ORIGINAL ARTICLE

Island hopping across the central Pacific: mitochondrial DNA detects sequential colonization of the Austral Islands by crab spiders (Araneae: Thomisidae)

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ABSTRACT

Aim Phylogenetic studies concerning island biogeography have been concentrated in a fraction of the numerous hot-spot archipelagos contained within the Pacific Ocean. In this study we investigate relationships among island populations of the thomisid spider *Misumenops rapaensis* Berland, 1934 across the Austral Islands, a remote and rarely examined southern Pacific hot-spot archipelago. We also assess the phylogenetic position of *M. rapaensis* in relation to thomisids distributed across multiple Polynesian archipelagos in order to evaluate the proposed hypothesis that thomisid spiders colonized Polynesia from multiple and opposing directions. The data allow an examination of genetic divergence and species accumulation in closely related lineages distributed across four Polynesian archipelagos.

Location The study focused on four Polynesian hot-spot archipelagos: the Austral, Hawaiian, Marquesan and Society islands.

Methods Mitochondrial DNA sequences comprising *c.* 1400 bp (portions of *cytochrome oxidase subunit I*, ribosomal *16S* and *NADH dehydrogenase subunit I*) were obtained from thomisid spiders (64 specimens, representing 33 species) collected in the Australs, the Hawaiian Islands, the Society Islands, the Marquesas, Tonga, Fiji, New Zealand, New Caledonia and North and South America. Phylogenetic analyses using parsimony, maximum-likelihood and Bayesian approaches were employed to resolve relationships of *M. rapaensis* to other Polynesian *Misumenops* and across the Austral Islands.

Results Rather than grouping with other *Misumenops* spp. from the archipelagos of the Society Islands, Marquesas and Hawaiian Islands, *M. rapaensis* appears more closely related to *Diaea* spp. from Tonga, Fiji, New Zealand and New Caledonia. Phylogenetic analyses strongly support *M. rapaensis* as monophyletic across the Austral Islands. *Misumenops rapaensis* sampled from the two older islands (Rurutu and Tubuai) form reciprocally monophyletic groups, while individuals from the younger islands (Raivavae and Rapa) are paraphyletic. Across the Austral Islands, *M. rapaensis* exhibits a surprising level of genetic divergence (maximally 11.3%), an amount nearly equivalent to that found across the 16 examined Hawaiian species (14.0%).

Main conclusions Although described as a single morphologically recognized species, our results suggest that *M. rapaensis* comprises multiple genetically distinct lineages restricted to different Austral Islands. Phylogenetic relationships among the island populations are consistent with sequential colonization of this lineage down the Austral archipelago toward younger islands. Analyses support the hypothesis that thomisid spiders colonized the central Pacific multiple times and suggest that *M. rapaensis* arrived in the Austral Islands from a westward direction, while *Misumenops* found in neighbouring archipelagos appear to be

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more closely related to New World congeners to the east. Finally, our data detect asymmetrical rates of morphological evolution and species diversification following colonization of four different Polynesian archipelagos.

INTRODUCTION

Remote oceanic islands are frequently cited as ideal settings for studying evolutionary processes because of their high levels of endemism (Simon, 1987; Wagner & Funk, 1995; Grant, 1998; Gillespie & Roderick, 2002), and have profoundly influenced the development of subjects ranging from species formation (Carson & Templeton, 1984; Grant & Grant, 1996; Losos *et al.*, 1998) to biogeography (MacArthur & Wilson, 1967; Simberloff & Wilson, 1969). Although three-quarters of the world's islands are found in the Pacific Ocean (Keast, 1996), phylogenetic studies focused on Pacific terrestrial endemics have largely been concentrated in the Hawaiian archipelago (e.g. Baker & DeSalle, 1997; Baldwin & Sanderson, 1998; Jordan *et al.*, 2003), the Galapagos Islands (e.g., Caccone *et al.*, 1999; Sequeira *et al.*, 2000; Burns *et al.*, 2002) and New Zealand (e.g., Trewick & Wallis, 2001; Buckley *et al.*, 2002), perhaps because of their fame for harbouring large adaptive radiations and possibly because of their greater accessibility to field collectors. With the exception of a few studies conducted within the Marquesas (Johnson *et al.*, 2000b; Gillespie, 2002) and the Society Islands (Craig *et al.*, 2001; Goodacre & Wade, 2001; Joy & Conn, 2001), limited information is available concerning the evolutionary history of the biota of most other Pacific islands, necessitating the construction of phylogenetic hypotheses for taxa occurring within such islands. In this study we investigate phylogenetic relationships among thomisid spiders distributed across the Austral Islands, a hot-spot archipelago situated in the southern Pacific Ocean.

