

Anisomeriini diving beetles—an Atlantic–Pacific Island disjunction on Tristan da Cunha and Robinson Crusoe Island, Juan Fernández?

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Abstract

Anisomeriini diving beetles contain only two enigmatic species, representing a remarkable disjunction between the Pacific Juan Fernández Islands (*Anisomeria bistriata*) and the South Atlantic Tristan da Cunha Archipelago (*Senilites tristanicola*). They belong to the Colymbetinae, which contain 140 species worldwide. Here we aim to reconstruct the evolutionary history of the Anisomeriini and use > 9000 bp DNA sequence data from 13 fragments of 12 loci for a comprehensive sampling of Colymbetinae species. Analyses under different optimization criteria converge on very similar topologies, and show unambiguously that *Anisomeria bistriata* and *Senilites tristanicola* belong to the Neotropical *Rhantus signatus* species group, a comparatively recent clade within Colymbetinae. Anisomeriini therefore are synonymized with Colymbetini and both species are transferred to *Rhantus* accordingly, resulting in secondary homonymy of *Rhantus bistriatus* (Brullé, 1835) with *Rhantus bistriatus* (Bergsträsser, 1778). We propose the replacement name *Rhantus selkirki* Jäch, Balke & Michat nom. nov. for the Juan Fernández species. Presence of these species on remote islands is therefore not relictary, but the result of more recent range expansions out of mainland South America. Finally, we suggest that Carabdytini should be synonymized with Colymbetini. Our study underpins the Hennigian principle that a natural classification can be derived only from the search for shared apomorphies between species, not from differences.

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Introduction

Islands are fascinating systems for the study of evolutionary processes as they have clear-cut boundaries and are to some degree easier to inventory than continental-size areas (Heaney, 2007; Whittaker et al., 2008; Gillespie and Clague, 2009; Losos and Ricklefs, 2010). Central questions include how and from where ancestral biota arrived on an island, no matter if the island is of oceanic or continental origin (Abegg and Thierry, 2002; Nikula et al., 2012; Salerno et al., 2012;

Toussaint et al., 2013), and how ecological conditions on the island affected the evolutionary fate of the colonists, or how arrivers utilized ecological opportunities over evolutionary time. This is the research ground where macroevolution and macroecology melt together. Here we investigate a remarkable disjunction, reported by Brinck (1948), between the very remote Tristan da Cunha Islands in the Atlantic Ocean (Ryan et al., 2007) and the Juan Fernández Islands off the Chilean coast (Haberle, 2009). The diving beetle tribe Anisomeriini Brinck, 1948 contains two enigmatic monospecific genera for *Anisomeria bistriata* (Brullé, 1835) (Juan Fernández: Robinson Crusoe Island) and *Senilites tristanicola* Brinck, 1948 (Tristan da Cunha:

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Nightingale and Inaccessible Island). They belong to the widespread subfamily Colymbetinae, which contains 140 species (Nilsson, 2013). Its species inhabit a wide variety of aquatic habitats, mainly standing water, showing greatest species diversity in northern temperate regions, while being mostly restricted to cooler high altitude habitats towards the Equator (Balke, 2001; Balke et al., 2009). The vast majority of species have an ovate, streamlined diving beetle habitus with flattened, paddle-like hind legs as adaptations to fast swimming (Ribera and Nilsson, 1995). The two species in Anisomeriini, in particular *A. bistriata*, deviate from this habitus, with a cordiform pronotum and less modified legs, thus somewhat resembling a ground beetle (Carabidae) (Michat and Balke, 2013). Their systematic position has never been addressed adequately despite advanced efforts to clarify the phylogeny of diving beetles (Dytiscidae) (e.g. Miller, 2001, 2003; Bergsten and Miller, 2007; Ribera et al., 2008; Alarie et al., 2009), mainly because the species are very rare in collections and fresh tissue has not been available for DNA sequencing so far.

Here we use information from five mitochondrial and eight nuclear gene fragments obtained from fresh samples to reconstruct phylogenetic relationships for a comprehensive sampling of most Colymbetinae genera and all relevant species groups delineated based on morphology, to (i) infer the phylogenetic relationships within the subfamily Colymbetinae as a framework, (ii) investigate the placement of *Anisomeria* and *Senilites* within Colymetinae, and (iii) understand the evolutionary origin of the enigmatic Juan Fernández and Tristan da Cunha colymbetine diving beetles.

Materials and methods

Taxon sampling

Colymbetinae contain the tribes Anisomeriini Brinck, 1948 [*Anisomeria* Brinck, 1943, *Senilites* Brinck, 1948], Colymbetini Erichson, 1837 [*Bunites* Spangler, 1972, *Colymbetes* Clairville, 1806, *Hoperius* Fall, 1927, *Meladema* Laporte, 1835, *Melanodytes* Seidlitz, 1887, *Neoscutopterus* J. Balfour-Browne, 1943, *Rhantus* Dejean, 1833], and Carabdytini Pederzani, 1995 [*Carabdytes* Balke, Hendrich & Wewalka, 1992]. Nilsson (2013) included *Rugosus* García, 2001 in Colymbetini but, based on the description and specimens we studied, this is not a member of the Colymbetinae but belongs to Copelatinae (M. Balke, unpublished). In Nilsson (2013), *Carabdytes* was still assigned to a valid Carabdytini, although Balke (2001) suggested a synonymy of the latter with Colymbetini. This was supported by Balke et al. (2007, 2009). We include 29 species (Table 1) of the subfamily Colymbetinae, rep-

resenting all extant genera except the Mediterranean *Melanodytes*, with a wide geographical coverage of the widespread genus *Rhantus*, including its major species complexes. We include *Agabus bipustulatus* (Linnaeus, 1767) as an outgroup representative as it has been shown in several recent studies that Agabinae are closely related to Colymbetinae (Ribera et al., 2004; Hunt et al., 2007), and *Amphizoa lecontei* (Matthews, 1872) (Amphizoidea) was used to root the tree.

