



Biogeography and diversification of the Pacific ant genus *Lordomyrma* Emery

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ABSTRACT

Aim This study addresses the origins of terrestrial biodiversity of the Fijian islands using the ant genus *Lordomyrma* (Hymenoptera: Formicidae: Myrmicinae) as a model system. We derive the evolution of the genus and determine its closest extra-Fijian relatives from geological data, molecular phylogenetic reconstruction and divergence estimates.

Location Ant taxa were sampled in the Southwest Pacific, Melanesia, Southeast Asia, Australia and mainland China.

Methods Phylogeny and divergence estimates of the ant genus *Lordomyrma* based on four nuclear genes (28S, ArgK, LW Rh, CAD) plus data on Indo-Pacific geological history are used to address current hypotheses regarding the origins of the Fijian biota.

Results The genus *Lordomyrma* probably originated in mainland Asia, with subsequent colonization of Australia and the Pacific. The Fijian *Lordomyrma* clade is monophyletic, and originated *c.* 8.8 Ma, when it diverged from a sister group in Papua New Guinea.

Main conclusions The colonization of Fiji by *Lordomyrma* is probably a result of long-distance dispersal from New Guinea, possibly aided by island hopping across the Vitiaz Arc. The timeline of diversification in *Lordomyrma* is broadly congruent with the Miocene fragmentation of the Vitiaz Arc and the Pliocene emergence of Vanua Levu. The biotic shuttle hypothesis, which posits 'Eua Island as the source of Fijian endemics, is rejected based on the sister relationship of Fiji and New Guinea lineages, as well as on the Miocene submergence of the terrane below sea level. The diversity of Fijian *Lordomyrma* results from the radiation of a single lineage, which diverged from a New Guinea sister group. The genus appears to have originated in Asia rather than in Australia.

Keywords

Divergence dating, diversification, 'Eua, Fiji, Formicidae, Hymenoptera, *Lordomyrma*, Melanesia, South Pacific, Vitiaz Arc.

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INTRODUCTION

The Fijian archipelago hosts a diverse terrestrial biota more typical of a mature continental ecosystem than of a collection of small remote islands (Raven & Axelrod, 1972; Keast, 1996; Evenhuis & Bickel, 2005). Fijian biogeographical anomalies include plants in the families Podocarpaceae and Araucariaceae, and a rich herpetofauna that includes *Platymantis* frogs, iguanid lizards, canoid boas, elapid snakes and extinct

mekosuchine crocodiles. The diversity of ants is equally enigmatic. More than 66% of Fijian ant species are endemics (Ward & Wetterer, 2006), some with extensive local radiations (Bolton *et al.*, 2006).

We reconstructed the phylogeny of the ant genus *Lordomyrma* Emery (Hymenoptera: Formicidae: Myrmicinae) and estimated divergence times of individual species and clades using DNA sequence data in order to determine where the genus *Lordomyrma* originated, whether the Fijian *Lordomyrma*

species derive from one or multiple colonizations, and where their closest extant relatives occur. Three hypotheses commonly invoked to explain the origins of Fiji's insular terrestrial assemblage are colonization of Fiji: (1) by long-distance dispersal from Australia or Melanesia, (2) by island hopping across the Vitiaz Arc, and (3) by 'Eua Island serving as biotic shuttle (Raven & Axelrod, 1972; Keast, 1996; Evenhuis & Bickel, 2005; Keppel *et al.*, 2009). This paper examines which of these hypotheses is most congruent with the patterns of historical biogeography of *Lordomyrma* (distribution shown in Fig. 1). Results of this study may be relevant to other terrestrial Fijian endemics with similar geographical distributions.

Geology of Fiji

Fiji comprises hundreds of islands, of which two (Viti Levu and Vanua Levu) possess land areas > 5000 km² (Ash, 1992; Neall & Trewick, 2008).

Viti Levu contains the oldest rocks of the archipelago, and is believed to be a remnant of the ancient Vitiaz Arc that formed on the Australian plate margin in the Late Eocene to Early Oligocene (Rodda, 1994; Hall, 2002). Viti Levu's emergence above sea level occurred in the early Miocene, 25–20 Ma (Whelan *et al.*, 1985), and serves as the earliest age estimate for Fijian terrestrial lineages. High-elevation ecosystems are expected to have formed much later, in the Early Pliocene, when a combination of volcanism and uplift raised the centre of Viti Levu above 1000 m (Rodda, 1994; Stratford & Rodda, 2000).

The oldest known rocks from Vanua Levu are dated to 8–6.5 Ma (Rodda & Kroenke, 1984; Yan & Kroenke, 1993; Rodda, 1994). Dry land is estimated to have become available c. 4 Ma, and most of the island was probably emergent by 4–3 Ma (Rodda, 1994).

The Vitiaz Arc formed a relatively unbroken chain of islands from the Philippines and northern New Guinea to Fiji. It was substantially established by 30 Ma, and volcanism continued to add to its landmass through the Oligocene (Ewart, 1988) (Fig. 2a). Fiji began to occupy its current position in the Middle Miocene (18 Ma), when the westward-moving Pacific Plate collided with the Vitiaz Arc, causing Fiji, Vanuatu and the Lau-Tonga regions (the Vanuatu Arc) to split from the Solomon Islands (Hall, 2002) (Fig. 2b). The Vanuatu Arc was itself disrupted 12–8 Ma, and subsequent spreading of the North Fiji Basin caused Fiji and the Lau-Tonga ridge to drift eastwards while Vanuatu drifted westwards (Carney *et al.*, 1985; Auzende *et al.*, 1995; Taylor *et al.*, 2000; Hall, 2002) (Fig. 2c).

