Edith Cowan University

Research Online

ECU Publications Post 2013

8-2-2017

Across the Indian Ocean: A remarkable example of trans-oceanic dispersal in an austral mygalomorph spider

Sophie E. Harrison

Mark S. Harvey
Edith Cowan University

Steve J.B. Cooper

Andrew D. Austin

Michael G. Rix

Follow this and additional works at: https://ro.ecu.edu.au/ecuworkspost2013

 Part of the Other Animal Sciences Commons

10.1371/journal.pone.0180139
Harrison, S. E., Harvey, M. S., Cooper, S. J., Austin, A. D., & Rix, M. G. (2017). Across the Indian Ocean: A remarkable example of trans-oceanic dispersal in an austral mygalomorph spider. *PloS one*, *12*(8), e0180139. https://doi.org/10.1371/journal.pone.0180139

This Journal Article is posted at Research Online.
https://ro.ecu.edu.au/ecuworkspost2013/3079

PLOS ONE

RESEARCH ARTICLE

Across the Indian Ocean: A remarkable example of trans-oceanic dispersal in an austral mygalomorph spider

Sophie E. Harrison[1]*, Mark S. Harvey[2,3,4], Steve J. B. Cooper[1,5], Andrew D. Austin[1], Michael G. Rix[1,2,6]

1 Australian Centre for Evolutionary Biology and Biodiversity, School of Biological Sciences, The University of Adelaide, Adelaide, SA, Australia, **2** Department of Terrestrial Zoology, Western Australian Museum, Welshpool DC, WA, Australia, **3** School of Biology, The University of Western Australia, Crawley, WA, Australia, **4** School of Natural Sciences, Edith Cowan University, Joondalup, WA, Australia, **5** Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, SA, Australia, **6** Biodiversity and Geosciences Program, Queensland Museum, South Brisbane, QLD, Australia

* sophie.e.harrison@adelaide.edu.au

Check for updates

OPEN ACCESS

Citation: Harrison SE, Harvey MS, Cooper SJB, Austin AD, Rix MG (2017) Across the Indian Ocean: A remarkable example of trans-oceanic dispersal in an austral mygalomorph spider. PLoS ONE 12(8): e0180139. https://doi.org/10.1371/journal.pone.0180139

Editor: Matjaž Kuntner, Scientific Research Centre of the Slovenian Academy of Sciences and Art, SLOVENIA

Received: January 26, 2017

Accepted: June 9, 2017

Published: August 2, 2017

Copyright: © 2017 Harrison et al. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All genetic data files are available from the Genbank database. Accession numbers can be found within Table 1.

Funding: This work was supported by Australian Biological Resources Study, https://www.environment.gov.au/science/abrs, grant number: CT212–07, author who received the funding: S.H.; Bioplatforms Australia DNA Barcoding Project, http://www.bioplatforms.com/, authors who received the funding: S.C., A.A.; The Australian

Abstract

The Migidae are a family of austral trapdoor spiders known to show a highly restricted and disjunct distribution pattern. Here, we aim to investigate the phylogeny and historical biogeography of the group, which was previously thought to be vicariant in origin, and examine the biogeographic origins of the genus *Moggridgea* using a dated multi-gene phylogeny. *Moggridgea* specimens were sampled from southern Australia and Africa, and *Bertmainus* was sampled from Western Australia. Sanger sequencing methods were used to generate a robust six marker molecular dataset consisting of the nuclear genes *18S* rRNA, *28S* rRNA, *ITS* rRNA, *XPNPEP3* and *H3* and the mitochondrial gene *COI*. Bayesian and Maximum Likelihood methods were used to analyse the dataset, and the key dispersal nodes were dated using BEAST. Based on our data, we demonstrate that *Moggridgea rainbowi* from Kangaroo Island, Australia is a valid member of the otherwise African genus *Moggridgea*. Molecular clock dating analyses show that the inter-specific divergence of *M. rainbowi* from African congeners is between 2.27–16.02 million years ago (Mya). This divergence date significantly post-dates the separation of Africa from Gondwana (95 Mya) and therefore does not support a vicariant origin for Australian *Moggridgea*. It also pre-dates human colonisation of Kangaroo Island, a result which is further supported by the intra-specific divergence date of 1.10–6.39 Mya between separate populations on Kangaroo Island. These analyses provide strong support for the hypothesis that *Moggridgea* colonised Australia via long-distance trans-Indian Ocean dispersal, representing the first such documented case in a mygalomorph spider.

Introduction

The historical view of the biogeographical history of the Southern Hemisphere postulated that the terrestrial biota had largely vicariant origins [1], and that dispersal played a relatively

Research Council, http://www.arc.gov.au/, grant number: LP120200092, authors who received the funding: A.A., S.C., M.R., M.H.; and The Nature Foundation of South Australia, https://www.naturefoundation.org.au/, author who received the funding: S.H. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

limited role in taxa with southern-temperate or 'Gondwanan' ranges [2]. The sequential separation of the southern continental blocks since the Mesozoic [3] has led to lineages on multiple post-Gondwanan land fragments forming independent clades. In contrast, oceanic dispersal [1] was often discarded *a priori* as a primary explanation of distribution patterns in the Southern Hemisphere [3]. The idea that seemingly remarkable feats of long-distance dispersal were needed to explain the evolutionary history of many groups of organisms was first postulated by Darwin [4], but the concept has often been considered speculative and difficult to test–"a science of the improbable, the rare, the mysterious and the miraculous" [5]. The apparent poor suitability of many austral groups for oceanic dispersal (e.g. marsupials and ratite birds) appeared to further support vicariance as the more likely biogeographical scenario [3]. Indeed, the idea that vicariance was the key theory to explain the Gondwanan distribution of many southern-temperate groups proved difficult to challenge for many decades [6].

Over the past 20 years, new discoveries and more advanced methods, particularly molecular phylogenetic and dating methods, have brought the dispersal-vicariance debate full-circle. Using the fossil record and/or gene-specific rates of nucleotide evolution, molecular phylogenies with dated nodes now provide new perspectives on the evolutionary history of the flora and fauna of the Southern Hemisphere [6, 7]. Most importantly, molecular divergence dating provides the temporal perspective necessary to test and, where appropriate, reject vicariant biogeographic hypotheses [7]. Calculating the probability of a successful dispersal requires taking into account the number of dispersers, their probability of survival, their likelihood of establishing upon landing, and also the presence of prevailing winds, oceanic currents, hosts, vectors or any other underlying mechanisms that may affect movement and survival (any or all of which may include rafting as a plausible hypothesis) [8]. Recent molecular studies have shown that successful long-distance dispersal events have occurred in many groups of taxa, such as monkeys [9], lemurs [10] and geckos [11], a previously counter-intuitive conclusion without accessible dated molecular phylogenies.

The now well-documented occurrence of long-distance dispersal via rafting in a large range of taxa [8], highlights that trans-oceanic dispersal is not only restricted to organisms capable of flight [12], aerial dispersal (e.g. ballooning spiders [13]) or oceanic buoyancy (e.g. floating seeds [14]). Rafting generally involves large chunks of land and/or vegetation being washed out to sea, with rafting events being implicated in the colonisation of numerous isolated land masses including Australia [3], Madagascar [10,15], South America [7, 9,11], New Zealand [16] and newly formed Darwinian Islands such as the Galapagos islands, Canary Islands and Hawaii [17]. A case in point, and not surprising, is the coastal araneomorph spider genus *Amaurobioides*, which is hypothesised to have undergone several long distance, transoceanic dispersal events, facilitated by rafting [18].Spiders of the infraorder Mygalomorphae are well featured in vicariance biogeography literature (e.g. [19–22]) and more recently in molecular studies of phylogeography and species delimitation [23]. Mygalomorphs are a monophyletic group with a worldwide distribution [24–26]. They have unusually long life cycles, with some species living up to 30 years and requiring 5–8 years to reach reproductive maturity [27]. They are univoltine [28] with females and juveniles leading sedentary lifestyles [29]. Although ballooning of spiderlings has been documented in several genera (e.g. [30–33]) most mygalomorphs do not disperse aerially and are known to be relatively non-vagile, with juveniles often moving only a few metres from the maternal site (e.g. [25,31,34,35]). These life-history traits predispose mygalomorph spiders to geographic isolation through mechanisms such as continental drift, glaciation, orogenic activity and habitat fragmentation, resulting in a large number of taxa that have small geographical distributions [36–38]. It is the poor vagility, sedentary habits and patterns of fine-scale genetic structuring characteristic of many mygalomorph spiders [28] that make this group especially amenable to testing the vicariance paradigm [25].