Laboratory procedures

Genomic DNA was extracted and purified from muscle tissue using the Qiagen DNeasy[®] tissue kits (Qiagen, Hilden, Germany). DNA samples were then used to conduct amplifications by PCR of five mitochondrial [*12s*, 352 bp, primers 12sai/12sbi (Simon et al., 1994); *16s*, 773 bp, primers M14/M223 (Simon et al., 1994); *cob*, 353 bp, primers Cb3/Cb4 (Barracough et al., 1999); *col*, 1417 bp, primers 5' part Hco/Lco 3' part Pat/Jerry (Simon et al., 1994) and *co2*, 527 bp, primers Co2f/George (Simon et al., 1994)] and eight nuclear gene fragments [*18s*, 1974 bp, primers 5' part 18s5'/18sb5.0–18sai/18sb2.5–18sa1.0/18sbi–3' part 18sa2.0/18s3'1 (Shull et al., 2001); *ark*, 674 bp, primers AK183f/AK939r (Wild and Maddison, 2008); *eno*, 677 bp, primers En37f/En731r (Wild and Maddison, 2008); *wng*, 500 bp, primers wg550f/wgAbr5 (Wild and Maddison, 2008); *ef1a*, 553 bp, primers 372s/747a (McKenna and Farrel, 2005); *h3*, 307 bp, primers H3af/H3ar (Colgan et al., 1998); *h4*, 159 bp, primers H4f2s/H4f2er (Pineau et al., 2005) and *cad*, 818 bp, primers Cd439f/Cd688r (Wild and Maddison, 2008)] using standard procedures (http://zsm-entomology.de/wiki/Coleoptera#The_Beetle_D_N_A_Lab). PCR products were purified and processed for sequencing using BigDye v3.1 (ABI, Darmstadt, Germany). The assembling and editing of the sequences was performed using Sequencher 4.10.1 (Gene Codes, Ann Arbor, MI, USA). The alignment for each gene was done in MEGA v5.1 (Tamura et al., 2011). Protein coding genes were aligned using the ClustalW algorithm (Thompson et al., 1994), whereas ribosomal genes (*12s*, *16s*, and *18s*) were aligned on the MAFFT portal (<http://mafft.cbrc.jp/alignment/server>). All protein coding genes were then imported into Mesquite v2.75 (Maddison and Maddison, 2011) in order to control the reading frames. Sequence data were then concatenated using Sequence Matrix v1.7.8 (Meier et al., 2006) to create a single nucleotide matrix. New sequences were submitted to the Barcoding of Life Database (BOLD - www.boldsystems.org - BOLD DOI - BOLD process IDs ZSMDB001-14 - ZSMDB031-14), where all the sequences were automatically transferred to Genbank accession numbers KJ637864–KJ638138 (Table 1).

Table 1
List of species studied, including museum voucher numbers, BOLD process IDs (for histone 4 - h4) and GenBank accession numbers

