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Biogeography of Australasian flightless weevils (Curculionidae, Celeuthetini) suggests permeability of Lydekker's and Wallace's Lines

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The Indo-Australian region was formed by the collision of the Australian and Asian plates, and its fauna largely reflects this dual origin. Lydekker's and Wallace's Lines represent biogeographic transition boundaries between biotas although their permeability through geological times was rarely assessed. Here, we explore the evolutionary history of flightless weevils of the tribe Celeuthetini in this geologically highly complex region. We generated a DNA sequence data set of 2236 bp comprising two nuclear and two mitochondrial markers for 62 species of the Indo-Australian tribe Celeuthetini. We used Bayesian Inference and Maximum Likelihood to reconstruct the first molecular phylogeny of the group. Based on this phylogenetic tree, we employed the program BioGeoBEARS to infer the biogeographical history of Celeuthetini in the region. The group's radiation begun east of Wallace's Line, probably during the mid-Eocene. We unveil multiple transgressions of Lydekker's and Wallace's Lines mostly during the Miocene with a significant role of founder-event speciation. The phylogeny of Celeuthetini is geographically highly structured with the first lineages occurring in New Guinea and the Moluccas, and a deep divergence between two clades largely confined to Sulawesi and their respective sister clades of the Lesser Sunda Islands. Wallace's Line was crossed once from Sulawesi and three times from the Lesser Sunda Islands to Java whilst Lydekker's Line was crossed once from New Guinea to the Moluccas. Although this beetle group shows extensive local diversification with little dispersal, the biogeographical demarcations of the Australasian region appear to have been rather porous barriers to dispersal.

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Introduction

The Indo-Australian Archipelago (IAA) has fascinated biologists ever since Alfred R. Wallace suspected geological history might explain seemingly complex distribution patterns across the archipelago (Wallace 1869). He was also the first to realize that the distribution of many taxa follows lines of shallow seas along the Asian Sunda Shelf and the Australian Sahul Shelf (Wallace 1860). One of the most famous biogeographical transitions was named after him (Huxley 1868), and the region between 'Wallace's Line' in the west and Lydekker's Line

(Lydekker 1896) in the east is today known as 'Wallacea', faunistically a melting pot of Oriental and Australian biota.

Generations of biogeographers have sought to understand patterns and processes behind the incredible biodiversity of the IAA with respect to its intricate geological history, leading towards integrative approaches involving biology, geology and geography (Hall 2002, 2012, 2013; Lohman *et al.* 2011; Brown *et al.* 2013; Toussaint *et al.* 2014). The region was subdivided into various areas of endemism (Turner *et al.* 2001; Brown *et al.* 2006), and examples for specific clades originating either in the west or the east are comparably well documented (Stelbrink *et al.* 2012; Webb & Ree 2012; Klaus *et al.* 2013). However, large-scale molecular phylogenies covering the entire IAA remain rare. Thus, the direction and frequency of dispersal events and the modes of biotic exchange between islands are not well understood (Lohman *et al.* 2011; Webb & Ree 2012). In general, biogeographical lines seem to be rather porous for plants with a higher proportion of dispersals from west to east than the opposite direction (Crayn *et al.* 2015). In *Begonia*, Thomas *et al.* (2012) document west to east dispersal and rapid diversification in Wallacea and New Guinea; wax plants (*Hoya*) also originated in south/South-East Asia and then colonized the IAA and eventually Australasia (Wanntorp *et al.* 2014).

Recently, comprehensive studies, however, helped to reveal a variety of ecologically different animals having crossed the lines. Peacock swallowtail butterflies with great flight capability colonized the Oriental and Australasian regions out of the Sunda-Wallacea region (Condamine *et al.* 2013), while *Delias* butterflies probably originated on the Australian plate periphery with Wallacea as an important area of their early radiation (Müller *et al.* 2013). Animals with less obvious over-seawater chance dispersal ability include fanged frogs that originated in SE Asia and spread across the IAA, with frequent exchange between Borneo, the Philippines and Sulawesi, crossing Wallace's and Huxley's Lines (Evans *et al.* 2003). Flightless *Trigonopterus* weevils crossed Wallace's Line three times to reach Bali from the east (Tänzler *et al.* 2014). The widespread diving beetle *Rhantus suturalis* also crossed Wallace's Line to colonize most of the Palearctic region out of New Guinean highlands in the Quaternary (Balke *et al.* 2009; Toussaint *et al.* 2013).

Two tribes of the megadiverse weevil subfamily Entiminae are almost entirely restricted to the IAA, that is the Pachyrrhynchini and the Celeuthetini. While both are extremely diverse with hundreds of species in the Philippines, Wallacea and Melanesia, they are almost absent from the neighbouring Asian and Australian shelf regions. Apparently, their evolution was largely staged in the emerging IAA. Species of both tribes are apterous, limiting their abilities of dispersal and boosting microendemism (Marshall 1956).

The Celeuthetini are less known than the Pachyrrhynchini, which are often found in ornamental display boxes of tropical insects. Nevertheless, Celeuthetini are an equally colourful and morphologically diverse group, and the long dorsolateral elytral extensions of some genera appear almost unreal. Marshall (1956) provides an excellent overview of the group and delineates it from other apterous entimine tribes, the Elytrurini and the Rhyncogonini. The monophyly of Celeuthetini appears plausible based on morphological characters such as the abbreviated metanepisternal suture. Their range extends from their area of highest diversity in Wallacea and Melanesia to the islands of Fiji and Samoa in the east; Taiwan and some southern Japanese islands are reached in the north (Alonso-Zarazaga & Lyal 1999); in Australia, only few species of Papuan affinities occur around Torres Strait (Pullen *et al.* 2014); few species are found in Borneo and Java (Marshall 1956), while the group is entirely absent from Sumatra and continental Asia. The majority of described species live on foliage and some are agricultural pests (Wesis *et al.* 2010). A large number of mostly unnamed species dwell the leaf litter, and some have fully reduced eyes as a consequence of their edaphic lifestyle. While many of the named species and genera have been described during the colonial era (e.g. Faust 1897; Heller 1900; Marshall 1956; Tanner 1969), the tribe seems to have fallen into obscurity in subsequent years. Few taxonomic revisions have treated selected genera (Thompson 1977; Riedel & Schönitzer 1996), but no attempts have been made to revise the confused generic classification.

Here, we use a representative sampling of species from across the IAA to (i) present the first phylogenetic inference for the tribe Celeuthetini, (ii) provide a temporal framework for the evolution of this group using a Bayesian relaxed clock to infer divergence time estimates and (iii) rely on the latest models to reconstruct the biogeographical history of the group and investigate the permeability of Wallace's and Lydekker's Lines to these flightless tropical weevils.