The Austral Archipelago is located approximately 500 km to the southwest of the Society Islands at their closest points (between Tahiti and Rurutu islands, Fig. 1), and extends over 1500 km from the southernmost island of Marotiri to Maria, a coral atoll. The Austral Islands are considered geologically continuous with the Cook Islands, which are located to the northwest of Maria (Dickinson, 1998; Bonneville *et al.*, 2002). Though the Austral–Cook chain is produced by volcanic hot-spot activity, its geological formation departs markedly from
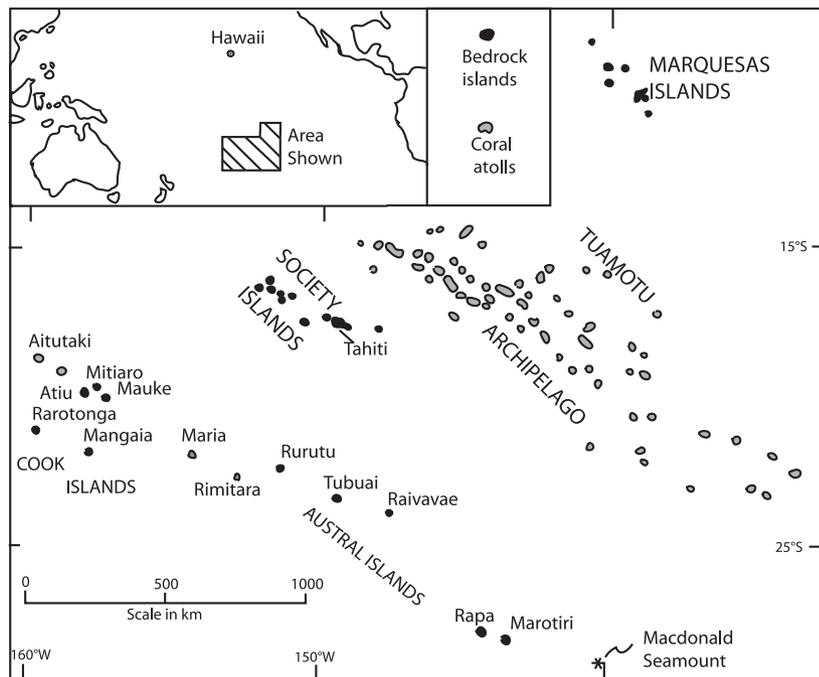
Figure 1 Map of Cook–Austral chain in relation to neighbouring archipelagos in the South Pacific Ocean.

that of the classic hot-spot archipelago model, exemplified by the Hawaiian–Emperor chain. An ideal hot-spot track consists of a singular alignment of volcanic islands formed as oceanic lithosphere drifts over a mantle plume (volcanic hot spot), similar to 'smoke carried downwind' (Wilson, 1963). Consequently, a linear array of islands is formed that are sequentially arranged in size and age, being both older and smaller with increasing distance from the hot spot. Islands 'downstream' from the hot spot decrease in size as a result of erosion and subsidence, ultimately becoming completely submerged, forming coral atolls and then seamounts. The Cook–Austral chain, by contrast, consists of multiple alignments of volcanic islands that have experienced repeated episodes of volcanism at several sites (Dickinson, 1998; Bonneville *et al.*, 2002). Bonneville *et al.* (2002) argue that the Austral Islands originated from at least two separate hot spots: (1) the Macdonald Seamount, a submarine volcano located 350 km southeast of Marotiri Island (Fig. 1) and a current site of hot spot activity, being the source of Rapa and Marotiri, and (2) the newly discovered Arago Seamount being the site of another extinct hot spot that produced the northern Austral islands of Raivavae, Tubuai, Rurutu and Rimatara.

The complex geological evolution of the islands in the Cook–Austral chain makes the precise origin and sequence of island formation an area of active debate amongst geologists (Dickinson, 1998; Bonneville *et al.*, 2002). Nevertheless, potassium–argon (K–Ar) age estimates indicate that the Cook–Austral chain began forming approximately 20–30 Ma (Keating, 1987; Munschy *et al.*, 1998) with the ages of the Austral islands ranging from the youngest island, Marotiri, at 4.3 Myr, to Maria at 15.7 Myr (Table 1). Though formed from different volcanic plumes, the islands of the Austral archipelago are sequentially ordered from southeast to northwest by increasing age due to the north-westward movement of the Pacific tectonic plate, much like the Hawaiian Islands (Fig. 2). The sequential arrangement of the Austral Islands, decreasing in age from northwest to southeast, predicts a phylogeographical pattern reflecting stepwise colonization from older to younger islands following island emergence (Fig. 2, inset), similar to the pattern Wagner & Funk (1995) termed the 'progression rule' in reference to the Hawaiian Islands.