The Migidae are a family of Mygalomorphae previously assumed to have a vicariant austral distribution. Eleven named genera occur in Africa, Madagascar, New Zealand, New Caledonia, South America and Australia [22,38]. The Australian migid fauna includes four genera: *Migas* L. Koch, 1873 and *Heteromigas* Hogg, 1902 from eastern Australia [39]; *Moggridgea* O. P.-Cambridge, 1904 from Kangaroo Island (KI), South Australia [40]; and *Bertmainius* Harvey *et al*., 2015 from south-western Australia [38]. Although displaying a putatively Gondwanan distribution, a cladistic study based on morphology suggested that the evolutionary history of the family cannot be explained by vicariance alone, with Australia appearing three times in the cladogram [22]. Recent molecular [35,38] and morphological [40] data suggest the only Australian *Moggridgea* species, *Moggridgea rainbowi* (Pulleine, 1919), groups with African *Moggridgea*, where all other congeneric species occur. The existence of an 'African' *Moggridgea* lineage in Australia immediately poses a number of tantalising biogeographic questions, and these form the basis of this study.

Here we test three alternative biogeographic hypotheses for the presence of *Moggridgea* in southern Australia, using a dated phylogenetic approach based on a comprehensive multi-gene dataset. The first (null) hypothesis is Gondwanan vicariance, which would be evidenced by a deep and very old divergence date from African congeners, consistent with the age of separation of Africa from the rest of Gondwana. This hypothesis was first suggested by Main [41] to explain the presence of *Moggridgea* (now treated as *Bertmanius*) in Western Australia. An alternative hypothesis (H_1) is a human-mediated introduction from Africa during the European colonisation of KI. This would be evidenced by a recent, extremely shallow (among conspecific) or low divergence date (among sister species) and, equally importantly, by a lack of phylogeographic structure on KI itself. The second alternative hypothesis (H_2) is trans-oceanic dispersal, which would be evidenced by both recent divergence from African species (relative to ancient African vicariance) and by demonstrable phylogeographic structuring among populations on KI. The implications of our results are discussed in regard to their broader impact, as an inability to reject H_2 would provide the first dated molecular evidence of long-distance oceanic dispersal in a mygalomorph spider, and would be an invaluable insight into the history and origins of southern hemisphere mygalomorph spider diversity. Our rejection of H_0 and H_2 provide the first solid evidence for long-distance oceanic dispersal in a mygalomorph spider, and has broader implications for better understanding the history and origins of southern hemisphere mygalomorph spider diversity.

Methods

Specimen sampling

Our dataset comprised seven specimens of *M. rainbowi* from two populations on KI separated by approximately 80 km (Western River [three specimens] and American River [four specimens]); five exemplar species of *Moggridgea* from South Africa; and seven species of *Bertmainius* from south-western Australia (see Table 1). The American River specimens were excavated from burrows above the high tide mark in May 2013, and initially preserved in 100% ethanol. These specimens were collected under permit number E26155-3 issued by the South Australian Department of Environment, Water and Natural Resources. All *M. rainbow* specimens from Western River, *Bertmainius* species from Western Australian and *Moggridgea* specimens from Africa were obtained from archived DNS samples stored in the Australian Biological Tissue Collection, provided with permission from the South Australian Museum. These DNA samples had been previously collected under annual collection permits issued to scientists from the Western or South Australian museums or donated by overseas colleagues. Legs 3 and 4 from the left side of each specimen were then kept in 100% ethanol, while the rest

Table 1. Registration numbers, locality data, and Genbank accession numbers for specimens used in the study.

Species	Registration numbers	Locality	Coordinates	Genbank accession numbers *COI*	Genbank accession numbers *ITS1-ITS2*	Genbank accession numbers *XPNPEP3*	Genbank accession numbers *18S*	Genbank accession numbers 28S	Genbank accession numbers *H3*
SCORPIONES									
Urodacus planimanus	T129654	WA: Bedfordale	32˚10'05"S, 116˚04'06"E	KY295225	-	KY295718	KY294838	KY294961	KY295099
ARANEAE									
Latrodectus hasseltii	T129059	WA: Welshpool	31˚59'08"S, 115˚55'57"E	KY295226	-	KY295719	KY294839	KY294962	KY295100
Aganippe sp.	T129362	WA: Serpentine NP	32˚22'05"S, 116˚00'26"E	KY295228	KY294976	KY295723	KY294841	KY294965	KY295103
Euoplos sp.	T129363	WA: Serpentine NP	32˚22'05"S, 116˚00'26"E	KY598258	KY294983	KY295725	KY294843	KY294970	KY295108
Cethegus fugax	T129260	WA: John Forrest NP	31˚53'54"S, 116˚05'49"E	KY295227	-	KY295722	KY294840	KY294963	KY295101
Moggridgea rainbowi	ABTC110307	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749981	MF169599	MF169538	MF169569	MF169628
Moggridgea rainbowi	ABTC110308	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749982	MF169600	MF169539	MF169570	MF169629
Moggridgea rainbowi	ABTC110309	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749983	MF169601	MF169540	MF169571	
Moggridgea rainbowi	SAM NN28257	SA: American River, Kangaroo Island	35˚46'35"S, 35˚46'35"S	MF169531	MF169535	MF169607	MF169547	MF169577	MF169632
Moggridgea rainbowi	SAM NN28345	SA: American River, Kangaroo Island	35˚46'36.5"S, 137˚46'33"E	MF169532	MF169536	MF169608	MF169548	MF169578	MF169633
Moggridgea rainbowi	SAM NN25429	SA: American River, Kangaroo Island	35˚46'37"S, 137˚46'3"E	MF169530	MF169534	-	MF169546	MF169576	MF169631
Moggridgea rainbowi	SAM NN28346.1	SA: American River	35˚46'36.5"S, 137˚46'33"E	MF169533	MF169537	-	MF169549	MF169579	MF169634
Moggridgea terrestris	MY357	South Africa: Eastern Cape Province	33˚07'31"S, 26˚36'40"E	JF749926	JF749986	MF169602	MF169541	MF169572	-
Moggridgea rupicoloides	MY360	South Africa: Eastern Cape Province	33˚23'26"S, 26˚26'11"E	JF749925	-	MF169603	MF169642	MF169573	-
Moggridgea intermedia	MY361	South Africa: Western Cape Province	33˚58'13"S, 23˚32'20"E	JF749928	JF749984	MF169604	MF169543	-	MF169630
Moggridgea mordax	MY371	South Africa: Northern Cape Province Hwy N14	28˚01'30"S, 22˚39'48"E	JF749929	-	MF169605	MF169544	MF169574	-

(*Continued*)

Table 1. (*Continued*)

