1980) argued that western U. S. trimerotropine grasshoppers (Section B *Trimerotropis* Stål, *Circotettix* Scudder and *Aerochoreutes* Rehn) form a unified phylogenetic group within the North American banded-wing Oedipodinae grasshoppers based upon the presence of a metacentric X chromosome and autosomal pericentric inversions. Yet Otte (1984) ignored such arguments when he transferred Section B *T. helferi* Strohecker to *Microtes* Scudder based solely upon morphological characters. Weissman (1984) argued that such convergence (homoplasy) between *T. helferi* and *Microtes* originated from inhabiting physically similar coastal sand dunes, and such convergence has now been confirmed with DNA data (Lightfoot *et al.*, unpubl.). Additionally, Weissman and Rentz (1980) speculated that blue in the hind wing indicated a

probable evolutionary subgroup within Section B *Trimerotropis* taxa, now also confirmed by Lightfoot *et al.* (unpubl.).

We believe that with continued progress in molecular cytogenetics (Dobigny *et al.*, 2004) and comparative chromosome painting (Carter, 1994; Wienberg, 2004; Murphy *et al.*, 2004), chromosomal data can have important impacts in phylogenetic investigations. Most ensiferan families have been examined cytologically. We discuss those families related to the Stenopelmatoidea in the order they appear in Fig. 2.

Schizodactylidae. India, 1 species, *Schizodactylus monstrosus* (Drury). $2n\male = 14$, all telocentric or rod-shaped chromosomes, including both sex chromosomes (McClung & Asana, 1933). While McClung & Asana (1933) didn't speculate on what phylogenetic significance this unusual orthopteran karyotype suggested, they noted that it "has no apparent extensive affinities with any groups and seems sui generis" (of its own kind).

Rhaphidophoridae. Various camel crickets in the Gondwana subfamily Macropathinae. $2n\male = 17–57$, some autosomes and always the X chromosome are metacentric (Hewitt, 1979; Mesa *et al.*, 1968, and references therein). Hubbell and Norton (1978) considered Macropathinae the sister group to all other Rhaphidophoridea, and Strauss and Lakes-Harlan (2009) note that the ancestral auditory situation of Ensifera is represented in Rhaphidophoridae.

Grylloidea. White (1973) and Hewitt (1979) list taxa within both the Gryllotalpidae and Gryllidae that have all rod-shaped chromosomes and other species with a combination of both rod-shaped and metacentric autosomes and X chromosome. No Myrmecophilidae have been karyotyped.

Prophalangopsidae. *Cyphoderris* Uhler. North America, 2 species, $2n\male=27$, some autosomes and always the X chromosome are metacentric (Mesa & Ferreira, 1984).

Tettigoniidae. A literature review (Hewitt, 1979; Ueshima & Rentz, 1979; White, 1973; Warchalowska-Sliwa, 1998) indicates that taxa with all rod-shaped chromosomes (including the X) as well as those with both rod-shaped and metacentric autosomes and a metacentric X, are known within the many katydid families. A distribution analysis of centromere position in the X chromosome for the 16 katydid subfamilies whose DNA was compared by Mugleston *et al.* (2013), would be of great interest.

