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Subfamilies Acridinae, Gomphocerinae and Oedipodinae are "fuzzy sets": a proposal for a common African origin

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Abstract

We propose that subfamilies Acridinae (including Truxalinae), Gomphocerinae and Oedipodinae are not monophyletic, and that, as a collective, originated in Africa some time before 100 mya.

Our conclusions are based on a phylogenetic analysis of portions of 5 mitochondrial genes, totalling up to about 2.7 kilobase pairs, in 117 species collected in the Americas, Eurasia, Africa and Australia. Sequences were analyzed by weighted and unweighted maximum parsimony, maximum likelihood and Bayesian methods. *Pyrgomorpha conica* served as the outgroup. Biogeographic origins and patterns were inferred by applying the programs "DIVA" and "r8s", for spatial and temporal analyses, respectively.

Maximum sorting of taxa using parsimony was achieved by assigning differential weights to the three codon positions. Resolution was, however, generally poor. Bayesian methods, by contrast, yielded a topology which was virtually identical to the maximum likelihood tree and, for the most part, fully resolved and interpretable. We provide arguments in support of favoring the use of the Bayesian tree to infer relationships and biogeographic origins.

Neither subfamily, as defined in the current on-line Orthoptera Species File 2, proved to be monophyletic. Instead, taxa assorted themselves into 3 broad categories: 1) Gomphocerinae, plus a small subset of acridines; 2) a sister group consisting of Oedipodinae, plus another small subset of acridines; and basal and paraphyletic to this pair, 3) the remaining taxa, all African and primarily members of the Acridinae. Very few tribes within these subfamilies proved to be monophyletic.

This phylogenetic pattern is reflected biogeographically and points to a common African origin for the subfamilies. The following migrations, initially those of (most likely) proto-acridines, are further suggested by the data: 1) movement from Africa to South America establishing genera of that continent's Gomphocerinae (*e.g.*, *Jagomphocerus*) and Acridinae (*e.g.*, *Metaleptea*), followed by incursions into North America, leading to species such as *Amblytropidia mysteca*; 2) a somewhat circuitous sequence of events involving a reverse migration from South America to Africa (establishing genera such as *Thyridota*) with ensuing dispersals to Eurasia (forming genera such as *Myrmeleotettix*) and to North America (leading to, for example, *Brunneria* and the bulk of that continent's Gomphocerinae); 3) almost simultaneous with the first event, migration of other early acridines from Africa to Eurasia, establishing the latter continent's Oedipodinae (*e.g.*, *Angaracris*). Subsequent dispersals to North America and the South Pacific led to genera such as *Camnula* and *Austroicetes*, respectively.

Keywords

Acrididae, Gomphocerinae, Oedipodinae, phylogeny, mitochondrial DNA, biogeography

Introduction

Previously, we described evolutionary and biogeographic relationships among selected genera within the subfamilies Gomphocerinae (Contreras *et al.* 2006) and Oedipodinae (Fries *et al.* 2007). Phylogenetic analyses of mitochondrial DNA sequences led us to conclude, provisionally, that each subfamily was monophyletic and that most tribes, as listed in the Orthoptera Species File 2, or OSF2 (Eades *et al.* 2011), were polyphyletic. Lacking in those studies was a sufficient sampling of the Acridinae, a subfamily possessing several morphological features that overlap those of the other two subfamilies. The inclusion of this group could have further supported, or challenged, our claims of subfamilial monophyly.

Currently, the OSF2 recognizes Acridinae, Gomphocerinae and Oedipodinae as legitimate subfamilies. Truxalinae, formerly considered a *bona fide* subfamily, has been subsumed within the Acridinae (Jago 1996, OSF2). Not that long ago, different subsets of these four groups were collapsed into single subfamilies. To cite a few examples: both gomphocerines and acridines — the so-called "slantheads" — formed the Acridinae (Bei-Bienko & Mishchenko 1951, Brooks 1958, Rehn 1958); acridines and oedipodines were combined within the Acridinae, with gomphocerines and truxalines placed within the Truxalinae (Dirsh 1965). Jago (1971, 1996a) provided a good account of the early history of the different taxonomic systems. More recently, Rentz *et al.* (2004), following Key (1993) and to some extent Rehn above, took a different view, maintaining that the amount of anatomical overlap between Acridinae and Oedipodinae (both *sensu* OSF2) is simply too great to accord them subfamily status; instead, each was downgraded to tribe within a larger, redefined, Acridinae. Otte (1981, 1984) did recognize the existence of certain annectant genera, such as *Stethophyma*, *Melanotettix* and *Machaerocera*. Nonetheless, each was assigned to a subfamily in his books; these placements have since been incorporated into the OSF2. Otte (1981) also regarded Acridinae as polyphyletic, owing to the ease with which stridulatory pegs, a trait commonly used to separate Gomphocerinae (pegs present) from Acridinae (pegs missing), could be lost (see also Jago 1996a). The borders separating these major groups still remain fuzzy and the question of their integrity and of their inter-relationships is far from resolved.

Our earlier studies also made inferences about the biogeographic origins of Gomphocerinae and Oedipodinae, primarily of their northern taxa. In both cases we proposed that North American genera had arisen from ancestors migrating from Eurasia. For the Oedipodinae (Fries *et al.* 2007), there was also some indication of more recent migrations from Eurasia to Australia and Africa. Vickery (1987, 1989) had made similar claims about the Eurasian origin of the Nearctic gomphocerines and oedipodines, and in the case of the former, added that some genera also had Neotropical origins. Still earlier, and contrasting with the last view, Carbonell (1977) proposed that Neotropical Acridinae, Gomphocerinae and Oedipodinae (among other subfamilies) were recently derived from incursives from the Old World via North America.

Gomphocerinae, Oedipodinae and Acridinae (including the Truxalinae), are clearly related (Rowell & Flook 1998). Apart from

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the aforementioned writings of Vickery, Rehn and Carbonell, very little has been written about the biogeographic origins of these subfamilies, individually or as a group — or indeed, of the family Acrididae in general. For the latter, Amédégnato (1993) did speculate that possibly the family radiated from the "Old World". Lovejoy *et al.* (2006) implied a time frame for the family's diversification in their statement: "…most subfamilies of the acridid grasshoppers have either exclusively Eastern or Western Hemisphere distributions … suggesting that much of the diversification of Acrididae occurred after Africa and South America were separated". That is, acridid diversification took place around 100 - 80 mya. Rowell and Flook (2004) made similar statements about a rapid proliferation of taxa within the Acridoidea during this time. Fossils potentially hold a clue, but here the record is rather exiguous. Reports on the earliest appearance of reliable fossils representing Acrididae range somewhat wildly from about 150 mya (Labandeira 1994) to about 55 mya (Zeuner 1939) to 24 mya (Carpenter 1992).

Molecular phylogenetic methods, however, have provided some independent insights into the date and order of appearance of taxa. In one such study involving one or a few representatives from each of these four subfamilies among a wide collection of Orthoptera, Rowell and Flook (1998) concluded that Acridinae (including Truxalinae) and Gomphocerinae are more recently evolved than Oedipodinae (see also Flook & Rowell 1997, Rowell & Flook 2004). Finally, we should mention, as a point of historical interest, Jago's (1979) novel approach to the subject of branching order. Using present day distributions of subfamily members and plate tectonic area measurements, he proffered this order of first appearance: Gomphocerinae (180 mya), Acridinae (120 mya) and then Oedipodinae (80 mya). As in the Flook and Rowell studies, continental origins are not mentioned.

The current study expands on our earlier research by including considerably more genera from the southern continents, particularly grasshoppers belonging to the Acridinae (*sensu* OSF2). Our objectives are to revisit the hypotheses of subfamily monophyly and, by including material from South America, Africa and Australia, to shed some light on the biogeographical origins of the entire group and its members. Of possible interest to orthopterists is the independent testing of relationships among genera, previously unexamined by molecular methods.

Materials and Methods

Species, along with sources and their biogeographic ranges, are listed in Table 1. Included, mostly from the Southern Hemisphere, are 22 species of Acridinae and 37 species of Gomphocerinae. For a few genera such as *Acrida*, *Aeropedellus*, *Amblytropidia* and *Gastrimargus*, two or more species were sampled, some from different continents. For phylogenetic analyses, *Pyrgomorpha conica* was employed as the outgroup.

Methodologies pertaining to DNA extraction, purification, amplification and sequencing are described elsewhere (Litzenberger & Chapco 2001a, 2001b; Contreras & Chapco 2006). Analyses were based on sequencing portions of mitochondrial genes encoding, cytochrome oxidase subunit I (CO1) and II (C02), cytochrome b (cytb), NADH dehydrogenase subunit V (ND5) and 16S ribosomal RNA (16S). For these genes, the maximum numbers of base pairs sequenced were 609, 378, 618, 642 and 502 respectively. These genes were used because in our previous studies, their analysis yielded topologies with reasonably high resolutions.

Sequences were aligned by visual inspection, imported into MacClade (Maddison & Maddison 2004) and analyzed using the software packages PAUP* (version 4.0b8 – Swofford 2003) and MrBayes (MB) (Version 3.0b4 — Huelsenbeck & Ronquist 2001). Both standard maximum parsimony (MP) and weighted maximum parsimony (wMP), following Farris' (1969) iterative weighting scheme, were used. Searches were repeated using all substitutions at the first 2 codon positions but only tranversional substitutions at the third position (methods referred to as MP123TV and wMP123TV). For the method of maximum likelihood, implemented through PAUP*, inputted parameter estimates consisted of output values obtained from the program Modeltest (Version 3.6 — Posada & Crandall 1998). [Modeltest identified the GTR + G +I model as the "best".] Bootstrapping using ML was not pursued owing to the inordinately long run times required. Levels of support for parsimony-derived relationships were estimated through 1000 bootstrap replicates. Bayesian analysis also used the GTR + G + I model and provided measures of nodal support in the form of posterior probabilities (% PP). For the MB analysis, 8 Monte Carlo Markov chains, one cold and 7 heated, were run simultaneously for 15 million generations and sampled every 500 generations, yielding 30,000 trees.

For all analyses, the 5 sequences were treated as a concatenated unit, a procedure that, as in all our previous studies (Chapco *et al.* 2001; Litzenberger & Chapco 2001a, 2001b), always yielded trees with greater resolution and support when compared to those based on single genes. Before proceeding with the analyses, sequences were evaluated to determine if they were in fact nuclear sequences of mitochondrial origin or "Numpts" (Bensasson *et al.* 2000). All sequences analyzed in this paper met the criteria set out by Zhang and Hewitt (1996) for excluding that possibility.