Colonization scenarios for the Fijian archipelago

Long-distance dispersal

The long-distance dispersal hypothesis posits that taxa from Asia, Australia or Melanesia colonized Fiji by means of rafting or flight, propelled by strong winds associated with tropical storms. The most dramatic example of long-distance dispersal to Fiji is that of the iguanids *Brachylophus* and *Lapitiguana*, which originated in South America (Gibbons, 1981; Zug, 1991; Pregill

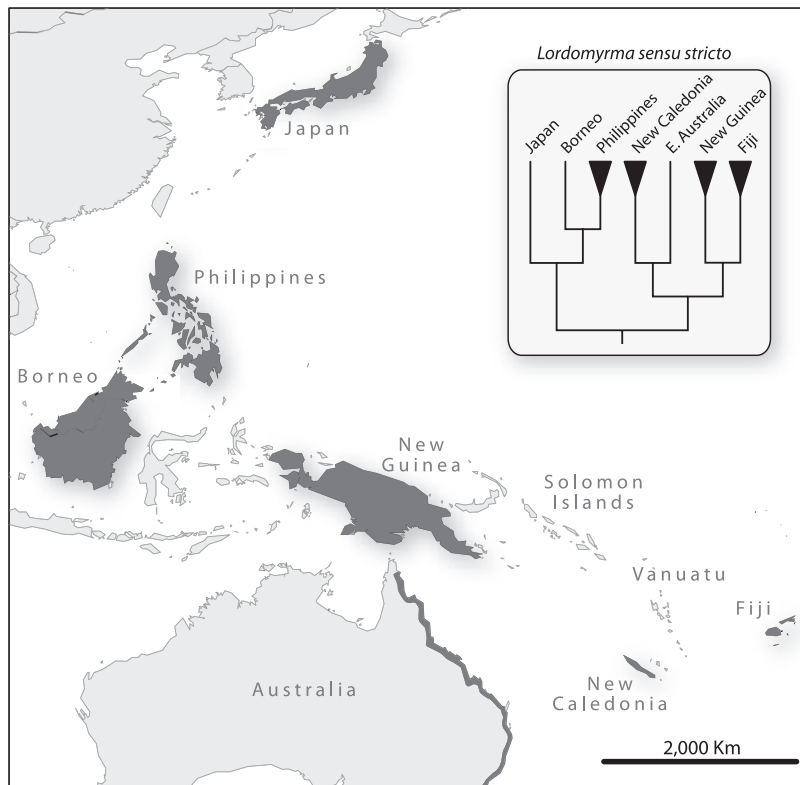


Figure 1 Geographical distribution of the genus *Lordomyrma sensu stricto*. Estimated species ranges are indicated by dark shading on the map (projection: world cylindrical equal area; scale: 1:50,000,000). The area cladogram (inset, top right) follows a Bayesian four-gene analysis of 33 taxa, partitioned by gene. The tree reflects relationships among clades in *Lordomyrma sensu stricto*, with triangles representing multiple species collapsed into a single terminal.

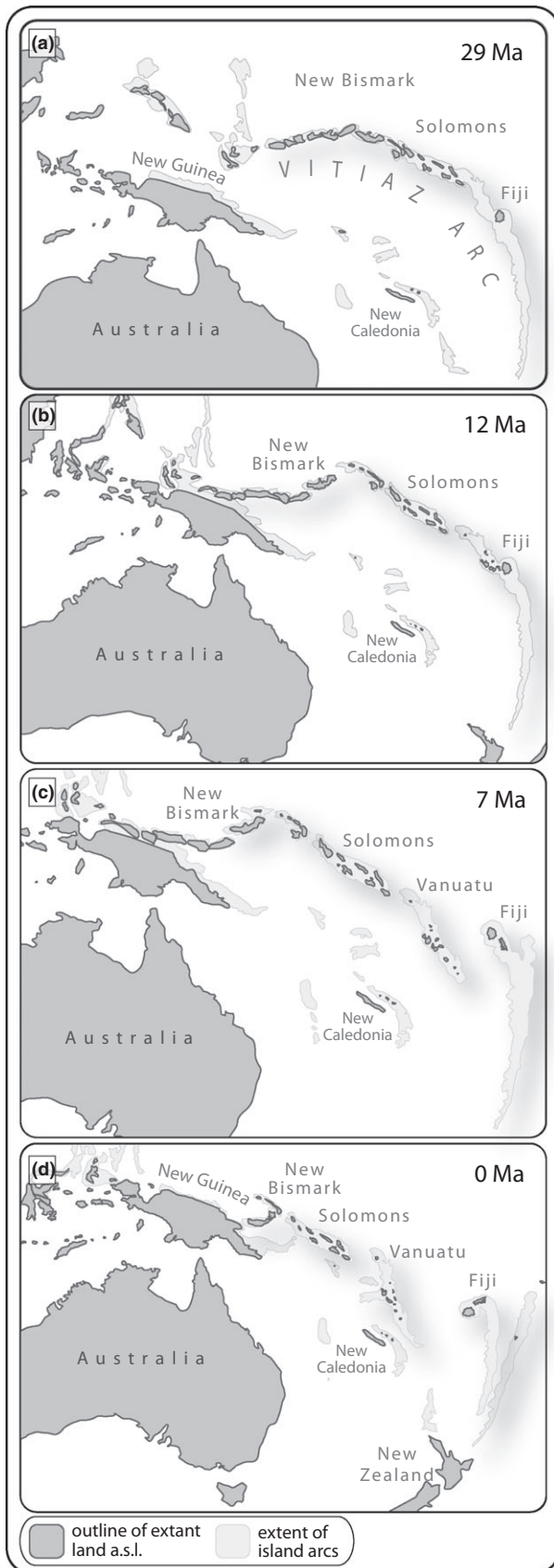


Figure 2 Fragmentation of the Vitiiaz Arc from 29 Ma to the present day (adapted from Hall, 2002).