GenBank accession numbers and BOLD process IDs															
Taxa	Voucher No	I2s	I6s	cob	5'col	3'col	co2	I8s	h3	h4	ark	cad	eno	wng	e/la
<i>Anisomeria histriata</i> (Brullé, 1835)	MB4325	-	KJ637885	KJ637924	KJ637865	-	-	KJ637902	-	ZSMDB001-14	KJ638123	KJ638037	KJ638060	-	KJ637942
<i>Agabus bipustulatus</i> (Linnaeus, 1776)	IR20	AY745642	AF428198	AY745659	-	AF309332	AY745659	AJ318687	EF670076	ZSMDB002-14	-	-	-	-	-
<i>Amphizoa lecontei</i> (Matthews, 1872)	IR-V-557	AY745639	AY071771	AY334160	-	AY071797	-	AJ318678	AY745673	ZSMDB003-14	-	EU677532	EU677555	EU677662	-
<i>Banites distigma</i> (Brullé, 1837)	IRBD	-	KJ637894	KJ637933	KJ637877	KJ637978	-	KJ637914	KJ638008	ZSMDB004-14	-	-	-	-	-
<i>Colymbetes fuscus</i> (Linnaeus, 1758)	MB0179	KJ637966	KJ637892	KJ637931	KJ637875	KJ637976	KJ637989	KJ637911	KJ638006	ZSMDB005-14	-	KJ638046	KJ638067	KJ638022	KJ637949
<i>Carabidytes upin</i> Balke et al., 1992	MB0306	KJ637964	KJ637891	FN356769	KJ637873	FN263070	KJ637988	FN257269	FN257567	ZSMDB006-14	KJ638129	KJ638044	KJ638066	FN256329	HF558697
<i>Hopertius planatus</i> Fall, 1927	MB0187	KJ637961	KJ637889	KJ637927	KJ637869	KJ637974	KJ637983	KJ637906	KJ638001	ZSMDB007-14	-	KJ638041	KJ638063	-	-
<i>Meladema imbricata</i> (Wollaston, 1871)	MB4793	KJ637969	KJ637898	KJ637937	KJ637881	-	KJ637993	KJ637919	KJ638011	ZSMDB008-14	KJ638135	-	-	-	-
<i>Neoscutipterus hornii</i> (Crotch, 1873)	MB0285	KJ637959	KJ637886	KJ637925	KJ637866	-	KJ637981	KJ637903	KJ637999	ZSMDB009-14	KJ638124	KJ638038	-	KJ638016	KJ637943
<i>Rhantus andinus</i> Balke, 1998a	MB3939	KJ637960	KJ637887	-	KJ637867	-	KJ637982	KJ637904	KJ638000	ZSMDB010-14	KJ638125	KJ638039	KJ638061	KJ638017	KJ637944
<i>Rhantus anisomychus</i> Crotch, 1873	MB0160	KJ637965	-	KJ637930	KJ637874	-	-	KJ637910	KJ638005	ZSMDB011-14	KJ638130	KJ638045	-	KJ638021	KJ637948
<i>Rhantus amecinus</i> Sharp, 1882	MB0467	FN257617	FN298848	FN356893	KJ637872	FN263072	KJ637987	FN257278	FN257576	ZSMDB012-14	KJ638128	KJ638043	KJ638065	FN256331	FN256345
<i>Rhantus atricolor</i> (Aubé, 1838)	MB0157	-	-	-	-	-	-	KJ637917	-	ZSMDB013-14	KJ638134	KJ638052	-	KJ638026	KJ637954
<i>Rhantus binotatus</i> (Harris, 1828)	MB0161	KJ637971	KJ637900	KJ637938	-	-	-	KJ637921	KJ638013	ZSMDB014-14	KJ638137	KJ638056	KJ638076	KJ638029	KJ637956
<i>Rhantus histriatus</i> (Bergsträsser, 1778)	MB0183	FN257606	FN298834	FN356762	-	FN263061	KJ637990	FN257259	FN257557	ZSMDB015-14	KJ638131	KJ638048	KJ638069	FN256319	-
<i>Rhantus hololei</i> Balke et al., 2002	MB0196	-	-	-	-	-	-	KJ637913	KJ638007	ZSMDB016-14	KJ638132	KJ638049	KJ638070	KJ638024	KJ637951
<i>Rhantus cheesmanae</i> Balke, 1993	MB1384	KJ637963	FN298824	FN356757	KJ637871	FN263051	KJ637985	FN257249	KJ638004	ZSMDB017-14	-	-	-	KJ638019	KJ637947
<i>Rhantus cvoletus</i> (Forster, 1771)	MB0180	KJ637972	FN298831	FN356886	KJ637883	FN263058	KJ637996	FN257256	FN257557	ZSMDB018-14	KJ638138	KJ638058	KJ638079	FN256316	KJ637957
<i>Rhantus graspi</i> (Gyllenhal, 1808b)	MB0193	KJ637968	KJ637897	KJ637936	KJ637880	KJ637979	KJ637992	KJ637918	KJ638010	ZSMDB019-14	-	-	KJ638054	KJ638027	KJ637955
<i>Rhantus gutticolis</i> (Say, 1830)	MB0198	KJ637958	KJ637884	KJ637923	KJ637864	KJ637973	KJ637980	KJ637901	KJ637998	ZSMDB020-14	KJ638122	KJ638036	KJ638059	KJ638015	KJ637941
<i>Rhantus incognitus</i> Scholz, 1927	MB3918	-	-	-	-	FN826906	KJ637986	KJ637909	-	ZSMDB021-14	KJ638127	-	KJ638064	KJ638020	-
<i>Rhantus signatus</i> kuscheli Guignot, 1952	MB4327	-	KJ637895	KJ637934	KJ637878	-	-	KJ637915	-	ZSMDB022-14	KJ638133	KJ638050	KJ638071	-	KJ637952
<i>Rhantus notatollis</i> (Aubé, 1837)	MB1330	KJ637970	KJ637899	-	-	-	KJ637994	KJ637920	KJ638012	ZSMDB023-14	KJ638136	KJ638055	KJ638075	KJ638028	-
<i>Rhantus phocaeorum</i> Guignot, 1957	MB4790	-	KJ637888	KJ637926	KJ637868	-	-	KJ637905	-	ZSMDB024-14	KJ638126	KJ638040	KJ638062	-	KJ637945
<i>Rhantus signatus</i> spec. (unpublished)	MB1222	-	KJ637896	-	-	-	xxxx	KJ637916	KJ638009	ZSMDB025-14	-	KJ638051	KJ638072	KJ638025	KJ637953

Table 1
(Continued)

GenBank accession numbers and BOLD process IDs															
Taxa	Voucher No	12s	16s	cob	5'col	3'col	co2	18s	h3	h4	ark	cad	eno	wng	efla
<i>Rhiantus signatus</i> (Fabricius, 1775)	MB0159	-	-	KJ637929	-	-	xxxx	KJ637908	KJ638003	ZSMDB026-14	-	-	-	-	-
<i>Rhiantus sozannae</i> Balke, 1990	MB0200	KJ637962	KJ637890	KJ637928	KJ637870	KJ637975	KJ637984	KJ637907	KJ638002	ZSMDB027-14	-	KJ638042	-	KJ638018	KJ637946
<i>Rhiantus saturalis</i> (MacLeay, 1825)	MB0006	FN257581	FN298810	FN356775	KJ637882	-	KJ637995	FN257231	FN257532	ZSMDB028-14	-	KJ638057	KJ638078	FN256293	FN256352
<i>Rhiantus vicinus</i> (Aubé, 1838)	MB3940	KJ637967	KJ637893	-	KJ637876	KJ637977	-	KJ637912	-	ZSMDB029-14	-	KJ638047	KJ638068	KJ638023	KJ637950
<i>Rhiantus vitifensis</i> J. Balfour-Browne, 1944	MB0469	FN257577	FN298849	FN356894	KJ637879	FN263073	KJ637991	FN257279	FN257548	ZSMDB030-14	-	KJ638053	KJ638073	FN256332	FN257220
<i>Senillites tristanicola</i> Brinck, 1948	MB3836	-	-	KJ637939	-	-	-	KJ637922	KJ638014	ZSMDB031-14	-	-	KJ638077	-	-