In order to place biogeographic events within an interpretably geological context, it was essential to estimate the times of divergence for various nodes. We initially applied the maximum likelihood ratio test (Page & Holmes 1998) to determine whether sequences evolved in a clock-like manner. Because sequences did not in fact conform to a model of rate constancy, we estimated divergence times by employing a semiparametric penalized likelihood (PL) method, which can accommodate rates that vary over lineages (Sanderson 2002). To this end, the program r8s, version 1.70 (Sanderson 2004) was used. As recommended by Sanderson, the TN (Truncated Newton) algorithm was applied in conjunction with PL. A cross-validation analysis was first performed to determine the most likely smoothing parameter (a measure of the relative contributions of parametric and nonparametric models that underlie PL), a procedure necessary for estimating optimal divergence times. Zero-length branches were collapsed. A more extensive description of the method and theory is given by Sanderson (2002). The program yields estimates of absolute times of divergence if at least one known divergence date is provided as input. In this case, and as had been done previously (Fries *et al.* 2007), we relied on Gaunt and Miles' (2002) estimate of 100 mya for the Gomphocerinae-Oedipodinae split (this value in turn was based on dated ancient cockroach fossils). This calibration point was then employed to estimate times of divergence for various nodes of interest — but with some degree of caution because, strictly speaking, the two subfamilies (*sensu* OSF2) proved not to be monophyletic, as will be demonstrated below. In addition, derived dates of events should only be viewed as very approximate, given the equally rough underpinnings behind the calibration.

Ancestral geographic areas were preliminarily reconstructed with the assistance of the program "DIVA" (Version 1.1) (Ronquist 1996, 1997). Each genus was coded with a string of 1s and 0s according to its recorded presence or absence in Africa, Australia, Eurasia, North America, South America or Oceana. For genera involving more than one species, we applied the 0/1 coding to each such species.

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For "maxareas", a parameter that limits the range of ancestral distributions, 2 sets of values were employed: 4 (the default — which favors vicariance) and 2 (which favors dispersal). While the results from DIVA proved helpful as a guide, further interpretation was performed in conjunction with the temporal analyses. For instance, for the node connecting A to F (see Results and Fig. 1), DIVA assigned to that node, among other possible land mass areas, "North America – South America – Africa", clearly not a possibility given the 99 mya suggested for that node by the temporal analysis.

Results

Among the different parsimony procedures used, wMP123TV yielded a tree with the greatest amount of resolution. Nevertheless, bootstrap support was generally poor, particularly at deeper levels. For the Bayesian procedure, the first 25,000 trees (burn-in value) were discarded, resulting in the 5000 trees that were used to obtain the consensus tree; this is depicted as chronograms in Figures 1 (a summary tree) and 2 (parts thereof). By comparison with parsimony, Bayesian methods yielded a highly resolved tree, with most nodes having sizeable PP values. Where there was good bootstrap support, PP values were also high. Relationships uncovered by ML were very similar to those in the MB topology.

To facilitate discussion, clusters of taxa are labelled A through N (Figs 1, 2). Overall, genera fall into three broad categories. The first group, spanning clades A to F, mostly comprises members of the Gomphocerinae; the single exception, clade E, consists of a *mélange* of acridines and gomphocerines. Support for clades A to F is somewhat weak (PP = 45 %) as is support for A to E (PP = 38%). For the inner subgroup A to D, however, support is very strong (PP = 88%). The second group (PP = 86%) spans clades G to M (plus *Duroniella*) and mostly comprises genera of Oedipodinae along with 2 genera of Acridinae (*Caledia* and *Froggattina*) and *Melanotettix*, a lone member of the Gomphocerinae. These two large clusters are labeled Gomphocerinae* and Oedipodinae*, respectively, and together are supported with a PP value of 99%. Basal and paraphyletic to the 2 groups is a third assemblage, labeled Acridinae*, which includes *Orthochtha*, clade N and a succession of taxa. Collectively, they form a set of acridine genera and one gomphocerine, *Pnorisa*. All are African, the significance of which will be discussed later.

Discussion

Choice of topology.—It is generally acknowledged that bootstrap and Bayesian support values are respectively conservative and liberal in their estimates of nodal confidence, and this is reflected in the present study with the Bayesian tree showing considerably greater resolution than the parsimony tree. Where parsimony does reveal good sorting of taxa, there is generally no disagreement with the Bayesian topology. The matter as to which approach is more accurate, however, is somewhat equivocal, given the opposite conclusions derived from various simulation studies (Suzuki *et al.* 2002, Wilcox *et al.* 2002, Alfaro *et al.* 2003, Simmons *et al.* 2004, Kelly 2005). As will be seen later, the Bayesian approach does yield numerous clades that "make sense" in terms of comprising large clusters of taxa from the same subfamily and/or continent. That is, recovered groupings are interpretable, as opposed to consisting of a gallimaufry of genera with no meaningful connections.

But this is not the only reason for favoring the Bayesian approach and downplaying the parsimony tree. There are, in fact, a few legitimate reasons for parsimony's poor resolution. Fuller *et al.* (2005) have pointed out that lower bootstrap support may be the result of comparatively higher AT content typically found in mitochondrial DNA, leading to a reduction in the number of informative sites in parsimony analysis. In the current study, the average AT was indeed relatively high at 70.3%. Other factors, pointed out by Flook and Rowell (1997), pertain to data which consist of a large number of taxa and involve sequences that exhibit significant departures from rate homogeneity. Both situations can lead to high levels of homogeneity and poor bootstrap support, as is the case here.

For our best parsimony tree (wMP123TV), the consistency index was in fact quite low, equaling 27.9%. The number of taxa in this study is fairly small, at least relative to the numbers in our previous studies and for which bootstrap support and resolution were respectably high. Furthermore, our data depart significantly from the molecular clock hypothesis. By contrast, the Bayesian method does use all the data and is able to accommodate rate heterogeneity with a proper choice of model. [As an added note, we should point out that a certain measure of confidence in the tree's robustness is provided by considering a study made by Yang and Rannala (2005), who showed that Bayesian phylogenies may be sensitive to choice of the prior probability distribution for branch length. Accordingly, we re-analyzed our data using different branch length priors and discovered that the resultant topologies were virtually the same as the one presented here.] Admittedly, a better resolved parsimony tree would have been desirable, especially one that turned out to be concordant with the Bayesian tree, if for no other reason than to provide greater overall confidence in the statements that follow. However, this not being the case, we would suggest that the Bayesian tree as it stands serve as a working hypothesis for further study.

Subfamily monophyly.—On the surface, it would appear that Gomphocerinae* is not monophyletic in terms of representing an uninterrupted subset of gomphocerine grasshoppers. One could regard the acridines within clade E as "peg-less gomphocerines" – a possibility, given Otte's (1981) statement concerning the relative ease with which stridulatory pegs can be lost over evolutionary time. Moreover, it should be noted that other genera in clade E, unequivocally classified as Gomphocerinae, do have elements (some populations within species, some species, one or both sexes) that also lack pegs (Jago 1971, Otte 1981). A case could therefore be made for regarding Gomphocerinae* as a monophyletic subset of gomphocerine grasshoppers, but not one centred around the "peg-trait". Nevertheless, the monophyletic status of the subfamily as a whole is still questionable because 2 other gomphocerines occur outside A to F: *Melanotettix* (part of clade L) and *Pnorisa* (part of clade N).

Similar reservations about the monophyly of Oedipodinae* (G – M plus *Duroniella*) can be expressed, given the presence of acridines within clades J, K and M and of *Melanotettix* within L. Interestingly, Oedipodinae* would appear to fit Rentz *et al.*'s (2004) broader view of Acridinae. Regarding their definition of tribes Acridini and Oedipodini, however, our analysis shows that neither is a unified group. As for the gomphocerine *Melanotettix*, it too could be considered part of Acridinae (*sensu* OSF2). The genus does lack stridulatory pegs, typical of the latter. It is noteworthy to mention that Otte (1981), having previously expressed some ambivalence about the genus' subfamily affiliation, "tentatively" (author's qualification) placed it within the Gomphocerinae. *Melanotettix* is part of a clade that also includes *Machaerocera*, another "bridge-genus" between Acridinae and Oedipodinae (Otte 1984).

There still remain the genera at the base of the entire phylogeny, clade N plus *Holopercna* to *Sherifuria*. All, except *Pnorisa*, are acridines (*sensu* OSF2) and all are African.

In light of these collective findings, we propose the following:

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Table 1. Species analyzed, locations and GenBank Accession numbers of mtDNA sequences.

Subfamily/Tribe†	Species	Source	Accession Nos CO1, CO2, cytb, nd5, 16S
Oedipodinae			
/Acrotylini	*Acrotylus insubricus*	Malatya, Turkey[CD]	EF151836, EF151816, EF151870, EF151904, JF932395
/Aiolopini	*Aiolopus strepens*	Sierra Nevada, Spain[CDEF]	EF151841, EF151821, EF151875, EF151907, JF932400
	Duroniella fracta	Malatya, Turkey[CD]	DQ230738, DQ230807, DQ230827, DQ230774, --
	Heteropternis couloniana	Mt Nimba, Guinea[D]	EF151858, EF151830, EF151892, EF151920, JF932431
	Heteropternis obscurella	Newcastle, Australia[F]	JN167816, --, JN167889, JN016776, JF932432
	Paracinema tricolor	‡loc?, South Africa[CD]	JN167829, JN002142, --, JN016786, JF932444
/Arphiini	*Arphia conspersa*	Jameson, SK, Can[A]	EF151839, EF151819, EF151873, --, U18065
/Bryodemini	*Angaracris barabensis*	Gansu Prov., China[C]	EF151856,--, EF151890, --, --
	Bryodema luctuosum	Gansu Prov., China[C]	EF151854, EF151829, EF151888, EF151917, JF932410
	Circotettix carlinianus	Condie, SK, Can[A]	EF151845, --, EF151879, EF151909, U18068
/Chortophagini	*Chorthophaga viridifasciata*	Jameson, SK, Can[A]	EF151864, --, EF151899, EF151924, JF932415
	Encoptolophus costalis	Regina, SK, Can[A]	EF151850, EF151827, EF151884, EF151913, JF932419
/Hippiscini	*Camnula pellucida*	Bummer, SK, Can[A]	JN167804, --, JN167870, JN016767, JF932411
	Pardalophora apiculata	Jameson, SK, Can[A]	--, --, JN167905, JN016789, JF932446
/Locustini	*Gastrimargus africanus*	Niamey, Niger[DE]	JN167812, EF151831, EF151893, --, JF932425
	Gastrimargus determinatus	Mt Nimba, Guinea[D]	JN167813, JN002130, JN167883, --, JF932426
	Gastrimargus musicus	Newcastle, Australia[F]	JN167814, JN002131, JN167884, JN016774, --
	Locusta migratoria	Genbank[CDEF]	X80245
	Oedaleus decorus	Massif Central, France[CDEF]	EF151834, EF151814, EF151868, EF151903, --
/Macherocerini	*Machaerocera mexicana*	Oaxaca, Mexico[A]	EF151861, --, EF151896, EF151923, JF932435
/Oedipodini	*Celes variabilis*	Massif Central, France[C]	EF151855, JN002120, EF151889, EF151918, --
	Oedipoda miniata	Erzingan, Turkey[C]	EF151840, EF151820, EF151874, EF151906, JF934441
/Parapleurini	*Stethophyma gracile*	Last Mountain, SK, Can[A]	DQ230737, DQ230806, DQ230826, DQ230773, --
	Stethophyma grossum	Massif Central, France[C]	DQ230735, DQ230804.-- , DQ230771, JF932460
/Psinidiini	*Trachyrhachys kiowa*	Condie, SK, Can[A]	EF151846, --, EF151880, EF151910, JF932461
/Sphingonotini	*Dissosteira carolina*	Bimidji, WI, USA	EF151851, EF151828, EF151885, EF151914, JF932417
	Spharagemon campestris	Condie, SK, Can[A]	EF151838, EF151818, EF151872, --, U18070
	Spharagemon collare	Jameson, SK, Can[A]	EF151852, --, EF151886, EF151915, U18071
	Sphingonotus caerulans	Sierra Nevada, Spain[BCDEF]	EF151844, EF151824, EF151878, EF151908, --
	Sphingonotus pachecoi	El Llano, Canary Is.[CD]	EF151857, --, EF151891, EF151919, JF932463
	Trimerotropis pallidipennis	Uspallata, Argentina[AB]	EF151863, --, EF151898, --, --

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Table 1. Continued.