Though generally taxonomically depauperate, the Austral Islands host a surprising number of endemic species of particular lineages. For example, Paulay (1985) documented a large radiation of flightless weevils of the genus *Miocalles* in Rapa. The land snail fauna of the Australs is considered particularly impressive, with 200 snail species being documented from Rapa alone (Cooke, 1934). In addition, studies by Clarke (1971) on the lepidopteran fauna of Rapa resulted in the description of a number of diverse groups. In all of these cases, phylogenetic hypotheses are unavailable, and to our knowledge no previous studies have presented phylogenetic hypotheses specifically assessing relationships across islands of the Austral archipelago. Some recent phylogenetic studies (Craig *et al.*, 2001; Wright *et al.*, 2001; Mitchell & Heenan, 2002) have incorporated a few species from some of these islands in the context of a broader biogeographical analysis, examining relationships among different sets of islands in the Pacific Basin.

The Thomisidae, commonly known as crab spiders, is a large cosmopolitan family characterized as cryptically coloured ambush predators that do not build webs (Chittka, 2001; Heiling *et al.*, 2003). Representatives of the genus *Misumenops* F.O.P.-Cambridge, 1900 are widely distributed across eastern Polynesia, reaching varying levels of species diversity within the different archipelagos in which it occurs. For example, the genus is represented by one to two endemic species in the Austral, Society and Marquesan archipelagos (where single species occur across multiple islands within each archipelago), while 17 endemic species of *Misumenops*, including several single-island endemics, are known from the Hawaiian Islands (Suman, 1970; Platnick, 2005). A second thomisid genus *Mecaphesa* Simon, 1900 has four species endemic to the Hawaiian archipelago. Based on his observations of morphology, Lehtinen (1993) hypothesized that the Hawaiian thomisids (including all species of *Misumenops* and *Mecaphesa*) represented a large monophyletic radiation being most closely related to *Misumenops* occurring in the Marquesas and Society Islands and in North and South America. While the genus *Misumenops* has not been documented from Central Pacific islands west of the Australs, representatives of the genus *Diaea* Thorell, 1869 are broadly distributed across western Polynesia (Samoa, Tonga and New Zealand) and Melanesia (Fiji, New Caledonia, New Guinea, the Solomon Islands and Vanuatu; Platnick, 2005). The juxtaposed distributions of these two groups, (1) eastern Polynesian *Misumenops*/*Mecaphesa* and (2) western Polynesian and Melanesian *Diaea*, led Lehtinen (1993) to argue further that thomisid spiders colonized the Central Pacific from opposite directions – the Hawaiian, Marquesan and Society Island thomisids arriving from the New World, and the western Polynesian thomisids from Melanesia. However, Lehtinen (1993) could not place the Austral Islands' *Misumenops rapaensis* within this scheme and regarded its origin as 'unknown'.

Table 1 Islands of the Austral Archipelago: current size, elevation and age estimates in millions of years since island emergence

Island	Size* (km²)	Maximum elevation† (m)	Maximal age estimate‡ (Myr)
Maria	1	3	15.70
Rimatara	18	95	14.80
Rurutu	32	389	12.68
Tubuai	45	402	10.40
Raivavae	18	437	6.96
Rapa	40	650	5.02
Marotiri	< 1	113	4.30

