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Original Article

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Rediscovery of *Melanesobasis* Donnelly, 1984 (Odonata: Coenagrionidae) in Vanuatu reveals a pattern of vicariance in insular damselflies

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ABSTRACT

The Vitiaz Arc provides a compelling opportunity to examine biogeographical patterns in the South Pacific. Previously, however, many groups lacked the appropriate taxon sampling to examine this system fully. Fieldwork aimed at improving our understanding of Vanuatu insect diversity and evolution resulted in the collection of two specimens of *Melanesobasis bicellulare* Donelly, 1984, a species previously known from a single specimen collected 40 years ago. Using a combination of morphological and molecular methods, we are able to associate the female, update distributional data, and record intraspecific variation, including the number of post-discoidal cells. We also use this genus, *Melanesobasis* Donnelly, 1984, found across Fiji and Vanuatu, to explore biogeographical patterns across the Vitiaz Arc. Our results provide additional evidence of the importance of the Vitiaz Arc in South Pacific damselfly biogeography and show a pattern of vicariance between the two island archipelagos.

Keywords: biogeography; damselfly; phylogeny; South Pacific; Vitiaz Arc; Zygoptera

INTRODUCTION

The origin of diversity on South Pacific islands has long fascinated biologists (Keppel *et al.* 2009). Although evidence exists for fauna evolving through both vicariance and dispersal mechanisms, debate remains about the prevalence of each (Rota *et al.* 2016, Swenson *et al.* 2019). The biogeography of the region is complicated by its complex geology, with dynamic, volcanic islands that have gone through multiple periods of submergence and re-emergence (Macfarlane *et al.* 1988, Polhemus 1996). This unstable history makes it difficult to track the composition of an archipelago through time, which makes coding geographical areas particularly difficult. Owing to this uncertainty, previous work has highlighted that island biogeography can benefit from examining patterns on the archipelago scale rather than by individual islands (Triantis *et al.* 2016, Saxton *et al.* 2023). This problem arises because most biogeographical analyses are still limited in their ability to account for extinct areas (i.e. sunken islands) (Sanmartín and Meseguer 2016). Historically, long-distance dispersal has been proposed as the primary mechanism of diversity on volcanic islands owing to their isolation from mainland continents (MacArthur and Wilson 2001). Under this model, the diversity of islands is a function of their size and distance from faunal sources. However, in recent years researchers have explored the idea that populations can evolve *in situ* by means of metapopulation vicariance, in which organisms are able to persist on archipelagos for long periods of time by

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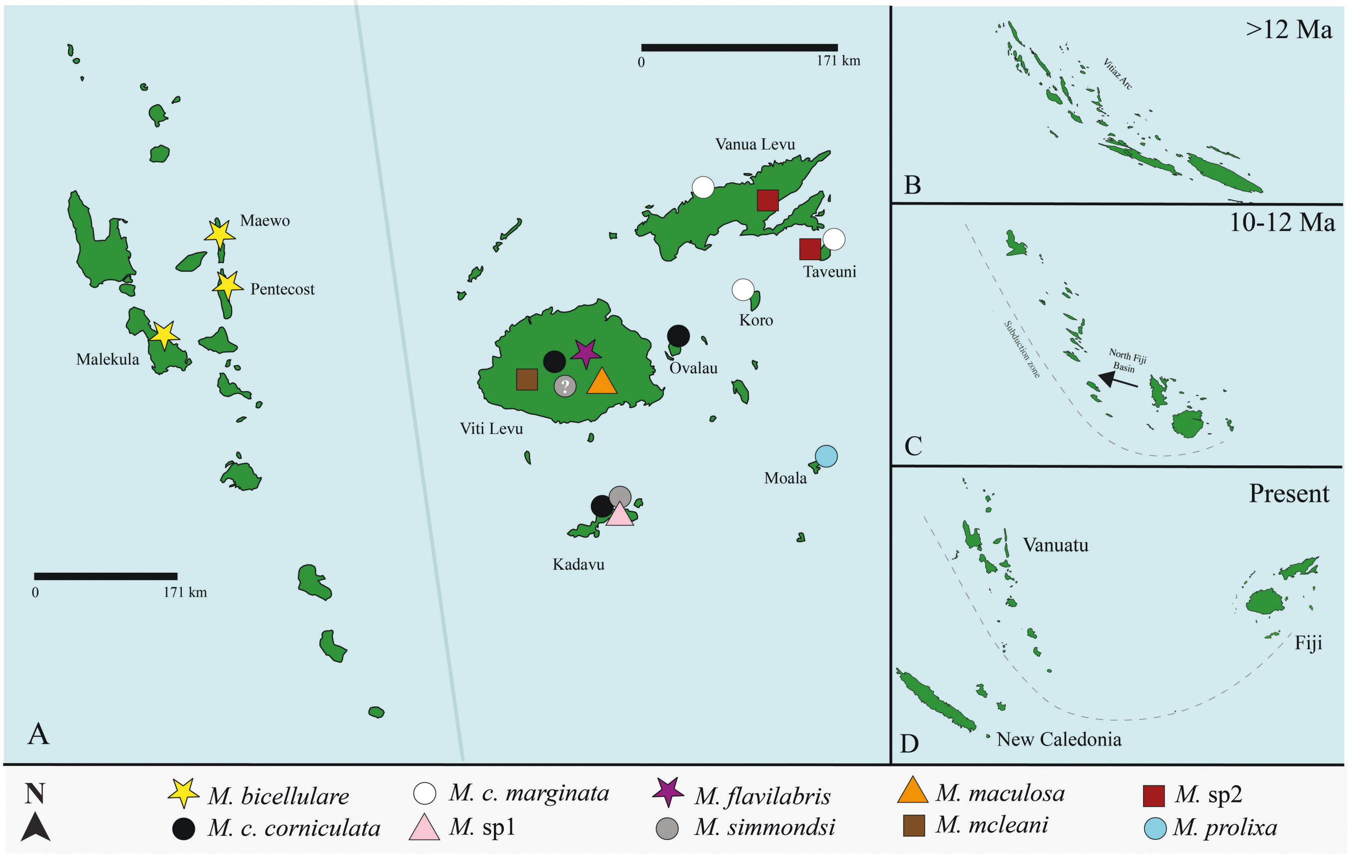

Figure 1. A, map of the distribution of *Melanesobasis* spp. in Vanuatu (left) and Fiji (right). Note the '?' inside *Melanesobasis simmondsi* on Viti Levu, indicating a potentially incorrect record (for more information, see Discussion). B, Vitiaz Arc prior to break-up. C, Vitiaz Arc as Vanuatu rotated clockwise away from Fiji. D, current position of Vanuatu and Fiji relative to New Caledonia. Palaeogeographical reconstructions based on the study by Gill *et al.* (2022).

dispersing short distances between islands in the same region. This will often lead to old lineages on recently emerged islands (Heads 2014, 2018).

The remnants of the Vitiaz Arc provide an ideal opportunity to explore some of these biogeographical patterns, owing to its long volcanic history and subsequent break-up that is conducive to metapopulation vicariance (Heads 2018). An oceanic arc that once spanned from Tonga to the Solomon Islands, the Vitiaz Arc included the island systems of both Fiji and Vanuatu (Crawford *et al.* 2003). Around 10–12 Mya, the archipelago of Vanuatu swung southwest from Fiji, possibly a result of the Ontong Java Plateau collision with the Solomon Islands (Begg and Gray 2002), forming what is now the North Fiji Basin (Meffre and Crawford 2001) (Fig. 1). The formation of this biogeographical barrier (i.e. the North Fiji Basin) could facilitate vicariance if the ancestor of a group was found throughout the region and predates the origin of this barrier. Alternatively, if the ancestor of the group is younger than the barrier and found on only one side of it, long-distance dispersal might best explain current distributions. As such, the ages of clades provide valuable information when examining biogeographical patterns.

Geological evidence suggests that the oldest rocks in Fiji (Yavuna group) are found on the main island of Viti Levu and date back to the Late Eocene to early Oligocene (~30–40 Mya) (Neall and Trewick 2008, Colley 2009). Owing to their age, these portions of the island are likely to represent remnants of the Vitiaz Arc. In contrast, the second largest Fijian island, Vanua Levu, is much younger, having been formed within only the past 7 Myr (Colley 2009, Keppel *et al.* 2009). In Vanuatu, the oldest islands make up the Western Chain, including Malekula and Espiritu Santo, which are estimated to have formed in the late Oligocene. This was followed by the Eastern chain, including the islands of Maewo and Pentecost, which are likely to have formed in the Late Miocene (Greene *et al.* 1994; see also Saxton *et al.* 2023).

In line with their former position in the Vitiaz Arc, the close alliance between the fauna in Fiji and Vanuatu has been noted in several groups (Ingleby and Colgan 2003, Bickel 2009, Grehan and Mielke 2020), including the endemic damselfly genera *Nesobasis* Selys, 1891, *Nikoulabasis* Ferguson *et al.*, 2023, and *Vanuatubasis* Ober & Staniczek, 2009 (Ferguson *et al.* 2023). Previous work exploring the biogeography of these damselfly genera suggests that the break-up of the Vitiaz Arc played an important role in their divergence (Saxton *et al.* 2023), highlighting the role of vicariance in the evolution of taxa on isolated island systems in the South Pacific. It is likely that the biology of a group, such as habitat and distributions, play an essential role in how organisms respond to similar or even the same evolutionary and biogeographical pressures (Salces-Castellano *et al.* 2020, Suárez *et al.* 2022). The damselfly genus *Melanesobasis* Donnelly, 1984 is distributed in a similar manner to the clade *Nesobasis* + *Nikoulabasis* + *Vanuatubasis* and was thought to be closely related (Beatty *et al.* 2017). Both groups are stream dwellers and, in some cases, are collected from the same localities (Marinov 2011, Saxton *et al.* 2021). This genus, therefore, provides a unique opportunity to see how the biogeography of similar lineages compare in the region.

The genus *Melanesobasis* was established for four undescribed species and three species previously belonging to *Nesobasis* (Donnelly, 1984). *Melanesobasis*, found in Fiji and Vanuatu, currently contains seven species and one subspecies. Six species are endemic to Fiji and one, *M. bicellulare* Donnelly, 1984, to Vanuatu. It also includes two undescribed species (treated here as *M.* sp1 and *M.* sp2) held in the personal collection of Donnelly (see Beatty *et al.* 2017). *Melanesobasis bicellulare* is known from a single specimen collected on the island of Maewo in 1979 (Donnelly 1984). This specimen represents the only record of *Melanesobasis* in Vanuatu. Morphologically similar to *Melanesobasis flavilabris* (Selys, 1891) from Fiji, *M. bicellulare* can be distinguished easily from *M. flavilabris* by the rounded terminal edge of the genital ligula in *Melanesobasis bicellulare* (distinctly pointed in *M. flavilabris*), quadrate mesostigmal laminae (triangular in *M. flavilabris*), and the presence of only two post-discoidal cells in the hindwing (three in *M. flavilabris*) (Donnelly 1984).