STENOPELMATOIDEA
Gryllacrididae. Australia only, 10 species, $2n\male$ from 11–31, some autosomes and always the X chromosome are metacentric (Rentz & John, 1990, and citations therein). Rentz and John (1990) discuss, p. 1153, a telocentric X chromosome in *Chauliogryllacris grahami* Rentz, but Fig. 241b, p. 1159, appears to show a submetacentric X chromosome, not a telocentric element where the centromere is terminal.
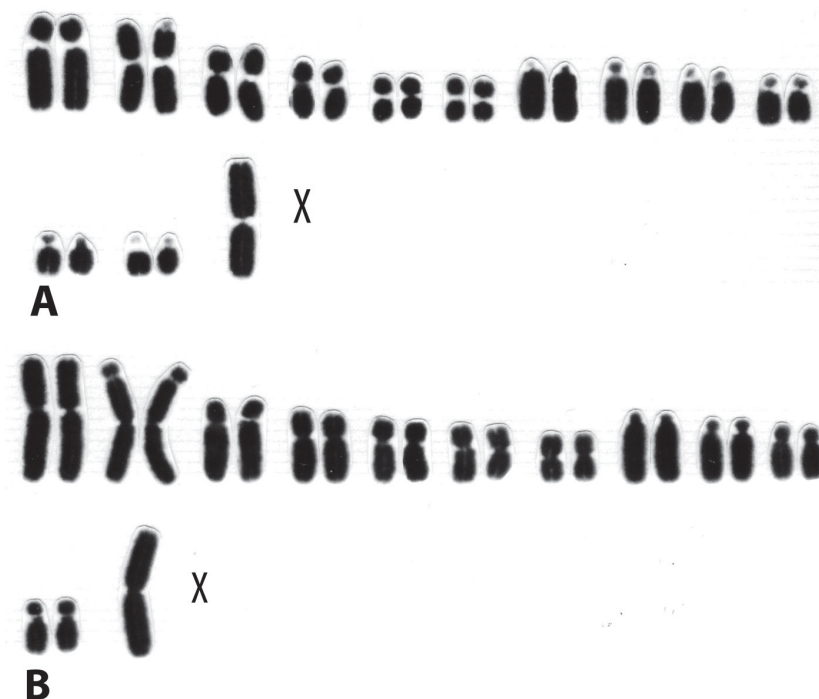

FIGURE S2-1: Karyotypes of North American Stenopelmatinae. **A:** Male from California, Inyo Co., $2n\male = 25$, showing 6 pairs each of metacentric and rod shaped autosomes and a metacentric X. **B:** Male from California, San Diego Co., $2n\male=23$, showing 7 pairs of metacentric and 4 pairs of rod shaped autosomes and a metacentric X.

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Stenopelmatidae

Siinae. (Clade A) Southern Africa and Southeast Asia. Karyotypes unknown but we predict a metacentric X and probably some metacentric autosomes.

Stenopelmatinae. (Clade B) North American *Stenopelmatus* species $2n\male$ vary from 19–27 (XO sex determination), with 23 and 25 most common (Fig. S2-1; John & Rentz, 1987; Weissman, 2001). Some autosomes and always the X chromosome are metacentric.