& Steadman, 2004). Most Pacific island taxa, however, appear to have originated in Melanesia, Southeast Asia or Australia (Sanmartín & Ronquist, 2004). Although colonization by long-distance dispersal can be difficult or impossible to distinguish from island hopping, we can predict that long-distance dispersals will bear signatures of the predominant wind patterns in the Pacific (Cook & Crisp, 2005) and of distance to source areas, in terms of diversity of colonizing lineages (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008). Furthermore, Fijian lineages recently diverged from geographically distant relatives are likely to have arrived by means of long-distance dispersal, whereas older splits allow for the possibility of island hopping according to the timeline of the Vitiiaz Arc.

Island hopping

Geological reconstructions, such as the Australian Margin model (Hall, 2002) and the Intra-oceanic model (Kroenke, 1996), offer an opportunity to examine how Fiji might have been colonized by means of short-distance island hopping along the developing Vitiiaz Arc. A 200–150 m drop in global sea-levels during the Oligocene lowstand (30–28 Ma) may have catalysed eastward biotic migration from Southeast Asia and Melanesia across the arc (Hallam, 1984; Haq *et al.*, 1987; Wade & Pällike, 2004).

The island hopping hypothesis predicts that close relatives of Fijian taxa are likely to be present on the intermediate islands of the former Vitiiaz Arc, and that phylogenetic patterns will reflect stepwise diversification towards Fiji (Burrett *et al.*, 1991). Several previous studies have invoked island hopping across the Vitiiaz Arc to explain other Fijian endemic invertebrate groups, including *Cosmopsaltria* cicadas (Hemiptera: Cicadidae) (Duffels & Turner, 2002), and Platynini ground beetles (Coleoptera: Carabidae) (Liebherr, 2005).

Biotic shuttle

An alternative hypothesis is that a fragment of ancient New Caledonia separated from the Norfolk Ridge 41 Ma, drifted eastwards to collide with Viti Levu in the Late Miocene, and introduced New Caledonian biota onto Fiji (Kroenke, 1996). The hypothesis has been invoked to explain the presence of many taxa on the archipelago, including relictual plants, vertebrates, arthropods and gastropods (Keast, 1996; Mueller-Dombois & Fosberg, 1998; Craig *et al.*, 2001; Goodacre & Wade, 2001; Mead *et al.*, 2002; Mueller-Dombois, 2002; Latke, 2003; Evenhuis & Bickel, 2005; Leigh *et al.*, 2007; Keppel *et al.*, 2009).

In order for 'Eua to have introduced New Caledonian taxa onto Viti Levu, four assumptions would have to be met: (1) the 'Eua Ridge was once connected to New Caledonia; (2) 'Eua was emergent when it sundered from New Caledonia and remained so through the following 35 Ma; (3) the taxa in question persisted on 'Eua throughout 35 Myr of transit; and (4) these taxa became established on Viti Levu when the two islands became confluent.

In the phylogenetic context, the hypothesis predicts that Fijian lineages are more closely related to New Caledonian than to Melanesian or Asian clades, and that dates of divergence should approximate 40 Ma, when 'Eua rifted from New Caledonia.

The genus *Lordomyrma*

The genus *Lordomyrma* comprises 27 described species and subspecies of rain forest ants known from Melanesia and the Pacific (Bolton, 1995; Sarnat, 2006; Lucky & Sarnat, 2008), with additional undescribed species occurring there and in Southeast Asia (Branstetter, 2009; Taylor, 2009). Eleven species are known from Fiji, the eastern range limit of the genus. Although all species of *Lordomyrma* possess winged queens and males, the restricted distributions of most species suggest limited dispersal capacity. Range limits of ants in Fiji and nearby Pacific Islands are relatively well known as a result of extensive sampling efforts (Sarnat, 2006; E.P. Economo and E.M. Sarnat, unpublished data).

Currently, the genus is characterized by 12-merous antennae, a simple sting with straight apex, triangular mandibles with seven or more teeth decreasing in size from apex to base, well-developed propodeal spines, a bicarinate clypeus and elongate frontal carinae (Bolton, 1994; Taylor, 2009). This definition, however, does not encompass all described species within the genus, nor does it exclude taxa belonging to morphologically similar genera. As a result, assigning species to *Lordomyrma* remains difficult, and a number of taxa related to *Lordomyrma* await inclusion or exclusion from the genus (Shattuck, 1999; Branstetter, 2009; Taylor, 2009).