Materials and methods

Taxon sampling and molecular biology

We sampled 62 Celeuthetini species from New Guinea, the Moluccas, Sulawesi, Java and the Lesser Sunda Islands (Table 1). Five outgroup representatives belong to two other tribes of Entiminae from the same region, that is Ottistirini and Pachyrrhynchini. Celeuthetini and Pachyrrhynchini are closely related and presumably sister groups based on morphological characters and our preliminary molecular analyses covering a larger number of entimine tribes. Species were selected to cover a range of lifestyles and habitats as well as the morphology-based species groups we defined based on studies of museum collections. Specimens were identified using the taxonomic literature, and in many cases names were verified by comparison with type material deposited in the museums of Dresden and London. Nomenclature follows Alonso-Zarazaga & Lyal (1999). Total genomic DNA was extracted non-destructively from whole beetles using the DNeasy kit (Qiagen, Hilden, Germany): the specimens preserved in absolute ethanol were opened at the prothorax–mesothorax joint before tissue lysis, retrieved after extraction and dry-mounted as collection vouchers. They are currently deposited at the State Museum of Natural History Karlsruhe (Germany); some will later be transferred to LIPI Research Center of Biology – Division of Zoology, Cibinong (Indonesia). We used standard PCR protocols (see Appendix S1) to amplify and then sequence the following gene fragments: cytochrome c oxidase subunit 1 (657 bp), 16S rRNA (511 bp), 18S (385 bp) and arginine kinase (683 bp). Sequences were edited using Sequencher v. 4.9 (GeneCodes Corp., Ann Arbor, MI, USA). Protein-coding genes were aligned and reading frames checked with MEGA 6 (Tamura *et al.* 2013). The non-coding genes 16S and 18S were aligned in MAFFT version 7 (Katoh & Standley 2013) using the Q-INS-i method, which considers the secondary structure of RNA. The different data sets used to infer phylogenetic relationships were generated in Sequence Matrix 1.7.2 (Meier *et al.* 2006). Sequences were deposited at European Nucleotide Archive (EMBL accession numbers LN866322-LN866564).

Molecular phylogenetics

We used Bayesian inference (BI) and maximum likelihood (ML) to reconstruct phylogenetic relationships using a concatenated data set. The partitions and corresponding optimal models of substitution were searched under PARTITIONFINDER 1.1.1 (Lanfear *et al.* 2012) using the '*greedy*' algorithm, either the '*mrbayes*' or '*raxml*' set of models, and the Akaike information criterion corrected (AICc) to compare the fit of the different models. The BI analyses were performed using MRBAYES 3.2.2 (Ronquist *et al.* 2012). Instead of selecting the substitution models *a priori* based on the results of PartitionFinder, we used the different partitions recovered but used reversible-jump Metropolis-coupled Markov chain Monte Carlo (MCMC) to explore the entire space of substitution models (Huelsenbeck *et al.* 2004). Two simultaneous and independent runs consisting of eight MCMC (one cold and seven incrementally heated) running 30 million generations were used, with a tree sampling every 5000 generations to calculate posterior probabilities (PP). To investigate the convergence of the runs, we investigated the split frequencies and effective sample size (ESS) of all the parameters and plotted the log-likelihood of the samples against the number of generations in TRACER 1.5 (http://BEAST.bio.ed.ac.uk/Tracer). A value of ESS > 200 was acknowledged as a good indicator of convergence. All the trees that predated the time needed to reach a log-likelihood plateau were discarded as burn-in, and the remaining samples were used to generate a 50% majority rule consensus tree. The ML analyses were conducted with the best partitioning scheme selected in PARTITIONFINDER 1.1.1 (Lanfear *et al.* 2012) using RAxML (Stamatakis 2006). We used the AutoFC option in RAxML to calculate the optimal amount of *bootstrap* (BS) replicates, which indicate the level of support at each node. A calculated PP ≥ 0.95 or a BS ≥ 70 was considered to indicate strong support for a given clade (Hillis & Bull 1993; Erixon *et al.* 2003).

Divergence time estimation

Divergence times were inferred with the BEAST 1.8.0 (Drummond *et al.* 2012). The partitions and models of nucleotide substitution were selected under PARTITIONFINDER 1.1.1 (Lanfear *et al.* 2012) using the '*greedy*' algorithm, the '*beast*' set of models and the AICc. We tested the hypothesis of molecular clock for both data sets using PAUP* (Swofford 2003), and as it was significantly rejected ($P < 0.001$), we used a Bayesian relaxed clock allowing rate variation among lineages as implemented in BEAST. To calibrate the tree, we used a substitution rate calculated for tenebrionid mitochondrial genes in Papadopoulou *et al.* (2010) based on a geological calibration. To account for uncertainty, we used a uniform prior encompassing the credibility interval calculated for both CO1 and 16S (i.e. 0.0131 ± 0.0013). Two runs performed under a *birth–death process* consisted of 30 million generations sampled every 1000 generations. The convergence of the runs was investigated using ESS, a conservative burn-in of 25% was applied after checking the log-likelihood curves, and the different runs were merged using LOGCOMBINER 1.8.0 (Drummond *et al.* 2012). The maximum credibility tree, median ages and their 95% highest posterior density (HPD) were generated afterwards under TREEANNOTATOR 1.8.0 (Drummond *et al.* 2012).

Ancestral range reconstruction

We used BIOGEOBEARS (Matzke 2013a) as implemented in R to infer the biogeographical history of Celeuthetini weevils across most of their range of distribution. This program allows reconstruction of the biogeographical history of a clade under different models such as DEC (Ree *et al.* 2005; Ree & Smith 2008), DIVA (Ronquist 1997) or BayArea (Landis *et al.* 2013). Additionally, it implements a parame-

Table 1 Taxon sampling. Overview of the specimens used in this study, their voucher identification number, classification, collecting locations and gene fragments used in the data set. Successful sequencing of a gene fragment is indicated (by +) for each species