Table 2
Partitioning schemes used in this study (numbers of partition in brackets)

Partitioning scheme	Description
P1 (1)	Unpartitioned dataset
P2 (2)	Mitochondrial genes versus nuclear genes
P3 (2)	Protein-coding genes versus non-coding genes (12s, 16s, and 18s)
P4 (9)	One partition for each codon position of the combined mitochondrial and combined nuclear genes versus the non-coding genes (12s, 16s, and 18s)
P5 (13)	One partition for each gene
P6 (33)	One partition for each codon position of each coding gene versus the non-coding genes, each as a separate position (12s, 16s, and 18s)

Phylogenetic inference

Phylogenetic inferences were conducted using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) to investigate if different inference methods in fact converge on a highly similar topology. The MP analyses were carried out under TNT v1.1 (Goloboff et al., 2008) with the Tree Ratchet and Tree Fusing algorithms (the settings were: initial level 100, find minimal length 5 times, memory set for 10 000 trees) and 1000 jackknife (JK) replicates (probability of character deletion: 0.36) to assess the stability of nodes. Maximum likelihood analyses were conducted under RAxMLGUI v0.93 (Stamatakis, 2006) with the autoFC command for automatic determination of sufficient fast bootstrap (BS) repeats. Outgroup taxa and gene partitions (one partition for each gene) were defined manually. For thorough bootstrap searches, GTRGamma was used as model of sequence evolution. Bayesian inference analyses of the combined dataset were performed on the CIPRES science gateway (Miller et al., 2010) with MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003) testing six different partitioning schemes (Table 2). The best fitting substitution model for each was selected using the Bayesian information criterion (BIC) (Table 3) in jModelTest v1.0.1 (Posada, 2008). Each analysis consisted of two independent runs, each started with a random tree and consisted of eight Markov chains Monte Carlo (MCMC, one cold and seven incrementally heated) run for 30 million generations and sampled each 1000th generation. A conservative burn-in of 25% was applied by checking the convergence statistics provided by the program and effective sample size (ESS) values in Tracer v1.5 (Rambaut and Drummond, 2007) (Table 4). The resulting trees were combined in a majority rule consensus topology with posterior probability (PP) of nodes calculated using

Table 3
Best fitting substitution models for each partition under the Bayesian information criterion (BIC) (corrected Akaike information criterion, AICc, in brackets)

Dataset	Partition	BIC (AICc)	
P1 (byall)		GTR + I + G (GTR + I + G)	
P2 (mtvsnuc)	(mt)	GTR + G (GTR + G)	
	(nuc)	SYM + G (GTR + G)	
P3 (pcvsnpc)	(pc)	GTR + G (GTR + G)	
	(npc)	GTR + G (GTR + G)	
P4 (by9)	(mt1)	TrN + G (GTR + G)	
	(mt2)	GTR + G (GTR + G)	
	(mt3)	GTR + G (GTR + G)	
	(nuc1)	GTR + G (GTR + G)	
	(nuc2)	TPM1uf + G (GTR + G)	
	(nuc3)	GTR + G (GTR + G)	
P5 (byeach)	(12s)	HKY + G (TIM1 + G)	
	(16s)	GTR + G (GTR + G)	
	(18s)	TrN + G (GTR + G)	
	(ark)	HKY + G (GTR + G)	
	(cad)	TrN + G (GTR + G)	
	(co1)	GTR + G (GTR + G)	
	(co2)	TrN + I + G (TIM1 + I + G)	
	(cob)	HKY + I + G (GTR + I + G)	
	(ef1a)	TrNef + G (TrNef + G)	
	(eno)	SYM + g (SYM + G)	
	(h3)	HKY + I + G (HKY + I + G)	
	(h4)	F81 + I (F81 + I)	
	(wng)	K80 + G (TIM1 + G)	
	P6 (1vs2vs3)	(ark1)	TrNef + G (TrNef + G)
		(ark2)	F81 (JC)
		(ark3)	TVM + G (TVM + G)
(cad1)		GTR + G (GTR + G)	
(cad2)		HKY + G (HKY + G)	
(cad3)		HKY + G (HKY + G)	
(co11)		TrN + G (TrN + G)	
(co12)		TrN + G (TrN + G)	
(co13)		TVM + G (TVM + G)	
(co21)		JC (JC)	
(co22)		HKY + G (JC)	
(co23)		TrN + G (HKY + G)	
(cob1)		TrN + I + G (TrNef + I + G)	
(cob2)		F81 + G (JC)	
(cob3)		TPM1uf + G (TPM1uf + G)	
(ef1a1)		F81 + G (JC + G)	
(ef1a2)		K80 (JC)	
(ef1a3)		TPM1uf + G (TPM1uf + G)	
(eno1)		TrN + G (TrN + G)	
(eno2)		JC + G (JC + G)	
(eno3)		TVM + G (TVM + G)	
(h31)		TrN (JC)	
(h32)		JC (JC)	
(h33)	GTR + G (HKY + G)		
(h41)	JC (F81)		
(h42)	JC + I (K80 + I)		
(h43)	TVM + G (TVM + G)		
(wng1)	TIM1ef + G (JC)		
(wng2)	JC + G (JC)		
(wng3)	TVMef + G (K80 + G)		

the `sumt` command in MrBayes. The different strategies of partitioning were compared based on Bayes factors (B_F) using the harmonic mean of the log likelihoods (Kass and Raftery, 1995) (Table 4).