Melanesobasis appears to share characteristics of some of the Platycnemididae, such as an undulate wing margin, long legs, wide head, and stout thorax, in addition to some nymphal characteristics (Donnelly 1984). However, despite these similarities, Donnelly (1984) suggested a close relationship to the endemic genus *Nesobasis*, citing wing and nymphal characters (i.e. lack of setae on mentum or labial palps). De Marmels (2007) placed *Melanesobasis* within the Teinobasinae, citing the cercal spur as a key character for the group. Dijkstra *et al.* (2014) tentatively placed the genus within the 'ridge-face' Coenagrionidae along with other Teinobasinae, such as *Vanuatubasis* and *Nesobasis*. Phylogenetic analyses completed by Beatty *et al.* (2017) included all but two species (*M. bicellulare* and *M. proxila* Donnelly, 1984) in the genus and did not recover *Melanesobasis* as sister to *Nesobasis* as was previously hypothesized. They did, however, establish two well-supported clades within the *Melanesobasis*, including the '*corniculata* clade', which contains *M. corniculata marginata* Donnelly, 1984, *M. corniculata corniculata* (Tillyard, 1924), *M. flavilabris* (Selys, 1891) and *M.* sp1, and the '*simmondsi* clade', which contains *M. simmondsi* (Tillyard, 1924), *M. mcleani* Donnelly, 1984, *M. maculosa* Donnelly, 1984, and *M.* sp2 (Beatty *et al.* 2017). Owing to limited generic taxon sampling available at the time, this phylogeny did not resolve its placement within Coenagrionidae. Most recently, Willink *et al.* (2024) reconstructed a densely sampled phylogeny across the entire family Coenagrionidae, which found consistent results with those major clades recovered in previous works (Dijkstra *et al.* 2014, Bybee *et al.* 2021), but was able to place three species of *Melanesobasis* within the 'ridge-face' Coenagrionidae *sensu* Dijkstra *et al.* (2014). *Melanesobasis* was recovered by Willink *et al.* (2024) as sister to *Bromeliagrion* De Marmels, 2005 + *Sangabasis* Villanueva, 2012 + *Pericnemis* Selys, 1863, albeit with low support.

Historically, Vanuatu has been undersampled, especially for insects, despite being in a unique biogeographical position owing to its former position in the Vitiaz Arc (Miller 1996, Cranston 2017, Marinov 2015). This oversight has left gaps in our understanding of the distribution and diversity of insect fauna in the South Pacific. Recent expeditions have taken large steps to begin to fill in these knowledge gaps. The results of these expeditions have led directly to a significant increase in our understanding of the diversity (Soldati *et al.* 2012, Kakinuma 2019, Gomy and Tishechkin 2020, Theischinger *et al.* 2020, Saxton *et al.* 2022), distribution (Marinov *et al.* 2019, Hadden *et al.* 2020, Sutherland *et al.* 2021, Gray 2023), natural history (Bouchet *et al.* 2011, Saxton *et al.* 2019, 2021), and evolutionary patterns (Toussaint and Balke 2016, Matos-Maraví *et al.* 2018, Saxton *et al.* 2023) of insects across the region. In continuation of this progress, additional fieldwork undertaken in 2019 resulted in the collection of two *Melanesobasis* specimens from the islands of Pentecost and Malekula, Vanuatu (Fig. 1). These represent the first *Melanesobasis* specimens collected in Vanuatu since the holotype of *M. bicellulare* in 1979. These records expand the distribution of *Melanesobasis* and provide the first molecular-grade samples, allowing for the incorporation of Vanuatu into previous phylogenetic hypotheses (see Beatty *et al.* 2017).

Here, with the incorporation of new material, we are able to associate and describe the female of *M. bicellulare* and to reconstruct a phylogeny incorporating important specimens from Vanuatu. With the incorporation of these specimens, we are able to examine, for the first time, the biogeographical patterns of the genus across both Fiji and Vanuatu in the context of their former placement in the Vitiaz arc. Specifically, here we use the age of the most recent common ancestor (MRCA) for *Melanesobasis* in addition to its reconstructed range to determine whether vicariance or dispersal best explains current distributions.

MATERIALS AND METHODS

Specimen methods

Fieldwork in Vanuatu took place in May–June 2019. Two specimens of *Melanesobasis* were collected on the islands of Malekula (female) and Pentecost (male) (see stars in Fig. 1) using aerial nets and immediately stored in 95% ethanol. Newly collected specimens were examined using an Olympus SZ51 stereo microscope. Identifications were made using the paper by Donnelly (1984) and comparisons with the holotype of *Melanesobasis bicellulare* deposited at the Bernice P. Bishop Museum. Images were taken using a Vision Digital Passport imaging system with a 65 mm lens. Images were stitched using ZERENE v.1.04 (Zerene Systems LLC, Richland, WA, USA). Dissections of genitalia were performed on the ethanol-preserved male from Pentecost. Label data are given verbatim, with '/' to indicate line breaks.

Specimens examined are deposited in the following institutions: Bernice P. Bishop Museum, Honolulu, HI, USA (BPBM) and Monte L. Bean Museum, Provo, UT, USA (BYU).

Molecular methods

Thoracic tissues from *Melanesobasis* specimens were used to extract DNA following the standard protocol for insects using Qiagen DNeasy extraction kits. We amplified portions of nuclear

Table 1. GenBank accession numbers of taxa included in phylogenetic analyses.

Genus	Species	Voucher	Pat/Jerry	LCO/HCO	12S	ITS
Ceriagrion	*auranticum*	RF2732	LC366839			LC366245
Ceriagrion	*auranticum*	mtGenome	NC_054209	NC_054209	NC_054209	
Ceriagrion	*fallax*	mtGenome	NC_054209	NC_054209	NC_054209	
Ceriagrion	*melanurum*	RF2022	LC366676			LC366082
Chromagrion	*conditum*		KU220873			KU245324
Mecistogaster	*linearis*		MK044580		MK032075	
Melanesobasis	*bicellular*	OD1705	PV577727	PV577730	PV583925	PV583929
Melanesobasis	*bicellular*	OD1706	PV577728	PV577731	PV583926	PV583930
Melanesobasis	*c. corniculata*	OD1707		PV577732	PV583927	PV583931
Melanesobasis	*c. marginata*	JSS16976	FJ812822	FJ812778	FJ812733	FJ812865
Melanesobasis	*c. corniculata*	JSS17153	FJ812819	FJ812775	FJ812730	FJ812862
Melanesobasis	*flavilabris*	JSS17158	FJ812820	FJ812776	FJ812731	FJ812863
Melanesobasis	*maculosa*	NE1572	MH348620			
Melanesobasis	*maculosa*	JSS16975	FJ812821	FJ812777	FJ812732	FJ812864
Melanesobasis	*mcleani*	NE1589	MH348619			
Melanesobasis	*mcleani*	JSS17159	FJ812823	FJ812779	FJ812734	FJ812866
Melanesobasis	*simmondsi*	OD1708	PV577729	PV577733	PV583928	PV583932
Melanesobasis	*simmondsi*	JSS16978	FJ812824	FJ812780	FJ812735	FJ812867
Melanesobasis	sp1		FJ812826	FJ812782	FJ812737	FJ812869
Melanesobasis	sp2		FJ812825	FJ812781	FJ812736	FJ812868
Pericnemis	*lestoides*		KF369484			
Platystigma	*asticutum*		MK044579		MK032074	
Platystigma	*martinezi*		PP110007		JQ966644	
Platystigma	*martinezi*		MK044583		MK032078	
Nehalennia	*gracilis*		GQ256041		GQ256007	
Nehalennia	*irene*		MG377572		GQ256015	
Nehalennia	*speciosa*		LC366879			LC366285
Nehalennia	*speciosa*		FN252223			HM598667

internal transcribed spacer I (ITS1) and the mitochondrial genes cytochrome *c* oxidase I (*COI*) (two regions treated here as Pat/Jerry and LCO/HCO) and small ribosomal RNA subunit (12S) using PCRs. Amplification conditions and primers followed those of Beatty *et al.* (2017). PCR products were sequenced at the DNA Sequencing Center of Brigham Young University.

Previously published *Melanesobasis* sequences used in study by Beatty *et al.* (2017) were gathered from GenBank, in addition to outgroups (i.e. *Ceriagrion* Selys, 1876, *Chromagrion* Needham, 1903, *Mecistogaster* Rambur, 1842, *Nehalennia* Selys, 1850, *Pericnemis*, and *Platystigma* Kennedy, 1920). Outgroups were selected based on the classification of ridge-faced Coenagrionidae given by Dijkstra *et al.* (2014) and the results obtained by Willink *et al.* (2024). For two *Ceriagrion* specimens, the published mitochondrial genomes were used to extract overlapping regions of *COI* and 12S (Shao *et al.* 2021) (see Table 1).

All sequences were aligned, trimmed, and concatenated in GENEIOUS PRIME v.2024.0.7 (https://www.geneious.com) using MAFFT v.7.490 (Katoh *et al.* 2013). We reconstructed a maximum likelihood tree using IQ-TREE v.1.6.12 (Nguyen *et al.* 2015). MODELFINDER (Kalyaanamoorthy *et al.* 2017) was used to select the best model of molecular evolution based on our sequence data (K3Pu+F+I+G4). We used 1000 ultrafast bootstraps (Minh *et al.* 2013) to assess node support.

Association of the female specimen was completed with both a pairwise distance matrix comparing the dissimilarity between barcode sequences (two regions of *COI*; see above molecular methods) across the diversity of *Melanesobasis* and the phylogenetic estimate performed for the group. Previously unknown female specimens that were recovered as sister to a known male and with a genetic similarity >98% (Hebert *et al.* 2003) were considered reliably associated.

Divergence time estimation

The ages of these clades are important when examining whether vicariance or dispersal explains present distributions. Endemic fauna that evolved *in situ* are expected to pre-date the formation of biogeographical barriers (i.e. separation of Fiji and Vanuatu), whereas organisms that evolved after the formation of a barrier are more likely to be the result of dispersal. As a result, it is often necessary to approach divergence time estimates using multiple strategies. Here, we applied two different dating strategies. The first strategy (D1) applied an amber fossil *Nehalennia* sp. (Ross *et al.* 2016) calibration point to the MRCA of the genus *Nehalennia* in addition to a fixed clock rate on the mitochondrial

Table 2. Ages obtained in all divergence time estimates.

Dating strategy	Tree model	Clock model	*Melanesobasis* MRCA	*Melanesobasis* (Fiji only)
D1: fossil calibration points and a fixed clock rate on mitochondrial DNA (partitioned alignment)				
D1.1	BD	RCE	26.25 [18.62–35.27]	24.69 [17.61–33.19]
D1.2	BD	RCLN	26.05 [19.02–36.10]	24.43 [17.74–33.78]
D1.3	Yule	RCE	25.31 [18.43–34.88]	23.82 [17.35–32.97]
D1.4	Yule	RCLN	26.03 [19.06–36.28]	24.41 [17.70–33.76]
D2: based on Willink *et al.* (2024) ages from the weakly informed root-prior ages (i.e. uniform root age 240–40 Mya)				
D2.1	BD	RCE	23.05 [9.02–42.35]	18.86 [7.68–35.19]
D2.2	BD	RCLN	23.60 [13.81–35.05]	20.44 [11.88–30.28]
D2.3	Yule	RCE	22.43 [9.26–40.48]	18.24 [7.69–31.70]
D2.4	Yule	RCLN	23.60 [13.81–35.05]	20.44 [11.88–30.28]

Median ages are given above, with 95% highest posterior density (HPD) given in square brackets. All D1 alignments were partitioned and mitochondrial DNA given a strict clock rate. Abbreviations: BD, birth–death; MRCA, most recent common ancestor; RCE, relaxed clock exponential; RCLN, relaxed clock log normal.