*†Island area and elevation obtained from Craig *et al.* (2001).
‡Ages for islands obtained as follows: Maria age estimated by Craig *et al.* (2001) based on distance from hot spot; Rimatara average age from Craig *et al.* (2001), Tubuai, Munschy *et al.* (1998), Raivavae, Duncan & McDougall (1976), Rapa, Munschy *et al.* (1998), Marotiri, from Craig *et al.* (2001).
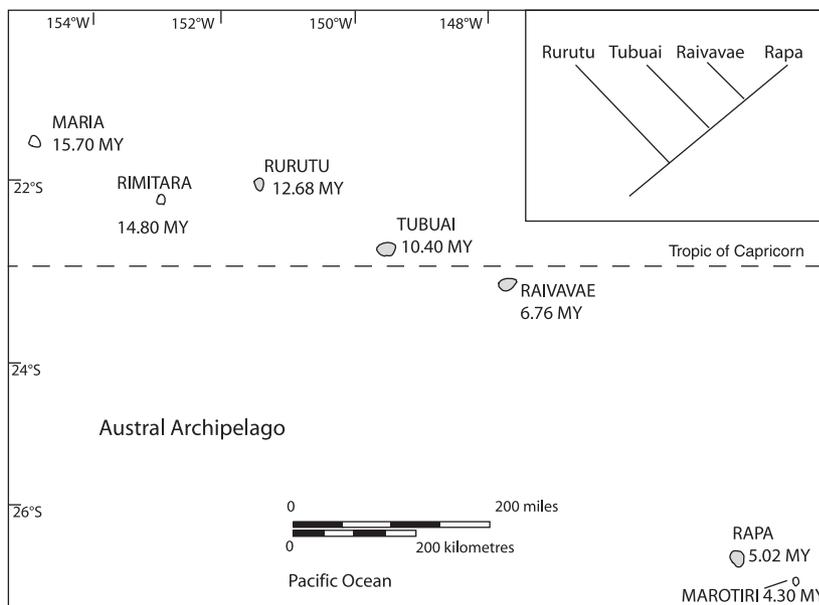
Figure 2 Map of the Austral Archipelago, including maximal ages of islands in millions of years (Myr). Shaded islands correspond to known distribution of *Misumenops rapaensis*. Inset: predicted phylogenetic hypothesis supporting stepwise colonization of islands.

Within the Austral Islands, *M. rapaensis* occurs on the islands of Rurutu, Tubuai, Raivavae and Rapa (Berland, 1934, 1942). Though these islands are widely separated (by as much as *c.* 1500 km), Berland (1942) concluded that across the different islands *M. rapaensis* represented a single morphologically uniform species. A more recent taxonomic treatment by Ledoux & Halle (1995) stated that the species was an endemic element of the archipelago (not introduced by humans) and further speculated that the lack of differentiation among islands might suggest that different island populations were capable of maintaining cohesion through inter-island migration. Here, we utilize mitochondrial DNA sequence data to investigate relationships among the different island populations of *M. rapaensis* in addition to the phylogenetic position of this species relative to other Pacific Thomisidae. In doing so, we aim to address outstanding questions regarding the biogeographical origin of *M. rapaensis* as well as to infer its history of colonization across the Austral Archipelago.

MATERIALS AND METHODS

Taxon sampling

The present study examined 64 specimens representing 33 species, focusing on Polynesian members of the thomisid genera *Misumenops*, *Mecaphesa* and *Diaea*. The thomisid genus *Misumenops* comprises 126 recognized species and is worldwide in distribution (North and South America, Africa, Asia and Europe). However, the majority of the described species of *Misumenops* occur in North and South America (67%) (Platnick, 2005). Representatives of the genus from the Central Pacific were extensively sampled, including specimens from the Austral Islands (*M. rapaensis* from the islands of Rurutu (three individuals), Tubuai (eight), Raivavae (five), and Rapa (nine)), Hawaiian Islands (13 of 17 described species from six islands),

Marquesas (*Misumenops delmasi* from the islands of Nuku Hiva, Hiva Oa, Tahuata and Fatu Hiva), Society Islands (*Misumenops melloleitaoi* from Moorea and Tahiti and *Misumenops* sp. from Raiatea and Huahine; J. Garb, in prep.). The study further included *Misumenops* from North America (five species) and South America (one species) that could be obtained for molecular analyses. The genus *Mecaphesa* includes six described species and is restricted to the Hawaiian Islands (four species), the Galapagos Islands (one species) and the Juan Fernandez Islands (one species). Three Hawaiian species of *Mecaphesa* were sampled in this study. The genus *Diaea* is large (86 described species) and has a nearly cosmopolitan distribution, but 92% of the species are contained within Africa and Australasia. The highest diversity of *Diaea* is in the southwest Pacific (52% of all species, largely occurring in Australia and New Zealand), where the *Misumenops* genus is absent (Platnick, 2005). Specimens of *Diaea* included in the current study were *Diaea praetexta* from Tonga (islands of Vava'u and Eua) and several unidentified species from Fiji, New Caledonia and New Zealand. In addition, we were able to include *Misumenoides formosipes* from North America. The four above-mentioned genera are considered members of the tribe Misumenini *sensu* Ono (1988), part of the thomisid subfamily Thomisinae, Sundevall, 1833. Accordingly, we included *Xysticus fraternus* Banks, 1895, also of the subfamily Thomisinae, but in the tribe Coriarachnini *sensu* Ono (1988), to serve as an outgroup. A complete list of all specimens used in this study and their species identity and collection locality is given in Table 2.