Species	Registration numbers	Locality	Coordinates	Genbank accession numbers *COI*	Genbank accession numbers *ITS1-ITS2*	Genbank accession numbers *XPNPEP3*	Genbank accession numbers *18S*	Genbank accession numbers 28S	Genbank accession numbers *H3*
Moggridgea peringueyi	MY372	South Africa: Northern Cape Province Hwy N14	28˚01'30"S, 22˚39'48"E	JF749927	JF749985	MF169606	MF169545	MF169575	-
Bertmainius monachus	WAM T57952	WA: Stirling Range NP, Talyuberlup	34˚24'51"S, 117˚57'22"E	JF749911	JF749976	MF169609	MF169550	MF169580	MF169635
Bertmainius monachus	WAM T63124	WA: Stirling Range NP, Talyuberlup	34˚24'51"S, 117˚57'22"E	JF749891	JF749948	MF169624	MF169565	MF169595	MF169645
Bertmainius monachus	WAM T63125	WA: Stirling Range NP, Talyuberlup	34˚24'51"S, 117˚57'22"E	JF749891	JF749972	MF169625	MF169566	MF169596	MF169646
Bertmainius pandus	WAM T57954	WA: Stirling Range NP, Toolbrunup	34˚23'27"S, 118˚03'31"E	JF749912	JF749975	MF169610	MF169551	MF169581	MF169636
Bertmainius pandus	WAM T57955	WA: Stirling Range NP, Toolbrunup	34˚23'27"S, 118˚03'31"E	JF749912	JF749973	MF169611	MF169552	MF169582	MF169637
Bertmainius colonus	WAM T57976	WA: Stirling Range NP, Ellen Creek	34˚22054"S, 118˚17'25"E	JF749906	JF749951	MF169613	MF169554	MF169584	MF169648
Bertmainius colonus	WAM T63126	WA: Stirling Range NP, Isongerup Track	34˚22'25"S, 118˚16'59"E	JF749907	JF749955	MF169626	MF169567	MF169597	MF169647
Bertmainius colonus	WAM T58045	WA: Stirling Range NP, Wedge Hill	34˚25'12"S, 118˚10058"E	JF749909	JF749931	MF169614	MF169555	MF169585	MF169639
Bertmainius tumidus	WAM T57961	WA: Porongurup NP	34˚40'57"S, 117˚50'56"E	JF749892	JF749937	MF169612	MF169553	MF169583	MF169638
Bertmainius tumidus	WAM T63106	WA: Waychinicup Nature Reserve	34˚54'29"S, 118˚15'56"E	JF749923	JF749964	MF169621	MF169562	MF169592	-
Bertmainius mysticus	WAM T60315	WA: Keystone State Forest	34˚58'59"S, 116˚37'53"E,	JF749901	JF749978	MF169615	MF169556	MF169586	MF169640
Bertmainius mysticus	WAM T60316	WA: Keystone State Forest	34˚58'59"S, 116˚37'53"E	JF749915	JF749977	MF169616	MF169557	MF169587	-
Bertmainius mysticus	WAM T63096	WA: Walpole–Nornalup NP	35˚00'23"S, 116˚38'37"E	JF749896	JF749961	MF169617	MF169558	MF169588	-
Bertmainius tingle	WAM T63102	WA: Walpole-Nornalup NP, Valley of the Giants	34˚58'47"S, 116˚52'44"E	JF749921	JF749958	MF169618	MF169559	MF169589	-
Bertmainius tingle	WAM T63103	WA: Walpole-Nornalup NP, Valley of the Giants	34˚58'47"S, 116˚52'44"E	JF749921	JF749956	MF169619	MF169560	MF169590	MF169641
Bertmainius tingle	WAM T63104	WA: Walpole-Nornalup NP, Valley of the Giants	34˚58'47"S, 116˚52'44"E	JF749921	JF749957	MF169620	MF169561	MF169591	MF169642

(*Continued*)

Table 1. (*Continued*)

Species	Registration numbers	Locality	Coordinates	Genbank accession numbers *COI*	Genbank accession numbers *ITS1-ITS2*	Genbank accession numbers *XPNPEP3*	Genbank accession numbers *18S*	Genbank accession numbers 28S	Genbank accession numbers *H3*
Bertmainius opimus	WAM T63108	WA: S. of Gracetown	33˚54'32"S, 115˚00'24"E	JF749900	JF749966	MF169622	MF169563	MF169593	MF169643
Bertmainius opimus	WAM T63179	WA: Shannon NP	34˚42'47"S, 116˚21'47"E	JF749920	JF749971	MF169627	MF169568	MF169598	-
Bertmainius opimus	WAM T63111	WA: Wellington Mill	33˚27'04"S, 115˚55'42"E	JF749917	JF749941	MF169623	MF169564	MF169594	MF169644

https://doi.org/10.1371/journal.pone.0180139.t001

of the body was transferred to 75% to allow for easier manipulation for morphological study. Cytochrome oxidase subunit I (*COI*) and internal transcribed spacer (*ITS*) sequences for *M. rainbowi* from Western River (KI), along with the *Moggridgea* species from South Africa and the *Bertmainius* species from Western Australia were taken from [35] and [38]. DNA from these specimens was sequenced for four additional genes: *XPNPEP3*, *28S*, *18S* and *H3* (see below).

Molecular methods

Approximately 3 mm^3 of muscle tissue was removed from the leg femora for DNA extraction. DNA was extracted using the Gentra DNA extraction PURE-GENE DNA Purification Kit (Gentra Systems, Minnepolis, MN, USA).

A 715 bp fragment of nuclear *18S* rRNA was amplified using the primers 18S_ai (5′-CCTGAGAAACGGCTACCACATC) and 18S_b0.5 (5′-GTTTCAGCTTTGCAACCAT-3′) [42]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing temperature of 50˚C for 35 s, then 72˚C for 2 mins, with a final elongation step of 72˚C for 10 mins.

An 852 bp fragment of nuclear *28S* rDNA was amplified using the primers 28Sa (5′-GACCCGTCTTGAAACACGGA-3′) and LSUR (5′-GCTACTACCACCAAGATCTGCA-3′) [42]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing temperature of 50˚C for 35 s, then 72˚C for 2 mins, with a final elongation step of 72˚C for 10 mins.

A 658 bp fragment of mitochondrial *COI* was amplified using the universal *COI* primers LCO1490 (5′-GGTCAACAAATCATAAAGATATTG-3′) and HC02198 (3′-TAAACTTCAGGGTGACCAAAAAATCA-5′) [43]. PCR was performed under the following conditions: an initial denaturation step of 94˚C for 5 mins, followed by 34 cycles of 94˚C for 45 s, annealing temperature of 48˚C for 45 s, then 72˚C for 1 min, with a final elongation step of 72˚C for 10 mins.

A 738 bp fragment of nuclear Xaa-Pro aminopeptidase 3 (*XPNPEP3*) was amplified using the primers XPNPEP3_f2 (5′-GAAAGAAGATTAAAACTAATGGAAC-3′) and (5′-XPNPEP3_Ar_r1 CCAGCATCCATYAANACCA-3′) [44]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing temperature dropping from 55˚C to 45˚C for 35 s, then 72˚C for 1 min, with a final elongation step of 72˚C for 10 mins.

An 838 bp fragment of nuclear *ITS* rRNA (including *ITS1*, *5.8S* rRNA, *ITS2*) was amplified using the primers G923 (5′-CGTAACAAGGTTTCCGTAGGTGA-3′) and G925 (5′AGAGAACTCGCGAATTCCACGG-3′) (see [35]). PCR was performed under the following conditions:

an initial denaturation step of 94˚C for 9 mins, followed by six cycles of 94˚C for 45 s, annealing 68˚C for 45 s (-1˚C each cycle); 72˚C 60 s, then 28 cycles of 94˚C for 45 s, annealing 62˚C for 45 s, 72˚C for 60 s, with a final elongation step of 72˚C for 6 min. The enzyme used was AmpliTaq Gold DNA polymerase.