Results

Dataset

The aligned dataset contained 9449 bp, including five mitochondrial (*co1*, *co2*, *cob*, *12s*, and *16s*) and eight nuclear genes (*h3*, *h4*, *ef1a*, *eno*, *ark*, *cad*, *wng*, and *18s*) (Table 1). Base composition features are given in Table 5. As expected, the mtDNA was more AT biased, whereas the nDNA more GC biased. Protein coding genes in general showed no insertions or deletions (indels), we only found an amino acid deletion (3 bp indels) in the alignments of *cad* and *wng* (for outgroup *Amphizoa lecontei*). The *cad* and *wng* sequences were therefore realigned and translated into amino acid sequences for quality control. As expected, the *18s* and *16s* rRNA genes showed several single or multiple base indels between regions of high nucleotide conservation [length of *16s*: 784 bp (771–778 bp); length of *18s*: 2187 bp (1896–1991 bp)]. No indels were found in the *12s* gene.

Molecular phylogeny

The different methods of phylogenetic inference revealed similar topologies (Fig. 1). For the BI analyses (Fig. 1), partitioning scheme P4 (by nine partitions) was statistically the best (Table 4). The recovered topology was mostly congruent with the MP and ML analyses (Figs 1 and 2), with two exceptions being (i) *Bunites distigma*, which we found in a different clade in the MP analysis from the one recovered in ML and BI, and (ii) *Rhantus atricolor*, which was placed as sister to the *Rhantus binotatus* group in the BI topology. Topologies of the other partitioning schemes used in this study showed similar results (data not shown).

The New Guinean *Carabdytes upin* is recovered as sister lineage of all other Colymbetinae. In former studies, *C. upin* was placed in a clade with several Oceanic species of *Rhantus* not included here (*Rhantus pacificus* group, sensu Balke, 1993), but these were also always outside the remainder of *Rhantus*. The Holarctic genus *Colymbetes* (21 species, here represented by *C. fuscus*) is the second most basal taxa in Colymbetinae. *Hoperius*, *Meladema*, and *Neoscutopterus* are together monophyletic with high Bayesian support (JK = 75, PP = 1.0, BS = 68). This is sister to a clade containing the remainder of Colymbetinae.

In both ML and BI analyses, the monospecific Neotropical genus *Bunites* (*B. distigma*) is placed as the sister species of the remaining *Rhantus* species clade (PP = 1.0, BS = 87). This finding is challenged using MP where *B. distigma* is placed in a weakly supported clade with *Rhantus atricolor* (JK = 44). A strongly supported clade (JK = 88, PP = 1.0, BS = 100) containing several Australo-Oceanic species of *Rhantus* (*R. annectens*, *R. cheesmanae*, *R. suturalis*, and *R. vitiensis*, all

Table 4

Partition strategies used in this study, with Bayes factor (B_F) estimates, Bayesian inference (BI) harmonic means (BHM) and effective sample size (ESS) values

Partitioning scheme	BHM	ESS	B_F						
			P1	P2	P3	P4	P5	P6	
P1	−50821.68	11021.19	–	0	0	0	0	0	0
P2	−49791.68	10536.25	∞	–	n.s.	0	0	0	0
P3	−49791.75	10106.63	∞	n.s.	–	0	0	0	0
P4	−46873.84	2614.09	∞	∞	∞	–	∞	∞	∞
P5	−49076.46	3971.62	∞	∞	∞	0	–	–	0
P6	−48215.53	2643.91	∞	∞	∞	0	∞	∞	–

Table 5

Base composition features of the used genes. Base compositions are written in percentages, fragment lengths are written as number of aligned bases

	<i>col</i>	<i>co2</i>	<i>cob</i>	<i>12s</i>	<i>16s</i>	<i>18s</i>	<i>ark</i>	<i>wng</i>	<i>eno</i>	<i>cad</i>	<i>h3</i>	<i>h4</i>	<i>ef1a</i>
A	29.4	34.3	30.9	42.0	33.4	23.5	22.0	24.7	26.6	27.9	19.2	20.8	25.3
T	37.7	38.5	38.5	37.8	15.5	23.1	18.4	18.7	24.7	26.0	15.3	16.4	25.5
C	16.2	15.6	19.8	14.5	8.7	28.2	34.3	30.2	25.8	20.4	36.7	32.1	26.0
G	16.8	11.6	10.8	5.7	42.4	25.2	25.4	26.2	22.9	25.8	28.6	30.8	23.1
bp	1417	527	353	352	773	1974	674	500	677	818	307	159	553

Rhantus suturalis group sensu Balke et al., 2009; Tous-saint et al., 2013) was recovered as the sister of a complex of three other *Rhantus* species groups. The first one, the *Rhantus exsoletus* group, contains several Palaeartic representatives (*R. bistriatus*, *R. exsoletus*, *R. incognitus*, and *R. notaticollis*) (JK = 97, PP = 1.0, BS = 100). The latter represents the sister of two clades of *Rhantus* species, the *Rhantus binotatus* group, the *Rhantus signatus* group (Peck and Balke, 1993), and the single species *Rhantus atricolor*. The *Rhantus binotatus* group contains mostly Neotropical (*R. anisonychus*, *R. bohlei*, *R. gutticollis*, and *R. souzannae*) as well as Nearctic (*R. anisonychus*, *R. gutticollis*, and *R. binotatus*) and Afrotropical (*R. phocaenarum*) species (JK = 91, PP = 0.97, BS = 99). The *Rhantus signatus* group consists only of Neotropical species (*R. andinus*, *R. signatus kuscheli*, *R. spec. near signatus* (indicated as *R. spec.*), *R. signatus*, and *R. vicinus*). Both Anisomeriini taxa, *Anisomeria bistriata* and *Senilites tristanicola*, were associated with this neotropical *Rhantus* clade with strong support (JK = 100, PP = 1.0, BS = 100). *Anisomeria* came out as sister to this group in BI and ML analyses and *Senilites* nested inside it (Figs 1 and 2). In the parsimony analysis both were nested inside this clade (Fig. 1).