MATERIALS AND METHODS

To test alternative hypotheses of the biogeographical origin and diversification of Fijian *Lordomyrma*, we inferred phylogeny based on DNA sequences sampled broadly from within the genus, as well as from known and suspected close relatives. Initial analyses involved a 33-taxon dataset based on four genes used to explore relationships of species within *Lordomyrma sensu lato* (the 'ingroup' dataset). The second dataset (the 'outgroup' dataset) was based on three genes from the ingroup taxa, and incorporated seven additional outgroup species, for a total of 40 taxa. Specimen data and details of nomenclature are reported in Appendix S1 in the Supporting Information.

Taxon sampling

Ten of Fiji's eleven *Lordomyrma* species were represented in each dataset (*Lordomyrma levifrons* was unavailable). Multiple representatives of three Fijian species (*Lordomyrma polita*, *Lordomyrma sukuna*, *Lordomyrma tortuosa*) were included to test morphological species boundaries (Mann, 1921, 1925; Sarnat, 2006).

In total, 29 specimens of described and undescribed *Lordomyrma* species (including *Ancyridris* sp.) made up the ingroup. An effort was made to include specimens from each region representing both conserved and highly derived morphologies. Images of several undescribed taxa are available at <http://www.antweb.org> (*Lordomyrma* AU01, *Lordomyrma* AU02 and *Lordomyrma* PI01). Genus undet. PH03 (which had been provisionally assigned to *Lordomyrma*) can be viewed at <http://www.discoverlife.org> under the name *Lordomyrma* sp. Phi1. We were unable to obtain molecular data from the type species of *Lordomyrma*, *Lordomyrma furcifera* from New Guinea, but included the morphologically similar *Lordomyrma* PG01, also from New Guinea. The term *Lordomyrma sensu stricto* is thus defined as the clade containing *L.* PG01 (Fig. 3).

Outgroup taxa included genera proposed as possible sister taxa to *Lordomyrma*: *Cyphoidris* Weber, *Rogeria* Emery and *Ancyridris* Wheeler (Taylor, 2009), plus representatives of seven likely myrmicine genera. Phylogenies were rooted with the distantly related genus *Myrmica* Latreille (Brady *et al.*, 2006; Moreau *et al.*, 2006).

Phylogenetic analyses

Gene sampling

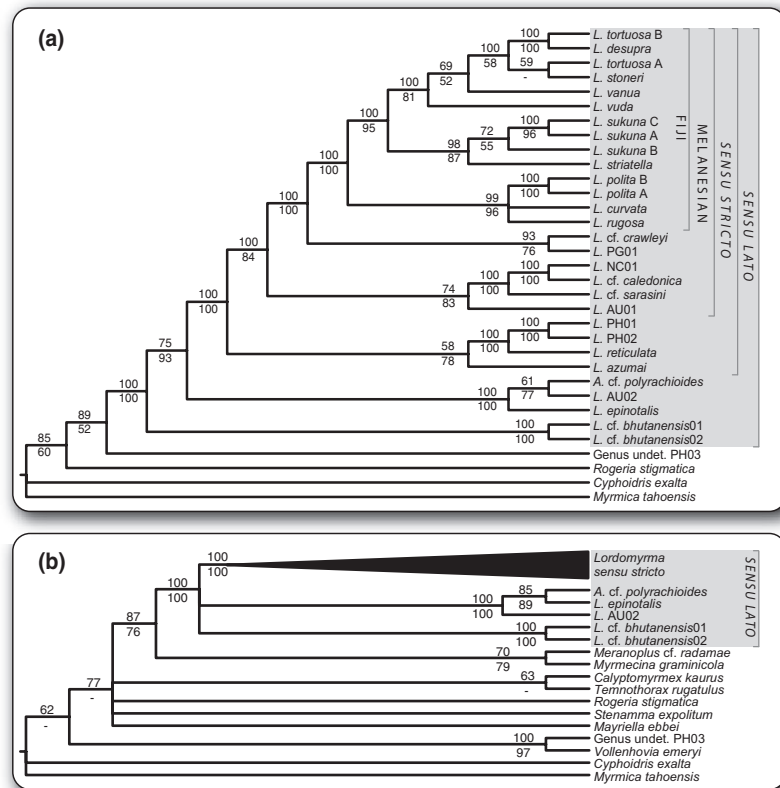
Four nuclear genes were chosen to infer divergence events across a range of evolutionary time-scales. The ingroup dataset included three nuclear protein-coding genes: arginine kinase (ArgK, 696 bp), rudimentary (CAD, 757 bp), long-wavelength rhodopsin (LW Rh, 539 bp) and nuclear ribosomal 28S (497 bp). These genes were previously shown to be informative for phylogenetic inference in ants (Ward & Downie, 2005; Brady *et al.*, 2006; Moreau *et al.*, 2006; Ward *et al.*, in press). The final ingroup dataset comprised *c.* 2.5 kb of sequence, from which uninformative and unalignable sequences were excluded (see Appendix S2). The outgroup dataset included only three genes: ArgK, LW Rh and 28S (*c.* 1.7 kb), as CAD was unavailable for seven outgroup taxa.

Molecular procedures

We extracted genetic material from specimens either destructively (entire ant pulverized) or non-destructively (body wall pierced prior to extraction), using the Qiagen DNeasy tissue kit (Qiagen Inc., Valencia, CA, USA) according to manufacturer protocols, with the exception of a final elution in water rather than in ethanol. Non-destructively extracted specimens were re-mounted and vouchered. Additional voucher specimens were deposited in the Australian National Insect Collection (Canberra, Australia). Polymerase chain reaction amplification followed previously published methodology (Ward & Downie, 2005). For primer sequences see Appendix S3.