Voucher ID	Tribe	Genus	Species	Author	Locality	CO1	AK	18S	16S
ARC3434	Celeuthetini	*Albertisius*	*excellens*	(Faust)	PNG, Central Prov., Moroka area, Kailaki, Beremutana ridge	+	+	+	+
ARC3550	Celeuthetini	*Apirocalodes*	*wegneri*	Voss	Flores Isl., Ruteng, Gn. Ranaka	+	+	+	+
ARC3441	Celeuthetini	*Apirocalus*	*ebrius*	Faust	PNG, Morobe Prov., Huon peninsula, mountain SW Pindiu	+	+	+	+
ARC3410	Celeuthetini	*Apotomoramphus*	sp 2		S-Sulawesi, Pc. Palopo, Gn. Sampuna	+	+	+	+
ARC3424	Celeuthetini	*Apotomoramphus*	sp 1		S-Sulawesi, Selayar Isl., Pagarangan	+	+	+	+
ARC3562	Celeuthetini	*Apotomorhamphus*	sp 3		N-Sulawesi, Tomohon, Rurukan, Gn. Mahawu	+	–	+	+
ARC3565	Celeuthetini	*Atactoglymma*	sp 1		N-Sulawesi, Kotamobagu, Matalibaru	+	+	+	+
ARC3413	Celeuthetini	*Coptorhynchus*	sp pr *niger*	Günther	S-Sulawesi, Tanah Toraja, Bittuang, Gn. Karoa	+	+	+	+
ARC3416	Celeuthetini	*Coptorhynchus*	sp		S-Sulawesi, Gn. Lompobattang, Malakaji, Parambintolo	+	+	+	+
ARC3418	Celeuthetini	*Coptorhynchus*	sp pr *subtilis*	Faust	S-Sulawesi, Tanah Toraja, Rantepao, Gn. Karre (= Gn. Wokim)	+	+	+	+
ARC3421	Celeuthetini	*Coptorhynchus*	sp 1		S-Sulawesi, Tanah Toraja, Ponding, Baruppu	+	+	+	–
ARC3436	Celeuthetini	*Coptorhynchus*	*ternatensis*	Guérin-Méneville	N-Maluku, Ternate Isl., Marikurubu, Gn. Gamalama	+	+	+	+
ARC3431	Celeuthetini	Gen 1	sp 1		W-PAPUA, Jayawijaya Reg., Jiwika, Kurulu	+	+	+	+
ARC3432	Celeuthetini	Gen 2	sp 1		W-PAPUA, Jayawijaya Reg., Jiwika, Kurulu	+	+	+	+
ARC3427	Celeuthetini	Gen 3	sp 1		W-PAPUA, Jayapura Reg., Cyclops Mts., Doyo	+	+	+	+
ARC3426	Celeuthetini	Gen 4	sp 1		W-PAPUA, Jayapura Reg., Sentani, Cyclops Mts.	+	+	+	+
ARC3422	Celeuthetini	Gen 5	sp 1		S-Sulawesi, Tanah Toraja, Ponding, Baruppu	+	+	+	+
ARC3423	Celeuthetini	Gen 5	sp 2		S-Sulawesi, Tanah Toraja, Ponding, Baruppu	+	+	+	+
ARC3415	Celeuthetini	Gen 6	sp 1		S-Sulawesi, Tanah Toraja, Ponding, Baruppu	+	+	+	+
ARC3566	Celeuthetini	Gen 7	sp 1		N-Sulawesi, Kotamobagu, Matalibaru	+	+	+	+
ARC3411	Celeuthetini	Gen 8	sp 1		S-Sulawesi, Tanah Toraja, Bittuang, Gn. Karoa	+	+	+	+
ARC3412	Celeuthetini	Gen 8	sp 2		S-Sulawesi, Tanah Toraja, Bittuang, Gn. Karoa	+	+	+	+
ARC3420	Celeuthetini	Gen 8	sp 3		S-Sulawesi, Tanah Toraja, Rantepao, Gn. Karre (= Gn. Wokim)	+	+	+	+
ARC3429	Celeuthetini	*Guineobius*	*baliemensis*	Riedel	W-PAPUA, Jayawijaya Reg., Jiwika, Kurulu	+	–	+	+
ARC3430	Celeuthetini	*Guineobius*	*niger*	Riedel	W-PAPUA, Jayawijaya Reg., Jiwika, Kurulu	+	+	+	–
ARC3409	Celeuthetini	*Heteroglymma*	*heteroglymmoides*	(K. Günther)	S-Sulawesi, Pc. Palopo, Gn. Sampuna	+	–	+	+
ARC3560	Celeuthetini	*Heteroglymma*	*biramosa*	Motschulsky	N-Sulawesi, Tomohon, Rurukan, Gn. Mahawu	+	–	+	+
ARC3561	Celeuthetini	*Heteroglymma*	*cimex*	Heller	N-Sulawesi, Tomohon, Rurukan, Gn. Mahawu	+	–	+	+
ARC3563	Celeuthetini	*Heteroglymma*	*albicans*	Heller	N-Sulawesi, Tomohon, Rurukan, Gn. Mahawu	+	–	+	+
ARC3567	Celeuthetini	*Heteroglymma*	sp pr *biramosa*	Motschulsky	N-Sulawesi, Kotamobagu, Matalibaru	+	–	–	+
ARC3568	Celeuthetini	*Heteroglymma*	sp 2		N-Sulawesi, Kotamobagu, Modoinding, Lake Moat area	+	–	+	+
ARC3569	Celeuthetini	*Heteroglymma*	sp 1		N-Sulawesi, Kotamobagu, Modoinding, Lake Moat area	+	+	+	+
ARC3546	Celeuthetini	*Javaulius*	Pr *rudis*	Marshall	C-Java, N slopes of Dieng plateau, Gn. Deles, Petungkriyono	+	+	+	+
ARC3548	Celeuthetini	*Javaulius*	sp 2		E-Java, Gn. Arjuno, road Batu – Pacet, Cangar	+	+	–	+
ARC3549	Celeuthetini	*Javaulius*	sp 1		E-Java, Krucil, Bremi, Gn. Argopuro (trail to Taman Hidup)	–	+	+	+
ARC3559	Celeuthetini	*Javaulius*	sp 3		Flores Isl., Ruteng, Gn. Ranaka	–	+	+	–
ARC3437	Celeuthetini	*Moluccobius*	sp 2		N-Maluku, Ternate Isl., Marikurubu, Gn. Gamalama	+	+	+	+
ARC3439	Celeuthetini	*Moluccobius*	sp 3		N-Maluku, Halmahera Isl., Sidangoli, Kali batu putih	+	+	+	+