Taxonomy

Carabdytini Pederzani, 1995 is here supported as a synonym of Colymbetini sensu Nilsson (2013) as already suggested by Balke (2001). The tribe was erected by Pederzani (1995) because at the time, *Carabdytes* appeared as an enigmatic and isolated taxon with

no obvious close relatives. Balke et al. (2009) show that several Oceanian *Rhantus* consistently group with *Carabdytes* and that the latter is merely highly derived morphologically due to adaptation to fast flowing stream habitats. Morphological characters mentioned by Pederzani (1995) to justify Carabdytini were all rejected by Balke (2001). Anisomeriini Brinck, 1948 is unambiguously a synonym of Colymbetini. Our analyses necessitate the following nomenclatural acts:

Colymbetini Erichson, 1837: 149

= Anisomeriini Brinck, 1948: 112, **syn. nov.**

= Carabdytini Pederzani, 1995: 45, **syn. nov.**

Rhantus Dejean, 1833: 54

= *Senilites* Brinck, 1948: 16, **syn. nov.**

= *Anisomeria* Brinck, 1943: 7, **syn. nov.**

Rhantus bistriatus (Brullé, 1835), **comb. nov.**

Rhantus bistriatus (Brullé, 1835) is a secondary junior homonym of *Rhantus bistriatus* (Bergsträsser, 1778). We here propose the replacement name *Rhantus selkirki* Jäch, Balke & Michat **nom. nov.**¹
Rhantus tristanicola (Brinck, 1948), **comb. nov.**

¹Alexander Selkirk (1676–13 December 1721), also known as Alexander Selcraig, was a Scottish sailor who spent more than 4 years as a castaway after being marooned on an uninhabited island in the South Pacific Ocean. An unruly youth, Selkirk joined buccaneering expeditions to the South Seas, including one commanded by William Dampier, which called in for provisions at the Juan Fernández Islands off Chile. Selkirk judged correctly that his craft, the Cinque Ports, was unseaworthy, and asked to be left there. By the time he was rescued, he had become adept at hunting and making use of the resources found on the island. His story of survival was widely publicized when he returned home, and probably became a source of inspiration for writer Daniel Defoe's fictional Robinson Crusoe.