A 327 bp fragment of nuclear histone *H3* was amplified using the primers H3aF (5′-ATGGCTCGTACCAAGCAGACVGC-3′) and H3aR (5′-ATATCCTTRGGCATRATRGTGAC-3′) [45]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing 48˚C for 35 s, then 72˚C for 2 mins, with a final elongation step of 72˚C for 2 mins. The enzyme used was MyTaq DNA polymerase.

The genes *18S*, *28S*, *XPNPEP3* and *H3* were amplified following [44], using MyTaq DNA Polymerase (Bioline, Taunton, MA), in a Bio-Rad T100 Thermal Cycler. For each 25 μL PCR reaction, 2 μL of template DNA, 5 μL of MyTaq buffer, 5 pm of each primer and 0.2 μL of MyTaq DNA polymerase were used. PCR products were visualised on 1.5% agarose gels using standard procedures, and PCR clean-up plus bi-directional sequencing was performed by the Australian Genome Research Facility (AGRF, Nedlands, WA). *COI* and *ITS* were amplified using Eppendorf Amplitaq Gold (Eppendorf, Westbury, NY, USA). For each 25 μL reaction, 2 μL of template DNA, 2.5 μL of PCR Gold Buffer, 3.5 μL of MgCl, 2.0 μL of deoxyribonucleotide triphosphate (dNTP), 10 pm of each primer, and 0.1μL Amplitaq Gold DNA polymerase was used. PCR products were verified by agarose gel electrophoresis (1% agarose), and PCR clean-up plus bi-directional Sanger sequencing was performed by AGRF (Waite Campus, Adelaide, S.A.). Sequences were submitted to GenBank (see Table 1 for accession numbers).

Phylogenetic analyses

Five non-migid outgroups were sourced from [44]: the scorpion *Urodacus planimanus* Pocock, 1893, the red-back spider *Latrodectus hasseltii* Thorell, 1870, the curtain-web mygalomorph spider *Cethegus fugax* Simon, 1908, and the idiopid trapdoor spiders *Aganippe* sp. O. P.-Cambridge, 1877 and *Euoplos* sp. (Table 1). All newly obtained sequences were edited with reference to chromatograms using Geneious [46]. Forward and reverse sequences were assembled, and the resulting consensus sequences were then aligned using the 'Geneious Alignment' function of Geneious. PartitionFinder [47] was used to select the model that best fit each gene, with the protein coding genes being divided into three codon positions. For *COI*, the General Time Reversible (GTR) [48] + gamma (G) [49] model was selected for the first codon position, the Felstein 81 (F81) [50] + invariant (I) I+G for the second codon position, and the Hasegawa, Kishino and Yano (HKY) [51] +I+G for the third. For *ITS1*, *ITS2* and *18S*, the model Kimura 80 (K80) [52] +G was chosen. For *5.8S* and *28S*, the GTR+I+G model was chosen. For *H3*, the GTR+I+G model was chosen for codon position one and the K80+G model was chosen for positions two and three. For *XPNPEP3*, the HKY+G model was chosen for all positions.

Phylogenetic reconstruction was undertaken using MrBayes 3.2.6 [53] employing the CIPRES Science Gateway [54]. In the Bayesian analysis, each codon position was modelled separately using the models listed above. All parameters were unlinked and the rates were allowed to vary over the partitions. For all reconstructions, two runs with four chains each were run simultaneously for 100 million generations, with every 1,000th tree sampled. A burnin of 1,000, chosen using the program Tracer 1.6 [55], was set for building the maximum clade credibility tree. The resulting tree was viewed using FigTree v1.3.1 [56] (Fig 1). A maximum likelihood analysis was also undertaken using RAxML [57] on the BlackBox server [58] with *COI*, *H3* and *XPNPEP3* partitioned by codons and *ITS1*, *5.8S*, *ITS2* and *28S* partitioned individually, with the GTR + G model used for all genes.

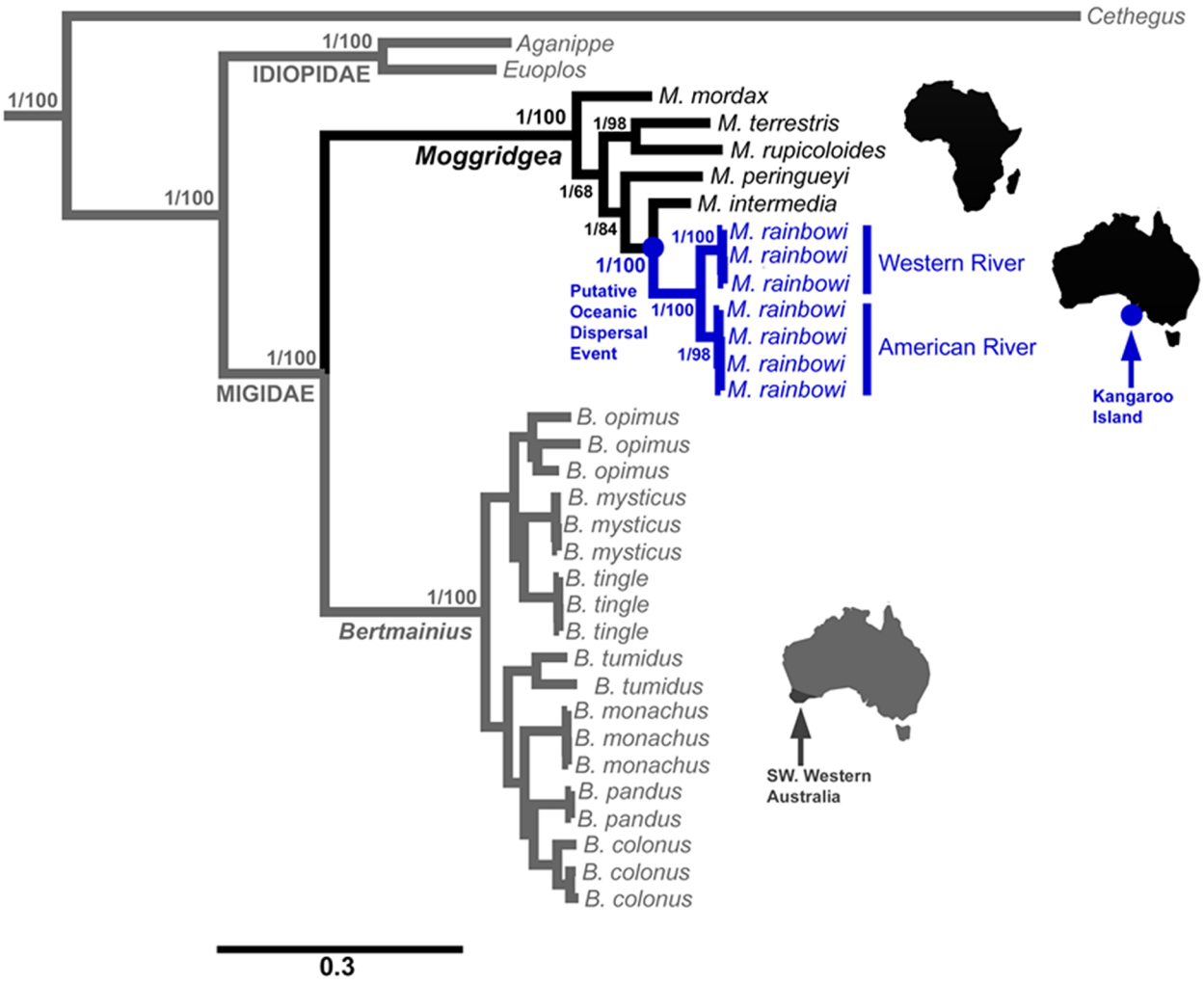


Fig 1. Combined *COI*, *ITS*, *H3*, *18S*, *28S* and *XPNPEP3* tree constructed using MrBayes and mixed models. Numbers on nodes represent posterior probabilities followed by maximum likelihood bootstrap values.

https://doi.org/10.1371/journal.pone.0180139.g001

Molecular clock analyses

Divergence dating analysis was performed using BEAST 1.8.0 [59] to determine the time of divergence of *M. rainbowi* from its African relatives. The program BEAUti 1.8.0 (part of the BEAST software package) was used to create.xml files to input into BEAST. Given the robustness of phylogenetic analyses placing *M. rainbowi* within the African *Moggridgea* clade (see Fig 1), we focused on the *Moggridgea* taxa only for our molecular clock analyses. Exclusion of distantly related taxa, such as *Bertmainius*, avoided potential issues with saturation of the third codon positions of *COI*. This still enabled us to effectively date the nodes of most interest, i.e. the divergence time between the closest African sister to *M. rainbowi*, *M. intermedia* (see [40]), and the divergence between the two KI *M. rainbowi* populations. We included only the specimens for which we had a complete set of sequence data; this allowed us to link the trees and resulted in a single tree for analysis. The gene *H3* had a larger proportion of missing data than the other genes, so was not included in the dating analysis. *28S* was also not included as it could not be sequenced for *M. intermedia*, which was found to be the closest relative to *M. rainbowi*.