Subfamily/Tribe†	Species	Source	Accession Nos CO1, CO2, cytb, nd5, 16S
	Trimerotropis pistrinaria	Findlater, SK, Can[A]	EF151848, EF151825, EF151882, EF151911, U18069
/Unassigned	*Austroicetes sp.*	Canberra, Australia[F]	EF185880, --, EF185881, --, JF932406
	Chortoicetes terminifera	Merriwah, Australia[F]	EF185877, EF185876, EF185878, EF185879, --
	Morphacris fasciata	Niamey, Niger[CDE]	JN167821, JN002136, JN167894, --, JF932437
Gomphocerinae			
/Acrolophitini	*Acrolophitus hirtipes*	Findlater, SK, Can[A]	JN167787, --, JN167852, JN016751, --
	Bootettix argentatus	Las Tablas, Mexico[A]	JN167802, JN002117, JN167866, JN016765, JF932408
/Amblytropidiini	*Amblytropidia australis*	Cerro Azul, Argentina[B]	JN167794, JN002111, JN167859, JN016757, --
	Amblytropidia mysteca	loc?, FL, USA[B]	JN167795, --,JN167860, JN016758, JF932401
	Boopedon nubilum	Newcastle, WY, USA	JN167801, JN002116, --, JN016764, JF932407
	Sinipta dalmani	Benito Juarez, Argentina[B]	JN167842, --, JN167916, JN016796, --
	Syrbula admirablis	loc?, FL, US[AB]	JN167846, JN002157, JN167920, JN016800, --
/Arcypterini	*Arcyptera fusca*	Massif Central, France[C]	JN167800, --, JN167864, JN016763, JF932404
	Ptygonotus gansuensis	Gansu Prov, China[C]	DQ230736, DQ230805, -- , DQ230772, --
	Ramburiella turcomana	Mulatya, Turkey[CD]	DQ230710, DQ230780, JN167912, DQ230744, JF932453
	Rhaphotittha levis	loc?, South Africa[CDE]	JN167835, JN002147, JN167908, --, JF932449
/Aulocarini	*Ageneotettix deorum*	Torrington, WY, USA	DQ230718, DQ230789, --, DQ230753, JF932399
	Aulocara elliotti	Torrington, WY, USA	DQ230719, JN002115, JN167865, DQ230754, JF932405
	Psoloessa delicatula	Last Mnt, SK, Can[A]	JN167838, JN002150, JN167911, JN016793, JF932452
/Chorthipini	*Chorthippus curtipennis*	Pinawa, MB, Can[A]	DQ230709, DQ230779, JN191382, DQ230743, JF932414
	Chorthippus parallelus	Budapest, Hungary[C]	DQ230723, DQ230793, JN167873,DQ230758, --
	Euchorthippus pulvinatus	Sierra Nevada, Spain[C]	DQ230711, DQ230781, JN167879, DQ230745, JF932421
	Glyptobothrus binotatus	Sierra Nevada, Spain[C]	DQ230724, DQ230794, JN167885, DQ230759, JF932427
	Glyptobothrus jacobsi	Sierra Nevada, Spain[C]	DQ230725, DQ230795, JN167886, DQ230760, JF932428
/Chrysochraontini	*Chloealtis abdominalis*	Jameson, SK, Can[A]	JN167823, DQ230787, DQ230817, DQ230751, --
	Chloealtis conspersa	Dilke, SK, Can[A]	JN191385, JN002121, JN167872, JN016768, JF932413
	Chrysochraon dispar	Massif Central, France[AC]	DQ230730, DQ230800, JN191383, DQ230766, --
	Euthystira brachyptera	Budapest, Hungary[C]	DQ230726, DQ230796, JN167880 , DQ230761, JF932422
/Compsacrini	*Staurorhectus longicornus*	La Pampa, Argentina[B]	JN167843, --, JN167917, JN016797, --
/Dnopherulaini	*Amesotropis valga*	06" 13′N, 05" 02′W, Ivory Coast[D]	JN167796, JN002112, JN167861, JN016759, JF932402
/Dociostaurini	*Dociostaurus jagoi*	Sierra Nevada, Spain[CDE]	DQ230734, JN002125, JN167876, DQ230770, JF932418
/Eritettigini	*Amphitornus coloradus*	Dilke, SK, Can[A]	JN167798, JN002114, * (in appendix), JN016761, JF932403

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Table 1. Continued.

Subfamily/Tribe†	Species	Source	Accession Nos CO1, CO2, cytb, nd5, 16S
	Eritettix simplex	Cypress Hills, SK, Can[A]	JN167809, JN002127, JN167878, JN016772, JF932420
	Opeia obscura	Last Mountain, SK, Can[A]	JN167827, JN002140, JN167900, JN016783, JF932443
/Gomphocerini	*Aeropedellus arcticus*	McKinley Park, AK, US[A]	JN167792, JN002109, -- , JN016754, JF932396
	Aeropedellus clavatus	Dilke, SK, Can[A]	DQ230708, DQ230777, EF565468, DQ230741, JF932397
	Aeropedellus reuteri	Khakasia, Russia[C]	JN167793, JN002110, JN167858, JN016755, JF932398
	Aeropedellus variegatus	Montpellier, France[C]	DQ230712, DQ230782, DQ230812, JN016756, --
	Brunneria brunnea	Dilke, SK, Can[A]	DQ230707, DQ230776, JN167867, DQ230740, JF932409
	Bruneria yukonensis	Kluane Nat'l Park, YT, Can[A]	JN167803, JN002118, JN167868, JN016766, --
	Gomphocerippus rufus	Massif Vercors, France[C]	DQ230733, DQ230803, JN167887, DQ230769, JF932429
	Myrmeleotettix maculatus	Bledwowska Desert, Poland[C]	JN167822, JN002137, JN167895, JN016781, JF932438
	Phlibostroma quadrimaculatum	Dilke, SK, Can[A]	JN167834, DQ230778, DQ230808, DQ230742, JF932448
/Melanotettigini	*Melanotettix dibelonius*	Guerrero, Mexico[AB]	JN167818, JN002134, JN167891, JN016778, --
/Mirmiriini	*Achurum carinatum*	loc?, FL, US[A]	DQ230717, DQ230788, JN167853, DQ230752, --
	Achurum minimipenne	Tamaulipas, Mexico[A]	JN167788, JN002105, JN167854, --, JF932394
	Mermiria bivittata	Goshen County, WY, US[A]	JN167819, JN002135, JN167892, JN016779, JF932436
/Ochrilidini	*Ochrilidia harterti*	Niamey, Niger[CD]	JN167824, --, JN167896, --, JF932439
	Ochrilidia tibialis	loc? Chad[CD]	JN167825, --, JN167897, --, --
/Orphulelini	*Dichromorpha viridis*	loc? FL, US[AB]	JN167807, JN002124, JN167875, JN016770, --
	Orphulella speciosa	Wellington, KS, US[AB]	JN167828, JN002141, JN167901, JN016784, --
	Orphulina balloui	Brasilia, Brazil[B]	--, --, JN167902, JN016785, --
/Paropomala group	*Paropomala wyomingensis*	Torrington, WY, US[A]	JN167831, JN002144, JN167904, JN016788, JF932445
/Scyllinini	*Jagomphocerus amazonicus*	Rio Ucayali, Peru[B]	--, JN002133, * (in appendix), --, --
	Parapellopedon uniformis	Savannah loc, Brazil[B]	JN167830, JN002143, JN167903, JN016787, --
	Rhammatocerus peragrans	Manabi, Equador[B]	JN167841, JN002153, JN167915, --, JF932456
	Rhammatocerus pictus	Ojeda, La Pampa, Argentina[B]	JN167839, JN002151, JN167913, JN016794, JF932454
	Rhammatocerus schistocercoides	Cajamarca, Peru[B]	JN167840, JN002152, JN167914, JN0167895, JF932455
/Stenobothrini	*Omocestus panteli*	Sierra Nevada, Spain[CD]	DQ230728, DQ230798, JN167899, DQ230763, JF932442
	Stenobothrus lineatus	Budapest, Hungary[CE]	DQ230729, JN002154, DQ230820, DQ230764, JF932457
/unassigned	*Pnorisa angulata*	loc?, South Africa[D]	JN167836, JN002148, JN167909, JN016791, JF932450
	Pseudogmothela yonlii	Tamou Reserve, Niger[D]	JN167837, JN002149, JN167910, JN016792, JF932451
	Stenohippus aequus	Tapoa, Niger	JN167844, JN002155, JN167918, JN016798, JF932458

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Table 1. Continued.