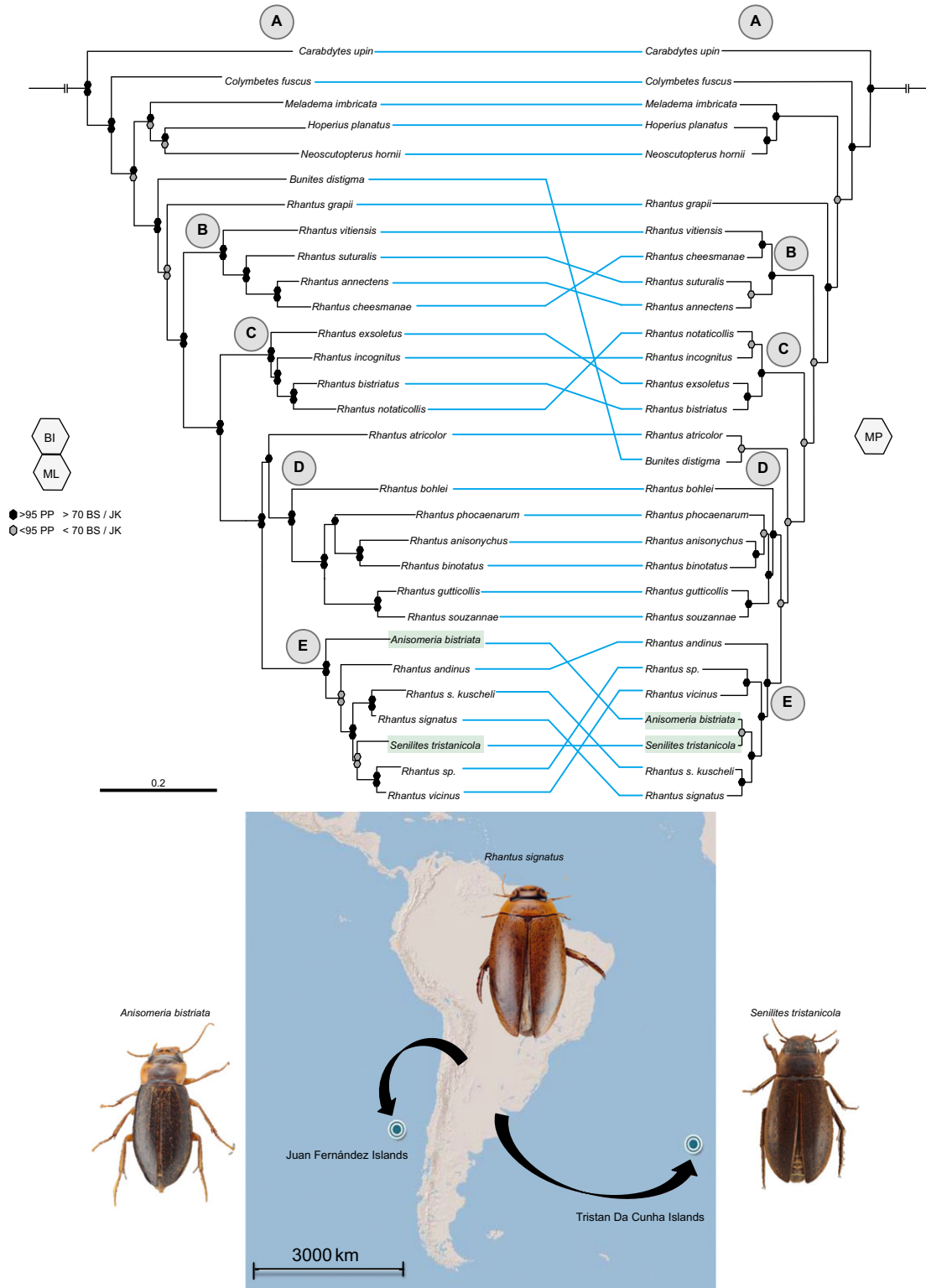


Fig. 1. Topology of the preferred Bayesian inference (BI) partitioning scheme (left), including node supports for posterior probability (PP) and bootstrap (BS) and preferred maximum parsimony (MP) topology of five most parsimonious trees (right). Jackknife values (based on 1000 replicates) are indicated on each node. Outgroups are pruned. Topological differences between both topologies. *Rhantus* species groups are indicated by letters in circles (A, *Rhantus pacificus* group; B, *Rhantus suturalis* group; C, *Rhantus exsoletus* group; D, *Rhantus binotatus* group; E, *Rhantus signatus* group).

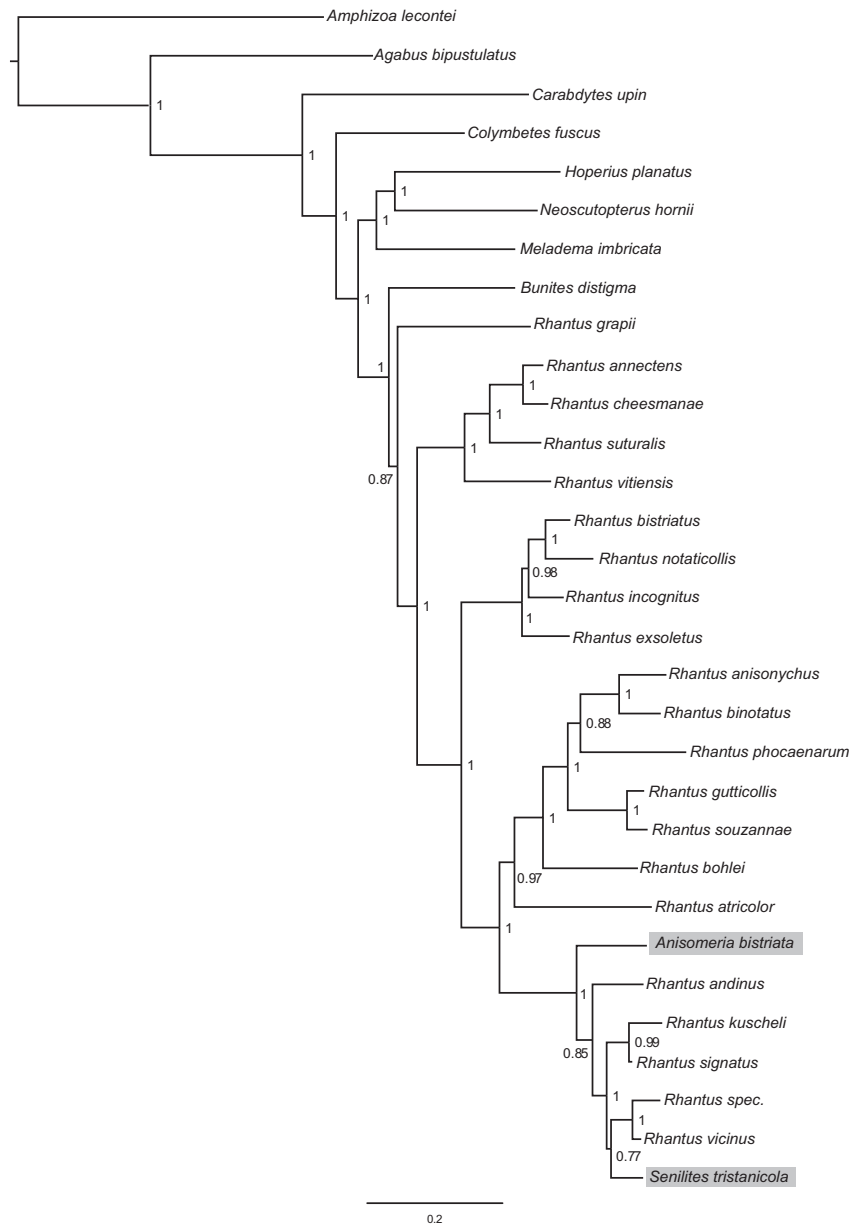


Fig. 2. Maximum likelihood (ML) topology. Bootstrap values are indicated on each node.