Six separate BEAST analyses were carried out using different clock models, including a strict clock, uncorrelated lognormal clock and exponential relaxed clock, and both the GTR + G + I and HKY nucleotide substitution modes. Each analysis was run for 20 million generations with a burnin of 1 million generations (i.e. 10%), and the program Tracer 1.6 [55] was used to analyse the parameter distributions estimated from BEAST and check for convergence of the chains. Stationarity was checked for, and no evidence of non-stationarity was found in all BEAST runs. As fossil calibrations were unavailable to date nodes of the *Moggridgea* phylogeny, the mean *COI* substitution rate was fixed at 0.02 substitutions per site per million years, based on the estimates of 4% divergence between lineages per million years [by 34] for the trapdoor spider *Aptostichus simus* Chamberlin 1917. Rates for all other genes were estimated. Site models and clock models were unlinked and trees were linked. The tree priors selected for separate analyses were Speciation: Yule Process and Birth-Death Process, as both are suitable for inter-species relationships. Priors on the ucld.mean for each gene were defined as uniform with an initial value of 0.00115, an upper value of 0.0115 and a minimum value of 0.0001. The universal substitution rate estimated for arthropod mtDNA [60] was used to define the upper value. Due to the average slower pace of nuclear genes compared with mitochondrial ones, the initial value was one order of magnitude slower (as per [61]). TreeAnnotator [59] was used to produce a single "target" tree which was then visualised using FigTree v1.3.1 [56].

Results

Phylogenetic analysis

A maximum clade credibility tree was generated for the MrBayes analysis of the combined six gene, 4118 character, 36 taxa dataset (Fig 1). This analysis resolved the genera *Moggridgea* and *Bertmainius* as reciprocally monophyletic, with *M. rainbowi* from KI clearly embedded within the African *Moggridgea* lineage and sister to *M. intermedia* (posterior probability = 1, bootstrap value 100) (Fig 1). Furthermore, *M. rainbowi* formed a monophyletic group, but showed phylogeographic structure, with haplotypes reflecting the two geographic locations (Western River and American River). The Maximum Likelihood analysis of the same dataset produced a completely concordant tree (see Dryad digital repository, doi:10.5061/dryad.9cp00).

Molecular clock analyses

The time to most recent common ancestor (TMRCA) estimate for the African *M. intermedia* and KI *M. rainbowi*, the TMRCA of the KI Western River and American River populations of *M. rainbowi*, and the Posterior Mean and Posterior ESS values for all three clocks with GTR, HKY and PartitionFinder models, using both Speciation: Yule Process and Speciation: Birth-Death Process tree priors are summarised in Table 2. All analyses performed using the GTR+I +G models failed to achieve adequate convergence for many of the parameter estimates (i.e. posterior statistics with effective sample sizes <10 after 20 million generations). Analyses performed using the HKY model had posterior ESS values of >1400 for every clock model used. Combinations of clocks and models gave TMRCA estimates ranging between 2.27 Mya (strict clock, HKY model, Speciation: Yule Process, 95% Highest Posterior Density [HPD] 1.89–2.65) to 16.02 Mya (strict clock, GTR model, Speciation: Yule Process, 95% HPD 8.97–25.60) between the African *M. intermedia* and *M. rainbowi* from KI. The TMRCA values for the divergence time between the two separate KI populations ranged between 1.10 Mya (Strict clock, HKY model, Speciation: Birth-Death Process, 95% HPD 0.86–1.34) to 6.39 Mya (strict clock, GTR models, Speciation: Yule Process, 3.48–10.23).

Table 2. Estimates of time (in millions of years) to most recent common ancestors (TMRCA) and 95% highest posterior density (HPD) intervals for key nodes and posterior mean and effective sample size [ESS] values, generated using BEAST.

Parameters	TMRCA Node 1 (Moggridgea Dispersal) + 95% Highest Posterior Density	TMRCA Node 2 (KI Population Divergence) + 95% Highest Posterior Density	Posterior Mean	Posterior ESS
Strict Clock, GTR Models, Speciation: Yule Process	16.02	6.39	-6059.22	20.04
	8.87–25.60	3.48–10.23		
Strict Clock, HKY Models, Speciation: Yule Process	2.27	1.10	-6478.87	1449.97
	1.89–2.65	0.87–1.34		
Strict Clock, GTR Models, Speciation: Birth-Death Process	15.98	6.35	-5813.92	8.93
	8.63–25.96	3.55–10.37		
Strict Clock, HKY Models, Speciation: Birth-Death Process	2.27	1.10	-6259.82	1672.67
	1.91–2.67	0.86–1.34		
Exponential Clock, GTR Models, Speciation: Yule Process	10.59	4.06	-6021.34	5.93
	4.01–19.94	1.59–7.66		
Exponential Clock, HKY Models, Speciation: Yule Process	3.54	1.75	-6155.69	2310.32
	2.35–4.96	1.17–2.45		
Exponential Clock, GTR Models, Speciation: Birth-Death Process	10.49	3.69	-5789.97	7.62
	3.97–19.71	1.60–7.45		
Exponential Clock, HKY Models, Speciation: Birth-Death Process	3.54	1.73	-5936.87	1607.35
	2.36–4.92	1.16–2.40		
Lognormal Clock, GTR Models, Speciation: Yule Process	15.44	5.96	-6035.79	9.76
	5.36–27.15	1.62–11.13		
Lognormal Clock, HKY Models, Speciation: Yule Process	8.48	3.56	-6172.48	1701.01
	3.33–13.97	1.25–6.53		
Lognormal Clock, GTR Models, Speciation: Birth-Death Process	15.40	5.77	-5821.38	10.17
	5.41–27.32	1.51–10.63		
Lognormal Clock, HKY Models, Speciation: Birth-Death Process	8.48	3.47	-5953.30	1825.83
	3.32–14.12	1.22–6.37		

https://doi.org/10.1371/journal.pone.0180139.t002

Discussion

Our analyses show that *M. rainbowi* from KI is unequivocally related to African *Moggridgea*, with KI populations rendering the latter paraphyletic–a result consistent with previous morphological findings [40]. Our six-gene Bayesian analysis is also concordant with previous molecular results [35], with a deep and reciprocally-monophyletic separation between true *Moggridgea* and Australian *Bertmainius*, although the latter study was limited in its taxon and gene sampling and appropriate outgroups to confirm the exact relationships, compared with the current study.