Subfamily/Tribe†	Species	Source	Accession Nos CO1, CO2, cytb, nd5, 16S
	Stenohippus mundus	Niamey, NigerCD	JN167845, JN002156, JN167919, JN016799, JF932459
	Thyridota dispar	loc?, South AfricaD	JN167847, JN002158, JN167921, --, (* in appendix)
Acridinae			
/Acridini	*Acrida bicolor*	Malatya, TurkeyCD	JN167789, JN002106, JN167855, JN016752, --
	Acrida conica	Silver Valley, QLD, AustraliaF	JN167790, JN002107, JN167856, JN016753, --
	Acrida turrita	Mt Nimba, GuineaD	JN167791, JN002108, JN167857, -- (* in appendix)
	Caledia captiva	Moomin, QLD, AustraliaF	-- , JN002119, JN167869, --, --
	Comacris lamottei	Mt Nimba, GuineaD	JN167806, JN002122, JN167874, JN016769, --
	Froggattina australis	Kuranda, QLD, AustraliaF	JN167811, JN002129, JN167882, --, JF932424
/Hyalopterygini	*Metaleptea adspersa*	Minas, UruguayAB	JN167820, --, JN167893, JN016780, --
	Parorphula graminea	Rio de Janeiro, BrazilB	JN167833, JN002146, JN167907, --, JF932447
/Phlaeobini	*Holopercna gerstaeckerii*	Mt Nimba, GuineaD	JN167817, --, JN167890, JN016777, JF932433
/Truxalini	*Truxalis nasuta*	Gran Canaria, Canary IslandsCDE	JN167848, JN002159, JN167922, JN016801, JF932462
/unassigned	*Anaeolopus socius*	loc?, South AfricaD	JN167799, --, JN167863, JN016762, --
	Cannula karschi	Mt Nimba, GuineaD	JN167805, --, JN167871, JN016767, JF932411
	Covasacris pallidinota	Benito Juarez, ArgentinaB	DQ230739, JN002123, JN191384, DQ230775, JF932416
	Duronia chloronota	Niamey, NigerD	JN167808, JN002126, JN167877, JN016771, --
	Eutryxalis filata	Madre de Dios, PeruB	JN167810, JN002128, JN167881, JN016773, JF932423
	Gymnobothrus temporalis	Mt Nimba, GuineaD	JN167815, -- (*in appendix), JN167888, JN016775, JF932430
	Odontomelus scalatus	Mt Nimba, GuineaD	JN167797, JN002113, JN167862, JN016760, --
	Odontomelus togoensis	Mt Nimba, GuineaD	JN167826, JN002139, JN167898, JN016782, JF932440
	Orthochtha dasycnemis	Lac Tanma, SenegalDE	JN167851, JN002162, JN167925, JN016803, JF932466
	Parga lamottei	Mt Nimba, GuineaD	JN167832, JN002145, JN167906, JN016790, --
	Sherifuria haningtoni	Niamey, NigerD	JN167850, JN002161, JN167924, --, JF932465
	Zacompsa festa	La Tapoa, NigerD	JN167849, JN002160, JN167923, JN016802, JF932464
Outgroup	*Pyrgomorpha conica*	Malatya, TurkeyABCDEF	EU031777, EU031776, EU031778, EU031779, JF932467

†- according to the OSF2; ‡ - loc? = unknown location; dashes signify no sequence obtained; * sequences placed in Appendix; Biogeographical Regions: A = Nearctic, B = Neotropics, C = Palaearctic, D = Africa, E = Oriental, F = Australia; Can = Canada; US = United States; MB – Manitoba, SK – Saskatchewan, YT – Yukon Territories, WI – Wisconsin, WY – Wyoming, FL – Florida, AK – Alaska, KS – Kansas.

Let Clades A to F define a "new" Gomphocerinae that is monophyletic; let Clades G to M define Acridinae, also monophyletic; and let N plus the basal taxa define – in this case, a paraphyletic group – perhaps labelled as "the ancient Acridinae". A more detailed morphological examination of fine structures using, for example, scanning electron microscopy (*e.g.*, Scali & Massimo 1977) or atomic-force microscopy (*e.g.*, Zhang *et al.* 2010) could potentially reveal characters that unify the monophyletic clusters.

Biogeographic origins of the subfamilies.—Gaunt and Miles (2002) estimated the age of common ancestry for, in their case, *Chorthippus* (a member of our Gomphocerinae*) and *Locusta* (a member of our Oedipodinae*) to be roughly 100 my. Accordingly, in calibrating our clock, we assigned that date to the node connecting our cluster

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of mostly gomphocerine grasshoppers with that of mostly oedipodine grasshoppers.

The following scenario points to an African origin for the Acridinae, Gomphocerinae and Oedipodinae. This interpretation, arrived at with the aid of DIVA, is consistent with the observation that all the taxa which are basal and paraphyletic to the Gomphocerinae* - Oedipodinae* node, are all unequivocally African. Their common ancestor was probably a proto-acridine. Diversification into two major lineages took place almost instantaneously, in geological terms, after the primary split. One subset of pre-acridines migrated to, and diversified within, South America about 99 mya, and then somewhat later some elements went on to establish the Gomphocerinae* in other continents (see below). About 96 mya, another subset entered Eurasia and radiated from there to form the Oedipodinae*. The connection between Africa and South America would still have been intact at the time (Sanmartin & Ronquist 2004, Smith *et al.* 2004), their disjunction not being completed until the end of the Late Cretaceous (Pitman *et al.* 1993); movement from Africa to Eurasia was made possible by several transitory connections that spanned the narrow Tethys sea (Goldblatt 1993). It is interesting to note that these almost concurrent, early events support Rowell and Flook's (1998) conclusion of a "single explosive radiation"having occurred within the Acridoidea, which appeared to correlate with — or to paraphrase their later words (Rowell & Flook 2004) be "triggered by" — the spread of flowering plants in the Cretaceous. Leys *et al.* (2002) made similar comments about another group of insects, the Apida, which perhaps, might be reflective of a general phenomenon. The acridines at the base of the tree had fairly ancient ancestors preceding the Gomphocerinae* — Oedipodinae* split by 10-70 my.

As a footnote, we should like to re-affirm our belief that dispersal rather than vicariance, accounted for the establishment of continental taxa, even though, to quote Voelker (1989), "…some dispersal across barriers is almost certainly required to explain the occurrence of the widespread ancestor". Notwithstanding this incisive remark, it is tempting to view the evolution of the two groups as a result of vicariance since the Oedipodinae* - Gomphocerinae* split roughly coincided with the breakup of Western Gondwanaland. That is, pre-acridines, having spread throughout the conjoined African - South American continent, became separated into two groups postfragmentation, one group giving rise to the gomphocerine – acridine complex that spread throughout South America and the other evolving into the oedipodine – acridine complex in Africa. However, given the overwhelming evidence that all the basal and paraphyletic taxa in the tree are African, the center of origin would have to be in Africa. Dispersion would have taken place from there.

*Gomphocerinae**.—The South American elements of clades F and E branched off in rapid succession 99 and 98 mya, respectively, from their African ancestors, with divergence within clades taking place in both cases, about 90 mya.

Members of clade F remained and diversified within South America. All but one genus, *Rhammatocerus*, are restricted to that continent. Of its 23 species, 21 are also endemic to South America (Otte 1981), including the 3 studied here. The other 2 occur throughout North America, but without knowing their sequences we cannot easily (see below) estimate the time of ancestral incursion.

Genera comprising clade E are more widespread. Many, such as *Orphulella*, include species, or populations within species, found in North America. *Amblytropidia* is another far-ranging genus, but here we do have sequences for continentally separated species. The program r8s estimates their time of divergence at about 50 mya, which would have been well within the time during which the two continents were intermittently connected by a series of land bridges (Pitman *et al.* 1993). One might speculate that the incursions of *Orphulella* and perhaps, *Rhammatocerus* (above), into North America had also taken place at this time and by this means.

About 92 mya, there was an unexpected reverse migration to Africa, still possible then, leading to the genera comprising clade D. The common ancestor of A to D could have been South American with, as stated, one branch leading to D and another to North America (clades A and C), with one offshoot from clade A moving on to Eurasia (clade B). This is an appealing scenario, given the relatively easy access between continents at the time. DIVA, however, identifies Africa as the ancestral area for clades A to D, and Eurasia as the common ancestral area for clades A to C. This implies three things: first, a movement from Africa to Eurasia would be required, still feasible as previously stated; second, the bulk of the North American gomphocerines had Eurasian ancestors; and third, genera such as *Eritettix* and *Opeia*, believed to have had a Neotropical origin (Vickery 1989), had instead a Holarctic origin.

*Oedipodinae**.—The second major group that migrated from Africa comprised mostly ancestors of the oedipodine grasshoppers, which, based on DIVA, initially settled in Eurasia. Incursion took place "soon" after the Gomphocerinae*- Oedipodinae* split, about 96 mya. In relatively short order, clades M (94 mya) to G (72 mya) were established. Movement into North America took place at least twice: 81 mya (clade L) and 53 mya (clade I). About 63 mya, there was a reverse dispersal to Africa (clade G). Certain elements of clades G, H, K and M have descendants in Australia and the Oriental region and represent more recent incursions. These will be discussed below.

Other subfamilies.—Similar studies of other subfamilies of Acrididae are few in number. Holarctic melanopline grasshoppers appear to have a South American origin (Amédégnato *et al.* 2003, Chapco 2006), but see Chintauan-Marquier *et al.* (2011) for a modification of this view. Whether the Melanoplinae also have an African link is presently unknown, although Lovejoy *et al.* (2006) did establish such a connection for Pan-American species of *Schistocerca*, a member of the Cyrtacanthacridinae, a subfamily related to the melanopline grasshoppers. Rowell and Flook (2004), using similar methods, described possible places of origin for the more spatially restricted Neotropical subfamily Proctolabinae. Outside of the Acrididae, the orthopteroid literature is not voluminous (*i.e.*, Huang *et al.* 2006, Maekawa *et al.* 2002) with respect to biogeographical origins.

The Clades

Clade A.—This clade (PP = 88%) is entirely North American, having evolved from Eurasian ancestors about 79 mya. Clade A includes genera/species not previously studied by Contreras and Chapco (2006): *Brunneria yukonensis*, *Bootettix argentatus*, *Eritettix simplex*, *Psoloessa delicatula*, *Opeia obscura* and the "banded-winged" gomphocerine, *Acrolophitus*.

Brunneria yukonensis, endemic to the Yukon Territory (Vickery 1997), is directly linked to *B. brunnea*, not a surprise in contrast to the case of *Chloealtis* below. According to our chronogram, the 2 species diverged about 8.3 mya. The northern region at that time would have been sufficiently warm for insects to survive, but it was predominantly forested (Reinink-Smith & Leopold 2005) and probably inhospitable to gramnivorous grasshoppers. More likely, the ancestor of *B. yukonensis* evolved in the grassland-dominated

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south (Jacobs *et al.* 1999), eventually migrating – perhaps "island hopping" between successive and numerous "nunataks" – and adapting to northern conditions during the intervening periods of glaciation.