All samples were sequenced using an ABI 3730 sequencer with ABI BigDye Terminator 3.1 (Applied Biosystems Inc., Foster City, CA, USA). Sequences were assembled and edited

Figure 3 Cladograms showing Bayesian topology with support values for relationships within *Lordomyrma* and to outgroup taxa. Bayesian posterior probabilities (PP) and maximum likelihood bootstrap values $\geq 50\%$ are shown above and below branches, respectively. Where PP values are $< 50\%$, branches are collapsed. Panel (a) presents a four-gene analysis of 33 taxa, partitioned by gene. Shading behind names indicates nested groups within *Lordomyrma*, as referred to in the text. In panel (b) a three-gene analysis of 40 taxa is shown, with the 24 *Lordomyrma sensu stricto* taxa collapsed into a triangle.



with SEQUENCHER 4.6 (Gene Codes Corporation, Ann Arbor, MI, USA) and aligned in CLUSTALX 1.38.1 (Thompson *et al.*, 1997) using default parameters; minor alignment errors were adjusted in MACCLADE 4.08 (Maddison & Maddison, 2005). Sequences for the majority of specimens were obtained through these protocols, and 25 sequences were obtained from GenBank. All novel sequences were deposited in GenBank (see Appendix S4).

Phylogenetic inference

Phylogeny was inferred using maximum likelihood with RAXML 7.0 (Stamatakis *et al.*, 2008) and using a Bayesian approach with MRBAYES 3.1 (Huelsenbeck & Ronquist, 2001), accessed through the CIPRES portal (http://www.phylo.org/sub_sections/portal/). Three data partitioning strategies were tested using both methods. The first involved no partitions, the second partitioned the data by gene, and the third partitioned the data by gene and by functional region (e.g. introns and exons).

We selected nucleotide sequence evolution models for all partitions using the Akaike information criterion in the program MRMODELTEST 2.3 (Posada & Crandall, 1998; Nylander, 2004) and PAUP* 4.0 (Swofford, 2002). See Appendix S2 for details on partitioning schemes and the selected models of evolution.

Likelihood analyses were performed on both datasets, using the partitioning schemes outlined above. Likelihood analyses were conducted using the program RAXML (Stamatakis *et al.*,

2008), which uniformly applies a GTR + G model to all partitions and performs rapid bootstrapping simultaneously to phylogeny reconstruction. The program was accessed through the Vital-IT Unit of the Swiss Institute of Bioinformatics (<http://phylobench.vital-it.ch/raxml-bb/>).

Bayesian analyses involved Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analysis employing two runs, each with four chains (one cold, three heated to temp. 0.5), sampled every 1000 generations. In partitioned runs, statefreq, shape, pinvar, revmat, and tratio were all unlinked. Each analysis was run for 2 million generations. All runs reached stationarity, as judged by the average standard deviation of split frequencies approaching 0.01. Approximately 10% of samples were excluded as burn-in before parameters and trees were summarized.

Results of different partitioning schemes in the Bayesian analyses were compared using Bayes factors. Bayes factors were calculated as twice the difference in marginal likelihoods between analyses, as estimated in the program TRACER 1.4 (Rambaut & Drummond, 2007). Significance was evaluated by comparing these values with standard tables (Newton & Raftery, 1994; Kass & Raftery, 1995; Suchard *et al.*, 2001; Nylander *et al.*, 2004).

Divergence dating

A chronogram for the genus was constructed using the program BEAST 1.4.8 (Drummond & Rambaut, 2007). The

analysis was limited to four genes from 27 taxa, with duplicates of three species removed. Among the taxa removed were the species *Lordomyrma desupra* and *Lordomyrma stoneri*, which form a species complex with *L. tortuosa*.

A relaxed-clock model was employed with a lognormal distribution and the Yule speciation process. The previously estimated age of the split between the core Myrmicinae (all taxa excluding *Myrmica*) and the genus *Myrmica* was used as a calibration point (Brady *et al.*, 2006). We took into account uncertainty associated with this date by assigning the node age a normally distributed prior with mean 73.5 Ma, and a standard deviation of one, reflecting the age range estimated in Brady *et al.* (2006). Core Myrmicinae were fixed as monophyletic, as were the Fiji + PNG *Lordomyrma sensu stricto*, as these clades emerged as sister taxa with strong support in previous analyses. Multiple BEAST analyses were performed, each running for 10 million generations with 10% burn-in removed. Stationarity was assessed by ensuring that effective sample size values were high for most parameters, thus indicating sufficient mixing, and by inspecting plots of posterior probability marginal density, where smooth curves indicated minimal stochastic noise. Results proved repeatable over multiple independent runs, and results from a single run were used to reconstruct a chronogram, visualized using the program FIGTREE 1.2.1 (<http://tree.bio.ed.ac.uk/software/figtree/>).

RESULTS

Phylogeny

Our analyses consistently supported monophyly of the Fijian *Lordomyrma* (Figs 3 & 4). The Fijian species form three well-supported clades (Fig. 3), which correspond to relationships predicted by morphological analyses (Sarnat, 2006). Short branch lengths in Fijian *Lordomyrma* suggest a relatively recent radiation (Fig. 4). Other clades (e.g. the Philippine clade)

possess much longer branches, possibly indicating under-sampling and/or high extinction rates in those lineages.