DNA (0.0115 substitutions per site) (Brower 1994). This amber specimen is mostly complete but is missing the abdomen and the tips of the wings, making it difficult to compare with extant species. The transverse ridges on the frons and supplementary tooth on the tarsal claws place this specimen within the 'ridge-faced' damselflies. Distinct thoracic carina and stripe pattern led authors to place it in *Nehalennia*, but could not determine whether it represented any of the extant species (Ross *et al.* 2016). To account for the uncertainty in the placement of this fossil, a log-normal distribution with a soft minimum age (15 Mya) was applied rather than an exponential distribution with a hard minimum. A hard maximum was placed at the base of the phylogeny based on the crown Zygoptera group Hemiphlebiidae (150 Mya) (*Mersituria ludmilae* Vasilenko, 2005).

The second strategy (D2) used ages obtained by Willink *et al.* (2024), in a superfamily-wide dating analysis based on weakly informed root-prior ages. These ages were chosen because they were largely in line with generic ages obtained in previous studies (i.e. *Ischnura* Charpentier, 1840, *Nesobasis*, and *Vanuatubasis*) (Beatty *et al.* 2017, Toussaint *et al.* 2019, Saxton *et al.* 2023). As such, log-normal distributions were applied for the MRCA of *Ceriagrion*, *Melanesobasis*, and *Mecistogaster* + *Platystigma*. A hard maximum was placed at the base of the phylogeny based on the crown Zygoptera group Hemiphlebiidae (*Mersituria ludmilae*, 150 Mya) (Vasilenko 2005).

We used the topology reconstructed in IQ-TREE (Supporting Information, File S1) as a fixed starting tree in all our divergence time estimates. Using a fixed topology ensures that ages between all models are directly comparable, in addition to minimizing computational time. We used the 'chronopl' command implemented within *ape* v.5.8 (Paradis and Schliep 2019), which applies a semi-parametric method based on penalized likelihood to force the topology to be ultrametric, and adjusts nodes based on minimum and maximum ages provided by the user to be within the distributions of the priors used in subsequent divergence time estimation. The tree was adjusted such that the *Melanesobasis* (node 43) was 8–40 Mya. *Ceriagrion* (node 40) set between 24 and 78 Mya. *Mecistogaster* + *Platystigma* (node 32) was specified to be 16–57 Mya. Finally, the root was set to be 50–150 Mya. The resulting ultrametric topology was exported and used as a fixed starting tree for both dating strategies in BEAUTi by setting all tree rearrangement operators to zero.

BEAUTi v.2.6.7 (Bouckaert *et al.* 2014) was used to set all analysis parameters, including clock and tree models in an XML file. We applied a combination of each of the tree and clock models across both dating strategies (i.e. birth–death, Yule, relaxed clock exponential, and relaxed clock log normal). For D1 analyses, the alignment was partitioned such that a strict clock could be applied to the mitochondrial DNA (e.g. *COI*, 12S). For D2 analyses, the alignment was not partitioned (for clock models, see Table 2). In order to incorporate the best-fitting site model into our analyses, TN93 was chosen, with the following modifications based on ModelFinder (Kalyaanamoorthy *et al.* 2017) results: gamma category count = 4, shape = 0.82, proportion invariant = 0.447. All transition rates were set to be estimated. We ran the resulting XML files in BEAST 2 v.2.6.6 (Bouckaert *et al.* 2014) on the CIPRES Science Gateway accessed through DeCIFR (https://decifr.cifr.ncsu.edu/), with a chain length of 300 000. Log files from each run were examined visually in Tracer v.1.7.2 (Rambaut *et al.* 2018) to ensure convergence and had effective sample size values of >200. A consensus tree was generated for each analysis using a 25% burn-in.

Biogeographical analyses

The historical ranges of these clades are important to determine whether the ancestor of *Melanesobasis* was widespread across the region (Vanuatu and Fiji) or found in only part of the region. This information, in conjunction with the age of the clade, can inform patterns of vicariance or relative dispersal. We would expect to find widespread ancestors pre-dating the formation of a barrier expected under a vicariance scenario and ancestors found in only a portion of the region after the formation of the barrier in a dispersal scenario. We performed a total of 18 biogeographical analyses using BioGeoBEARS (Matzke 2013), using two different methods of coding areas in addition to time-stratified analyses. These included models with and without jump-dispersal events (+J), allowing for founder speciation (Matzke 2022). The three main models tested (i.e. DEC, DIVALIKE, and BAYAREALIKE) allow for or restrict different types of anogenic and cladogenic events, allowing the user to determine which model best accounts of the data given. For a more detailed account and comparison of the three main models tested, see Matzke (2013, 2014). In order to perform biogeographical analyses, the resulting dated topology D1.2 was trimmed using the 'drop.tip' function in *phytools* v.2.3 (Revell 2024), such that each species in *Melanesobasis* was represented by one tip. We chose topology D1.2 because our dataset contains intraspecific sampling, and the birth–death tree model has been shown to be robust to mixed sampling (Ritchie *et al.* 2017). This model (D1) also relied on fossil calibration points rather than previous divergence time estimations. However, we note that the ages recovered for all models are largely congruent (Table 2). For the first six models, biogeographical areas were coded as Fiji (A) and Vanuatu (B), with the maximum areas allowed set equal to two. This model, coded at the archipelago level, examines broader patterns of biogeography, which is important when trying to account for extinct areas (Triantis *et al.* 2016, Saxton *et al.* 2023).

An additional six models were run based on biogeographical areas coded as: southwest Fiji (Viti Levu, Ovalau, Kadavu) (A); northeast Fiji (Vanua Levu, Koro, Taveuni) (B); and Vanuatu (C). The maximum number of areas was set to three. In this model, we split Fiji into southwestern and northeastern regions based on a natural barrier found in species distributions (see also Beatty *et al.* 2017). This method of coding was then used in conjunction with a time-stratified analysis that restricted lineage movements between Vanuatu (C) and regions of Fiji (A and B) prior to 10 Mya, corresponding to the estimated time when the two archipelagos split. Results from all models were compared using the Akaike information criterion (AIC) to assess best fit.

RESULTS

Variation in male and association of the female

The two male specimens investigated in the present study show some variation in post-discoidal cells, numbering two (Maewo) and three (Pentecost) (Fig. 2). In both, the male cerci bear long, curved setae along their rounded apex, with the Pentecost male appearing more hirsute. In the Pentecost male, the penis also appears expanded dorsally before constricting to a rounded terminal segment (Fig. 3). This expansion is not visible in the illustration of the Maewo male genitalia given by Donnelly (1984). However, for the moment, both are considered *Melanesobasis bicellulare* with the following shared characters: pale occipital bar, broadly rounded mesostigmal plate, shape of the penis, and thoracic colour pattern (see Donnelly 1984: figs 5, 7, 8, 10, 11).

The female specimen collected in Malekula had a pairwise genetic similarity to the Pentecost male that was 98.69% (Pat/Jerry) and 98.60% (LCO/HCO). The Malekula female specimen was also recovered sister to the Pentecost male *Melanesobasis bicellulare* with 100% bootstrap support (BS).

Melanesobasis bicellulare **Donnelly (Figs 2–4)**

Melanesobasis bicellulare Donnelly 1984: 100.

Type material examined: Holotype (one ♂, *BPBM*), 'NEW HEBRIDES [Vanuatu]: Maewo I: Sounwari: 0–360 m, 4–5. IX.1979' 'G.M. Nishida Coll. / BISHOP Museum / Acc. No. 1979.380'.

Additional material examined: (one ♂, BYU), 'VANUATU: Pentecost Is., / Ranmawat, May 30, 2019; / −15.8126, 168.1770 / Coll: SM Bybee, GS Powell / #BYU-VU-2019' 'OD1706'.

(one ♀, BYU), 'VANUATU: Malekula Is., / Wiaru River, May 13th 2019 / −16.0787, 167.2726 / Coll. SM Bybee, GS Powell / BYU-VU-2019' 'OD1705'.

Description of female

Head: Labium beige; labrum light yellow with darker posterolateral corners, medial posterior edge with dark brown spot; anteclypeus and genae green, mandibles (except for reddish tips) yellow; postclypeus, frons, and scape black with bronze shimmer; antennae with black scape, pedicels yellow, flagella dark brown and darkening apically (Fig. 4D); vertex and rear of head black except for pale yellow–white patches extending from the base of the scape to the lateral ocelli; pale occipital bar present; eyes dark green on dorsal two-thirds and lighter on basal one-third.

Thorax: Prothorax dorsally black with strong bronze shimmer; laterally black with pale stripes; hind lobe with a straight medially edge; mesostigmal plates light brown, roughly triangular, and without a prominent caudal depression, lateral corner broadly rounded (Fig. 4B). Pterothorax with black carina; laterally black with bronze shimmer except for a pale stripe along the mesopleural suture, a pale spot on the apical corner of the mesinfraepisternum, a short pale stripe on the posterior one-third of the interpleural suture, and a pale stripe that runs along the ventral edge of the metepisternum but reaches the metapleural suture on its posterior half; anterior carina pale along the metepisternum and metepimeron. Coxae black; legs light brown ventrally and dark brown dorsally; trochanters and femora with dark brown spines; tibiae with lighter spines than that of the femora; tarsi reddish-brown and small recurved spines; claws reddish brown.

Wings: Hyaline, with dark brown venation; brown pterostigma; three post-discoidal cells. Nodal index: forewing 18/2–2/15; hindwing 17/2–2/14.