Table 1 Continued

Voucher ID	Tribe	Genus	Species	Author	Locality	CO1	AK	18S	16S
ARC3440	Celeuthetini	*Moluccobius*	sp 1		N-Maluku, Halmahera Isl., Sidangoli, Kali batu putih	+	+	+	+
ARC3544	Celeuthetini	*Nothes*	sp 2		W-Java, Cianjur, Gn. Gede above Kebun Gede	+	–	+	+
ARC3545	Celeuthetini	*Nothes*	sp 1		W-Java, Maja, Gn. Ciremai	+	+	+	+
ARC3547	Celeuthetini	*Nothes*	sp 3		W-Java, Gn. Sawal, Ciamis, Panjalu, Tembong	+	+	+	+
ARC3438	Celeuthetini	*Opterus*	*echinatus*	Marshall	N-Maluku, Halmahera Isl., Sidangoli, Kali batu putih	+	+	+	+
ARC3442	Celeuthetini	*Opterus*	sp 1		W-PAPUA, Biak Reg., Biak Island, Nernu	+	+	+	+
ARC3433	Celeuthetini	*Oribius*	sp 1		W-PAPUA, Jayawijaya Reg., Jiwika, Kurulu	+	+	+	+
ARC3428	Celeuthetini	*Parasphenogaster*	cf ottonis	Heller	W-PAPUA, Jayapura Reg., Sentani, Cyclops Mts.	+	+	+	+
ARC3564	Celeuthetini	*Picronotus*	*asper*	Pascoe	N-Sulawesi, Tomohon, Rurukan, Gn. Mahawu	+	+	+	+
ARC3417	Celeuthetini	*Piezonotus*	*kalidupae*	Heller	SE Sulawesi, Buton Isl., Bau Bau, Lapodi	+	+	+	+
ARC3425	Celeuthetini	*Piezonotus*	*dammerincola*	Heller	S-Sulawesi, Selayar Isl., Pagarangan	+	+	+	+
ARC3553	Celeuthetini	*Piezonotus*	*segnis*	Heller	Flores Isl., Ruteng, Hotel garden	+	+	+	+
ARC3539	Celeuthetini	*Syntrophus*	*virescens*	Heller	C-Bali, Bedugul, Gn. Pohen (= Gn. Tapak = Gn.Keramat)	+	–	+	+
ARC3540	Celeuthetini	*Syntrophus*	*setosapex*	(Heller)	C-Bali, Bedugul, Tamblingan	+	–	+	+
ARC3541	Celeuthetini	*Syntrophus*	cf *radiatifrons*	(Heller)	C-Bali, Bedugul, Tamblingan	+	–	+	+
ARC3542	Celeuthetini	*Syntrophus*	*carinulifer*	(Heller)	C-Bali, Bedugul, Gn. Catur	+	+	+	+
ARC3554	Celeuthetini	*Syntrophus*	sp 2		E-Java, Meru Betiri N.P., Sukamade	+	+	+	+
ARC3556	Celeuthetini	*Syntrophus*	*bipusulosus*	(Heller)	Lombok Isl., Gn. Rinjani, Senaru, Rinjani-track	+	+	+	+
ARC3557	Celeuthetini	*Syntrophus*	*echinatus*	(Heller)	Lombok Isl., W Sengigi, Gn. Pusuk	+	–	+	+
ARC3558	Celeuthetini	*Syntrophus*	sp 1		Lombok Isl., W Sengigi, Gn. Pusuk	+	+	+	+
ARC3543	Celeuthetini	*Temnogastrus*	*humeralis*	(Heller)	C-Bali, Bedugul, Gn. Catur	+	–	+	+
ARC3552	Celeuthetini	*Temnogastrus*	*granulatus*	Voss	Flores Isl., Ruteng, Gn. Ranaka	+	–	+	+
ARC3555	Celeuthetini	*Temnogastrus*	cf *javanus*	(Faust)	E-Java, Meru Betiri N.P., Sukamade	+	–	+	+
ARC3435	Celeuthetini	*Trigonospartus*	*rufidorsum*	Faust	PNG, Central Prov., Moroka area, Kailaki, Beremutana ridge	+	+	+	+
ARC3508	Ottistirini	*Ittostira*	pr *costulata*	Heller	S-Sulawesi, Tanah Toraja, Ponding, Baruppu	+	–	+	+
ARC3513	Ottistirini	*Ottistira*	*dani*	Riedel	W-PAPUA, Jayawijaya Reg., Jiwika, Kurulu	+	+	+	+
ARC3507	Pachyrhynchini	*Pachyrrhynchus*	*forsteni*	Snellen van Vollenhoven	N-Maluku, Halmahera Isl., Jailolo, Payo, Gn. Jailolo	+	+	+	+
ARC3512	Pachyrhynchini	*Pantorhytes*	*huonarius*	Stibick	PNG, Morobe Prov., Huon peninsula, Sattelberg	+	+	+	+
ARC3506	Pachyrhynchini	*Sphenomorpha*	cf wallacei	Behrens	N-Maluku, Halmahera Isl., Jailolo, Payo, Gn. Jailolo	–	+	+	+

ter describing founder-event speciation (+J), which is assumed to be significant in archipelagic settings (Matzke 2013b, 2014). This program also allows the comparison of the different models tested in a statistical framework. We conducted the analyses using the BEAST maximum clade credibility tree with outgroups pruned. The following regions were used in the analyses: A, Java; B, Bali; C, Sulawesi; D, Lesser Sunda Islands; E, Moluccas; and F, New Guinea. Bali was coded as a separate area as it is in a critical zoogeographical position west of Wallace's Line; moreover, it had proved to be unrelated to Java in another weevil genus (Tänzler *et al.* 2014) raising doubts on the previously accepted opinion that the faunas of Java and Bali are very closely related. The distribution of each taxon was recovered from the literature (Faust 1895, 1896, 1897; Heller 1914, 1940, 1941; Günther 1938; Voss 1940, 1961; Marshall 1956) and/or from our field notes from the past 25 years. Some species will be described, respectively, transferred to other genera in a separate publication (Riedel, in prep.). Because of the extremely dynamic palaeogeographical and palaeoclimatic histories of the region during the past 50 million years (Myr) (Miller *et al.* 2005; Hall 2012, 2013), we designed two time slices with differential dispersal rate parameters between the areas as summarized in Table 2.

Results

Phylogenetic relationships

The phylogenetic reconstructions obtained by MrBayes and RAxML (Fig. 1) were largely congruent and retrieved the tribe Celeuthetini as monophyletic. There is some uncertainty resolving the first clades of New Guinea genera, but a clade comprising all the taxa from Sulawesi and the Sunda Arc plus the Papuan genera *Albertisius*, *Apirocalus*, *Opterus*, and genus 4 is strongly supported. The phylogeny of species from Sulawesi, the

Table 2 Matrices of time slices and dispersal rates used in BIOGEOBEARS

	Java	Bali	Sulawesi	Lesser S.	Moluccas	New Guinea
0–15.0 Ma						
Java	1	1	0.5	0.5	0	0
Bali	1	1	0.5	0.5	0.1	0
Sulawesi	0.5	0.5	1	0.1	0.5	0.1
Lesser S.	0.5	0.5	0.1	1	0	0
Moluccas	0	0.1	0.5	0	1	1
New Guinea	0	0	0.1	0	1	1
15.0–50.0 Ma						
Java	1	1	0.5	0.1	0	0
Bali	1	1	0.5	0.1	0	0
Sulawesi	0.5	0.5	1	0.1	0.5	0.1
Lesser S.	0.1	0.1	0.1	1	0	0
Moluccas	0	0	0.5	0	1	1
New Guinea	0	0	0.1	0	1	1

Lesser Sunda Islands and Java is well resolved and usually strongly supported, with the exception of the clade containing *Javaulius* partly showing weaker support. The genera *Piezonotus* and *Picronotus* are deeply nested in *Coptorhynchus*, and the genera *Javaulius* and *Apirocalodes* are nested in *Syntrophus*.