All analyses recovered strong support for the Fijian clade being most closely related to New Guinean taxa. Monophyly was also well supported for New Caledonian *Lordomyrma*, which was recovered with moderate support as sister to an Australian species. Together, all of the aforementioned taxa form a well-supported clade referred to here as the Melanesian *Lordomyrma*.

All analyses recovered the Southeast Asian plus Japanese species as falling outside the clade of Melanesian *Lordomyrma*, but whether these Asian taxa themselves form a clade or a grade remains uncertain, as support values are low. All of the aforementioned taxa are included in the grouping *Lordomyrma sensu stricto*.

The Solomon Islands species, *Lordomyrma epinotalis* Mann, fell outside *Lordomyrma sensu stricto*, and emerged within a clade including *Ancyridris cf. polyrachioides* and *Lordomyrma* AU02. The grouping of these three species plus the *sensu stricto* group is here referred to as *Lordomyrma sensu lato*.

The sister group to *Lordomyrma sensu lato* remains uncertain. Although we recovered moderate support for the association of *Lordomyrma* with Genus undet. PH03 in analyses of the ingroup dataset, analyses of the outgroup dataset failed to recover this relationship, and weakly associated *Lordomyrma* with *Meranoplus* plus *Myrmecina*.

Maximum likelihood and Bayesian methods recovered nearly identical tree topologies from each analysis, regardless of partitioning scheme. Differences in tree topology between analyses of ingroup versus outgroup datasets were confined to relationships among outgroup taxa (Fig. 3).

Topological differences among the three partitioning schemes were negligible for both datasets. Bayes factor (BF) comparisons of partitioning schemes for the ingroup dataset showed that partitioning by gene and by functional region provided a significantly better fit to the data than either partitioning by gene or not partitioning at all (Table 1,

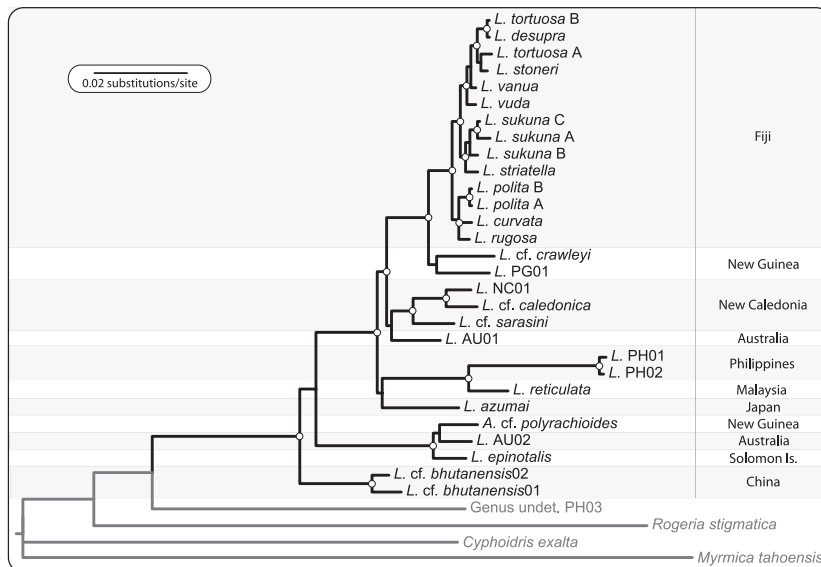


Figure 4 Phylogram of the ant genus *Lordomyrma* with Bayesian topology and branch lengths, based on analysis of the ingroup dataset (four genes, 33 taxa) partitioned by gene and by functional region. Nodes with posterior probabilities 95–100% are represented by open circles. Where support is < 50%, branches are collapsed. Branches to outgroups appear in grey.

Table 1 Bayes factor comparisons evaluating the fit of the three partitioning schemes used to analyse both *Lordomyrma* datasets. Bayes factors are calculated as twice the difference in marginal likelihoods from two analyses. Marginal likelihoods for all analyses are given below with standard error (SE) based on 1000 bootstrap replicates. A comparison value ≥ 10 is considered significant, and therefore all comparisons below are significant. Negative values favour the column over the row. For the ingroup dataset (four genes, 33 taxa), the favoured partitioning scheme is by gene and by functional region. For the outgroup dataset (three genes, 40 taxa), the favoured partitioning scheme is by gene.

Partitioning scheme	Unpartitioned	By gene	By gene and by functional region	Marginal likelihood \pm SE
Ingroup dataset				
Unpartitioned	–	–	–	–9829.099 \pm 0.426
By gene	189.83	–	–	–9734.082 \pm 0.741
By gene and by functional region	317.08	127.24	–	–9670.560 \pm 0.538
Outgroup dataset				
Unpartitioned	–	–	–	–8539.250 \pm 0.639
By gene	120.55	–	–	–8478.974 \pm 0.613
By gene and by functional region	75.81	–44.74	–	–8501.345 \pm 0.555

$2\ln$ BF = 127.24 and 317.08, respectively). For the outgroup dataset, however, the best partitioning scheme was by gene, rather than by gene and by functional region (more complex; $2\ln$ BF = 44.74) or not partitioning at all (less complex; $2\ln$ BF = 120.55).