Anostostomatidae. (Clade C) *Cnemotettix* (this report, Fig. S2-2), California, 2 species, $2n\male = 25$ and 27, some autosomes and always the X chromosome are metacentric. *Glaphyrosoma* (this report, Fig. S2–3), Honduras, one species, $2n\male=28$ (XY sex determination) and Mexico, four species, $2n\male=29$ (XO sex determination), some autosomes and the X chromosome are metacentric. *Lezina concolor,* Israel. $2n\male=29$ (this report, Fig. S2–4). There are 4 pairs of metacentric and 10 pairs of telocentric autosomes with a metacentric X chromosome. Meiosis was common in the two adult males examined.
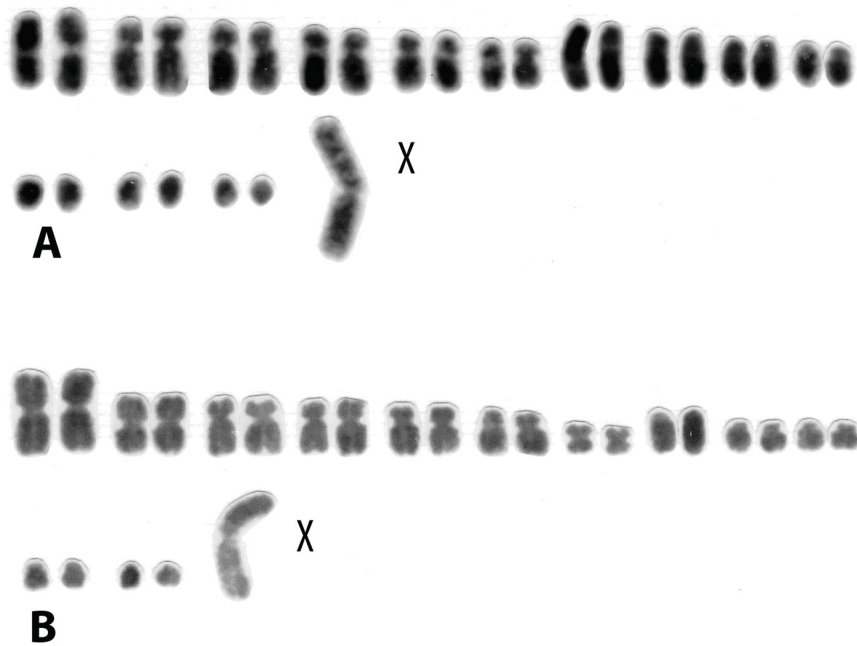
FIGURE S2-2: Karyotypes of *Cnemotettix*. **A:** Male from California, Monterey Co., $2n\male=27$ with 6 pairs of metacentric and 7 pairs of rod shaped autosomes and a metacentric X. **B:** Male from California, Santa Barbara Co. $2n\male=25$ with 7 pairs of metacentric and 5 pairs of rod shaped autosomes and a metacentric X.
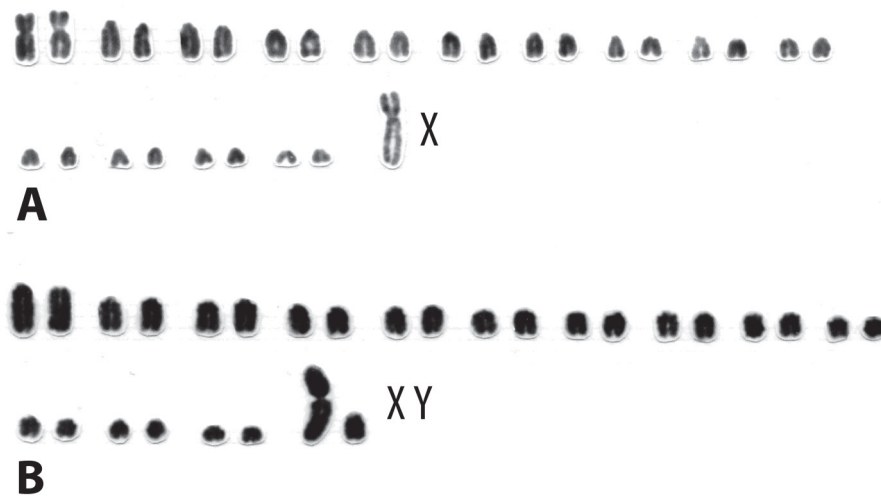
FIGURE S2-3: Karyotypes of *Glaphyrosoma* **A:** Male from Mexico, Nuevo Leon. $2n\male=29$ with 1 pair of metacentric and 13 pairs of rod shaped autosomes and a metacentric X. **B:** Male from Honduras, Cortes, $2n\male=28$ with 13 pairs of rod shaped autosomes and a metacentric X and rod shaped Y chromosome.

FIGURE S2–4. Karyotype of *Lezina.* There are 4 pairs of metacentric and 10 pairs of telocentric autosomes with a metacentric X chromosome.

Anostostomatidae. (Clade D) Australia, South Africa, New Zealand, Papua New Guinea. Australia, *Anostostoma* (*Australostoma*) *opacum* Brunner von Wattenwyl with 2n♂= 21 with metacentric autosomes and a metacentric X chromosome (John & Rentz, 1987). Brasil, *Lutosa*, 2n♂=15, some autosomes and the X chromosome metacentric (Piza, 1947). New Zealand, Morgan-Richards (pers. comm. to D.B.W., July, 2013) believes that *Motuweta isolata* Johns may have all 23 male chromosomes metacentric. *Hemideina* and Deinacrida, 19 species, 2n♂ varies from 11–29, some autosomes and always the X chromosome are metacentric or submetacentric (Morgan-Richards, 1997; Morgan-Richards & Gibbs, 2001; Morgan-Richards *et al.*, 2000; Morgan-Richards & Wallis, 2003; M. Morgan-Richards pers. comm. to D.B.W., July, 2013). Australia, *Cooloola ziljan*, 2n♂ = 21, some autosomes and the X chromosome are metacentric (John & Rentz, 1987).