Divergence time estimates and ancestral range reconstruction

Our BEAST analysis recovered the split between the tribe Celeuthetini and its sister clade at 48.9 Ma (95% HPD: 37.1–62.1 Ma). A chronogram derived from our BEAST analysis and showing the divergence time estimates for the tribe is presented in Fig. 2. We infer an early origin of the tribe Celeuthetini in the late Eocene (43.5 Ma, 95% HPD: 34.0–55.4 Ma). The three main clades of Celeuthetini weevils diversified at the Eocene/Oligocene transition, while most branching events occurred during the Miocene. The latest diversification events are recovered in the genera *Heteroglymma* and *Moluccobius* during the Quaternary.

The results of the different models used in the program BIOGEOBEARS are presented in Table 3. In the null model M0 as well as in the model M1 comprising two time slices and optimized dispersal rates between areas, the model DEC+J was recovered as significantly better than the other models. A graphic representation of the biogeographical history under this model is presented in Fig. 3.

We infer a joint origin in New Guinea + Lesser Sunda Islands + Sulawesi, east of Wallace's Line (Figs 2 and 3). We find four independent transgressions of Wallace's Line possibly in the Miocene: three times from the Lesser Sunda Islands and one from Sulawesi to Java. We also infer one colonization event of Bali from Java, back towards the east, in the mid-Miocene without further transgression of Wallace's Line eastwards. We also infer the colonization of Moluccas out of New Guinea at the same period. We recover two signatures of range expansion via founder-event speciation in the history of the group. The first one is the colonization of Sulawesi and Lesser Sunda Islands from New Guinea and in a more derived position of this same clade the colonization of the Lesser Sunda Islands from Sulawesi. Most of the biogeographical dynamics took place in the early stages of the history of the group with no main biogeographical event after the mid-Miocene.

Discussion

Phylogenetics and taxonomy

The phylogeny obtained is largely congruent with the generic classification and/or with important morphological characters. A separate publication will focus on taxonomic and nomenclatural issues (Riedel, in prep.), but few comments need to be made here as well. The genus *Coptorhynchus* Guérin-Méneville (*sensu strictu*, as defined by the concept of the junior synonym *Stereogastrus* Marshall; Alonso-Zarazaga & Lyal 1999) comprising >50 species from Sulawesi and the Moluccas is not monophyletic. It is characterized by a sexually dimorphic modification of the female venter with ventrites 1 and 2 enlarged and ventrites 3–5 unusually small and retracted (Voss 1940; Marshall 1956). A similar modification is also found in *Piezonotus* Schoenherr and *Picronotus* Marshall (see Marshall 1956, p. 126), which according to our reconstruction are part of the *Coptorhynchus* clade. At least two other genera not included in our phylogeny (*Machaerostylus* Heller from New Britain and *Tarunus* Marshall from the Sangihe Islands) have a similar morphology and may also need to be synonymized after a more comprehensive study.

Syntrophus Marshall is also polyphyletic: the main character separating it from the largely edaphic *Javaulius* Marshall is a longer funicular article 2. However, in edaphic genera of Celeuthetini, the articles of the antennal funicle are always short and subovate, so apparently this change of character is related to a change of habitat. *Apirocalodes* Voss was described as a monotypic genus because of its unusual elytral flanges resembling the Papuan genus *Apirocalus* Pascoe otherwise not closely related (Voss 1961). More interesting is the convergent gain, respectively, the secondary loss of a peculiar conical eye shape. However, this character has long been known as homoplastic (Heller 1940; pp. 93–94) and is found equally unstable in the genus *Trigonops* Guérin-Méneville (Tanner 1969).

More taxonomic work on Celeuthetini is needed, and ideally studies based on morphology should go hand-in-hand with molecular phylogenetic work, to arrive at a stable classification. Nomenclature, systematics and ultimately biogeography could greatly benefit from an expansion of the