Abdomen: Overall black with bronze shimmer; S8 reddish-brown dorsally; S9 and S10 black (Fig. 4E); cerci dark brown and roughly limuloid, lightening apically; paraproct dark brown on dorsal side, fading to a brownish red on ventral side; valve with excision on dorsal apex forming small tooth, stylus extending

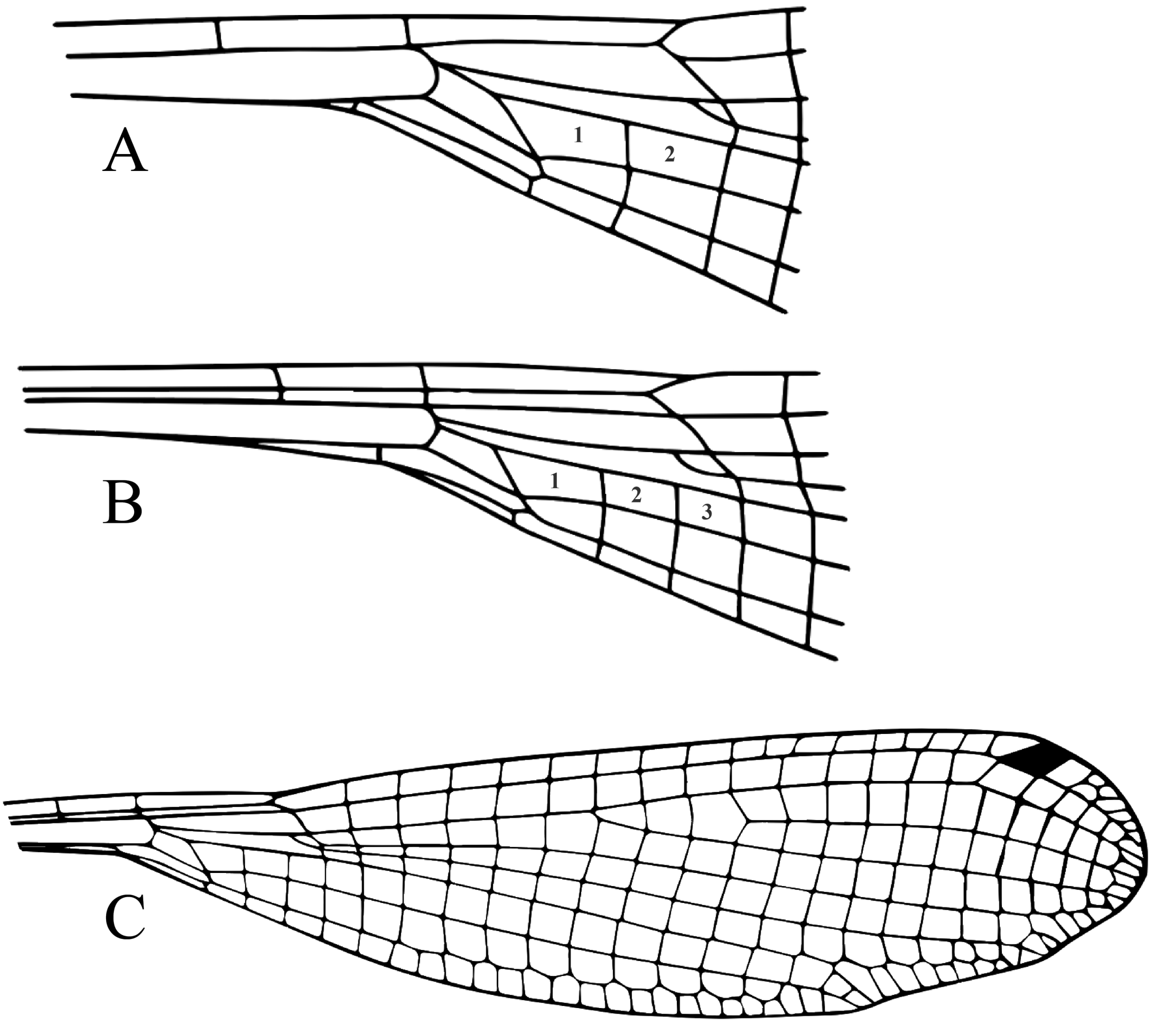

Figure 2. Hindwing venation in *Melanesobasis bicellulare.* A, male, holotype, Maewo, with two post-discoidal cells. B, male, Pentecost, with three post-discoidal cells. C, Female, Malekula; note undulating wing margin.

Figure 3. Male *Melanesobasis bicellulare* from Pentecost. A, dorsal view of terminal appendages, showing setae. B, lateral view of penis.

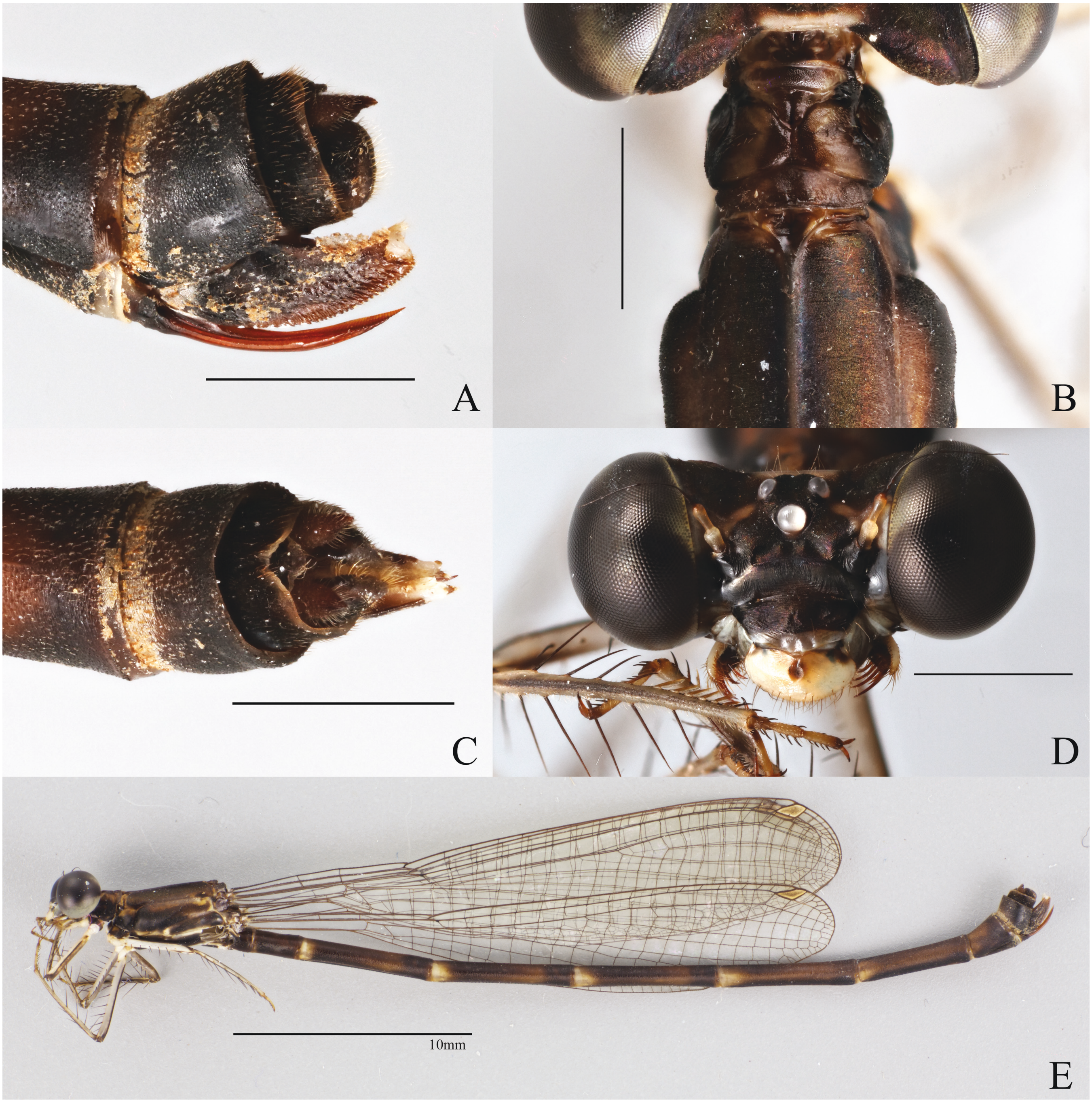

Figure 4. Female *Melanesobasis bicellulare*. A, lateral view of ovipositor. B, dorsal view of pronotum. C, dorsal view of ovipositor. D, face. E, lateral view of habitus. Unless otherwise labelled, scale bars represent 1 mm.

beyond cerci, narrow and broadly rounded, gonapophysis reddish-brown (Fig. 4A, C).

Measurements: Total length 41 mm, abdomen 33 mm, and hindwing 24 mm.

Distribution: Vanuatu (Maewo, Pentecost, and Malekula).

Molecular phylogenetics and divergence time estimates

In total, we included 28 specimens in the maximum likelihood phylogeny (Table 1), composing 2596 bp. Seven of the eight known species of *Melanesobasis* were included, in addition to one subspecies. Currently *M. c. marginata* is treated as a subspecies of *M. c. corniculata*. The maximum likelihood phylogeny recovered a monophyletic *Melanesobasis* (98% BS). Vanuatu specimens of *Melanesobasis bicellulare* were recovered as sister to all Fijian species. Congruent with previous analyses (i.e. Beatty *et al.* 2017), we recovered a well-supported '*corniculata*' clade (100% BS) and '*simmondsi*' clade (100% BS). Of the species tested for monophyly, *Melanesobasis c. corniculata* is recovered as non-monophyletic (51% BS), with undescribed species *Melanesobasis* sp2 sister to the subspecies *M. c. marginata* (71% BS) (Fig. 5).