DNA sequencing and alignment

Total DNA was extracted from one or two legs of each specimen stored in 70–100% ethanol, using either a phenol–chloroform preparation (Palumbi *et al.*, 1991) or using the

Table 2 Taxa sampled in this study, their collecting locality, and GenBank accession numbers

ID no.*	Species	Locality†	COI	r16S-ND1
649	*Misumenops rapaensis*	AUS: Rurutu Island, Mt Manureva, *c.* 200 m	DQ174427	–
662	*M. rapaensis*	AUS: Rurutu Island, Mt Manureva	DQ174426	–
663	*M. rapaensis*	AUS: Rurutu Island, above Moerai, 130 m	DQ174425	DQ174356
664	*M. rapaensis*	AUS: Tubuai Island, Mt Taita, 60–400 m	DQ174418	–
665	*M. rapaensis*	AUS: Tubuai Island, Mt Taita, 60–400 m	DQ174417	–
666	*M. rapaensis*	AUS: Tubuai Island, Mt Taita, 310–400 m	DQ174419	–
667	*M. rapaensis*	AUS: Tubuai Island, Mt Taita	DQ174420	–
668	*M. rapaensis*	AUS: Tubuai Island, Mt Taita	DQ174421	DQ174358
669	*M. rapaensis*	AUS: Tubuai Island, Mt Taita, 350–400 m	DQ174422	–
670	*M. rapaensis*	AUS: Tubuai Island, Mt Taita, 350–400 m	DQ174423	–
671	*M. rapaensis*	AUS: Tubuai Island, Mt Taita, 60–400 m	DQ174424	–
672	*M. rapaensis*	AUS: Raivavae Island, Maunanui, 150 m	DQ174403	DQ174357
673	*M. rapaensis*	AUS: Raivavae Island, Mt Hiro, 380 m	DQ174404	–
674	*M. rapaensis*	AUS: Raivavae Island, Mt Hiro, 380 m	DQ174405	–
675	*M. rapaensis*	AUS: Raivavae Island, Mt Hiro, 380 m	DQ174406	–
676	*M. rapaensis*	AUS: Raivavae Island, Mt Hiro, 380 m	DQ174407	–
677	*M. rapaensis*	AUS: Rapa Island, Mt Perahu, 600 m	DQ174408	–
678	*M. rapaensis*	AUS: Rapa Island, Mt Perahu, 600 m	DQ174409	–
679	*M. rapaensis*	AUS: Rapa Island, along road (western side of Haurei Bay), 10 m	DQ174411	–
680	*M. rapaensis*	AUS: Rapa Island, Pariati, 200 m	DQ174410	DQ174359
681	*M. rapaensis*	AUS: Rapa Island, Pariati, 200 m	DQ174413	–
682	*M. rapaensis*	AUS: Rapa Island, Maitua, 200 m	DQ174415	–
683	*M. rapaensis*	AUS: Rapa Island, Maungaoa, 400 m	DQ174414	–
684	*M. rapaensis*	AUS: Rapa Island, Akao	DQ174412	–
685	*M. rapaensis*	AUS: Rapa Island, Maii	DQ174416	–
461	*Misumenops* sp.	SOC: Raiatea Island, Temihana Plateau, 780 m	DQ174371	DQ174328
701	*Misumenops* sp.	SOC: Huahine Island, Mt Turi, *c.* 650 m	DQ174372	DQ174329
484	*M. melloleitaoi*	SOC: Moorea Island, Mt Mouaputa, 840 m	DQ174373	DQ174330