References

Carter, N.P. (1994) Cytometry. *Communications in Clinical Cytometry*, 18, 2–10.
https://doi.org/10.1002/cyto.990180103

Dobigny, G., Ducroz, J.-F., Robinson, T.J. & Volobouev, V. (2004) Cytogenetics and cladistics. *Systematic Biology*, 53, 470–484.
https://doi.org/10.1080/10635150490445698

Hewitt, G.M. (1979) Orthoptera. Grasshoppers and crickets. *In:* John, B. (Ed.), *Animal Cytogenetics*. Gebrüder Borntraeger, Berlin, pp. 1–170.

Hubbell, T.H. & Norton, R.M. (1978) The systematics and the biology of the cave-crickets of the North American tribe Hadenoecinni (Orthoptera: Saltatoria: Rhaphidophoridae: Dolichopodinae). *Miscellaneous Publications Musuem of Zoology University of Michigan*, 156, 1–125.

John, B. (1981) Chromosome change and evolutionary change: a critique. *In:* Atchley, W.R. & Woodruff, D.S. (Eds.), *Evolution and Speciation. Essays in Honor of M.J.D. White*. Cambridge University Press, Cambridge, pp. 23–51.

John, B. & Rentz, D.C.F. (1987) The chromosomes of four endemic Australian fossorial orthopterans: a study in convergence and homology. *Bulletin Sugadaira Montane Research Center*, 8, 205–216.

Lewis, K.R. & John, B. (1963) *Chromosome Marker*. Churchill, London, X + 489 S.

McClung, C.E. & Asana, J.J. (1933) The chromosomes of *Schizodactylus monstrosus*. *Journal of Morphology*, 55, 185–191.
https://doi.org/10.1002/jmor.1050550111

Mesa, A. & Ferreira, A. (1984) A cytogenetic look at the Haglidae through study of the chromosomes of two of its four relict species: *Cyphoderris monstrosa* and *C. strepitans* (Orthoptera: Ensifera). *Occasional Papers of the Museum of Zoology University of Michigan*, 705, 1–11.

Mesa, A., Ferreira, A. & de Mesa, R.S. (1968) The karyotype of some Australian species of Macropathinae (Gryllacridoidea-Rhaphidophoridae). *Chromosoma (Berl.)*, 24, 456–466.
https://doi.org/10.1007/BF00285019

Morgan-Richards, M. (1997) Intraaspecific karyotype variation is not concordant with alloyme variation in the Auckland tree weta of New Zealand, *Hemideina thoracica* (Orthoptera: Stenopelmatidae). *Biological Journal of the Linnean Society*, 60, 423–442.

Morgan-Richards, M. & Gibbs, G.W. (2001) A phylogenetic analysis of New Zealand giant and tree weta (Orthoptera : Anostostomatidae : Deinacrida and Hemideina) using morphological and genetic characters. *Invertebrate Taxonomy*, 15, 1–12.
https://doi.org/10.1071/IT99022

Morgan-Richards, M., Trewick, S.A. & Wallis, G.P. (2000) Characterization of a hybrid zone between two chromosomal races of the weta *Hemideina thoracica* following a geologically recent volcanic eruption. *Heredity*, 85, 586–592.
https://doi.org/10.1046/j.1365-2540.2000.00796.x

Morgan-Richards, M. & Wallis, G.P. (2003) A comparison of five hybrid zones of the weta Hemideina thoracica (Orthoptera : Anostostomatidae): Degree of cytogenetic differentiation fails to predict zone width. *Evolution*, 57, 849–861.
https://doi.org/10.1111/j.0014-3820.2003.tb00296.x

Mugleston, J.D., Song, H. & Whiting, M.F. (2013) A century of paraphyly: a molecular phylogeny of katydids (Orthoptera: Tettigoniidae) supports multiple origins of leaf-like wings. *Molecular Phylogenetics and Evolution*, 69, 1120–1134. https://doi.org/10.1016/j.ympev.2013.07.014

Murphy, W.J., Pevzner, P.A. & O'Brien, S.J. (2004) Mammalian phylogenomics comes of age. *Trends in Genetics*, 20, 631–639. https://doi.org/10.1016/j.tig.2004.09.005

Otte, D. (1984) *The North American grasshoppers. Vol. II. Acrididae. Oedipodinae*. Harvard University Press, Cambridge, Massachusetts, 366 pp.