But how did an otherwise African spider lineage end up on KI in southern Australia? To address this question we used two lines of evidence: divergence dating between African and Australian exemplars; and divergence dating between both the KI populations of *Moggridgea*. The (null) hypothesis of Gondwanan vicariance requires a very old divergence date of 110 + Mya between African and Australian *Moggridgea* to be consistent with the vicariant breakup of Gondwana [3]. The inferred split between *M. rainbowi* and African *M. intermedia* ranged from 2.27–16.02 Mya (Table 2), and the inferred age for the divergence of the two KI populations of *M. rainbowi* ranged from 1.10–6.39 Mya. Although there may be considerable uncertainty in the use of a 'borrowed' rate for *COI* to estimate divergence times, even if the HPD error margins for our dating estimate were doubled or tripled, it is clear that the dates for these

nodes are relatively recent, and not concordant with Africa's long isolation from the rest of Gondwana. Therefore, vicariance must be rejected as a plausible hypothesis for the presence of *Moggridgea* on KI.

The first of two alternative hypotheses (H_1) is that *Moggridgea* was accidentally introduced from Africa to KI by humans, such as explorers, sealers or European settlers who arrived in 1802 [62]. The sealers came from North America, and settled at what is now American River [63]. If humans brought *Moggridgea* to KI at any time from 1802 onwards (assuming a single introduction), intra-specific phylogeographic structure and genetic divergence equating to 1.10–6.39 Mya of isolation in different regions of KI would be highly unlikely.

While we cannot disprove more than one introduction of the same species, each with divergent mtDNA, to different locations on KI, the probability of two successful dispersal events for the same African species must be very low. Similarly, this hypothesis cannot be rejected on the basis of the divergence of *M. rainbowi* from *M. intermedia* alone, given our incomplete sampling of African taxa and the possibility of another unknown species in Africa being a closer relative to *M. rainbowi*. There is also the possibility of putatively unsampled littoral zone lineages from Africa, which would be more likely to be carried by explorers or oceanic vessels. However, no littoral species are so far known, although concentrated fieldwork would be required to confirm this. More than one introduction also seems highly unlikely due to the significant level of genetic differentiation between *M. rainbowi* populations at American River and Western River, which is consistent with *Moggridgea* arriving well before humans colonised the island.

The final hypothesis (H_2) predicts that *Moggridgea* is present in Australia due to long-distance dispersal from southern Africa. This proposition, which best fits the estimated divergence date of 2.27–16.02 Mya, cannot be rejected given current morphological and molecular evidence, and is our preferred explanation for the data. Long-distance dispersal of 10,000 km may be improbable for a sedentary trapdoor spider such as *Moggridgea*, but oceanic dispersal is not unprecedented for this genus, at least over shorter distances. Most species occur on mainland Africa, but three species are known from offshore islands. These include *M. occidua* (Simon, 1907) from Príncipe, *M. nesiota* Griswold, 1987 from Comoros, and *M. socotra* Griswold, 1987 from Socotra [64,40]. Príncipe and Socotra are both continental fragments of mainland Africa, and therefore their fauna may have originated by vicariance and not dispersal. However, the Comoros are volcanic in origin and were formed between 0.1 and 7.7 Mya [65]. *Moggridgea nesiota* Griswold 1987b is found on the island of Moheli, which was formed 5.5 Mya, suggesting that the presence of this species there can only be explained by dispersal from mainland Africa (approximately 340 km away). Although only a small fraction of the distance between the south-western Cape and KI, this distribution does suggest that *Moggridgea* is capable of oceanic dispersal, most likely facilitated by rafting given their burrow-dwelling existence. Colonisation by individuals who have arrived via rafting will inevitably occur in the littoral zone [66] which is consistent with the habitat of *M. rainbowi* at American River, where their burrows have only been found in vertical banks just above the high tide mark [40]. This habitat also provides further evidence of an unusual, possibly high degree of salt tolerance.

While this study represents the first robust evidence of long-distance trans-oceanic dispersal in a mygalomorph spider, oceanic dispersal at a smaller scale (e.g. as for *M. nesiota*) can be inferred for several other mygalomorphs. This is especially so for those species that occur on newly formed islands of volcanic origin (e.g. Galapagos Islands and Hawaii), and those that were once connected to a continental landmass, such as the Seychelles, the latter of which are part of the granitic Mascarene Plateau which broke off from the Indian Plate about 66 Mya) [17]. While some mygalomorphs found on non-continental islands are capable of ballooning (e.g. *Ummidia* Thorell, 1878 which is present on the volcanic island Saint Vincent in the Caribbean [67]; and *Conothele* Thorell, 1878 which occurs on some Pacific Islands and the

Seychelles [68,69]), there are also other mygalomorphs that cannot disperse this way, and yet are present on young, isolated landforms. The barychelid *Nihoa hawaiiensis* (Raven, 1988) [70] occurs on the Leeward Islands [71] which form part of the Society islands and has a very recent age progression of 1–4.5 Mya [72]. Species of a second barychelid genus, *Idioctis* L. Koch, 1874 inhabit numerous islands (i.e. Fiji, Western Samoa, Madagascar, the Seychelles, Christmas Island, and Caroline and Marshall Islands), as well as the intertidal or littoral zones of northern Australia, New Caledonia and the Solomon Islands [71]. Their habitat and distribution suggests oceanic dispersal may be the most plausible hypothesis to explain their distribution patterns [70]. A third barychelid genus, *Sason* Simon, 1887, occurs in the Seychelles, the Andaman and Mariana Islands, southern India, Ceylon, northern Australia and New Guinea [73]. Their arboreal nests may render them more amenable to oceanic travel; if an entire log or tree was dislodged and became oceanic flotsam, survival of a trans-oceanic journey may have been possible [19,20]. However, while the evidence supporting these hypothesised oceanic dispersals is compelling, none are yet supported by dated molecular phylogenies.

The direction of dispersal events can help draw conclusions about the origin of taxa. For example, taxa in Hawaii which rely on wind dispersal, such as birds and spiders, come primarily from the east [66], as predicted by storm patterns. However, taxa that disperse via rafting come mostly from the west, as predicted by oceanic currents. For dispersal via rafting, these currents may assist in the movement of buoyant objects, such as seed pods, over long distances [14]. Similarly, these currents could also be a driving force in the movement of a large vegetation rafts and other debris from Africa to Australia.

The origin of much of Australia's mygalomorph fauna has been attributed to invasion from the north and south of the continent [74], however the potential mechanisms of dispersal are not known [see 73]. The main difficulties with trans-oceanic dispersal for mygalomorphs have been discussed for ground spiders [75], and include prolonged exposure to desiccating atmosphere, lack of non-saline water, and the extremely small probability of juveniles settling in a suitable habitat, maturing, and mating [20]. However, dispersal via rafting cannot be ruled out for migids [22]. There are a number of other factors worth considering which may lead trapdoor spiders to be suited to oceanic dispersal, such as their low metabolic rate [76]. The use of silk-lined burrows with a snugly fitting trapdoor provides a relatively stable microhabitat, enabling trapdoor spiders to regulate temperature and humidity [77]. If a rafting event was facilitated by the movement of a large mass of earth or whole trees, it is plausible that spider burrows may remain intact for long periods. Nest building, defined as thickened silk placed in a pre-existing niche or cavity (requiring minimal excavation) has been well documented in African *Moggridgea*, and is more prevalent than true burrow building [64]. This method allows spiders to colonise arboreal habitats, which may aid their dispersal. Dispersal by a gravid female capable of producing numerous juveniles, would enhance the chance of a successful dispersal event and subsequent mating [20]. In addition, the ability of mygalomorph spiders to resist drowning and use stored oxygen is a critical survival tactic in terrestrial environments when burrows are temporarily flooded [78], and the same is likely to be true on oceanic rafts. While there is no doubt that large expanses of seawater pose a significant challenge to oceanic dispersal, they are clearly not insurmountable barriers, given enough time. With their low food intake requirements, protective burrows, and ability to 'hold their breath', small trapdoor spiders may be even better equipped for dispersal than previously realised.