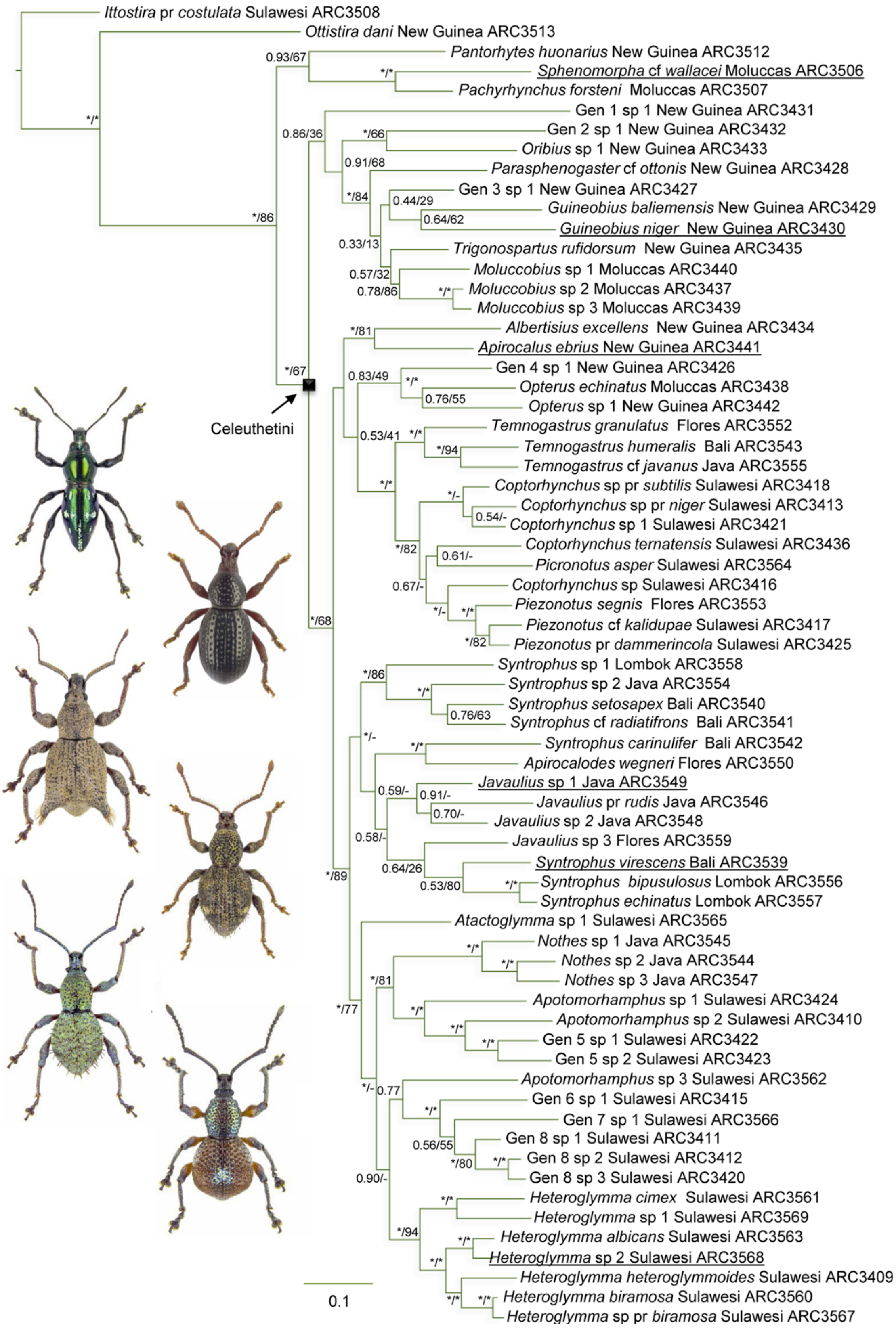
Ittostira pr costulata Sulawesi ARC3508
Ottistira dani New Guinea ARC3513
Pantorhytes huonarius New Guinea ARC3512
Sphenomorpha cf wallacei Moluccas ARC3506
Pachyrhynchus forsteni Moluccas ARC3507
Gen 1 sp 1 New Guinea ARC3431
Gen 2 sp 1 New Guinea ARC3432
Oribius sp 1 New Guinea ARC3433
Parasphenogaster cf ottonis New Guinea ARC3428
Gen 3 sp 1 New Guinea ARC3427
Guineobius baliemensis New Guinea ARC3429
Guineobius niger New Guinea ARC3430
Trigonospartus rufidorsum New Guinea ARC3435
Moluccobius sp 1 Moluccas ARC3440
Moluccobius sp 2 Moluccas ARC3437
Moluccobius sp 3 Moluccas ARC3439
Albertisius excellens New Guinea ARC3434
Apirocalus ebrius New Guinea ARC3441
Gen 4 sp 1 New Guinea ARC3426
Opterus echinatus Moluccas ARC3438
Opterus sp 1 New Guinea ARC3442
Temnogastrus granulatus Flores ARC3552
Temnogastrus humeralis Bali ARC3543
Temnogastrus cf javanus Java ARC3555
Coptorhynchus sp pr subtilis Sulawesi ARC3418
Coptorhynchus sp pr niger Sulawesi ARC3413
Coptorhynchus sp 1 Sulawesi ARC3421
Coptorhynchus ternatensis Sulawesi ARC3436
Picronotus asper Sulawesi ARC3564
Coptorhynchus sp Sulawesi ARC3416
Piezonotus segnis Flores ARC3553
Piezonotus cf kalidupae Sulawesi ARC3417
Piezonotus pr dammerincola Sulawesi ARC3425
Syntrophus sp 1 Lombok ARC3558
Syntrophus sp 2 Java ARC3554
Syntrophus setosapex Bali ARC3540
Syntrophus cf radiatifrons Bali ARC3541
Syntrophus carinulifer Bali ARC3542
Apirocalodes wegneri Flores ARC3550
Javaulius sp 1 Java ARC3549
Javaulius pr rudis Java ARC3546
Javaulius sp 2 Java ARC3548
Javaulius sp 3 Flores ARC3559
Syntrophus virescens Bali ARC3539
Syntrophus bipusulosus Lombok ARC3556
Syntrophus echinatus Lombok ARC3557
Atactoglymma sp 1 Sulawesi ARC3565
Nothes sp 1 Java ARC3545
Nothes sp 2 Java ARC3544
Nothes sp 3 Java ARC3547
Apotomorhamphus sp 1 Sulawesi ARC3424
Apotomorhamphus sp 2 Sulawesi ARC3410
Gen 5 sp 1 Sulawesi ARC3422
Gen 5 sp 2 Sulawesi ARC3423
Apotomorhamphus sp 3 Sulawesi ARC3562
Gen 6 sp 1 Sulawesi ARC3415
Gen 7 sp 1 Sulawesi ARC3566
Gen 8 sp 1 Sulawesi ARC3411
Gen 8 sp 2 Sulawesi ARC3412
Gen 8 sp 3 Sulawesi ARC3420
Heteroglymma cimex Sulawesi ARC3561
Heteroglymma sp 1 Sulawesi ARC3569
Heteroglymma albicans Sulawesi ARC3563
Heteroglymma sp 2 Sulawesi ARC3568
Heteroglymma heteroglymmoides Sulawesi ARC3409
Heteroglymma biramosa Sulawesi ARC3560
Heteroglymma sp pr biramosa Sulawesi ARC3567
Celeuthetini
0.93/67
/
0.86/36
*/66
0.91/68
*/84
0.44/29
0.64/62
0.33/13
0.57/32
0.78/86
/
*/86
/
*/81
0.83/49
/
0.76/55
0.53/41
/
*/94
/
*/-
0.54/-
*/82
0.61/-
0.67/-
*/-
/
*/82
*/67
*/68
*/86
/
0.76/63
*/-
/
0.59/-
0.91/-
0.70/-
0.58/-
0.64/26
0.53/80
/
*/89
/
/
*/81
*/77
/
/
/
*/-
0.77
/
0.56/55
*/80
/
0.90/-
/
*/94
/
/
/
/
0.1

Fig. 1 Phylogenetic relationships as recovered in the MrBayes analysis of the concatenated data set. Values at each node (A/B) are (A) posterior probability of MrBayes analysis, (B) bootstrap support value of RaxML analysis; a hyphen indicates that this node is not found in the ML-based topology. Asterisks indicate strongly supported nodes with a posterior probability ≥0.95 or a bootstrap support value ≥70. The species for which a habitus is shown on the left have their names underlined, and the ordering of the pictures follows the ordering of the phylogeny from top to bottom.

current data set to include other zoogeographical regions, that is the Philippines, Solomons etc., which would allow a test of the currently recognized genera for monophyly.

Origins and biogeography

Our divergence time estimates are based on the BEAST analysis using a Bayesian relaxed clock calibrated with a Tenebrionidae substitution rate (Papadopoulou *et al.* 2010). This dating might be debatable as the rate is not extracted from a Curculionidae clade but from a fairly distant family. No reliable fossil-based phylogeny of weevils is available to date, and the only one published does not contain a representative of Celeuthetini (McKenna *et al.* 2009). The proposed timing of events might be slightly older than the reality as some flightless taxa supposedly have an accelerated rate of evolution (Ikeda *et al.* 2012; Vogler & Timmermans 2012; Mitterboeck & Adamowicz 2013). We consider the proposed time frame as reasonable enough to serve as a base for further discussion despite these uncertainties. In any case, the directionality of the biogeographical events was robustly established here.