There is a strong association among *Eritettix*, *Opeia* and *Psoloessa*. Vickery (1989) maintained that they, among other genera, are united in having a Neotropical origin. They are indeed linked, but their South American counterparts, at least of the last 2 genera, arose from the north. Somewhat earlier, Carbonell (1977) expressed a similar view on the origin of Neotropical gomphocerines. While *Eritettix* and *Opeia* belong to the same tribe, Eritettigini, *Psoloessa* belongs to another tribe, Aulocarini. Neither tribe is monophyletic. Eritettigini includes *Amphitornus*, part of clade C, and the South American *Sinipta*, part of clade F; Aulocarini includes *Aulocara* and *Ageneotettix*, both of which are positioned within clade B. Curiously, *Eritettix* and *Psoloessa* shared a very recent common ancestor (4.5 mya), whereas *Eritettix* and *Opeia* shared an ancestor long before that, 51.4 mya. Jago (1971) had pointed out a resemblance between *Eritettix* and the African genus *Pnorisa*, but given the phylogeny, the phenotypic similarity is probably the result of convergence.

OSF2 assigns *Bootettix* and *Acrolophitus* to the tribe Acrolophitini. Our results indicate that both are part of the same subclade, but they are not directly connected and are separated by members of other tribes. Their positions, however, should be regarded as tenuous, given that support for *Bootettix*'s location is weak (PP < 50 %) and the number of sequenced base pairs for *Acrolophitus* is rather low (1386 bp).

Clade B.—Clade B, a sister clade of A, consists almost entirely of Eurasian and Eurasian-derived North American Gomphocerinae. In its entirety, clade B is weakly supported (PP = 55%). In a previous study (Contreras & Chapco 2006), *Dociostaurus* and *Arcyptera* (different species) were closely linked and, apart from *Ramburiella* (see below), formed a sister group to other Eurasian gomphocerines and their North American derivatives. *Pseudogmothela*'s topological location is quite equivocal, given that in repeated MB runs, the genus emerges elsewhere. Confidence in the integrity of the remaining assemblage encompassing *Aeropedellus* to *Mermiria* is, however, much greater (PP = 82%). Divergence within this subclade occurred about 73 mya.

Out of roughly 20 species of *Aeropedellus*, four were analyzed. At one time, *A. arcticus* was considered a subspecies of *A. variegatus* (Hebard 1935), but subsequent work by Vickery (1967, 1997) showed them to be quite morphologically distinct, a difference reinforced by our molecular data. The two Eurasian species are paraphyletic to the two North American species, as are the Eurasian genera *Glyptobothrus* and *Gomphocerippus*. It is therefore probable that *A. reuteri* or its ancestor gave rise to the North American species, about 10 mya, during a warm interglacial period when Beringia was in place (Vickery 1989).

The discovery that two species of the North American genus *Chloealtis* are not directly related is somewhat unexpected, given their similar appearance (Otte 1981) [but not, apparently, with respect to choice of oviposition site – see Stauffer & Whitman 1997]. Each is directly connected to a different Eurasian genus: *C. abdominalis* to *Chrysochroan* (both members of the tribe Chrysochranotini) and *C. conspersa* to *Ptygonotus* (tribe Arcypterini). In both cases, times of separation predate that of the *Aeropedellus* radiation by about 20 - 30 my. Either Beringia or one of the north Atlantic bridges could have served as conduits to the Nearctic.

An association among the three Eurasian genera *Myrmeleotettix*, *Omocestus* and *Stenobothrus* is strongly supported, and appears to agree with morphologically-based phylogenies provided by Jago (1971) and Clemente *et al.* (1990). Although Jago (1971) regards the 3 as subgenera of *Stenobothrus*, the OSF2, curiously, assigns them to different tribes: *Myrmeleotettix* to tribe Gomphocerini and the other 2 to tribe Stenobothrini. Contreras and Chapco (2006) proposed combining the 2 tribes.

Mermiria is the first genus to branch off from the base of the aforementioned subclade. It belongs to the Mermiriini, as does *Achurum*, but as can be seen from Figure 2a, the two are quite far apart. According to Vickery (1989), *Mermiria* is related to the South American genus *Staurorhectus* (clade F) (see also Jago 1971), but undoubtedly the resemblance must be the result of convergence.

Clade C.—Clade C is basal to A and B and is strongly supported (PP = 85%). Its sole Eurasian genus, *Ramburiella*, is also basal to the bulk of gomphocerines in Contreras and Chapco (2006). *Ramburiella* and the two North American genera, according to DIVA, shared a common Eurasian ancestor, splitting from one another about 77 mya. *Amphitornus* and *Boopedon* evolved from a common ancestor about 70 mya; they belong to different tribes, Eritettigini and Amblytropidiniini respectively. Other members of these tribes occur elsewhere in the tree. Two other species of *Ramburiella* are found in Africa, probably the result of recent migrations.

Clade D.—This interesting clade represents a "return" to Africa from South America about 92 mya, well within a time period during which dispersal across the chasm separating the two southern continents was still possible for some organisms (Pitman *et al.* 1993). Diversification took place about 80 mya. Support for this aggregate of five African gomphocerine genera is very strong (PP = 93%). The group is external to clades A, B and C. *Stenohippus* and *Thyridota* have not yet been assigned to tribe by the OSF2. The remaining three genera belong to different tribes. Jago (1996a) erected the Dnopherula Complex, defined by a geophilous lifestyle and morphologically, by a fronto-vertical angle >40°, placing within it, among other genera, *Pnorisa*, *Rhaphotittha*, *Pseudogmothela*, *Ramburiella* and *Stenohippus*. Of these, only *Rhaphotittha* and *Stenohippus* are closely related, albeit not directly. Other members of clade D (*Amesotropis*, *Ochrilidia* and *Thyridota)* are regarded as phytophilous and are not included in Jago's Dnopherula Complex.

The genus *Ochrilidia* is centered in Africa, but some species also occur in southern Europe and south-west Asia including India (Bei-Bienko & Mishchenko 1951, Dirsch 1965, OSF2). The two species studied here occupy somewhat different ranges, but overlap in northern Africa; they diverged about 15 mya, coinciding with a time of transition from tropical forest habitat to that of open grasslands (Micheels *et al.* 2009).

Stenohippus is phylogenetically older than *Ochrilida*, having diverged about 58 mya. Ranges of *S. harteri* and *S. mundus* overlap in west-central Africa, perhaps the genus' place of origin. The genus itself has a broader African distribution, encompassing the Arabian peninsula, and extends into southwest India. For this genus and *Ochrilidia* above, estimation of times of entry outside Africa would require having sequences for species from those continents.

Clade E.—This clade (PP = 99%) diversified about 90 mya from a common neotropical ancestor and is external to A – D, consisting of a mixture of acridine and gomphocerine genera. Most genera including *Metaleptea* – the eponymous title of the Orthoptera Society newsletter – had not been studied previously by Contreras and Chapco (2006). These taxa are well represented in South America with some elements of *Amblytropidia*, *Dichromorpha* and *Orphulella* appearing in North America. *O. speciosa*, the species studied here,

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is found entirely within North America.

Most tribes within the clade are not monophyletic. *Achurum* belongs to the tribe Mermiriini, but is far removed from another member, *Mermiria* (part of clade A). In contrast, the unified trio *Dichromorpha*, *Orphulella* and *Orphulina* all belong to one tribe, Orphulellini, an association supported here. *Amblytropidia* belongs to the tribe Amblytropidini, which also includes, among others, the genus *Sinipta* (part of F), *Boopedon* (part of Clade C) and *Syrbula* (part of Clade B). Interestingly, some reservations about the legitimacy of Amblytropidini had been previously expressed by Otte (1981). Although *Eutryxalis* and *Covasacris* have not been assigned to tribe by OSF2, Donato (2003a, 2003b) placed them in the tribe Hyalopterygini along with *Metaleptea* and *Parorphula* (some species of which have been synonymized with *C. pallidinota*), a union which agrees with our phylogenetic findings.

It is worth noting that most gomphocerines that make up this gomphocerine/acridine mix lack stridulatory files on their hind femora. For example, some species of *Orphulella* (not *speciosa*) and some populations of *Achurum carinatum* lack this acridine-defining trait (Otte 1981).

The two species of *Amblytropidia* separated about 50 mya. *A. mysteca* occurs in the southern US and parts of Mexico and Central America, whereas *A. australis* is found in southern South America. A series of island arcs, in place at the time, periodically linked the two continents (Pitman *et al.* 1993) and could have served as a conveyance for a South American ancestor of *A. mysteca*.

The two closely linked genera, *Orphulella* and *Orphulina*, together with *Dichromorpha* form part of the tribe Orphulellini, an association supported here. They arose from a common South American ancestor about 60 mya, spreading to different extents into Central and North America.

The genus *Achurum* occurs in south, southeastern US and Mexico. The two species analyzed here separated about 33 mya and presently have nonoverlapping distributions. *A. minimipenne* is found in the southern US (excluding Florida); *A. carinatum* is in Florida. Their common ancestor must have occurred elsewhere since the Florida Peninsula would have been submerged (Lane 1994) at that time.

Clade F.—This clade branched off from a common South American stock about 99 mya and soon after (90 mya) diverged into five genera. All taxa making up this group are gomphocerines and most are exclusively restricted to that continent. *Jagomphocerus*, *Parapellopedon* and *Rhammatocerus* belong to the tribe Scyllini and that association is strongly supported here. *Rhammatocerus*, however, is not monophyletic. *Sinipta* (tribe Amblytropidiini) and *Staurorhectus* (tribe Compsacrini) are linked and external to the Scyllini. Other members of Amblytropidiini (*Boopedon*, *Amblytropidia*) analyzed here, are far removed from this clade. In Carbonell's (1977) morphological descriptions of some South American tribe members, he acknowledges that these aggregations are not necessarily of phylogenetic significance.

Clade G.—*Oedipoda* is external to all other taxa comprising Clade G, but its phylogenetic location is weakly supported (PP = 59%); in Fries *et al.* (2007), the genus' position is somewhat ambivalent. The remaining cluster by contrast, has maximal support (PP = 100%). Relationships among genera previously studied (Fries *et al.* 2007) appear unaltered with the inclusion of *Morphacris* and additional species of *Heteropternis* and *Gastrimargus*. Analysing trees based on 12S and 16S rDNA sequences, Rowell and Flook (2004) also united *Oedipoda*, *Locusta* and *Morphacris*, but not in the same branching order as that here. Yin *et al.* (2008), using the latter's 16S data set and adding sequences from *Gastrimargus* and *Heteropternis*, also revealed the same associations, except that the position of *Heteropternis* was external to all the oedipodine genera studied (see Lu & Huang 2006 for a similar study but without *Heteropternis*). More recently, Ma *et al.* (2009) in their phylogenetic analysis of complete mitochondrial genomes involving seven genera of Acrididae, directly linked *Oedaleus* with *Gastrimargus*, two genera which are also very similar morphologically (Ritchie 1981, 1982). The two particular species analyzed by Ma *et al.* differed from ours. In their analysis, *Locusta* was external to the pair. Other findings by Ma *et al.* are discussed under clade M.