Chronology

A relaxed clock analysis (Fig. 5) recovered tree topology consistent with the previously described maximum likelihood and Bayesian results. The stem group of *Lordomyrma sensu lato* originated c. 44.2 Ma (95% highest posterior density (HPD) lower and upper bounds 58.5–30.0 Ma). Divergence of the insular lineages from mainland China congeners occurred c. 26.5 Ma (95% HPD 36.1–16.7 Ma). The origination of the stem group of *Lordomyrma sensu stricto* is estimated as c. 24.4 Ma (95% HPD 33.4–15.8 Ma), and, within this clade, the Melanesian *Lordomyrma sensu stricto* lineage emerged 17.1 Ma (95% HPD 20.5–9.0 Ma).

The stem group of the Fijian lineage split from a New Guinea sister lineage c. 8.8 Ma (95% HPD 13.0–5.0 Ma). Within the Fijian taxa, *Lordomyrma curvata* and *Lordomyrma vanua*, the two Fijian *Lordomyrma* species endemic to the island of Vanua Levu, originated 2.3 Ma (95% HPD 4.1–0.9 Ma) and 1.2 Ma (95% HPD 2.3–0.4 Ma), respectively.

DISCUSSION

Our results offer support for dispersal, rather than vicariance, as the means by which Fijian taxa colonized the archipelago. Whether this occurred as a result of multiple short-distance events or a single long-distance dispersal event from biotic source populations remains unclear in the case of the ant genus *Lordomyrma*.

Long-distance dispersal

Colonization of Fiji by means of long-distance dispersal from Melanesia is supported by the fact that Fijian *Lordomyrma*

comprise a single monophyletic radiation that is most closely related to that of the New Guinean *Lordomyrma*, and by the absence of extant congeners on intermediate islands. At the time of divergence of the Fijian lineage from the New Guinean lineage (8.8 Ma), Fiji was closer to New Guinea (Fig. 2), which increases the likelihood of a dispersal event.

Island hopping

The eastward spread of *Lordomyrma* from New Guinea to Fiji by means of island hopping across the Vitiav Arc is a compelling scenario. The Miocene fragmentation of the Arc, the ancient emergence of Viti Levu, and the more recent emergence of Vanua Levu are broadly congruent with *Lordomyrma* diversification.

Support for the island hopping scenario is tempered by the lack of extant close relatives on the intermediate Bismark Archipelago, Solomon Islands and Vanuatu. If *Lordomyrma* did colonize Fiji by island hopping from New Guinea, extinction must be presumed for the *Lordomyrma sensu stricto* lineages that once occurred between Fiji and New Guinea.

Biotic shuttle

We reject the biotic shuttle hypothesis, which posits 'Eua Island as the source of Fijian endemics, on both phylogenetic and geological grounds. Fijian *Lordomyrma* are more closely related to New Guinean than to New Caledonian lineages, and the origin of the Fijian species is far too recent (c. 8.8 Ma) to reflect vicariance from Australia 40 Ma. Geological evidence for 'Eua does not fulfil the biotic shuttle hypothesis for the following four reasons. (1) The ancient connection between 'Eua and New Caledonia remains unclear; few studies have investigated 'Eua's geological origin (Kroenke, 1996). (2) 'Eua was submerged to bathyal depths (> 200 m below sea level) during the Middle Miocene after it sundered from New Caledonia, as the Eocene limestones are overlain by deep-water volcanic rocks (Tappin & Ballance, 1994). As a result, none of the original terrestrial taxa could (3) have persisted on this landmass or (4) become established on Fiji.