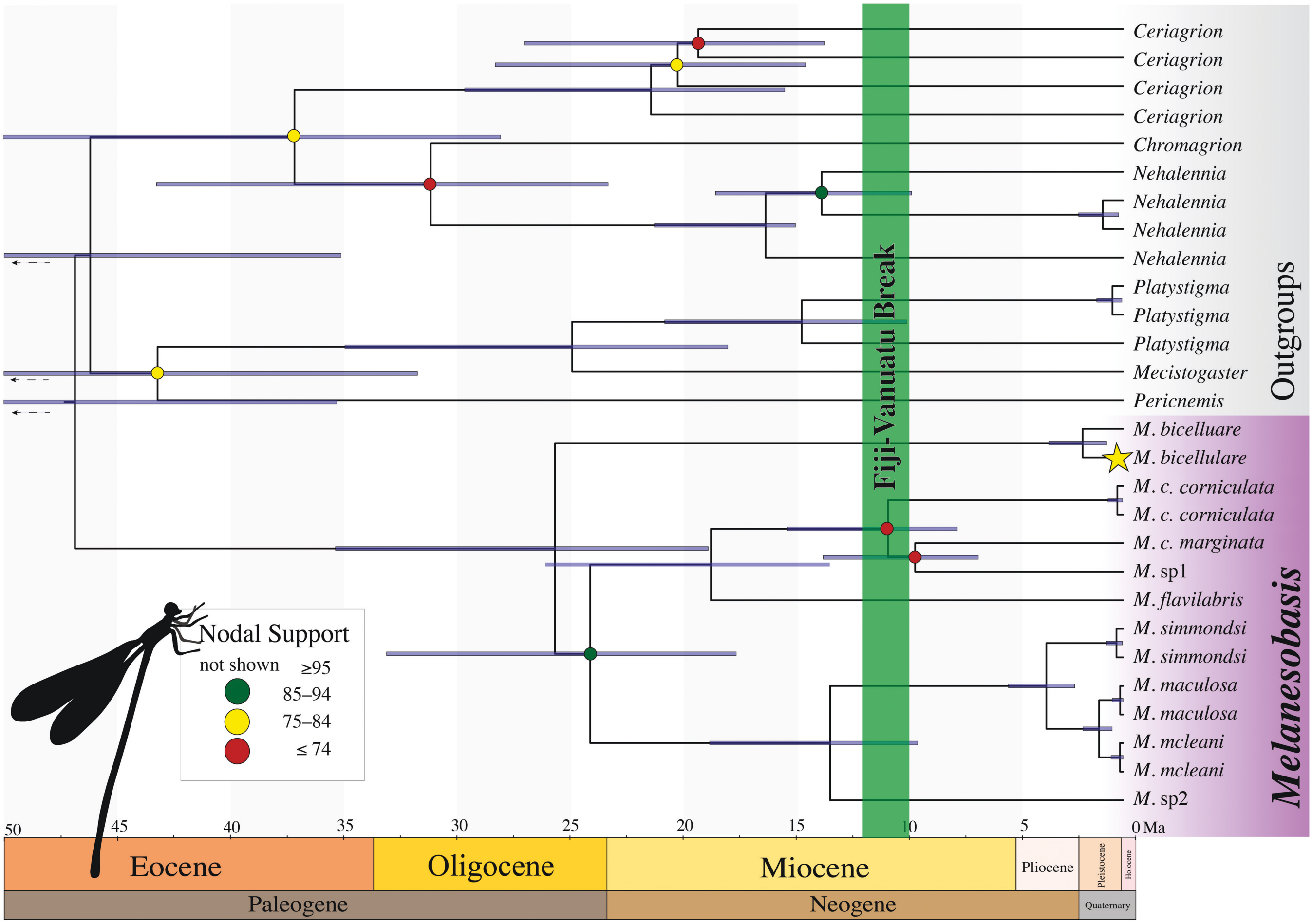

Figure 5. Results of divergence time estimation in BEAST 2 based on D1.2. Node support <95% is shown at nodes. The yellow star indicates placement of the previously unknown female specimen.

Divergence time analyses (D1 and D2) recovered overall similar median ages (Table 2; Supporting Information, File S1). Both recovered the age of *Melanesobasis* around 23–26 Mya [9–40 Mya highest posterior density (HPD)] and specifically the age of Fijian *Melanesobasis* at 18–24 Mya (7–33 Mya HPD). Most extant species are estimated to have originated within the last 5 Myr in both analyses. The second dating strategy (D2) consistently recovered broader 95% HPD than the first dating strategy (D1), often with ranges spanning an additional 10–15 Myr.

Biogeography

Results of all models, including ancestral state probabilities for all internal nodes, can be found in the Supporting Information, File S2. Of all biogeographical models tested, DIVALIKE was recovered as the best fit for our two-area models, with an AIC score of 5.386 (Table 2). In both DEC and DIVALIKE models, the MRCA of all *Melanesobasis* (node 10) was recovered as Fiji + Vanuatu (AB) with >99% ancestral state probabilities, supporting a vicariance event in which descendants were split between Fiji (A) and Vanuatu (B). The remaining internal nodes were recovered as Fiji (A) with >99% probability (Fig. 6). Conversely, the BAYAREALIKE model (AIC 15.49) recovered the MRCA of all *Melanesobasis* (node 10) as Fiji (A) (80%), with a subsequent dispersal event to Vanuatu. The remaining internal nodes for this model recovered Fiji as the ancestral range with >90% probability. BAYAREALIKE+J recovered a similar result but with Fiji (A) and Vanuatu (B) as equally likely (50%) to be the ancestral state for *Melanesobasis* (node 10), with subsequent jump-dispersal events (founder-event speciation) to either Vanuatu or Fiji. All remaining internal nodes were reconstructed as Fiji (A) with >99% probability.

Using three-area models, the DIVALIKE+J model (Fig. 7) was recovered as the best fit with an AIC score of 19.87. In this model, the MRCA of all *Melanesobasis* (node 10) was reconstructed with the highest probability (52%) to be southwest Fiji + Vanuatu (AC). A vicariance event was reconstructed, with the descendants of node 10 being found in either southwest Fiji (A) or Vanuatu (C). Jump dispersal (founder-event speciation) was inferred for the species *M.* sp2 and *M. c. marginata* from southwest Fiji (A) to northeast Fiji (B). DIVALIKE reconstructed a highly similar scenario, in which vicariance was inferred with node 10 reconstructed as AC (85%) and the direct descendants being found in only A or C. Under this model, however, dispersal to northeast Fiji (B) occurred after cladogenesis leading to a range expansion (nodes 14 and 15; AB), which was followed by vicariance in both major clades of Fijian *Melanesobasis*.

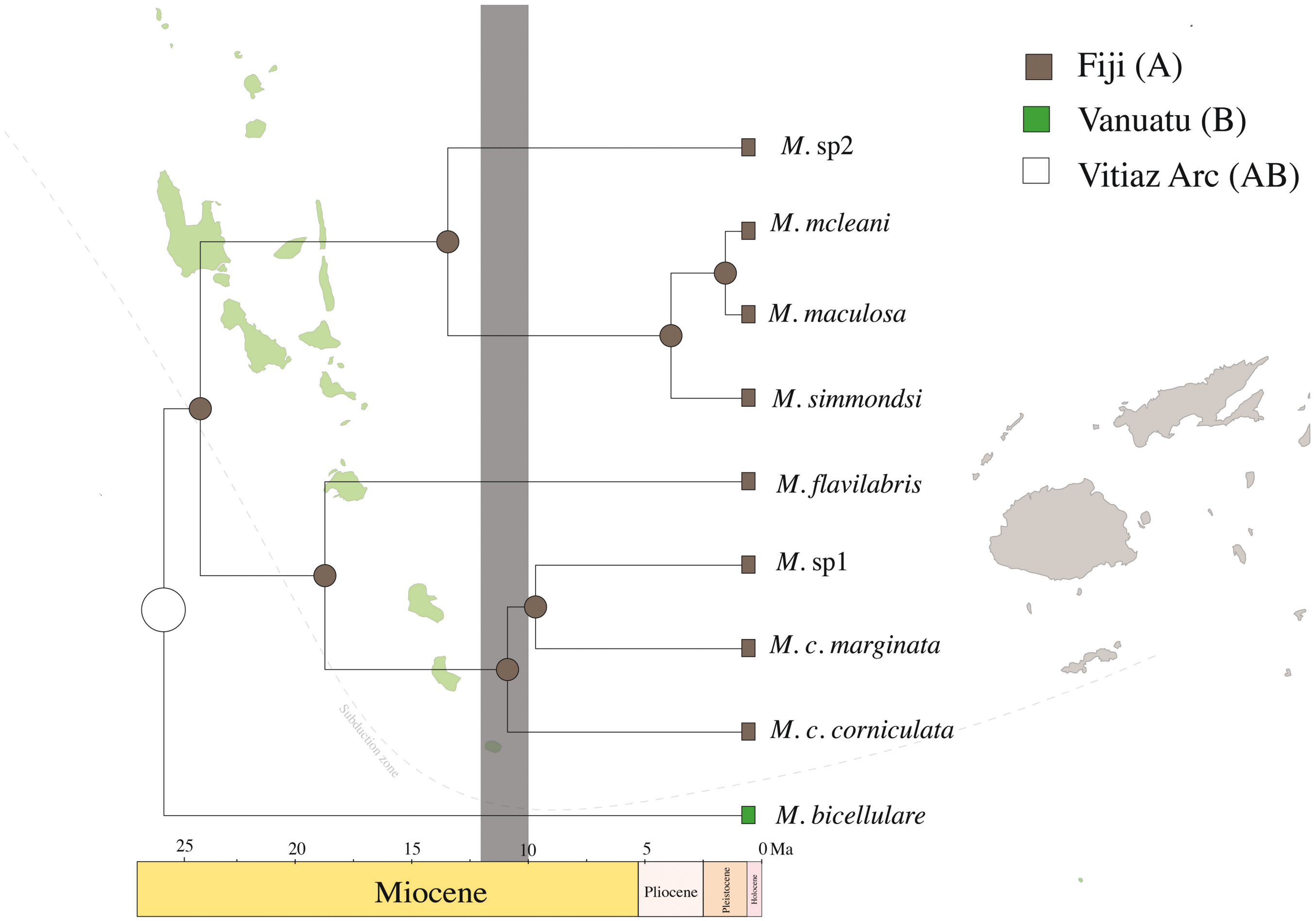

Figure 6. Results of BioGeoBEARS best-fitting model (DIVALIKE) using a two-area model. Grey bar indicates estimated timing of Vitiaz Arc break-up (10–12 Mya).

In the three-area DEC model, all areas (ABC 46%) were recovered at node 10. The descendants of the MRCA of *Melanesobasis* under this model had range contraction in northeast Fiji (B) (extinction) and vicariance into Fiji (A) and Vanuatu (C). Within the Fijian *Melanesobasis* there was back dispersal to northeast Fiji (B) leading to nodes 14 and 15 (AB) followed by vicariance. DEC+J had a largely unresolved ancestral area for all *Melanesobasis* at node 10 (AC 33%; A 20%; C 23%). Vicariance was recovered as the mostly likely scenario, with descendants of node 10 in area A or C. This was followed by jump-dispersal to northeast Fiji (B).

Under BAYAREALIKE, node 10 had the greatest probability to inhabit all three areas (ABC 38%) or all of southwest and northeastern Fiji (AB 31%). This reconstruction suggested either range contraction (extinction) leading to descendants in AB (node 11) and C (node 1), or subsequent dispersal to Vanuatu. Additional range contraction events were reconstructed in Fiji (AB), leading to extant distributions in only southwestern Fiji (A) or northeastern Fiji (B). BAYAREALIKE+J recovered node 10 as C (50%) or A (42%). Based on the highest probabilities, jump-dispersal from Vanuatu to southwestern Fiji (A) occurred, with subsequent jump-dispersal to northeastern Fiji (B).

When the three-area model was time constrained to limit movement between Vanuatu and Fiji after 10 Mya, we recovered almost identical results to the unconstrained three-area model (Supporting Information, File S2). DIVALIKE+J was recovered as the best-fitting model in this case, with an AIC score of 19.87. The MRCA for all *Melanesobasis* was recovered as both Fiji and Vanuatu (AC), followed by vicariance.

DISCUSSION

The results presented here highlight the importance of vicariance in the evolution of taxa on remote islands in the South Pacific, while also exhibiting the importance of complete geographical sampling to explore these patterns fully. Previous phylogenetic hypotheses of *Melanesobasis* were able to include only Fijian species, limiting biogeographical analyses to those islands. With the incorporation of Vanuatu specimens, we are able to examine biogeographical patterns fully, gaining insight into the origin of the genus.