A small point of interest: *Acrotylus*, *Morphacris*, (perhaps) *Locusta* and *Oedaleus*, although belonging to different tribes (OSF2), appear unified in possessing a common defence mechanism (Whitman 1990). The point in mentioning this is to illustrate the need for probing more deeply into these insects' biology in order to discover other commonly inherited traits which our molecular phylogeny, if accurate, would suggest must exist. *Morphacris* has not yet been assigned to tribe according to the OSF2, although Petit *et al.* (2006) place the genus within the (North American) tribe Tropidolophini, clearly an error.

The two African species of *Gastrimargus* are directly linked, sharing an ancestor about 31 mya. The genus, however, is not monophyletic. The Australian *G. musicus* is somewhat phylogenetically removed from the pair, despite its striking resemblance to *G. africanus* (Ritchie 1982). Like *G. musicus*, the species, *Heteropternis obscurella*, is autochthonous to Australia-Australasia (Rentz *et al.* 2004); at one time they were believed to be descendants of fairly recent invaders (Key 1959, Ritchie 1981). Our phylogeny shows however, that they descended from African ancestors further back in time: 44 mya for *H. obscurella* and 56 mya for *G. musicus*. Fries *et al.* (2007) describe possible colonization scenarios, one involving "long-distance island hopping" and the northward moving "island" India. *Oedaleus* is another wide-ranging genus (Ritchie 1981) and its only Australian species, *australis*, may have had a similar ancient history, given that the two species of *Oedaleus* analyzed by Fries *et al.* (2007) – one African and the other Asian – separated about 35 mya.

Clade H.—These are the same Eurasian genera studied previously (Fries *et al.* 2007); there are no changes to their relative associations within the present, larger body of data. Diversification within the clade took place about 55 mya, roughly within the same time frame as noted in Fries *et al.* Its close relationship to clade I also remains unchanged.

Clade I.—All members of clade I (PP = 100%) are North American, having split off from a Eurasian ancestor about 60 mya. Most tribes of Oedipodinae were shown not to be monophyletic by Fries *et al.* (2007), and with the addition of *Camnula* and *Pardalophora*, that conclusion may be extended to include the Hippiscini to which both genera belong. The relative positions of genera in Fries *et al.* (2007) remain approximately the same. Otte (1984) does point out *Camnula's* apparent lack of a nearest relative within the tribe. Here, it would seem that the genus' nearest relative is *Trachyrhachys*, a member of the tribe Psinidiini.

Clade J.—This clade is external to Clades G – I, having branched off from a Eurasian ancestor about 80 mya. Most genera of Clade J have wide-ranging members; at least three dispersals have occurred. One led to the African acridine, *Anaeolopus*, another to the North American *Stethophyma gracile* and at least one migration established *Aiolopus*

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strepens throughout the Old World and Asia-Australia. *Aiolopus* and *Stethophyma* were previously shown (Fries *et al.* 2007) to be linked and remain so here. *Aiolopus*'s closer relationship with *Anaeolopus* is interesting and was perhaps adumbrated by Hollis (1967) who, in re-examining synonymies within the genus *Aiolopus*, transferred one species, *A. tamulus*, to *Anaelopus*. The scheme presented by Rentz *et al.* (2004) would undoubtedly have placed all members of clade J, a mix of Oedipodinae and Acridinae (*sensu* OSF2), into a redefined Acridinae.

Clade K.—Clade K diverged from a common Eurasian ancestor about 81 mya, preceding the previous division by 1 my. Within clade K, a split occurred 12 my later, giving rise to the Eurasian/African genus *Paracinema* and the remaining taxa, all centered in Australia. One possible route to that distant continent could have been achieved via a series of steps from Eurasia to Africa to India (on its northward drift) and on to Australia. Fuller *et al.* (2005) had proposed just such a long-range pathway for the allodapine bee genus *Braunsapis*, which may well have served as a dispersal route for other insects capable of long-distance migration.

The tight relationship between the oedipodines, *Austroicetes* and *Chortoicetes*, previously established (Fries *et al.* 2007), remains the same with successive links to the acridines, *Caledia* and *Froggattina*. As a matter of historical interest, Colgan (1989, 1991) had demonstrated the same close association using the older technologies of allozyme and restriction enzyme analyses. With respect to tribal affiliation, *Caledia* and *Froggattina* both belong to the Acridini, but are not directly linked; other tribal members appear elsewhere in the phylogeny. The tribe Epacromiini, of which *Paracinema* is a member, is also nonmonophyletic with other genera such as *Aiolopus*, *Duroniella* and *Heteropternis* scattered throughout the tree.

Clade L.—The evolution of these North American genera predates those comprising clade I (*Arphia* to *Pardalophora*) by about 30 my. At the time of divarication, Laurasia, still intact, would have facilitated movement between regions. All but the gomphocerine *Melanotettix* are oedipodines. Otte (1981, 1984) had expressed some ambivalence about the subfamily affiliation of *Melanotettix*, as well as that of *Machaerocera*, both sharing some features (absence of stridulatory pegs and habitat type, respectively) with the Acridinae.

Clade M and Duroniella.—Clade M, comprising two acridine genera, is basal to clades G – L. Its ancestor, probably Eurasian in origin, diverged soon after the Oedipodine* explosion, 96 mya. One genus, *Acrida*, is distributed worldwide, excluding the Americas, and comprises over 40 species, of which three were studied here. The genus is at least 39 my old. *A. conica* occurs in Australia and New Guinea, and, according to DIVA, shared a common ancestor with the largely African *A. turitta* about 30 mya. Migration to the Australian region would have been more recent than the time of dispersal for the ancestor of the Australian genera in clade K. Also, the pathways were likely different. By 39 mya, India would have reached its northern limit, cutting off that part of the route to Australia. Given the widespread distribution of the genus, the ancestor of *A. conica* could well have come from Southeast Asia from whence we know island-hopping would have been possible (Jønsson & Fjeldså 2006). *Truxalis* is similarly widely distributed, but without having samples from other geographical regions, all we can propose is that diversification took place since about 71 mya.

Others have examined the phylogenetic position of *Acrida* with respect to a limited number of acridines, gomphocerines and oedipodines. *Acrida's* relationship to *Truxalis* had already been demonstrated by Rowell and Flook (1998) in their phylogenetic analysis of mitochondrial 12S + 16S rDNA sequences for a very wide sample of Acridoidea. Directly linked to one another, the two genera were part of a large, mostly unresolved, tree. Liu *et al.* (2008), in their analysis of a 795 bp portion of the same two rDNA sequences, showed that *Acrida* (sp = *willemsei*) was external to four genera of Oedipodinae, a result broadly similar to that in our present work. A recent phylogenetic analysis (Fenn *et al.* 2008) of the complete mitochondrial genomes of a small number of orthopteran taxa, including three species of Acrididae, showed that *Acrida* (*willemsei*) was directly linked to a member of the Calliptaminae (genus *Calliptamus*); both were associated with *Locusta*, an unexpected result. Expanding on the latter study, Ma *et al.* (2009) analyzed four additional Acrididae. Their investigation showed that *Acrida* was external to the trio *Chorthippus – Calliptamus – Oxya*, and that this set emerged as a sister group to the aggregate, *Locusta-Oedaleus-Gastrimargus*. The relative positions of *Chorthippus*, *Acrida* and the oedipodines appear to be reversed to the topology uncovered in the present study in which *Acrida* is shown to be more closely aligned with the Oedipodinae.

Given the vast amount of data that complete sequences do provide, it is tempting to regard their phylogenies as being somewhat more accurate, but Zwickl and Hillis (2002) have shown, through simulation studies, that increased taxon sampling is perhaps more important than increasing the number of sequences in achieving greater phylogenetic confidence. Whether the relationships revealed in this paper will remain invariant with greater genomic scrutiny, however, remains to be seen.

Duroniella is located in southwestern Asia, the Middle East and north Africa, probably derived from a Eurasian or African ancestor about 96 mya. Over its taxonomic history, this genus has been assigned to various subfamilies from Acridinae (Bei-Bienko & Mishchenko 1951, Jago 1971) to Oedipodinae (OSF2) to Gomphocerinae (Fries *et al.* 2007). From the present phylogeny, which encompasses a greater sampling of the three subfamilies, it would appear that *Duroniella* is more closely aligned with a complex of taxa composed of members of Oedipodinae and (a subset of) the Acridinae, but not of the Gomphocerinae.

Orthochtha, Clade N and remaining taxa.—These genera diverged before the Gomphocerinae* - Oedipodinae* split at different times, ranging from the more recent offshoot, *Orthochtha* (111 mya), to those of clade N (118 mya) to the genus with the most ancient ancestor, *Sherifuria* (174 mya). This basal group, a mixture of resolved and unresolved relationships, is paraphyletic to all the preceding taxa. All are African and, except for *Pnorisa* (Gomphocerinae – see Clade D above), all belong to the Acridinae. *Orthochtha* is the only genus with species outside the continent (four are in southern India – OSF2); they are probably the descendants of (not necessarily recent) incursives from Africa.

Clade N consists of six genera. The two species of *Odontomelus*, are not directly linked but instead are connected through the genus *Parga*. In Jago's (1983) study of several African acridine genera, both are placed within the *Parga* genus group, which also includes *Comacris*, *Duroniella*, *Gymnobothrus*, *Holopercna* and *Zacompsa*. Apart from *Duroniella*, *Holopercna* and *Pnorisa*, our results concur approximately with Jago's grouping. Jago (1983) defines yet another genus group, *Phlaeoba*, for which we unfortunately have analyzed only one genus, *Sherifuria*. Jago alludes to yet another (unnamed) group to which *Orthochtha* belongs, and in our study, the genus is phylogenetically apart from the others, internal to clade N, albeit with weak support.