Piza, S. de Toledo, Jor. (1947) Short notice upon spermatogenesis in *Lutosa brasiliensis* Bruner (Tettigoniodea-Stenopelmatidae). *Anais da Escola Superior de Agricultura "Luiz de Queiroz"*, 4, 202–208.

Rentz, D.C.F. & John, B. (1990) Studies in Australian Gryllacrididae: taxonomy, biology, ecology and cytology. *Invertebrate Taxonomy*, 3, 1053–1210.
https://doi.org/10.1071/IT9891053

Strauss, J. & Lakes-Harlan, R. (2009) The evolutionary origin of auditory receptors in Tettigonioidea: the complex tibial organ of Schizodactylidae. *Naturwissenschaften*, 96, 143–146.
https://doi.org/10.1007/s00114-008-0450-4

Ueshima, N. & Rentz, D.C. (1979) Chromosome systems in the North American Decticinae with reference to Robertsonian changes (Orthoptera, Tettigoniidae). *Cytologia*, 44, 693–714.
https://doi.org/10.1508/cytologia.44.693

Warchalowska-Sliwa, E. (1998) Karyotype characteristics of katydid Orthopterans (Ensifera, Tettigoniidae), and remarks on their evolution at different taxonomic levels. *Folia Biologica*, 46, 143–176.

Weissman, D.B. (2001) North and Central America jerusalem crickets (Orthoptera: Stenopelmatidae): taxonomy, distribution, life cycle, ecology and related biolgy of the American species. *In:* Field, L.H. (Ed.), *The Biology of Wetas*, *King Crickets and Their Allies*. CABI Pub., New York, pp. 57–72.
https://doi.org/10.1079/9780851994086.0057

Weissman, D.B. & French, E. (1980) Autecology and population structure of *Trimerotropis occidentalis*, a grasshopper with a reproductive dormancy. *Acrida*, 9, 145–157.

Weissman, D.B. & Rentz, D.C.F. (1980) Cytological, morphological, and crepitational characteristics of the trimerotropine (*Aerochoreutes*, *Circotettix*, and *Trimerotropis*) grasshoppers (Orthoptera: Oedipodinae). *Transactions of the American Entomological Society*, 106, 253–272.

White, M.J.D. (1973) *Animal Cytology and Evolution*. Cambridge University Press, New York, 961 pp.

Wienberg, J. (2004) The evolution of eutherian chromosomes. *Current Opinion in Genetics & Development*, 14, 657–666.
https://doi.org/10.1016/j.gde.2004.10.001

SUPPLEMENT 3. Acoustic Communication Behaviors

We discuss groups in the order they appear in Fig. 2.

Schizodactylidae. Stridulatory apparatus present in both described genera (Mason, 1961; Strauss & Lakes-Harlan, 2010, p. 4574). The latter authors comment (p. 4578) that "…communication signals used by Schizodactylidae are not described." J. Strauss (pers. comm. to D.B.W., 2017) says that the stridulatory apparatus makes a very faint sound that is difficult to induce by disturbing the insect, and that they meant "not described" as to frequency content and spatial pattern. Since both genera are atympanate, the produced sound is probably defensive (J. Strauss, pers. comm. to D.B.W., 2017). Picker *et al.* (2004) note stridulation in South African male *Comicus.*

Rhaphidophoridae. Abdominal and hind leg drumming in males (Weissman, 2001), and tremulation (Stritih & Cokl, 2012) known.

Gryllotalpidae. Tegminal stridulation only known (Walker, 2017) in this worldwide group.

Grylloidea. Tremulation, drumming, and tegminal stridulation known (Walker & Masaki, 1989).

Prophalangopsidae. *Cyphoderris.* Tegminal stridulation only known (S. K. Sakaluk, pers. comm. to D.B.W., March, 2012).

Tettigoniidae. Several mechanisms known (Gwynne, 2001) including tegminal, femoro-abdominal, and coxae stridulation, plus abdominal and hind leg drumming.