Previously, *M. bicellulare* was known from only one specimen collected in 1979 from Maewo, Vanuatu, and these new collecting events represent not only a significant temporal result, demonstrating the continued presence of the taxon 45 years later, but also a distributional expansion onto two additional islands of Vanuatu. The specimens that were collected as part of this study have allowed for the reliable association of female *M.*

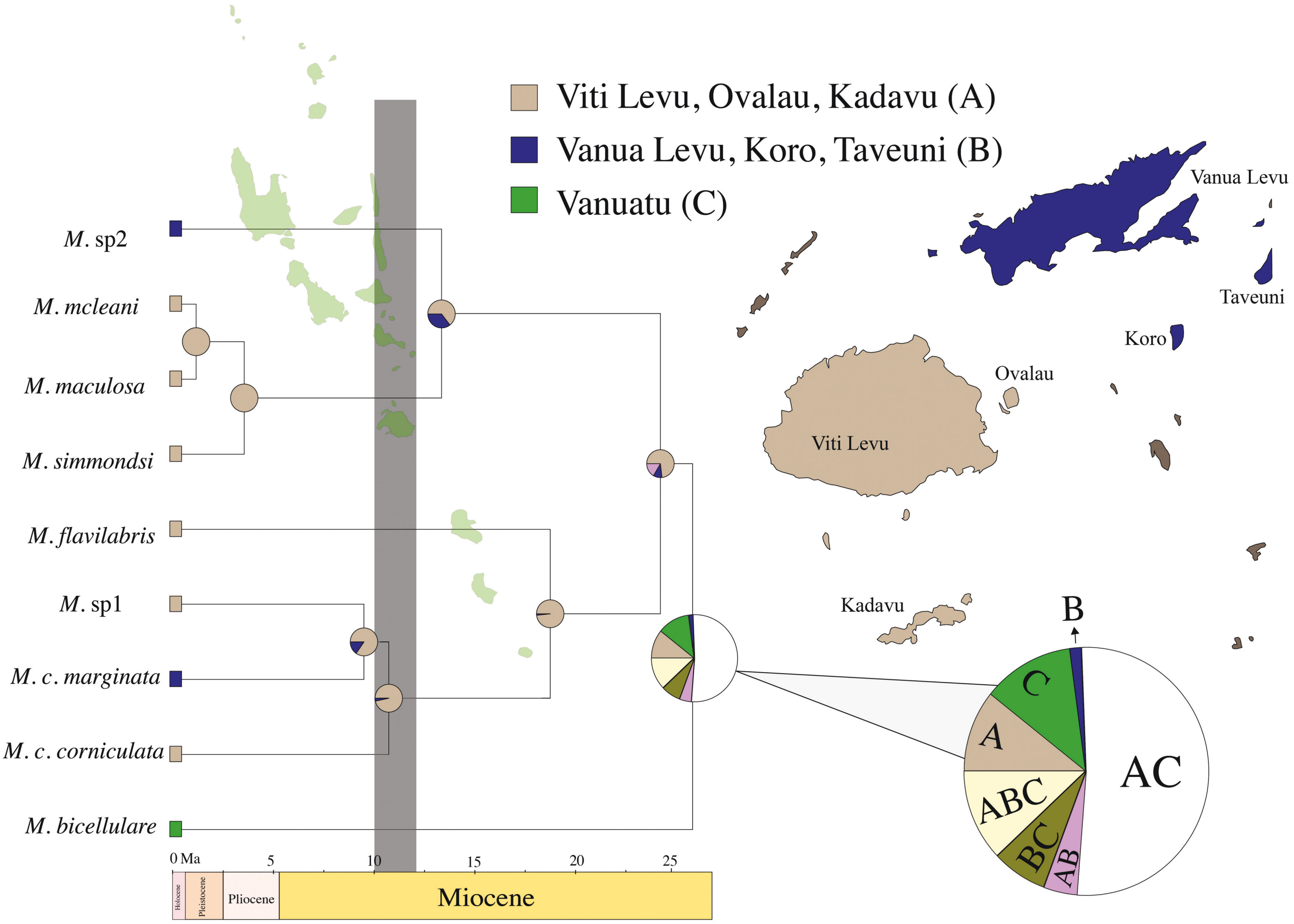

Figure 7. Results of BioGeoBEARS best-fitting model (DIVALIKE+J) using a three-area model, in which Fiji was divided into two areas. For the full breakdown of the ancestral state probabilities at each node, see Supporting Information, File S2. Grey bar indicates estimated timing of Vitiaz Arc break-up (10–12 Mya).

bicellulare and add to what we know about the distribution and morphology of this group. These specimens, in conjunction with the known diversity and distributional patterns in Fiji, suggest that the diversity of *Melanesobasis* in Vanuatu might be greater than is currently understood. Additional fieldwork targeting this genus should be undertaken across the archipelago to improve our understanding of both the distribution and the phenology of this genus.

Donnelly (1984) suggested that *M. bicellulare* was easily mistaken for *M. flavilabris* but was diagnosed by the presence of only two post-discoidal cells, in addition to the shape of the cerci, penis, and mesostigmal plates. However, in Coenagrionidae, the number of post-discoidal ('post-quadrangular') cells has been known to vary within species (De Marmels 1984, Garrison and Von Ellenrieder 2018). In some genera, such as *Argia* Rambur, 1842, it is common to find specimens of the same species with three to five post-discoidal cells (Garrison and Von Ellenrieder 2018). The male specimen of *M. bicellulare* collected in Pentecost appears to show that variation in the number of cells is also occurring in *Melanesobasis*. The male specimen strongly resembles the holotype of *M. bicellulare* in head coloration (i.e. labrum, antennal pattern, pale spots lateral to the ocelli, and a transverse occipital bar), thorax coloration (i.e. dark), paraproct configuration, broadly rounded mesostigmal plates, and penis shape, with the major difference being that the Pentecost specimen has three post-discoidal cells. At the moment, the observed differences are attributed to suspect intraspecific variations between members of populations inhabiting neighbouring islands. However, the collection of additional specimens is needed to provide sufficient material to explore this hypothesis fully. The female *M. bicellulare*, in addition to having >98% pairwise genetic similarity with the male identified as *M. bicellulare*, also shares the following characters: labrum pale with medial brown spot, pale spots on the dorsum of head, coloration of antennae, coloration of legs, and general coloration of the abdomen. Redefining the diagnostic morphology of this taxon to include the observed intraspecific variation is vital to aid in future identification of this species within Vanuatu. Future studies should examine *Melanesobasis* morphology in the context of phylogenetic results to gain a better understanding of the evolution of this genus. For example, there appear to be two major clades of Fijian *Melanesobasis*, which also align with the presence or absence of a small tooth on the inner edge of the cerci.

The topology, with the addition of *M. bicellulare*, remains largely unchanged from those results obtained by Beatty *et al.* (2017). All species except for *M. prolixa* have now been

Table 3. BioGeoBEARS analysis results for all models tested.

Model	Number of areas	n	d	e	j	LnL	AIC
DEC	2	2	1.0×10^{-12}	1.0×10^{-12}	0	−1.79	7.58
DEC+J	2	3	1.0×10^{-12}	1.0×10^{-12}	1.0×10^{-5}	−1.79	9.58
DIVALIKE*	2	2	1.0×10^{-12}	1.0×10^{-12}	0	−0.69	5.39
DIVALIKE+J	2	3	1.0×10^{-12}	1.0×10^{-12}	1.0×10^{-5}	−0.69	7.39
BAYAREALIKE	2	2	0.0069	0.0092	0	−5.74	15.49
BAYAREALIKE+J	2	3	1.0×10^{-12}	1.0×10^{-7}	0.067	−3.01	12.03
DEC	3	2	0.0068	0.0069	0	−12.58	29.16
DEC+J	3	3	1.0×10^{-12}	1.0×10^{-12}	0.15	−7.53	21.07
DIVALIKE	3	2	0.0076	1.0×10^{-12}	0	−11.06	26.11
DIVALIKE+J*	3	3	1.0×10^{-12}	1.0×10^{-12}	0.13	−6.93	19.87
BAYAREALIKE	3	2	0.0079	0.043	0	−14.47	32.93
BAYAREALIKE+J	3	3	1.0×10^{-7}	1.0×10^{-7}	0.17	−8.25	22.51
Time-stratified analyses							
DEC	3	2	0.010	0.0060	0	−12.05	28.09
DEC+J	3	3	1.0×10^{-12}	1.0×10^{-12}	0.15	−7.53	21.07
DIVALIKE	3	2	0.011	1.0×10^{-12}	0	−10.78	24.56
DIVALIKE+J*	3	3	1.0×10^{-12}	1.0×10^{-12}	0.13	−6.93	19.87
BAYAREALIKE	3	2	0.016	0.040	0	−14.76	33.52
BAYAREALIKE+J	3	3	1.0×10^{-7}	1.0×10^{-7}	0.17	−8.25	22.51

*The best-fitting model for each method used to code geographical areas.

included, with the single missing taxon being known from a single specimen collected in 1924 from Moala, Fiji. At the time of this study, the holotype of this species was unable to be located, meaning that interpretations including this missing taxon are limited. Our results also suggest the necessity to elevate the rank of the subspecies *M. c. marginata*. This result was also shown by Beatty *et al.* (2017), although with slightly different relationships. The '*corniculata*' clade was recovered in both analyses, but in the study by Beatty *et al.* (2017) *M. flavilabris* + *M.* sp1 was sister to *M. c. marginata*. We recovered *M. c. marginata* as sister to *M.* sp1, although the node support for this relationship was not high (71% BS). The clade containing both these species (*M. c. marginata* + *M.* sp1) was recovered sister to *M. c. corniculata* (Fig. 5). If valid, the elevation of this subspecies would add to the two undescribed species that were known previously.

Previous estimates for the crown age of Zygoptera have found 189 Mya (Suvorov *et al.* 2022) to 240 Mya (Kohli *et al.* 2021). Estimates for Coenagrionoidea have recovered 115 Mya (Suvorov *et al.* 2022) to 128 Mya (Kohli *et al.* 2021) and Coenagrionidae at 95 Mya (Suvorov *et al.* 2022). Estimates have placed the 'ridge-faced' Coenagrionidae at 115 Mya (Toussaint *et al.* 2019) and 78 Mya (Suvorov *et al.* 2022). Previous divergence time estimates for damselflies in Vanuatu and Fiji have found the clade *Nesobasis* + *Nikoulabasis* + *Vanuatubasis* as 18–23 Mya, with individual genera originating right around the time Vanuatu is estimated to have swung away from Fiji (*Nesobasis* 15–19 Mya, *Nikoulabasis* 12–19 Mya, and *Vanuatubasis* 7–10 Mya) (Saxton *et al.* 2023). Willink *et al.* (2024) recovered the age of *Melanesobasis* as 21 Mya including three species (*M. c. corniculata*, *M. flavilabris*, and *M. mcleani*). Here, we recover a median age of *Melanesobasis* as 23–26 Mya (9–40 Mya HPD), an estimate that is congruent overall with previous work, and placing the origin of the genus well before the break-up of the Vitiaz Arc. The origin of the two main Fijian clades within *Melanesobasis* is also recovered before or around the same time as the break-up of the Vitiaz Arc (Fig. 5; Table 2). Only two analyses, D2.1 and D2.3, recovered an HPD that included 9 Mya as the earliest potential age of *Melanesobasis*, which would have been right after the break-up of Vanuatu and Fiji, pointing to the split of the islands being a driver of evolution in the clade.