368	*M. melloleitaoi*	SOC: Tahiti Island, Tahiti iti, Taravao Plateau, 640 m	DQ174374	DQ174331
479	*M. delmasi*	MARQ: Nuku Hiva Island, Mt Muake, 800 m	DQ174367	DQ174324
482	*M. delmasi*	MARQ: Tahuata Island	DQ174369	DQ174326
657	*M. delmasi*	MARQ: Fatu Hiva Island, Omoa, 800 m	DQ174370	DQ174327
412	*M. delmasi*	MARQ: Hiva Oa Island, Mt Temetiu Ridge, 1140 m	DQ174368	DQ174325
099	*M. anguliventris*	HAW: Oahu Island (K, Ma, H), Mt Ka'ala summit	DQ174376	DQ174333
095	*M. discretus*	HAW: Kauai Island, Alakai Swamp	DQ174375	DQ174332
072	*M. junctus*	HAW: Molokai Island (K, O, Ma, H), Pu'u Kolekole	DQ174388	DQ174345
101	*M. cavatus*	HAW: Hawaii Island, Mauna Kea	DQ174377	DQ174334
547	*M. kanakanus*	HAW: Oahu Island (K, Ma, H), Manoa Cliff Trail, Ko'olau Mts	DQ174390	DQ174347
153	*M. imbricatus*	HAW: Oahu Island (Ma), Pauoa Flats, Ko'olau Mts	DQ174380	DQ174337
238	*M. facundus*	HAW: Hawaii Island, Saddle Rd Kipuka#3	DQ174381	DQ174338
343	*M. nigrofrenatus*	HAW: Hawaii Island (K, O), Pu'uwa'awa'a Forest bird sanctuary	DQ174383	DQ174340
542	*M. aridus*	HAW: Maui Island (H), Auwahi, East Maui	DQ174385	DQ174342
500	*M. rufithorax*	HAW: Oahu Island, Manoa Cliff Trail, Ko'olau Mts	DQ174389	DQ174346
103	*M. editus*	HAW: Oahu Island, Mt Ka'ala summit	DQ174378	DQ174335
537	*M. insulanus*	HAW: Necker Island (K, O, Ma, H), Summit Hill	DQ174384	DQ174341
554	*M. hiatus*	HAW: Maui Island, Auwahi East Maui	DQ174386	DQ174343
653	*Mecaphesa semispinosa*	HAW: Oahu Island, Mt Ka'ala summit	DQ174382	DQ174339
120	*Mecaphesa perkins*	HAW: Oahu Island, Wa'ahila Ridge, Ko'olau Mts	DQ174379	DQ174336
340	*Mecaphesa naevigerum*	HAW: Oahu Island (K, Ma, H), Pahole NARS	DQ174387	DQ174344
410	*M. rothi*	USA: California: San Luis Obispo Co.	DQ174391	DQ174348
661	*M. celer*	USA: California, Riverside Co.	DQ174393	DQ174350
658	*M. importunus*	USA: California, San Diego Co.	DQ174392	DQ174349
660	*M. devius*	USA: California, Riverside Co.	DQ174395	DQ174352
659	*M. sp.*	USA: California, Riverside Co.	DQ174394	DQ174351
647	*M. pallidus*	Argentina: Carrizo Plain	DQ174397	DQ174354
076	*Misumenoides formosipes*	USA: Maryland	DQ174396	DQ174353
703	*Diaea praetexta*	Tonga: Vava'u Island	DQ174401	DQ174365