Acknowledgments

We thank Nick Birks for collecting the specimens of *Moggridgea rainbowi* at American River, without which this research would not have been possible. We are also extremely grateful to

Marshall Hedin (San Diego University) and Jason Bond (Auburn University) for generously providing the African exemplars for our study, and Kate Sparks at the South Australian Museum for providing access to specimens. In addition, we thank Kathleen Saint (South Australian Museum) for technical support.

Author Contributions

Conceptualization: Sophie E. Harrison, Mark S. Harvey, Steve J. B. Cooper, Andrew D. Austin, Michael G. Rix.

Formal analysis: Sophie E. Harrison, Steve J. B. Cooper, Michael G. Rix.

Funding acquisition: Sophie E. Harrison, Steve J. B. Cooper, Andrew D. Austin.

Investigation: Sophie E. Harrison, Michael G. Rix.

Methodology: Sophie E. Harrison, Steve J. B. Cooper.

Project administration: Andrew D. Austin.

Resources: Andrew D. Austin.

Supervision: Andrew D. Austin.

Writing – original draft: Sophie E. Harrison.

Writing – review & editing: Sophie E. Harrison, Mark S. Harvey, Steve J. B. Cooper, Andrew D. Austin, Michael G. Rix.

References

1. Nelson G, Platnick NI (1981) Systematics and biogeography: cladistics and vicariance. New York: Columbia University Press.
2. Platnick NI (1991). Patterns of biodiversity: tropical vs temperate. J. Nat. Hist. 25: 1083–1088.
3. Sanmartín I, Ronquist F (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. Syst. Biol. 53: 216–243. https://doi.org/10.1080/10635150490423430 PMID: 15205050
4. Darwin C (1859) The origin of species by means of natural selection. John Murray, London.
5. Nelson G (1978) From Candolle to Croizat: comments on the history of biogeography. J. Hist. Biol. 11: 269–305. PMID: 11610435
6. Crisp M, Cook L, Steane D (2004) Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? Philos. T. Roy. Soc. B 359: 1551–1571.
7. de Queiroz A (2014) The monkey's voyage: how improbable journies shaped the history of life. New York: Basic Books.
8. Giribet G, Boyer SL (2010) 'Moa's Ark' or 'Goodbye Gondwana': is the origin of New Zealand's terrestrial invertebrate fauna ancient, recent, or both? Invertebr. Syst. 24: 1–8.
9. Perez S, Tejedor M, Novo N, Aristide L (2013) Divergence times and the evolutionary radiation of New World monkeys (Platyrrhini, Primates): an analysis of fossil and molecular data. PLoS One 8: e68029. https://doi.org/10.1371/journal.pone.0068029 PMID: 23826358
10. Yoder AD, Cartmill M, Ruvolo M, Smith K, Vilgalys R. (1996) Ancient single origin of Malagasy primates. P. Natl. Acad. Sci. USA 93: 5122–5151
11. Gamble T, Bauer AM, Colli GR, Greenbaum E, Jackman TR, Vitt LJ et al. (2010) Coming to America: multiple origins of New World geckos. J. Evolution. Biol. 24: 231–244.
12. Schwarz MP, Fuller S, Tierney SM, Cooper SJB (2006) Molecular phylogenetics of the exoneurine allodapine bees reveal an ancient and puzzling dispersal from Africa to Australia. Syst. Biol. 55: 31–45. https://doi.org/10.1080/10635150500431148 PMID: 16507522
13. Hayashi M, Bakkali M, Hyde A, Goodacre SL (2015) Sail or sink: novel behavioural adaptations on water in aerially dispersing species. BMC Evol. Biol. 15: 1–8. https://doi.org/10.1186/s12862-014-0274-0

14. Baum DA (1995) A systematic revision of Adansonia (Bombacaceae). Ann. Missouri Bot. Gard. 82: 440–470.
15. Yoder AD, Nowak MD (2006) Has vicariance or dispersal been the predominant biogeographic force on Madagascar? Only time will tell. Annu. Rev. Ecol. Evol. S. 37: 405–431.
16. McGlone MS (2005) Goodbye Gondwana. J. Biogeogr. 32: 739–740.
17. Gillespie RG, Roderick GK (2002) Arthropods on islands: colonization, speciation, and conservation. Annu. Rev. Entomol. 47: 595–632. https://doi.org/10.1146/annurev.ento.47.091201.145244 PMID: 11729086
18. Ceccarelli SF, Opell BD, Haddad CR, Raven RJ, Soto EM, Ramirez MJ (2016) Around the world in eight million years: historial biogeography and evolution of the spray zone spider *Amaurobioides* (Araneae: Anyphaenidae). PLoS ONE 11(10): e0163740. https://doi.org/10.1371/journal.pone.0163740 PMID: 27732621
19. Legendre R (1979) Les Araignées et la dérive des continents. Ann. Biol. 18: 37–68.
20. Raven RJ (1980) The evolution and biogeography of the mygalomorph spider family Hexathelidae. J. Arachnol. 8: 251–266.
21. Platnick NI (1981) Spider biogeography: past, present, and future. Rev. Arachnol. 3: 85–96.
22. Griswold CE, Ledford J (2001) A monograph of the migid trap door spiders of Madagascar and review of the world genera (Araneae, Mygalomorphae, Migidae). Occas. Pap. Calif. Acad. of Sci. 151: 1–120.
23. Hendrixson BE, Guice AV, Bond JE (2015) Integrative species delimitation and conservation of tarantulas (Araneae, Mygalomorphae, Theraphosidae) from a North American biodiversity hotspot. Insect Conserv. and Diver. 8: 120–131.
24. Raven RJ (1985) The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bull. Am. Mus. Nat. Hist. 182: 1–180.
25. Bond JE, Hendrixson BE, Hamilton CA, Hedin M (2012) A reconsideration of the classification of the spider infraorder Mygalomorphae (Arachnida: Araneae) based on three nuclear genes and morphology. PLoS ONE, 7: e38753. https://doi.org/10.1371/journal.pone.0038753 PMID: 22723885
26. Bond JE, Garrison NL, Hamilton CA, Godwin RL, Hedin M, Agnarsson I (2014) Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. Curr. Biol. 15: 1765–1771.
27. Main BY (1978) Biology of the arid-adapted Australian trapdoor spider Anidiops villosus (Rainbow). Bull. Brit. Arachnol. Soc. 4: 161–175.
28. Ferretti NE, Gonzalez A, Fernando PM (2012) Historical biogeography of mygalomorph spiders from the peripampasic orogenic arc based on track analysis and PAE as a panbiogeographical tool. Syst. Biodivers. 10: 179–193.
29. Coyle FA, Icenogle WR (1994) Natural history of the California trapdoor spider genus Aliatypus (Araneae, Antrodiaetidae). J. Arachnol. 22: 225–255.
30. Coyle FA (1983) Aerial dispersal by mygalomorph spiderlings (Araneae, Mygalomorphae). J. Arachnol. 13: 283–286.
31. Coyle FA (1985) Ballooning mygalomorphs: estimates of the masses of Sphodros and Ummidia ballooners (Araneae: Atypidae, Ctenizidae). J. Arachnol. 13: 291–296.
32. Main BY (1956) Observations on the burrow and natural history of the trap-door spider Missulena (Ctenizidae). West. Austr. Nat. 5: 73–80.
33. Main BY (1957) Occurrence of the trap-door spider Conothele malayana (Doleschall) in Australia (Mygalomorphae: Ctenizidae). West. Austr. Nat. 5: 209–216.
34. Bond JE, Hedin M, Ramirez M. Opell B(2001) Deep molecular divergence in the absence of morphological and ecological change in the Californian coastal dune endemic trapdoor spider Aptostichus simus. Mol. Ecol. 10: 899–910. PMID: 11348499
35. Cooper SJB, Harvey MS, Saint KM, Main BY (2011) Deep phylogeographic structuring of populations of the trapdoor spider Moggridgea tingle (Migidae) from southwestern Australia: evidence for long-term refugia within refugia. Mol. Ecol. 20: 3219–3236. https://doi.org/10.1111/j.1365-294X.2011.05160.x PMID: 21689192
36. Harvey MS (2002) Short-range endemism among the Australian fauna: some examples from non-marine environments. Invertebr. Syst. 16: 550–570.
37. Bond JE, Hedin M (2006) A total evidence assessment of the phylogeny of North American euctenizine trapdoor spiders (Araneae, Mygalomorphae, Cyrtaucheniidae) using Bayesian inference. Mol. Phylogenet. Evol. 41: 70–85. https://doi.org/10.1016/j.ympev.2006.04.026 PMID: 16857391