STENOPELMATOIDEA

Gryllacrididae. Worldwide. Femoral-abdominal stridulation (Field & Bailey, 1997; Rentz & John, 1990; Rentz, 1997) and hind leg drumming in both sexes (Rentz, 1997; Field & Bailey, 1997) known. Abdominal drumming mentioned by Rentz (1997, p. 57) and Hale & Rentz (2001, p. 102) but no reference cited. D.C.F.Rentz (unpublished) notes that he has observed

abdominal drumming in several gryllacridids during courtship and mating. This is performed often simultaneously with femoro-abdominal stridulation and hind leg drumming. Often this is performed so quickly that it is difficult to observe and record, indicating that video analysis would be helpful.

Stenopelmatidae
Siinae. (Clade A) Southern Africa. Drumming apparently absent (Weissman & Bazelet, 2013); femoro-abdominal stridulation rare to common depending upon species (Weissman & Bazelet, 2013).

Stenopelmatinae. (Clade B) New World. Abdominal drumming known in males and females (Weissman, 2001); femoro-abdominal stridulation rare (Weissman, 2001).

Anostostomatidae. (Clade C) New World, North America. Hind leg drumming known in males of both *Cnemotettix* and *Glaphyrosoma* (Weissman, 2001). Stridulation of any kind unknown (D.B.W., unpubl). In contrast, the other New World anostostomatid sequenced by us, *Anabropsis*, in Clade D, apparently do not drum (D.B.W., unpub.), emphasizing the potential phylogenetic importance of this behavior. *Lezina.* No sound production mentioned by Popov (1984) but G. Wizen (pers. comm. to D.B.W., May, 2012) documents femoro-abdominal stridulation in *L. concolor* with investigations continuing.

Anostostomatidae. (Clade D) Old World. Femoro-abdominal stridulation (Monteith & Field, 2001; Field & Jarman, 2001) and abdominal drumming in both sexes (Chappell *et al.*, 2012; Field & Jarman, 2001; Gwynne, 2004) known. Mandibular stridulation also known in South African *Henicus* (Brettschneider *et al.*, 2007). Deinacridinae, New Zealand, femoro-abdominal stridulation (Field, 1993; Field, 2001; McVean & Field, 1996), tremulation (Field, 2001) and tergo-tergal stridulation known. *Cooloola,* Australia, no sounds produced (D.C.F.R., unpubl.).

References

Brettschneider, H., Chimimba, C.T., Scholtz, C.H. & Bateman, P.W. (2007) Review of southern African Anostostomatidae (Orthoptera: Ensifera), with a key to genera. *African Entomology,* 15, 103–119.
https://doi.org/10.4001/1021-3589-15.1.103
Chappell, E.M., Trewick, S.A. & Morgan-Richards, M. (2012) Shape and sound reveal genetic cohesion not speciation in the New Zealand orthopteran, *Hemiandrus pallitarsis*, despite high mitochondrial DNA divergence. *Biological Journal of the Linnean Society,* 105, 169–186.
https://doi.org/10.1111/j.1095-8312.2011.01777.x
Field, L.H. (1993) Observations on stridulation, agonistic, and mating behavior of *Hemideina ricta* (Stenopelmatidae: Orthoptera), the rare Banks Peninsula weta. *New Zealand Entomologist,* 16, 68–74.
https://doi.org/10.1080/00779962.1993.9722653
Field, L.H. (2001) Stridulatory mechanisms and associated behaviour in New Zealand wetas. *In*: Field, L.H. (Ed.), *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New York, New York, pp. 271–295.
https://doi.org/10.1079/9780851994086.0271
Field, L.H. & Bailey, W.J. (1997) Sound production in primitive Orthoptera from Western Australia: Sounds used in defence and social communication in *Ametrus* sp. and *Hadrogryllacris* sp. (Gryllacrididae: Orthoptera). *Journal of Natural History,* 31, 1127–1141.
https://doi.org/10.1080/00222939700770591
Field, L.H. & Jarman, T.H., 2001. Mating behaviour. *In*: Field, L.H. (Ed.), *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New York, New York, pp. 317–332.
https://doi.org/10.1079/9780851994086.0317
Gwynne, D.T. (2001) *Katydids and Bush-crickets. Reproductive Behaviour and Evolution of the Tettigoniidae.* Cornell University Press, Ithaca, New York, 317 pp.
Gwynne, D.T. (2004) Reproductive behavior of ground weta (Orthoptera : Anostostomatidae): Drumming behavior, nuptial feeding, post-copulatory guarding and maternal care. *Journal of the Kansas Entomological Society,* 77, 414–428.
https://doi.org/10.2317/E-34.1
Hale, R.J. & Rentz, D.C.F. (2001) The Gryllacrididae: an overview of the world fauna with emphasis on Australian examples. *In*: Field, L.H. (Ed.), *The Biology of Wetas, King Crickets and Their Allies.* CAB International, New York, New York, pp. 95–110.
https://doi.org/10.1079/9780851994086.0095
Mason, J.B. (1961) Stridulatory mechanism in the family Schizodactylidae. *EOS,* 37, 505–508.
McVean, A. & Field, L.H. (1996) Communication by substratum vibration in the New Zealand tree weta, *Hemideina femorata* (Stenopelmatidae: Orthoptera). *Journal of Zoology,* 239, 101–122.
https://doi.org/10.1111/j.1469-7998.1996.tb05440.x
Monteith, G.B. & Field, L.H. (2001) Australian king crickets: distribution, habitats and biology (Orthoptera: Anostostomatidae). *In*: Field, L.H. (Ed.), *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New