Both methods of area coding recovered similar results, with the combined regions including both Vanuatu and Fiji (i.e. Vitiaz Arc) being recovered as the ancestral area for all *Melanesobasis* (Fig. 6). This result is consistent with a vicariance scenario in which the MRCA of all *Melanesobasis* (23–26 Mya) was found across the Vitiaz Arc, with its descendants being found in only Vanuatu or Fiji. These results suggest that the lineage inhabiting the southern portion of the Vitiaz Arc (now Fiji) might have been distinct from the lineage inhabiting the northern portion of the arc (now Vanuatu) prior to the split of the two archipelagos (Fig. 6). It is also interesting to note the long branch length for the MRCA to the Vanuatu species *M. bicellulare*, suggesting that there might be additional undescribed species and/or extinction that has taken place along that branch. The former explanation is highly plausible because comprehensive sampling has not been completed for the entire region, particularly in Vanuatu. Assuming, however, that the long branch length is not attributable to missing taxa but represents an older split between Fiji and Vanuatu prior to the break-up of the Vitaiz Arc, it is likely that other geological or ecological change can explain this divergence. Natural disasters, which are commonplace in the South Pacific, are certainly a plausible explanation for this division by introducing uninhabitable or sunken islands serving as barriers. Alternatively, if one island or archipelago experienced rapid ecological change, whether in response to natural disaster or climate change, it could lead to adaptation and vicariant speciation in the absence of physical geographical barriers.

In order to increase our resolution while still retaining biologically meaningful areas, we also ran a three-area model based on a natural break between southwest and northeast Fiji. In the three-area model, vicariance was reconstructed with the MRCA of all *Melanesobasis* found in both southwestern Fiji and Vanuatu and its direct descendants found in only one of those areas (Fig. 7). Dispersal was inferred as the most likely mechanism of spread to younger Fijian islands within the past ~5–10 Myr, with the origin of extant lineages (Fig. 7). The MCRA of *Melanesobasis* was found in Vanuatu and the southwest portion of Fiji, including the islands of Viti Levu, Kadavu, and Ovalau. This result would also be consistent with Viti Levu having the oldest rocks in Fiji (Neall and Trewick 2008), which are likely to be remnants of the original Vitiaz Arc (Colley 2009). Interestingly, rocks from the Yavuna group formation have also been detected in Maewo (Colley 2009), despite the estimated age of Maewo being much younger. This is of note because the only islands in Vanuatu known to have *Melanesobasis* include the eastern chain (Maewo and Pentecost) and Malekula. When time constrained to allow movement between Vanuatu and Fiji only prior to the break-up of the islands, the fit of the model performed as well as (if not better than) unconstrained models (Table 3), further indicating how the southwest movement of Vanuatu limited movement between the landmasses.

At present, *Melanesobasis* species display less restricted distributions than the genera *Nesobasis* and *Nikoulabasis* in Fiji, which are usually single-island endemics. However, preliminary taxonomic work suggests that *M. c. marginata* should be elevated to species rank, and *M. c. corniculata* displays variation in Kadavu that needs to be investigated further. *Melanesobasis simmondsi* was reported by Tillyard (1924) to be from Viti Levu; however, since that time *M. simmondsi* has been collected only from Kadavu, where it is almost as common as what Marinov and Rashni (2023) recorded as *Melanesobasis c. corniculata*. This is similar to *N. brachycerca* Tillyard, 1924, which was reported from Viti Levu but has been found only on Vanua Levu and Rabi (Donnelly 1990, Marinov and Rashni 2023, Rashni *et al.* 2023). These taxonomic changes would result in a similar pattern of highly endemic species as found in other Fijian damselfly genera. *Melanesobasis bicellulare*, found on three islands in Vanuatu, would be a stark exception to this pattern (also different from single-island endemics found in *Vanuatubasis*). Future work might prove that the variation noted in males cannot be explained by intraspecific variation. A full revision of the genus is needed to resolve these distributional patterns and reflect the true diversity of the genus.

The results obtained here provide an additional piece of evidence of the role of vicariance in the evolution of damselfly taxa in the South Pacific, specifically across the Vitaiz Arc (see also Saxton *et al.* 2023). These results could provide compelling evidence for future research examining how organisms with similar biologies (i.e. *Melanesobasis*, *Nesobasis*, and *Vanuatubasis*) respond to the same biogeographical pressures. A similar pattern has also been hypothesized in taxa of Lepidoptera (Grehan and Mielk 2020, Grehan and Ramik 2024). This is in contrast to a study that found no such evidence of vicariance in the plant genus *Planchonella* and suggested that long-distance dispersal was the best explanation (Swenson *et al.* 2019). In the ongoing task of understanding Coenagrionidae biogeography in the South Pacific, the results of endemic genera in Vanuatu and Fiji provide valuable insights into the important role of Vanuatu in fully understanding their evolutionary history. Future workers, building upon phylogenetic hypotheses presented here and in previous papers (i.e. Beatty *et al.* 2017, Ferguson *et al.* 2023, Saxton *et al.* 2023), should remain aware of the unique geology of the region and how this might influence both the coding of geographical areas and the interpretation of results of biogeographical analysis.

CONCLUSION

The results of this study provide important insight into the biogeographical history of taxa on remote islands, underscoring the importance of vicariance in their evolutionary history. However, they also illustrate the importance of fieldwork and integrative taxonomy in understanding the evolutionary history of lineages. Fieldwork undertaken in 2019 on islands in Vanuatu, many of which were largely undersampled (Marinov 2015), led to a rediscovery of a rarely collected and poorly understood taxon. Through a combination of morphological and molecular data, we were able to associate the female specimen reliably to the largely unknown *M. bicellulare*, greatly expanding on its natural history and distribution.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We would like to thank the late Jim Boone for providing images of the holotype of *Melanesobasis bicellulare* and for hosting us at the Bishop Museum. Donna Kalfatakmoli assisted in the permits for all Vanuatu specimens used in this study. Laura Sutherland is thanked for imaging the female specimen.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY STATEMENT

All molecular sequences used in this study can be found on GenBank. All other data are published in the Supplementary Data accompanying this study.

REFERENCES

Beatty C, Sánchez Herrera M, Skevington J *et al.* Biogeography and systematics of endemic island damselflies: the *Nesobasis* and *Melanesobasis* (Odonata: Zygoptera) of Fiji. *Ecology and Evolution* 2017;**7**:7117–29.

Begg G, Gray DR. Arc dynamics and tectonic history of Fiji based on stress and kinematic analysis of dikes and faults of the Tavua Volcano, Viti Levu Island, Fiji. *Tectonics* 2002;**21**:5-1–5-14.

Bickel DL. Biogeography of Diptera in the southwest Pacific. In: Pape T, Bickel D, Meier R (eds), *Diptera Diversity: Status, Challenges and Tools*. Boston, MA: Brill Academic, 2009, 257–75.

Bouchet P, Le Guyader H, Pascal O. *The Natural History of Santo*. Marseille, Paris: IRD, Pro-Natura International, Muséum national d'Histoire Naturelle, 2011.

Bouckaert R, Heled J, Kühnert D *et al.* BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 2014;**10**:e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Brower AV. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences of the United States of America* 1994;**91**:6491–5. https://doi.org/10.1073/pnas.91.14.6491

Bybee SM, Kalkman VJ, Erickson RJ *et al.* Phylogeny and classification of Odonata using targeted genomics. *Molecular Phylogenetics and Evolution* 2021;**160**:107115. https://doi.org/10.1016/j.ympev.2021.107115

Colley, H. Fiji, geology. In: Gillespie RG, Clague D (eds), *Encyclopedia of Islands*. Berkeley, CA: University of California Press, 2009, 305–9.

Cranston PS. Chapter 6: biodiversity of Australasian Insects. In: Foottit RG, Adler PH (eds), *Insect Biodiversity: Science and Society*. Hoboken, NJ: John Wiley and Sons, 2017, 111–39.

Crawford AJ, Meffre S, Symonds PA. 120 to 0 Ma tectonic evolution of the southwest Pacific and analogous geological evolution of the 600 to 220 Ma Tasman Fold Belt System. In: Hillis RR, Müller RD (eds), *Evolution and Dynamics of the Australian Plate*. Boulder, CO: Geological Society of Australia Special Publication and Geological Society of America Special Paper, 2003, 384–404.

De Marmels J. The genus *Nehalennia* Selys, its species and their phylogenetic relationships (Zygoptera: Coenagrionidae). *Odonatologica* 1984;**13**:501–27.

De Marmels J. *Tepuibasis* gen. nov. from the Pantepui region of Venezuela, with descriptions of four new species, and with biogeographic, phylogenetic and taxonomic considerations on the Teinobasinae (Zygoptera: Coenagrionidae). *Odonatologica* 2007;**36**:117–46.

Dijkstra KDB, Kalkman VJ, Dow RA *et al.* Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). *Systematic Entomology* 2014;**39**:68–96. https://doi.org/10.1111/syen.12035

Donnelly TW. *Melanesobasis* gen. nov., a new genus of Fijian damselflies: a possible link between the platycnemidid Lieftinckia and certain coenagrionids (Zygoptera). *Odonatologica* 1984;**13**:89–105.

Donnelly TW. The Fijian genus *Nesobasis* Part 1: species of Viti Levu, Ovalau, and Kadavu (Odonata: Coenagrionidae). *New Zealand Journal of Zoology* 1990;**17**:87–117. https://doi.org/10.1080/03014223.1990.10422587

Ferguson DG, Marinov M, Saxton NA *et al.* Phylogeny and classification of *Nesobasis* Selys, 1891 and *Vanuatubasis* Ober & Staniczek, 2009 (Odonata: Coenagrionidae). *Insect Systematics & Evolution* 2023;**54**:555–72.

Garrison RW, Von Ellenrieder N. Damselflies of the genus *Argia* (Odonata: Coenagrionidae) from Ecuador with descriptions of five new species. *Zootaxa* 2018;**4470**:1–69.

Gill J, Todd E, Hoernle K *et al.* Breaking up is hard to do: magmatism during oceanic arc breakup, subduction reversal, and cessation. *Geochemistry, Geophysics, Geosystems* 2022;**23**:e2022GC010663.

Gomy Y, Tishechkin A. Contribution à la connaissance des Histeridae de l'archipel du Vanuatu (Coleoptera). *Faunitaxys* 2020;**8**:1–20.

Gray KW. *Biodiversity and Biogeography of Myrmecosymbioses and Vanuatuan Ants*. Doctoral Dissertation, Arizona State University. 2023.

Greene HG, Collot JY, Fisher MA *et al.* Neogene tectonic evolution of the New Hebrides island arc: a review incorporating ODP drilling results. *Proceedings of the Ocean Drilling Program, Scientific Results*, 1994;**134**:19–46.

Grehan JR, Mielke CG. How to survive along a tectonic subduction zone: the western Pacific islands ghost moth *Phassodes* Bethune-Baker, 1905 (Lepidoptera: Hepialidae). *News of the Lepidopterists' Society* 2020;**62**:173–6.

Grehan JR, Ramik M. Confirming predicted presence of *Phassodes* ghost moth on Vanuatu (Lepidoptera: Hepialidae). *News of the Lepidopterists' Society* 2024;**66**:140–2.