38. Harvey MS, Main BY, Rix MG, Cooper SJB (2015) Refugia within refugia: in situ speciation and conservation of threatened Bertmainius (Araneae: Migidae), a new genus of relictual trapdoor spiders endemic to the mesic zone of south-western Australia. Invertebr. Syst. 29: 511–533.
39. Raven RJ (1984) Systematics and biogeography of the mygalomorph spider family Migidae (Araneae) in Australia. Aust. J. Zool. 32: 379–390.
40. Harrison SE, Rix MG, Harvey MS, Austin AD (2016) An African mygalomorph lineage in temeprate Australia: the trapdoors spider genus Moggridgea (Araneae: Migidae) on Kangaroo Island, South Australia. Austral Entomol. 55: 208–216.
41. Main BY (1991) Occurrence of the trapdoor spider genus Moggridgea in Australia with descriptions of two new species (Araneae: Mygalomorphae: Migidae). J. Nat. Hist. 25: 383–397.
42. Rix MG, Harvey MS, Roberts JD (2008). Molecular phylogenetics of the spider family Micropholcommatidae (Arachnida: Araneae) using nuclear rRNA genes (18S and 28S). Mol. Phylogenet. Evol. 46: 1031–1048. https://doi.org/10.1016/j.ympev.2007.11.001 PMID: 18162409
43. Folmer O, Black M., Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotech. 3: 294–299.
44. Rix MG, Cooper SJB, Meusemann K, Klopfstein S, Harrison SE, Harvey MS et al. (2017). Post-Eocene climate change across continental Australia and the diversification of Australasian spiny trapdoor spiders (Idiopidae: Arbanitinae). Mol. Phylogenet. Evol. 109: 302–320. https://doi.org/10.1016/j.ympev.2017.01.008 PMID: 28126515
45. Colgan DJ, McLauchlan A, Wilson GDF, Livingston SP, Edgecombe GD, Macaranas J, Cassis E, Gray MRV (1998) Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Aust. J. Zool. 46: 419–437.
46. Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, et al. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199 PMID: 22543367
47. Lanfear R, Calcott B, Ho S, Guidon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29: 1695–1701. https://doi.org/10.1093/molbev/mss020 PMID: 22319168
48. Rodríguez F, Oliver JF, Marín A, Medina JR (1990) The general stochastic model of nucleotide substitutions. J. Theoret. Biol. 142: 485–501.
49. Yang Z (1996). Among-site rate variation and its impact on phylogenetic analyses. Trends Ecol. Evol. 11: 367–372. PMID: 21237881
50. Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. J. Mol. Evol. 17: 368–376. PMID: 7288891
51. Hasegawa M, Kishino H, Yano T (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. J. Mol. Evol. 22: 160–174. PMID: 3934395
52. Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. 16: 111–120. PMID: 7463489
53. Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, et al. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61: 539–542. https://doi.org/10.1093/sysbio/sys029 PMID: 22357727
54. Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop, pp. 1–8. LA: New Orleans.
55. Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. Available from http://beast.bio.ed.ac.uk/Tracer.
56. Rambaut A, Drummond AJ (2010) FigTree v1.3.1. Institute of Evolutionary Biology. Available from http://tree.bio.ed.ac.uk/software/figtree/
57. Stamatakis A (2014) RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 22: 2688–2690.
58. Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootsrap algorithm for the RAxML web-servers. Syst. Biol. 57: 758–771. https://doi.org/10.1080/10635150802429642 PMID: 18853362
59. Drummond AJ, Rambaut A (2007) Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7: 214. https://doi.org/10.1186/1471-2148-7-214 PMID: 17996036
60. Brower AVZ (1994) Rapid morphological radiation and convergence among races of the butterfly Heliconius erato inferred from patterns of mitochondrial DNA evolution. Proc. Natl. Acad. Sci. USA 91: 6491–6495. PMID: 8022810

61. Opatova V, Arnedo MA (2014) From Gondwana to Europe: inferring the origins of Mediterranean Macrothele spiders (Araneae: Hexathelidae) and the limits of the family Hexathelidae. Invertebr. Syst. 28: 361–374.
62. Davies M, Twidale CR, Tyler MJ (2002) Natural history of Kangaroo Island, 2nd edn. South Australia: Royal Society of South Australia.
63. Bell G (1997) Kangaroo Island–this remote island of the southern sea: Kangaroo Island history 1836–1996. Kingscote: Published by Author.
64. Griswold CE (1987) The African members of the trap-door spider family Migidae (Araneae: Mygalomorphae) 1. The genus Moggridgea O.P.-Cambridge 1875. Ann. Natal Mus. 28: 1–118.
65. Schlüter T, Trauth MH (2008) Geological atlas of Africa; with notes of stratigraphy, tectonics, economic geology, geohazards, geosites and geoscientific education of each country. Berlin: Springer-Verlag.
66. Gillespie RG, Baldwin BG, Waters JW, Fraser CI, Nikula RS, Roderick GK (2012) Long-distance dispersal: a framework for hypothesis testing. Trends Ecol. Evol. 71: 47–56.
67. Simon E (1891) On the spiders of the island of St. Vincent. Part 1. Proc. Zool. Soc. Lond. 1891: 549–575.
68. Roewer CF (1963) Araneina: Orthognatha, Labidognatha. Insects of Micronesia 3: 104–132.
69. Saaristo MI (2002) New species and interesting new records of spiders from Seychelles (Arachnida, Araneaea). Phelsuma 10: A1–31.
70. Raven RJ (1988) A revision of the mygalomorph spider genus Idioctis (Araneae, Barychelidae). Am. Mus. Novit. 2929: 1–14.
71. Churchill TB, Raven RJ (1992) Systematics of the intertidal trapdoor spider genus Idioctis (Mygalomorphae: Barychelidae) in the Western Pacific with a new genus from the Northeast. Mem. Queensl. Mus. 32: 9–30.
72. Neall VE, Trewick SA (2008) The age and origin of the Pacific Islands: a geological overview. Phil. Trans. Biol. Sci. 363: 3293–3308.
73. Raven RJ (1986) A revision of the spider genus Sason Simon (Sasoninae, Barychelidae, Mygalomorphae) and its historical biogeography. J. Arachnol. 14: 47–50.
74. Main BY (1981) Eco-evolutionary radiation of mygalomorph spiders in Australia. Biogeography and Ecology of New Guinea 2: 853–872. Junk: The Hague.
75. Platnick NI (1976) Drifting spiders or continents?: Vicariance biogeography of the spider subfamily Laroninae (Araneae: Gnaphosidae). Syst. Zool. 25: 101–109.
76. Canals M, Veloso C, Solis R (2015) Adaptation of the spiders to the environment: the case of some Chilean species. Front. Physiol. 6: 220. https://doi.org/10.3389/fphys.2015.00220 PMID: 26321957
77. Framenau VW, Baehr BC, Zborowski P (2014) A guide to the spiders of Australia. Sydney: New Holland Publishers.
78. Main BY (1993) From flood avoidance to foraging: adaptive shifts in trapdoor spider behaviour. Mem. Queensl. Mus. 33: 599–606.