Table 2 continued

ID no.*	Species	Locality†	COI	r16S-ND1
704	*Diaea praetexta*	Tonga: Eua Island	DQ174402	DQ174366
692	*Diaea* sp.	New Caledonia, Mt Koghis	DQ174399	DQ174363
089	*Diaea* sp.	New Zealand	DQ174398	DQ174355
699	*Diaea* sp.	Fiji: Viti Levu, Monasavu	DQ174428	DQ174362
696	*Diaea* sp.	Fiji: Viti Levu, Singatoka Dunes	DQ174430	DQ174360
697	*Diaea* sp.	Fiji: Viti Levu, Singatoka Dunes	DQ174429	DQ174361
079	*Xysticus fraternus*	USA: New York	DQ174400	DQ174364

*Number refers to specimen code in authors' database.

†AUS, Austral Islands; SOC, Society Islands; MARQ, Marquesan Islands; HAW, Hawaiian Islands. Letters in parentheses after Hawaiian island locality indicate additional islands where species is distributed, as follows: K = Kauai, O = Oahu, Ma = Maui, H = Hawaii. More specific locality information available upon request.

Qiagen DNAeasy Tissue kit (Qiagen Inc., Valencia, CA, USA). The remainder of the specimen was stored in 70% ethanol for deposition in the UC Berkeley Essig Museum of Entomology (note: voucher of specimen 692 = QVM13:44871, loaned from the Queen Victoria Museum, Tasmania). Two separate fragments of the mitochondrial genome were amplified by polymerase chain reaction (PCR):

1. A portion of the *cytochrome oxidase I* (*COI*) gene in three overlapping fragments using either primer combinations LCOI 1490: 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′ (Folmer *et al.*, 1994) with C1-N-2568 5′-GCT ACA ACA TAA TAA GTA TCA TG-3′ (Hedin & Maddison, 2001) resulting in a *c.* 1078 base-pair (bp) fragment, LCOI 1490 with HCOI 2198: 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′ (Folmer *et al.*, 1994), to produce a *c.* 700 bp fragment, or universal primers C1-J-1718: 5′-GGA GGA TTT GGA AAT TGA TTA GTT CC-3′ and C1-N-2191: 5′-CCC GGT AAA ATT AAA ATA TAA ACT TC-3′ (Simon *et al.*, 1994), generating a *c.* 473 bp fragment.

2. A portion of the mitochondrial genome spanning sections of ribosomal *16S* to *NADH dehydrogenase subunit I* (henceforth referred to as *16S-ND1*), amplified using the primers LR-N-12945 5′-CGA CCT CGA TGT-TGA ATT AA-3′ (Hedin, 1997) with ND1Thom 5′-GAG CTA CTC TTC GAA TTG ATC C-3′ (this study), resulting in *c.* 600 bp.

PCR conditions to amplify either *COI* or *16S-ND1* segments included an initial 95 °C denaturation of 90 s, followed by 35 cycles of 30 s at 94 °C, 40 s ranging from 45 to 55 °C, 45 s at 72 °C, followed by a final 10 min 72 °C extension. The amplified portion of *COI* was collected from all 64 examined specimens; whereas the *16S-ND1* segment was collected from one individual of *M. rapaensis* for each of the four Austral Islands in addition to all other included specimens (for a total of 43 sequences).

PCR products were purified using the QIAquick PCR Purification Kit (Qiagen) and sequenced in both directions using the ABI 377, ABI 310, or ABI 3700 automatic sequencers (Applied Biosystems, Foster City, CA, USA) with the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit. Sequence chromatograms were visually edited against

chromatograms of complementary strands and translated to identify codon positions. GenBank accession numbers for each included sequence are listed in Table 2. Both sets of mitochondrial fragments were manually aligned. The *COI* sequences contained no indels and were highly conserved in their first and second codon positions, such that alignment of these sequences was straightforward. The sequences spanning *16S-ND1* exhibited considerable length variability outside of the protein-coding *ND1* gene. After manual alignment, three sections of the fragment that could not be unambiguously aligned, totalling 36 bp, were excluded from phylogenetic analyses.

Phylogenetic analyses

Phylogenetic tree searches of the combined matrix of mitochondrial data (*16S-ND1* + *COI*) for all available taxa were conducted using PAUP* β10 (Swofford, 2002). Maximum parsimony (MP) tree searches were initiated treating all characters as unweighted, reversible and unordered with gaps considered to be missing data. Heuristic searches were performed by stepwise addition of taxa, with tree-bisection–reconnection (TBR) branch swapping rearrangement and 1000 stepwise random taxon addition replicates. A strict consensus of the trees was computed where multiple equally most parsimonious trees (MPTs) were recovered in a search. Relative branch support was assessed by computing non-parametric bootstrap (BS) values (Felsenstein, 1985) using 1000 pseudoreplicates but with 10 random taxon additions per replicate and by calculating decay indices (DI), or the number of steps required to collapse a branch (Bremer, 1988), using the program TREEROTV2 (Sorenson, 1999). A best-fit model of sequence evolution and model parameters was determined by evaluating nested hypotheses of evolutionary models using the likelihood ratio test as implemented in the program MODEL-TEST 3.06 (Posada & Crandall, 1998). The best-fit model of sequence evolution and model parameters selected by MODELTEST, was used to find maximum likelihood (ML) tree(s). Maximum likelihood heuristic tree searches included TBR branch swapping rearrangement with 10 random taxon

addition replicates. Maximum likelihood clade support was assessed by computing 100 ML bootstrap pseudoreplicates. Comparison of different bootstrap search strategies by DeBry & Olmstead (2000) concluded that TBR branch swapping, saving only one tree at a time (MULTREES option off), resulted in an unbiased estimate of bootstrap values computed when multiple trees are saved. Thus, to expedite ML bootstrap support computation, one random taxon addition replicate was executed per bootstrap replicate, with the MULTREES option turned off for TBR branch swapping. Using the model of nucleotide substitution selected by MODELTEST, Bayesian tree searches were executed with the program MR. BAYES 3.0 (Huelsenbeck & Ronquist, 2001). Three independent runs were conducted, each with four Markov chain Monte Carlo (MCMC) chains for 3,000,000 generations, sampling trees every 1000 generations, and were initiated using default uniform priors and the 'random tree' option. The ML scores of sampled trees were plotted against generation time to determine the point at which log likelihood values reached stationarity (i.e. the 'burn-in' period). A 50% majority rule consensus tree was computed from trees retained after burn-in to determine clade posterior probability values (PP). Results generated from the three independent runs were compared to assess convergence of likelihood scores and clade posterior probability values.