Hadden RA, Saxton NA, Gerlach PS *et al.* Nitidulidae (Coleoptera: Cucujoidea) of Vanuatu. *Journal of Asia-Pacific Entomology* 2020;**23**:470–6. https://doi.org/10.1016/j.aspen.2020.03.005

Heads MJ. *Biogeography of Australasia: a Molecular Analysis*. New York: Cambridge University, 2014.

Heads MJ. Metapopulation vicariance explains old endemics on young volcanic islands. *Cladistics* 2018;**34**:292–311. https://doi.org/10.1111/cla.12204

Hebert PD, Cywinska A, Ball SL *et al.* Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences* 2003;**270**:313–21. https://doi.org/10.1098/rspb.2002.2218

Ingleby S, Colgan D. Electrophoretic studies of the systematic and biogeographic relationships of the Fijian bat genera *Pteropus*, *Pteralopex*, *Chaerephon* and *Notopteris*. *Australian Mammalogy* 2003;**25**:13–29. https://doi.org/10.1071/am03013

Kakinuma S. Description of a new species of *Melanesiandra* Santos-Silva *et al.* (Coleoptera: Cerambycidae: Parandrinae) found in Vanuatu. *Insecta Mundi* 2019;**0686**:1–5.

Kalyaanamoorthy S, Minh BQ, Wong TK *et al.* ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 2017;**14**:587–9.

Katoh K, Standley DM. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 2013;**30**:772–80. https://doi.org/10.1093/molbev/mst010

Keppel G, Lowe AJ, Possingham HP. Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *Journal of Biogeography* 2009;**36**:1035–54. https://doi.org/10.1111/j.1365-2699.2009.02095.x

Kohli M, Letsch H, Greve C *et al.* Evolutionary history and divergence times of Odonata (dragonflies and damselflies) revealed through transcriptomics. *iScience* 2021;**24**:103324–35. https://doi.org/10.1016/j.isci.2021.103324

MacArthur RH, Wilson EO. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press, 2001.

Macfarlane A, Carney JN, Crawford AJ. *et al.*, Vanuatu: a review of the onshore geology. In: Green HG, Wong FL (eds), *Geology and Offshore Resources of Pacific Island Arcs: Vanuatu Region*. Houston, TX: Circum-Pacific Council for Energy and Mineral Resources Earth Science Series, 1988, 45–91.

Marinov M. The seven 'oddities' of Pacific Odonata biogeography. *Journal of the International Dragonfly Fund* 2015;**11**:1–62.

Marinov M, Rashni B. Contribution to the Odonata of Kadavu, Fiji with erection of three new species (Insecta: Odonata). *Journal of the International Dragonfly Fund* 2023;**41**:1–34.

Marinov M, Bybee S, Doscher C *et al.* Faunistic studies in South-east Asian and Pacific Island Odonata. *Journal of the International Dragonfly Fund* 2019;**26**:1–46.

Matos-Maraví P, Clouse RM, Sarnat EM *et al.* An ant genus-group (*Prenolepis*) illuminates the biogeography and drivers of insect diversification in the Indo-Pacific. *Molecular Phylogenetics and Evolution* 2018;**123**:16–25. https://doi.org/10.1016/j.ympev.2018.02.007

Matzke N. *BioGeoBEARS: BioGeography with Bayesian (and Likelihood) Evolutionary Analysis in R Scripts*. Berkeley, CA: University of California, 2013.

Matzke NJ. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology* 2014;**63**:951–70. https://doi.org/10.1093/sysbio/syu056

Matzke NJ. Statistical comparison of DEC and DEC+J is identical to comparison of two ClaSSE submodels, and is therefore valid. *Journal of Biogeography* 2022;**49**:1805–24. https://doi.org/10.1111/jbi.14346

Meffre S, Crawford AJ. Collision tectonics in the New Hebrides arc (Vanuatu). *Island Arc* 2001;**10**:33–50. https://doi.org/10.1046/j.1440-1738.2001.00292.x

Miller SE. Biogeography of Pacific insects and other terrestrial invertebrates: a status report. In: Keast A, Miller SE (eds), *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. Amsterdam: SPB Academic, 1996, 463–75.

Minh BQ, Nguyen MAT, Von Haeseler A. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 2013;**30**:1188–95. https://doi.org/10.1093/molbev/mst024

Neall VE, Trewick SA. The age and origin of the Pacific islands: a geological overview. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2008;**363**:3293–308. https://doi.org/10.1098/rstb.2008.0119

Nguyen LT, Schmidt HA, Von Haeseler A *et al.* IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 2015;**32**:268–74. https://doi.org/10.1093/molbev/msu300

Paradis E, Schliep K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 2019;**35**:526–8. https://doi.org/10.1093/bioinformatics/bty633

Polhemus DA. Island arcs, and their influence on Indo-Pacific biogeography. In: Keast A, Miller SE (eds), *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. Amsterdam, The Netherlands: SPB Academic, 1996: 51–66.

Rambaut A, Drummond AJ, Xie D *et al.* Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 2018;**67**:901–4. https://doi.org/10.1093/sysbio/syy032

Rashni B, Donnelly T, Sakiti-Waqa H *et al.* On the Fijian endemic *Nesobasis brachycerca* Tillyard, 1924 (Odonata: Coenagrionidae) with first description of the female and updated description of the male. *Zootaxa* 2023;**5311**:251–66. https://doi.org/10.11646/zootaxa.5311.2.5

Revell LJ. Phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ* 2024;**12**:e16505. https://doi.org/10.7717/peerj.16505

Ritchie AM, Lo N, Ho SY. The impact of the tree prior on molecular dating of data sets containing a mixture of inter- and intraspecies sampling. *Systematic Biology* 2017;**66**:413–25.

Ross AJ, José MAC, Nel A. The first records of coenagrionid damselflies (Odonata: Zygoptera: Coenagrionidae: *Neoerythromma* sp. and *Nehalennia* sp.) from Mexican amber (Miocene). *Boletín de la Sociedad Geológica Mexicana* 2016;**68**:81–6.

Rota J, Peña C, Miller SE. The importance of long-distance dispersal and establishment events in small insects: historical biogeography of metalmark moths (Lepidoptera, Choreutidae). *Journal of Biogeography* 2016;**43**:1254–65. https://doi.org/10.1111/jbi.12721

Salces-Castellano A, Patiño J, Alvarez N *et al.* Climate drives community-wide divergence within species over a limited spatial scale: evidence from an oceanic island. *Ecology Letters* 2020;**23**:305–15. https://doi.org/10.1111/ele.13433

Sanmartín I, Meseguer AS. Extinction in phylogenetics and biogeography: from timetrees to patterns of biotic assemblage. *Frontiers in Genetics* 2016;**7**:35. https://doi.org/10.3389/fgene.2016.00035

Saxton NA, Powell GS, Serrano SJ *et al.* Natural history and ecological niche modelling of coastal *Atyphella* Olliff larvae (Lampyridae: Luciolinae) in Vanuatu. *Journal of Natural History* 2019;**53**:2771–80. https://doi.org/10.1080/00222933.2020.1749955

Saxton NA, Paxman EM, Dean AM *et al.* Factors influencing the distribution of endemic damselflies in Vanuatu. *Insects* 2021;**12**:670. https://doi.org/10.3390/insects12080670

Saxton NA, Marinov MG, Bybee SM. Revision of *Vanuatubasis* Ober & Staniczek, 2009 (Odonata, Coenagrionidae), with description of seven new species. *ZooKeys* 2022;**1128**:129–69. https://doi.org/10.3897/zookeys.1128.89751

Saxton NA, Powell GS, Bybee SM. A story of vicariance? How the geology of oceanic archipelagos influenced the evolutionary history of endemic damselflies. *Molecular Phylogenetics and Evolution* 2023;**186**:107831. https://doi.org/10.1016/j.ympev.2023.107831

Shao H, Li Q, Liu Y. The complete mitochondrial genome of *Ceriagrion fallax* (Odonata: Zygoptera: Coenagrionidae) and phylogenetic analysis. *Mitochondrial DNA. Part B, Resources* 2021;**6**:491–2. https://doi.org/10.1080/23802359.2020.1870891

Soldati L, Kergoat GJ, Condamine FL. Preliminary report on the Tenebrionidae (Insecta, Coleoptera) collected during the SANTO 2006 expedition to Vanuatu, with description of a new species of the genus *Uloma* Dejean, 1821. *Zoosystema* 2012;**34**:305–17. https://doi.org/10.5252/z2012n2a8

Suárez D, Arribas P, Jiménez-García E *et al.* Dispersal ability and its consequences for population genetic differentiation and diversification. *Proceedings of the Royal Society B: Biological Sciences* 2022;**289**:20220489.

Sutherland LN, Powell GS, Bybee SM. Validating species distribution models to illuminate coastal fireflies in the South Pacific (Coleoptera: Lampyridae). *Scientific Reports* 2021;**11**:17397. https://doi.org/10.1038/s41598-021-96534-x

Suvorov A, Scornavacca C, Fujimoto MS *et al.* Deep ancestral introgression shapes evolutionary history of dragonflies and damselflies. *Systematic Biology* 2022;**71**:526–46. https://doi.org/10.1093/sysbio/syab063

Swenson U, Havran JC, Munzinger J *et al.* Metapopulation vicariance, age of island taxa and dispersal: a case study using the Pacific plant genus *Planchonella* (Sapotaceae). *Systematic Biology* 2019;**68**:1020–33. https://doi.org/10.1093/sysbio/syz025

Theischinger G, Marinov M, Bybee S *et al.* The genus *Gynacantha* Rambur, 1842 in the South Pacific (Odonata: Anisoptera: Aeshnidae). *Zootaxa* 2020;**4778**:171–95.

Tillyard R. The Dragonflies (order Odonata) of Fiji, with special reference to a collection made by Mr. H.W. Simmonds, F.E.S., on the island of Viti Levu. *Transactions of the Entomological Society London* 1924;**71**:305–46.

Toussaint EF, Balke M. Historical biogeography of *Polyura* butterflies in the oriental Palaeotropics: trans-archipelagic routes and South Pacific island hopping. *Journal of Biogeography* 2016;**43**:1560–72.

Toussaint EF, Bybee SM, Erickson RJ *et al.* Forest giants on different evolutionary branches: ecomorphological convergence in helicopter damselflies. *Evolution* 2019;**73**:1045–54.

Triantis K, Whittaker RJ, Fernández-Palacios JM *et al.* Oceanic archipelagos: a perspective on the geodynamics and biogeography of the World's smallest biotic provinces. *Frontiers of Biogeography* 2016;**8**:e29605.

Vasilenko DV. New damselflies (Odonata: Synlestidae, Hemiphlebiidae) from the Mesozoic Transbaikalian locality of Chernovskie Kopi. *Paleontological Journal* 2005;**39**:280–3.

Willink B, Ware JL, Svensson EI. Tropical origin, global diversification, and dispersal in the pond damselflies (Coenagrionoidea) revealed by a new molecular phylogeny. *Systematic Biology* 2024;**73**:290–307. https://doi.org/10.1093/sysbio/syae004