Discussion

Here we present a comprehensively sampled phylogenetic analysis of Colymbetinae diving beetles. Topologies from parsimony, likelihood, and Bayesian inference were highly similar and compatible in the focus area, suggesting sufficiently strong phylogenetic signal over different hierarchical levels. Phylogenetic relationships within the Colymbetinae had generally strong support in the model based analyses, whereas support levels were lower using the parsimony criterion. This might be due to different substitution rates in different genes, and especially among codon positions in the protein coding genes which strongly

dominate the dataset. Another explanation for slightly lower support values is insufficient gene coverage for some species (e.g. *Bunites distigma*). Incomplete character sampling can have a great effect on the parsimony based phylogenetic reconstruction depending on the percentage of missing data and also depending on the genes missing (Wiens and Morrill, 2011). This is, however, not a problem here due to the overall size of the dataset. A molecular dating approach was not applied in this study, as the fossil records of the Colymbetinae are very scarce (Nilsson, 2013). The aim of this analysis was to investigate the remarkable disjunction of Anisomeriini between the Tristan da Cunha and Juan Fernández Islands reported by Brinck

(1948), and we found (1) that both Anisomeriini genera *Senilites* and *Anisomeria* are in fact synonyms of *Rhantus*; and that both species, *R. selkirki* and *R. tristanicola*, belong to a Neotropical species group previously referred to as *R. signatus*-group. The MP analysis reveals a weakly supported clade of “*Senilites*” and “*Anisomeria*” inside the *R. signatus*-group. The BI and ML analyses reject a sister group relation of “*Senilites*” and “*Anisomeria*”. Both topologies would imply a mainland South American origin and two range expansion events: one into the South Pacific, one into the South Atlantic (Fig. S1). A Tristan da Cunha Islands and Juan Fernández Islands disjunction remains a valid concept, possibly even monophyly of the two species, as suggested in the parsimony analysis. Our study, however, suggests that the species are comparably recent, and we identified close relatives in South America. Anisomeriini as a valid tribe lacks any support, because monophyly of Colymbetini requires Anisomeriini in a sister group relationship. Such a topology would imply an old age and true relic character of Anisomeriini—this was clearly rejected here.

Interestingly, Juan Fernández Islands were also reached by the widespread southern South American *Rhantus signatus* (Fabricius, 1775), the island population being named as *R. signatus kuscheli* Guignot, 1952, and in need of taxonomic reinvestigation based on extensive material of *Rhantus signatus* in general. Reaching the islands required transoceanic dispersal or passive transport, as neither archipelago had land connections with mainland South America. *Rhantus selkirki* and *R. tristanicola* have vestigial wings, reduced probably in response to harsh environmental conditions on windy islands (McCulloch et al., 2009; Medeiros and Gillespie, 2011; Vogler and Timmermans, 2012). Wing and wing musculature reduction allow for habitus modification (Vogler and Timmermans, 2012) and might lead to the ground beetle-like habitus observed. Interestingly, the New Guinea *Carabdytes* has a similar, rather ground beetle like habitus, but does fly. Remarkably, *Rhantus tristanicola* occurs on two islands, Nightingale and Inaccessible (Brinck, 1948), about 20 km apart.

Geological studies of the Juan Fernández Islands indicate a volcanic origin, forming above the hotspot of the eastward drifting Nazca plate (Haberle, 2009). Investigations of geological material of the Islands of the archipelago, Alejandro Selkirk, Robinson Crusoe, and Santa Clara, indicate ages from 1 to 2, 4, and 5 Myr, respectively, whereas the underlying Nazca plate comprises a much older Eocene origin (Stuessy et al., 1984). The archipelago harbours a stunning insect fauna with a high level of endemism (70%), the majority of these species probably being derived from South American ancestral species that reached the archipelago (Stuessy et al., 1984; Haberle, 2009). Whereas the Juan Fernández Islands are situated about 750–600 km off

the coastline of Chile, the archipelago of Tristan da Cunha lies 3360 km off the coastline of the South American continent and about 2800 km from the African continent (Gillespie and Clague, 2009). The islands of the Tristan archipelago are small, volcanic islands in the central South Atlantic (Gillespie and Clague, 2009) and the youngest (c. 200 000 years) and largest (96 km²) island is Tristan, which is still an active volcano (Ryan et al., 2007). It first erupted some 3 Ma from the deep ocean floor in a depth of 3500 m. The present-day volcano is 5500 m high, and its peak is 2060 m above sea level. Inaccessible Island is thought to be around 3–4 Myr old; the oldest island of the archipelago is Nightingale, with an approximate age of 18 Myr (Ollier, 1984; Ryan et al., 2007). The Tristan da Cunha Archipelago was never connected to a continental mainland, which means that all present terrestrial flora and fauna had to disperse across the ocean. Most species arrived from South America, which can be explained by the prevailing westerly winds. However, some species have arrived from southern Africa. Once they reached the isolated archipelago, they adapted to their new habitats, resulting in many endemic species (Gillespie and Clague, 2009). Adaptation to new environments and extreme bottlenecks might then also mask “generic boundaries”, leading to “creation” of higher taxa by taxonomists when in fact there exist closely related species (cf. Balke and Ribera, 2004). Here lies the very strength of phylogenetic analysis, the search for commonalities rather than deviations in the quest for a natural classification (Hennig, 1950). The results of our study indicate a South American origin for *Rhantus selkirki* and *R. tristanicola*. The latter colonized the Tristan da Cunha Archipelago by transcending more than 3000 km from the South American mainland. Although this distance seems to be unrealistic for a dispersal event, the present phylogenetic topology indicates a possible trans-Atlantic long distance range expansion, as suggested, for example, for South Atlantic finches with a South American origin (Ryan et al., 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. MacClade reconstruction of geographical traits for mapping the biogeographical history of the *Rhantus signatus* clade.