York, New York, pp. 79–94.
https://doi.org/10.1079/9780851994086.0079

Picker, M.D., Griffiths, C. & Weaving, A. (2004) *Field Guide to the Insects of South Africa*. South Africa Struik Publishers, Cape Town.

Popov, G.B. (1984) Insects of Saudi Arabia. (Orthoptera: Fam. Stenopelmatidae and Gryllacrididae). *In*: Wittmer, W. & Buttiker, W. (Eds.), *Fauna of Saudi Arabia.* Ciba-Geigy Ltd., Basle, pp. 175-202.

Rentz, D.C.F. (1997) The world's most unusual gryllacridid (Orthoptera: Gryllacrididae). *Journal of Orthoptera Research,* 6, 57–68.
https://doi.org/10.2307/3503536

Rentz, D.C.F. & John, B. (1990) Studies in Australian Gryllacrididae: taxonomy, biology, ecology and cytology. *Invertebrate Taxonomy,* 3, 1053–1210.
https://doi.org/10.1071/IT9891053

Strauss, J. & Lakes-Harlan, R. (2010) Neuroanatomy of the complex tibial organ in the splay-footed cricket *Comicus calcaris* Irish 1986 (Orthoptera: Ensifera: Schizodactylidae). *Journal of Comparative Neurology,* 518, 4567–4580.
https://doi.org/10.1002/cne.22478

Stritih, N. & Čokl, A. (2012) Mating behaviour and vibratory signalling in non-hearing cave crickets reflect primitive communication of Ensifera. *PLoS One,* 7(10): e47646. doi:10.1371/journal.pone.0047646.
https://doi.org/10.1371/journal.pone.0047646

Walker, T.J. (2017) *Singing Insects of North America*. Available from: http://entnemdept.ufl.edu/walker/buzz/s341a.htm

Walker, T.J. & Masaki, S. (1989) Natural History. *In*: Huber, F., Moore, T.E., Loher, W. (Eds). *Cricket Behavior and Neurobiology*. Cornell University Press, Ithaca, New York, pp. 1–42.

Weissman, D.B. (2001) Communication and reproductive behaviour in North American Jerusalem crickets (*Stenopelmatus*) (Orthoptera: Stenopelmatidae). *In*: Field, L.H. (Ed.), *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New York, New York, pp. 351–375.
https://doi.org/10.1079/9780851994086.0351

Weissman, D.B. & Bazelet, C.S. (2013) Notes on southern Africa Jerusalem crickets (Orthoptera: Stenopelmatidae: *Sia*). *Zootaxa,* 3616, 49–60.
https://doi.org/10.11646/zootaxa.3616.1.4