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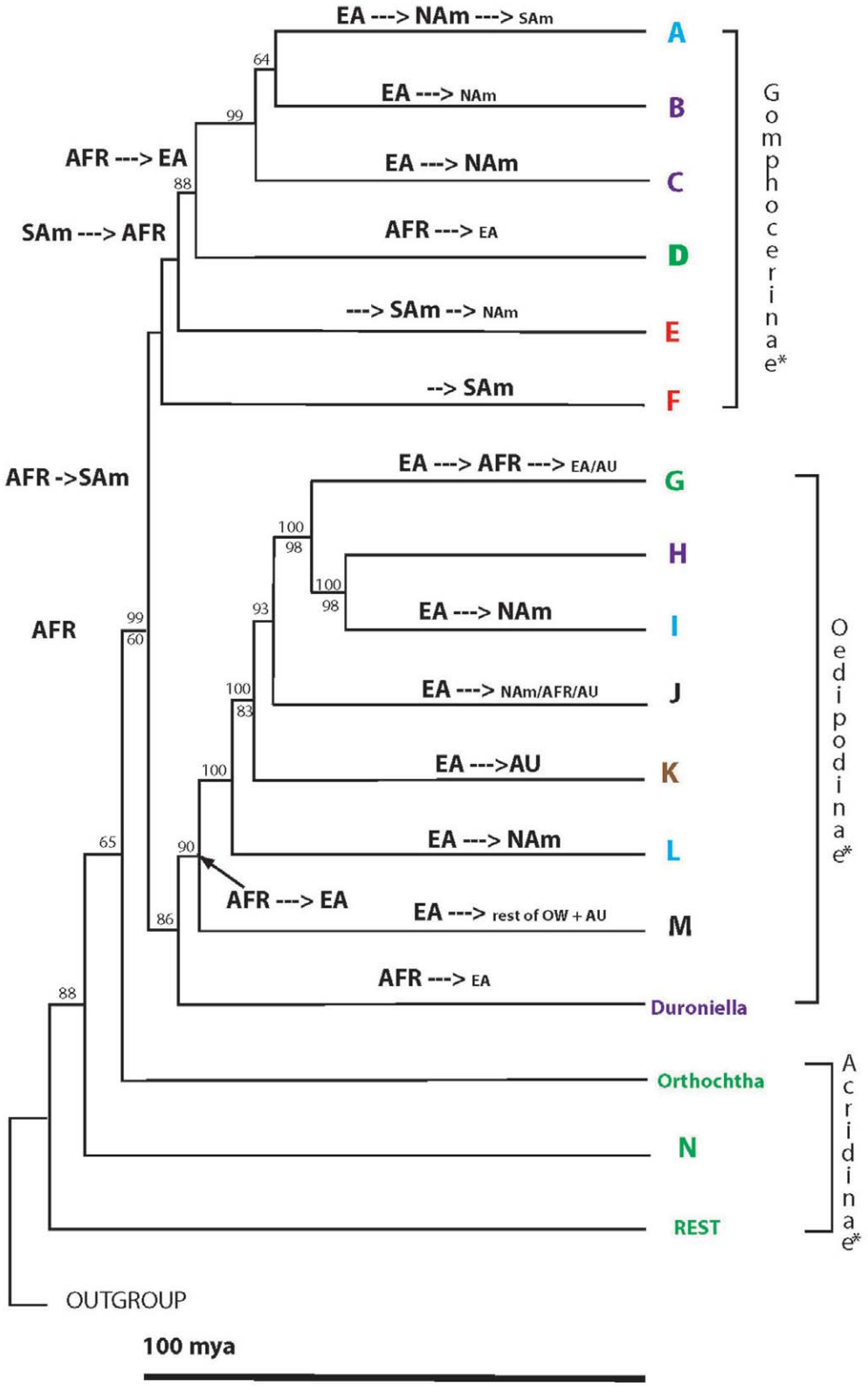


Fig. 1. Chronogram for Acridinae, Gomphocerinae and Oedipodinae evolution. Relationships are those obtained by Bayesian methods (see text). Branch lengths are proportional to times of divergence estimated by r8s. Numbers at nodes refer to Bayesian posterior probabilities (% PP). Numbers (>50%) at nodes are % PP (above line) and % bootstrap values (below line). Clades A to N are referenced in the text. "Rest" refers to basal taxa (see Fig. 2D). NAm = North America, EA = Eurasia, SAm = South America, AFR = Africa, AU = Australia. Items with arrows – *e.g.*, EA--> NAm --> SAm – reflect direction of migration. Smaller scripts indicate that a minor number of clade members have descendants in the targeted continent. Colors refer to geographical distribution of the majority of the clade's members. Blue: North America; purple: Eurasia; green: Africa; red: South America; brown: Australia. Black is used for members with widespread distributions.

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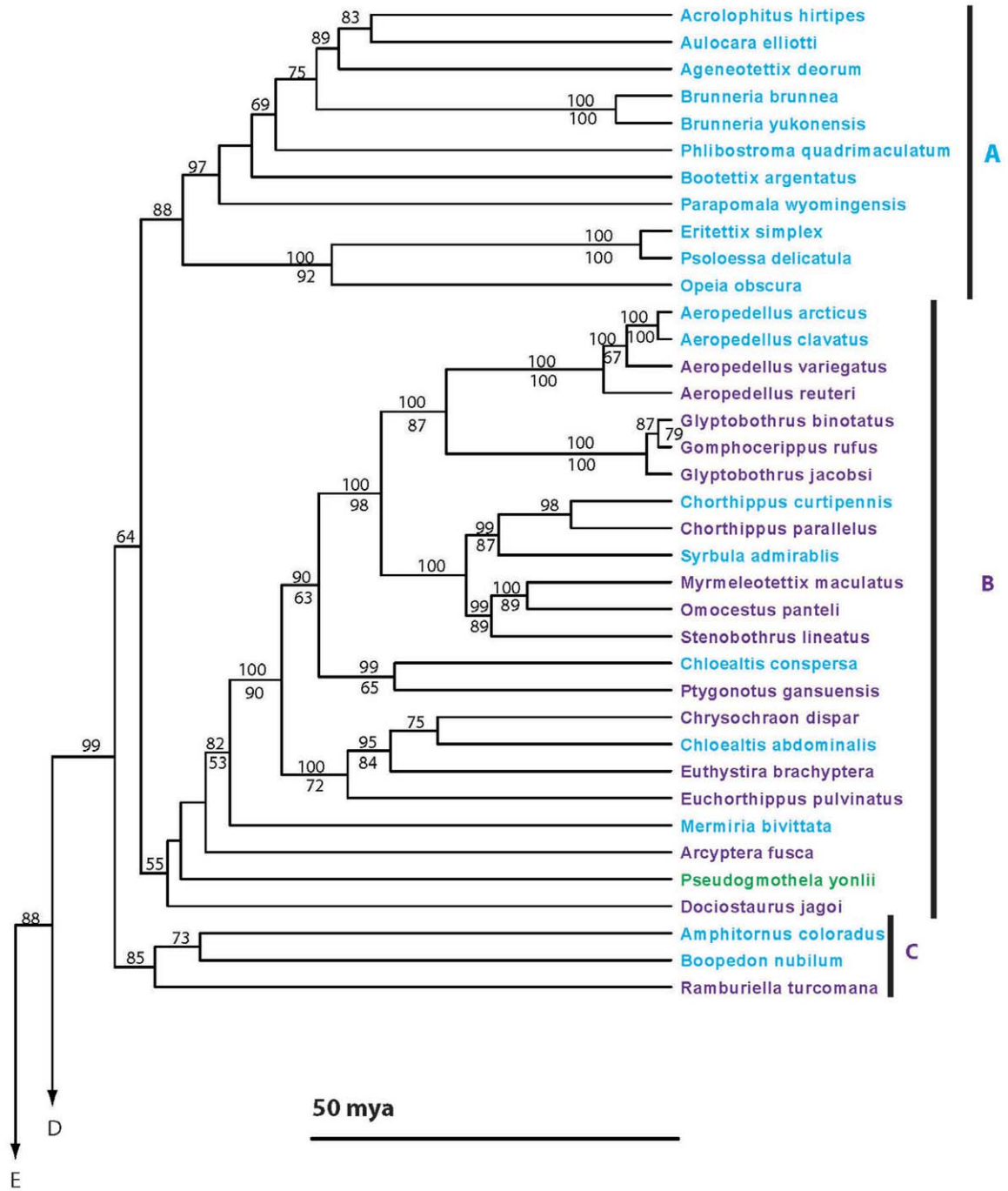


Fig. 2a. Elements of clades depicted in Figure 1. (Figs 2b-d on successive pages.) Clades A to C. Numbers (>50%) at nodes are % PP (above line) and % bootstrap values (below line). Color codes are described in the legend for Figure 1.

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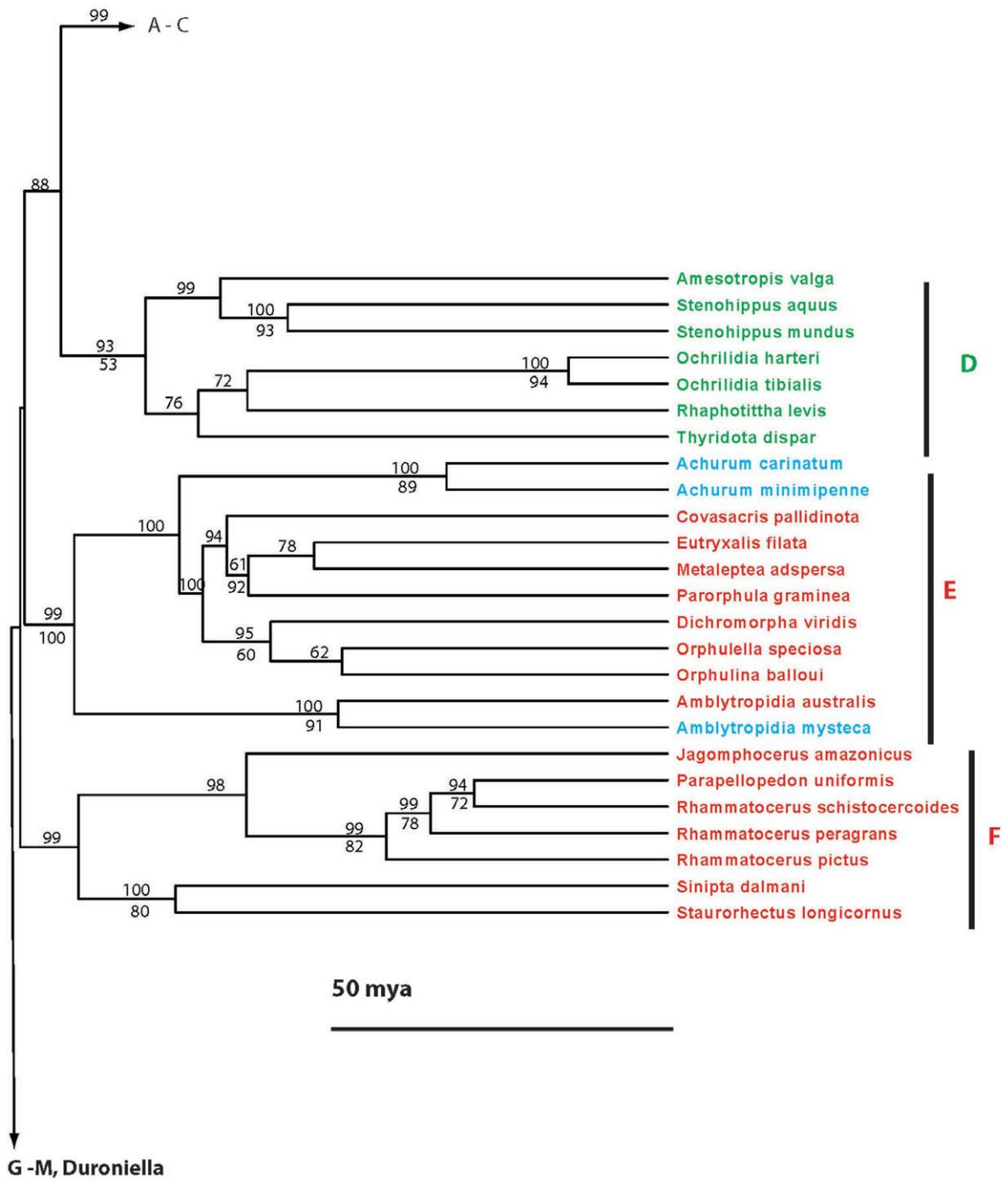


Fig. 2b. Elements of clades depicted in Figure 1. Clades D to F. Numbers (>50%) at nodes are % PP (above line) and % bootstrap values (below line). Color codes are described in the legend for Figure 1.