We here suggest a mid-Eocene origin of the tribe Celeuthetini somewhere east of Wallace's Line in a region spanning the Lesser Sunda Islands, New Guinea and Sulawesi. In the mid-Eocene, most of the extant Lesser Sunda Islands were not subaerial yet, and Sulawesi as we know it today consisted of three fragments separated by thousands of kilometres ocean (Hall 2012, 2013). One of these fragments was part of the Sula Spur, a promontory of the Australian plate and in proximity to the proto Papuan arc (Hall 2012, 2013). Large parts of the Moluccas and potentially of the Lesser Sunda Islands were formed by the fragmentation of the Sula Spur and the collision of some of these fragments with the Sunda Shelf during the Miocene (Hall 2013). Additionally, most of New Guinea emerged from the collision of the Australian and Asian plates in the past 10 Myr (Toussaint *et al.* 2014 for a geological review). Therefore, during the Eocene, most of what constitutes these islands today was part of the Gondwanan stock moving northwards, and it seems unlikely that the ancestor of Celeuthetini originated in one of the two remaining parts of Sulawesi, that is on the Sunda Shelf (western part of the island) or on drifting oceanic terranes (northern part of the island). Hence, we hypothesize that these weevils originated in an Australo-Papuan setting east of Wallace's Line (Fig. 3), a scenario already suggested in corvoid birds (Jønsson *et al.* 2011; Aggerbeck *et al.* 2014) and presumably also exhibited by other taxa, for example rainbowfishes (Unmack *et al.* 2013). At that time, Australia and emerged parts of New Guinea featured a somewhat subtropical to tropical climate (Martin 2006). It was only during the mid-Miocene that Australia experienced a dramatic aridification that led to the loss of tropical habitats. Based on the current environmental preferences of Celeuthetini, such a landmass would have been a very suitable setting for their rapid evolution. This scenario is compatible with our results as we only recover a segregation of lineages in the Lesser Sunda Islands, New Guinea and Sulawesi until the early to mid-Miocene (Fig. 3). It is possible that Celeuthetini are closely related to Elytrurini and/or Rhyncogonini, tribes restricted to the islands of the West Pacific, respectively, Polynesia, and possibly sharing a common ancestry having evolved in this setting at tropical latitudes.

The assemblage of Sulawesi as well as the aggregation and emergence of the Lesser Sunda Islands with the Greater Sunda Islands is dated to the early Miocene. Celeuthetini weevils at that time present in New Guinea, Lesser Sunda Islands and eastern Sulawesi were able to cross Lydekker's and Wallace's Lines several times to colonize the western part of the archipelago in Bali and Java. The genus *Moluccobius* endemic to the Moluccas and West New Guinea results from the crossing of Lydekker's Line by New Guinean ancestors in the early to mid-Miocene. A few hundred kilometres south, ancestors from the Lesser Sunda Islands crossed Wallace's Line repeatedly to give rise to at least three independent lineages in Java (Fig. 3). We also recover a transgression of Wallace's Line from Sulawesi towards Java in the mid-Miocene. All these events are associated with founder-event speciation meaning that a part of the ancestral population dispersed and colonized a new geographical area not previously occupied by the ancestor. These dynamic biogeographical events could possibly be accounted for by passive dispersal in/on flotsam or drifting terrane blocks. Unfortunately, the life cycle of these weevils is mostly unknown, and future investigations of their biology might bring new insights into the understanding of their biogeographical history.

Conclusion

We suggest a mid-Eocene origin of Celeuthetini weevils east of Wallace's Line. Throughout their evolution, these beetles have been able to cross biogeographical lines in

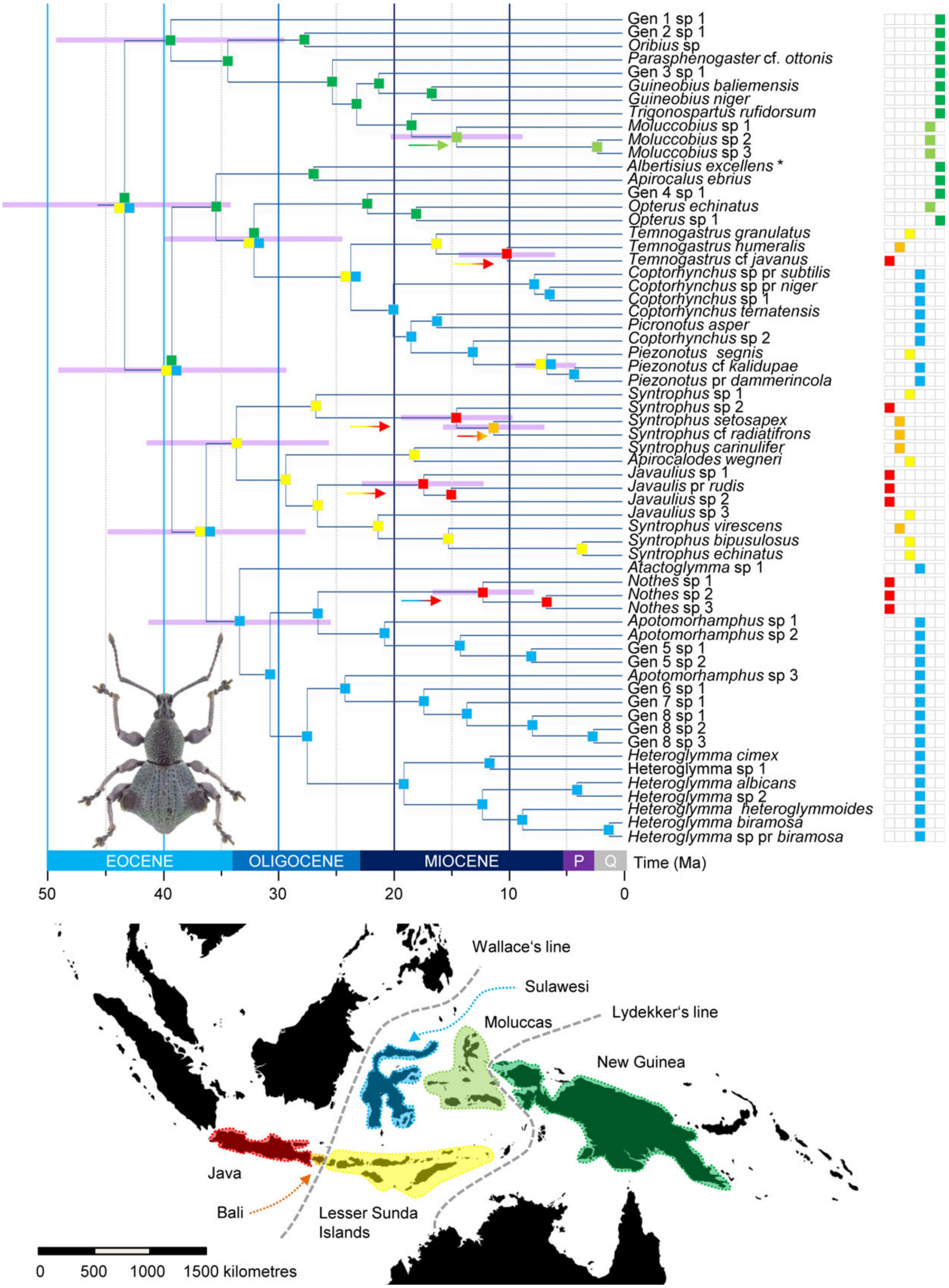
Gen 1 sp 1
Gen 2 sp 1
Oribius sp
Parasphenogaster cf. ottonis
Gen 3 sp 1
Guineobius baliemensis
Guineobius niger
Trigonospartus rufidorsum
Moluccobius sp 1
Moluccobius sp 2
Moluccobius sp 3
Albertisius excellens *
Apirocalus ebrius
Gen 4 sp 1
Opterus echinatus
Opterus sp 1
Temnogastrus granulatus
Temnogastrus humeralis
Temnogastrus cf javanus
Coptorhynchus sp pr subtilis
Coptorhynchus sp pr niger
Coptorhynchus sp 1
Coptorhynchus ternatensis
Picronotus asper
Coptorhynchus sp 2
Piezonotus segnis
Piezonotus cf kalidupae
Piezonotus pr dammerincola
Syntrophus sp 1
Syntrophus sp 2
Syntrophus setosapex
Syntrophus cf radiatifrons
Syntrophus carinulifer
Apirocalodes wegneri
Javaulius sp 1
Javaulis pr rudis
Javaulius sp 2
Javaulius sp 3
Syntrophus virescens
Syntrophus bipusulosus
Syntrophus echinatus
Atactoglymma sp 1
Nothes sp 1
Nothes sp 2
Nothes sp 3
Apotomorhamphus sp 1
Apotomorhamphus sp 2
Gen 5 sp 1
Gen 5 sp 2
Apotomorhamphus sp 3
Gen 6 sp 1
Gen 7 sp 1
Gen 8 sp 1
Gen 8 sp 2
Gen 8 sp 3
Heteroglymma cimex
Heteroglymma sp 1
Heteroglymma albicans
Heteroglymma sp 2
Heteroglymma heteroglymmoides
Heteroglymma biramosa
Heteroglymma sp pr biramosa
EOCENE
OLIGOCENE
MIOCENE
P
Q
Time (Ma)
50
40
30
20
10
0
Wallace's line
Sulawesi
Moluccas
Lydekker's line
New Guinea
Java
Bali
Lesser Sunda Islands
0
500
1000
1500 kilometres