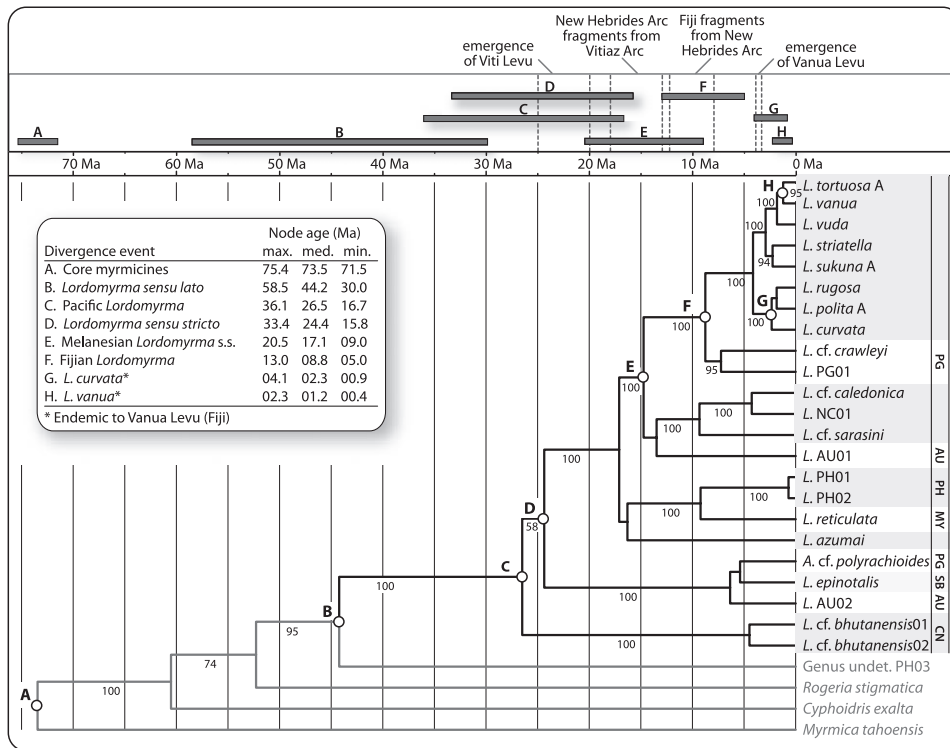


Figure 5 Chronogram of the evolutionary history of the ant genus *Lordomyrma*, with scale in millions of years ago (Ma), based on a four-gene BEAST analysis of 27 taxa. Bayesian posterior probabilities > 50% are shown beside branches. Minimum, median and maximum node ages are given for eight nodes (inset), which are indicated by open circles on the phylogeny (labelled with capital letters). The phylogenetic events associated with these nodes are described in the inset table. Bars representing 95% highest posterior density of node ages are located above the phylogeny, with major geological events in the history of the Fijian islands indicated. Geographical ranges of ingroup taxa are to the right of the phylogeny, with abbreviations as follows: AU, Australia; CN, China; FJ, Fiji; JP, Japan; MY, Malaysian Borneo; NC, New Caledonia; PG, Papua New Guinea; PH, Philippines; and SB, Solomon Islands.

Origins of the Fijian *Lordomyrma*

Unanimous support for monophyly of the Fijian *Lordomyrma* provides evidence for the single-origin hypothesis. Morphological diversity in the Fijian *Lordomyrma*, thought to be a product of multiple lineages (Sarnat, 2006), can now be interpreted as convergence with the morphology observed in New Guinean and Australian lineages.

The Fijian lineage of *Lordomyrma* established and radiated in Fiji well after the archipelago emerged above sea level (Fig. 2). Evidence of this pattern and its timing in *Lordomyrma* provides concrete support for the longstanding hypothesis that many Pacific island assemblages include endemic radiations of Melanesian ant lineages (Wilson, 1958a,b, 1959a,b).

Lordomyrma sensu lato colonized Melanesia in the Miocene, c. 17 Ma (Fig. 5), apparently from an ancestral Asian lineage. This origin has been hypothesized for other Fijian ant taxa, including *Cerapachys* (Wilson, 1959b) and *Strumigenys* (Bolton, 2000), as well as proposed for other terrestrial Fijian invertebrates (Balke *et al.*, 2007). Nevertheless, we cannot discount the possibility that the genus arose in Australia and only later colonized Asia and the Pacific, given the relationship of the *Lordomyrma sensu stricto* group to the Australian *Lordomyrma* AU02.

Lordomyrma within the Fijian archipelago

Dating analysis recovered a sequence of diversification within Fiji that is congruent with the geological history of the archipelago. Diversification of the Fijian *Lordomyrma* occurred in Viti Levu prior to several lineages independently colonizing the northern island of Vanua Levu. The two *Lordomyrma* species endemic to Vanua Levu (*L. curvata* and *L. vanua*) diverged from their nearest living relatives c. 2.3 Ma (4.1–0.9 Ma) and 1.2 Ma (2.3–0.4 Ma), respectively, which corresponds to the date of Vanua Levu’s first emergence above sea level, c. 3–4 Ma (Rodda, 1994). This coincidence of island emergence and speciation suggests that interisland divergence in these taxa was initiated by the colonization of Vanua Levu.

Taxonomic implications

Our results show that the current concept of *Lordomyrma* is paraphyletic with respect to *Ancyridris* (Brown, 1956; Taylor, 2009). We suggest two alternatives. The genus *Lordomyrma* could be restricted to the *sensu stricto* clade, and *L. epinotalis*, *Lordomyrma* AU02 and the *Lordomyrma bhutanensis* complex could be reassigned to new genera. Alternatively, the genus could be defined more inclusively, encompassing *Ancyridris* as a junior synonym of *Lordomyrma*.

Although we were unable to determine the sister group to *Lordomyrma sensu lato*, we have demonstrated that previously suggested close relatives (*Cyphoidris*, *Rogeria*) are not sister to this group. Additional data have likewise disproved suggested sister-group relationships with *Bariamyрма* and *Lachnomyrmex* (P. S. Ward, UC Davis, unpublished data). Future studies may look to the following genera for possible sister-group relationships with *Lordomyrma*: *Lasiomyrma* (Terayama & Yamane, 2000), *Indomyrma* (Brown, 1986) and *Dacatinops* (Brown & Wilson, 1957).

CONCLUSIONS

The Fijian *Lordomyrma* form a monophyletic group whose ancestor colonized Viti Levu c. 8.8 Ma. The biogeographical origins of the clade are traced to New Guinea. The Melanesian species of *Lordomyrma sensu stricto* also form a monophyletic group that was probably derived from Asian origins during the Miocene. Phylogenetic patterns and dates of divergence correspond to the geological reconstruction of the Southwest Pacific, and support the hypothesis of ancient long-distance dispersal from New Guinea to Fiji, followed by local radiation. Phylogenetic and geological data weakly support the island hopping hypothesis and refute the biotic shuttle hypothesis as a source of the Fijian terrestrial biota.

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SUPPORTING INFORMATION

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

Appendix S1 Collection data sorted by taxon ID.

Appendix S2 Models of sequence evolution for selected data partitions.

Appendix S3 Primers used for sequencing arginine kinase, 28S rDNA, long-wavelength rhodopsin and CAD.

Appendix S4 GenBank accession numbers for DNA sequences.

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