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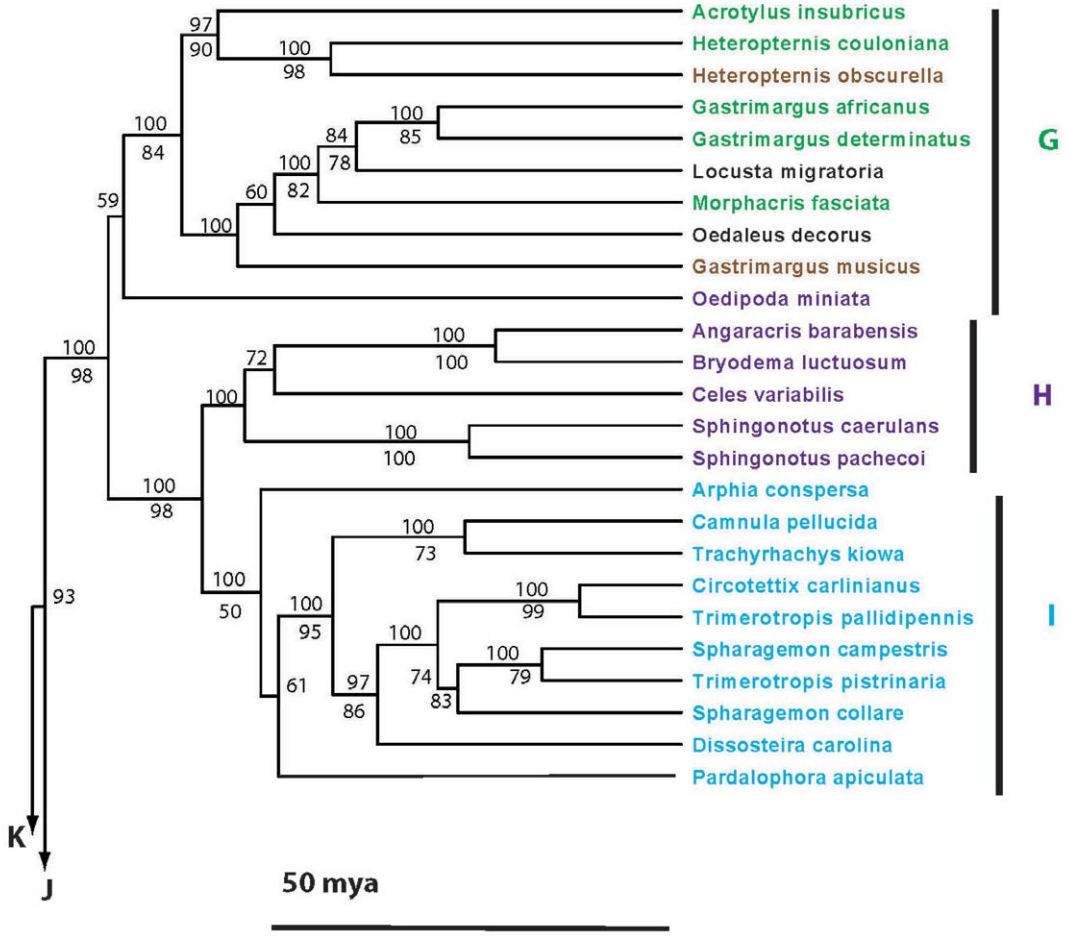


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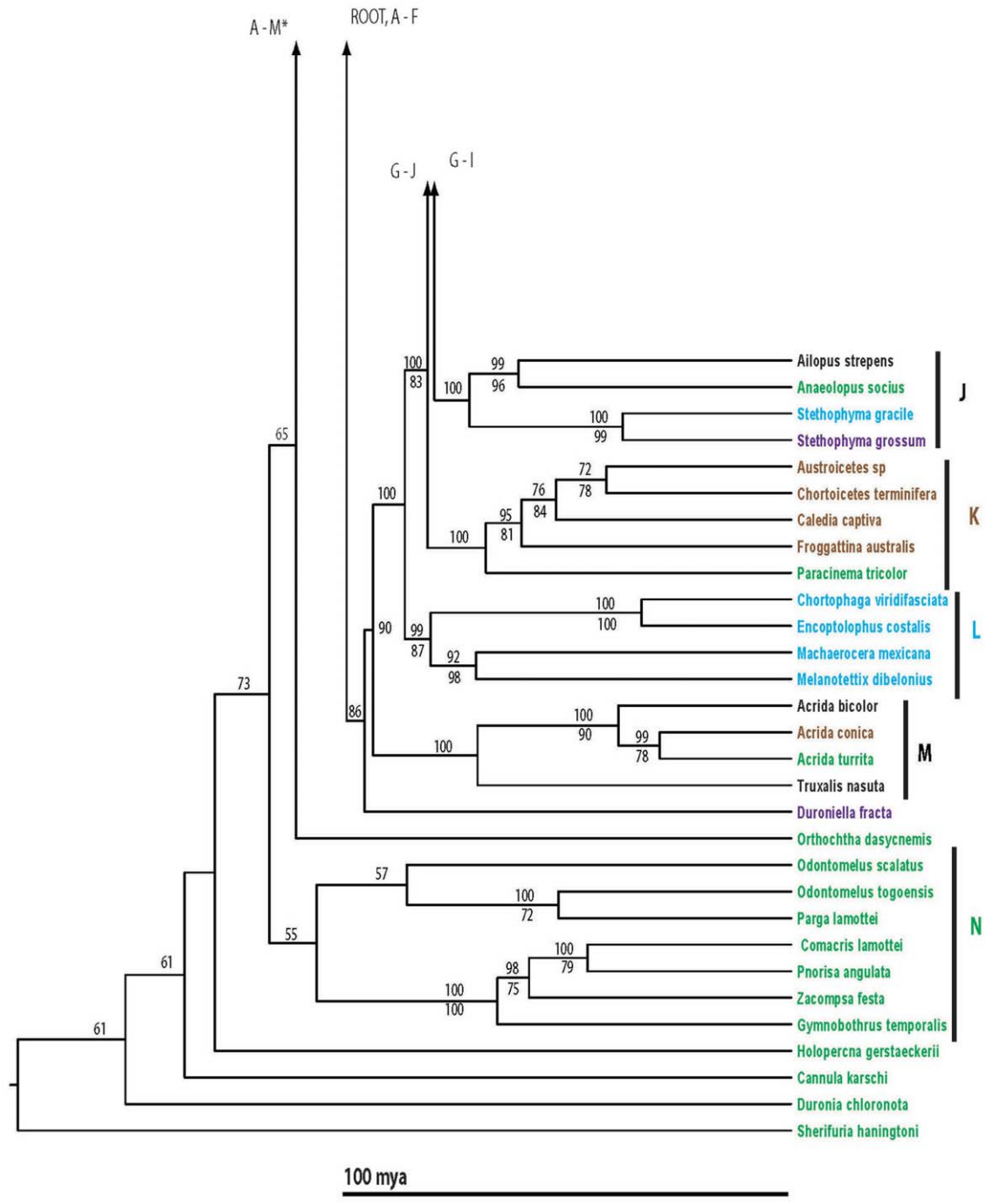


Fig. 2d. Elements of clades depicted in Figure 1. Clades J to M plus *Duroniella*; clade N plus remaining basal taxa. Numbers (>50%) at nodes are % PP (above line) and % bootstrap values (below line). Color codes are described in the legend for Figure 1.

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Appendix 1. The following sequences, owing to Genbank's limitations regarding length, are reproduced here.

Acrida turrita 16S ribosomal RNA gene
ATTGAGCTACTGCACCCAAAAATAATCTTAATCCAACATCGAGGTCGCACTCTGCTTTGTCGATAAGAGCTCTCAAAAACAATTACGCTGT-
TATCCCTAAGGTAACTTAATCTTATAATCATAAATTATGGATCATAAAAACATAAATTAATGAATTCATAATGAAGAGTTTATTTATTCTTCATGT-
CACCCCAA

Thyridota dispar 16S ribosomal RNA gene
ATTGGGCTACTGCACCCTAAAACTTTTCTTAATCCAACATCGAGGTCGCAATTTATTTTGTCGATATGAGCTCTCAAAAATAATTACGCTGT-
TATCCCTAAGGTAACTTAATCTTATGATCATAAATTATGGATCAAAATTAACATAAATTAATGATTATATAAATGAAGAGTTTATTGATTCTAC

Gymnobothrus temporalis COII gene (translation starts at base 1)
GATACATATATAACACCAGAAAGAGATCTTAATAATGAAGGATTTCGACTATTAGATGTAGACAACCGGACAATTTTACCTATAAATACAGAAG-
TACGTATTCTTACCAGAGCATCAGACGTACTTCACTCATGAGCAGTACCAGCATTAGGGATTAAAATTGATGCCACACCAGGACGACTAAAC

Achurum minimipenne cytb gene (translation starts at base 1)
ATATTTTTCATCTGTATTTACCTTCATGTAGGACGAGGAATCTATTATGGATCATATATGTATATACATACATGAATAATTGGAACGTTAATTT-
TATTCCTTGTTATA

Amphitornus coloradus cytb gene (translation starts at base 3)
TTGGTACAATTATTCTATTTTTAGTAATAGCAACTGCATTTATAGGTTATGTATTACCATGAGGACAAATATCTTTCTGAGGGGCAACAGTAAT-
TACAAACCTATTATCAGCAATTCCATATTTA

Jagomphocerus amazonicus cytb gene (translation starts at base 3)
GGACAGTAATCTTATTTCTAGTAATAGCAACAGCATTTATAGGATATGTATTACCATGAGGACAAATATCATTCTGAGGAGCTACAGTAATCA-
CAAATCTATTATCAGCAATCCCTTATTTA

Stethophyma grossum cytb gene (translation starts at base 1) GGATCATATATACATATAAATACATGAATAATTGAAACGCTAATTCTATTTTTAGT-
TATACCAACAGCATTTATAGGTTATGTATTACCATGAGGACAAATATCATTCTGAGGAGCAACAGTAATTACAAATTTATTATCAGCTATCCCT-
TATCTTGCAACAGAATTAGTACAAA

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