Fig. 2 Historical biogeography of the Indo-Australian Celeuthetini weevils. Chronogram presenting the median divergence time estimates resulting from the BEAST analysis. The distribution of each taxon is given in a geographical matrix on the right side of the chronogram with colours referring to the geographical map at the bottom of the figure. Coloured squares indicate the most likely ancestral area recovered at each node. Coloured arrows indicate founder-event speciation as implemented in BioGeoBEARS using the +J parameter. The 95% HPD of the median ages are highlighted by horizontal pink bars. The habitus picture shows *Albertisius excellens* as indicated by the asterisk next to the name.

Table 3 Results of the BIOGEOBEARS analyses

	N. param.	AIC	*P*-value	LnL	j	d	e
M0							
DEC	2	198.6	–	−97.31	NA	0.0022	0.0023
DEC+J	3	138.6	***	−66.28	0.0345	0.0000	0.0000
DIVALIKE	2	181.2	–	−88.60	NA	0.0026	0.0000
DIVALIKE+J	3	139.6	–	−66.79	0.0364	0.0000	0.0000
BAYAREALIKE	2	224.3	–	−110.17	NA	0.0036	0.0074
BAYAREALIKE+J	3	154.8	–	−74.42	0.0324	0.0010	0.0010
M1							
DEC	2	195.9	–	−95.95	NA	0.0071	0.0040
DEC+J	3	141.2	***	−67.58	0.1025	0.0000	0.0000
DIVALIKE	2	183.3	–	−89.67	NA	0.0077	0.0000
DIVALIKE+J	3	142.2	–	−68.12	0.1077	0.0000	0.0000
BAYAREALIKE	2	204.9	–	−100.44	NA	0.0057	0.0063
BAYAREALIKE+J	3	151.0	–	−72.48	0.0989	0.0010	0.0010

The *** symbol indicates that this model is significantly supported as the best model. M0, no time slice, all dispersal rates equal, all areas allowed. M1, two time slices, optimized dispersal rates, all areas allowed.

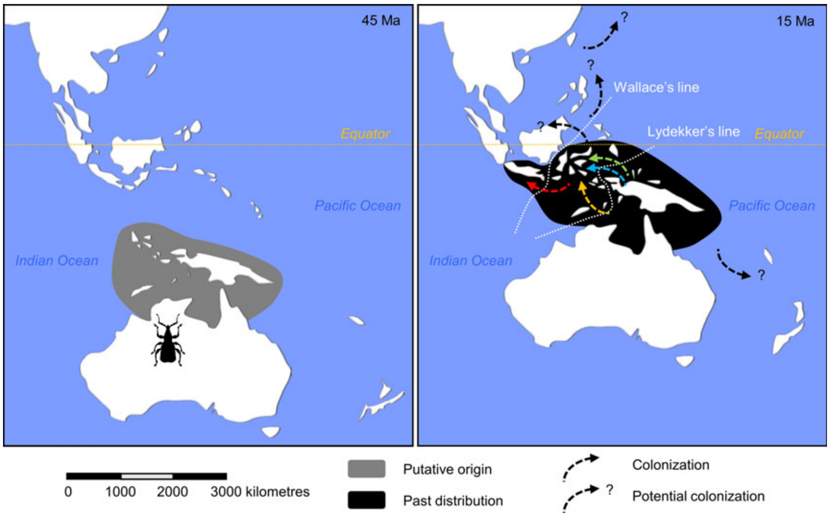

Fig. 3 Biogeographical scenario of Celeuthetini evolution in a palaeogeological framework. Maps illustrating the geological setting of the Indo-Australian archipelago 45 and 15 million years ago redrawn from Hall (2002, 2012, 2013) and Toussaint *et al.* (2014). The colours of the arrows indicate the area towards which the colonization event is directed. Because the taxon sampling does not include specimens from Borneo, Japan, the Philippines, Taiwan or the West Pacific region, we presented putative colonization events in the second map.

the IAA despite their flightlessness. This study adds to the growing body of evidence suggesting a more limited role of Wallace's and Lydekker's Lines in the biogeographical history of IAA arthropods. Waterways may not be as much of a barrier to some terrestrial organisms as they appear to us, but instead offer the opportunity of passive transportation, at least at times of favourable currents and weather conditions. Whether significant diversification can follow such a dispersal event will depend on ecological factors and the time available. To explore these mechanisms of dispersal will be the next big challenge of biogeography.

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Supporting Information

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

Appendix S1. Molecular biology protocols used in this study.