Based on the results of the phylogenetic analyses described above, taxa appearing closely related to *M. rapaensis* were retained for further analyses with all available sequences obtained from *M. rapaensis*. Because the *16S-ND1* fragment could not be amplified from most specimens of *M. rapaensis*, these analyses were based on the *COI* sequences alone. For this data set, MP, ML and Bayesian tree searches were conducted as described above. However, the reduced set of taxa allowed for ML bootstrap replicates retaining all trees, with three random taxon addition replicates executed per bootstrap replicate. Uncorrected as well as ML-corrected estimates of sequence divergence (Yang & Kumar, 1996) were computed for each pairwise taxon comparison, using the model and parameters as selected by MODELTEST. Finally, uncorrected genetic distance was plotted against ML-corrected sequence divergence for each pairwise sequence comparison to assess sequence saturation.

RESULTS

Sequence variability

Initial alignment of sequences spanning *16S-ND1* collected from the 43 sampled specimens resulted in a 597 bp character matrix, with 395 bp corresponding to the protein-coding sequence. Translation of the protein-coding sequence did not reveal unexpected stop codons and was appropriately conserved relative to *ND1* sequences published for other spiders. Following exclusion of the ambiguously aligned sections (36 bp), the remaining 561 bp contained 245 variable positions, 186 (75.9%) were in the protein-coding region. Third-

codon positions were most variable, with 119 (90.8%) positions being variable, followed by 45 (34.1%) of all first-codon position, and 22 (16.7%) of all second-codon positions. The sequenced portion of *COI* resulted in an 820 bp alignment. As with *ND1*, the *COI* sequences appeared appropriately conserved relative to previously published spider *COI* sequences and did not contain unexpected stop codons. These sequences included 299 (36.5%) variable sites and were more conserved relative to the sequenced fragment of *ND1*, with 230 (84.2%) third-codon positions being variable, 52 (19.0%) variable first-codon positions and 17 (6.2%) variable second-codon positions. The maximum uncorrected genetic distance computed from the combined mitochondrial data was 16.6% for all sampled taxa, with maximum ML-corrected distances scaling to 47.8%. Maximum genetic distances computed for taxa restricted to different archipelagos are reported in Table 3. A scatter plot of pairwise uncorrected genetic distance against pairwise ML-corrected distance indicated evidence of sequence saturation beyond an uncorrected distance of 10%, corresponding to ML-corrected distances of *c*. 15% (data not shown). Accordingly, lack of resolution of relationships among taxa exhibiting an ML-corrected distance greater than 15% may be due to substitutional saturation overwhelming the phylogenetic signal.

Phylogenetic analyses

The concatenated *16S-ND1* and *COI* fragments resulted in a character matrix 1381 bp in length containing 544 variable characters, 447 of which were parsimony informative. Parsimony tree searches of the combined data resulted in 14 equally parsimonious trees (MPTs), each being 2302 steps long [consistency index (CI) = 0.348, retention index (RI) = 0.556, rescaled consistency index (RC) = 0.194]. A strict consensus of the 14 MPTs (Fig. 3) found strong support for monophyly of *M. rapaensis* from the four Austral Islands

Table 3 Maximum pairwise genetic distance (%) estimated for different archipelagos and all sampled taxa and maximal ages of each archipelago

	Genetic distance		
	Uncorrected	ML distance	Maximal ages (Myr)*
Austral Islands	8.4	11.3	15.7
Society Islands	7.2	10.1	7.2
Marquesas	7.3	10.4	6.1
Hawaiian Islands†	8.9	14.0	30–34
All taxa	16.6	47.8	–

*Dates represent the earliest age at which islands within each archipelago were available for colonization, obtained from Clague & Dalrymple (1987), Keating (1987), Craig *et al.* (2001) and Duncan & McDougall (1974, 1976).

†Maximal pairwise distance for Hawaiian Islands is same whether or not *M. anguliventris* (which does not appear in clade with all other sampled Hawaiian taxa) is included.
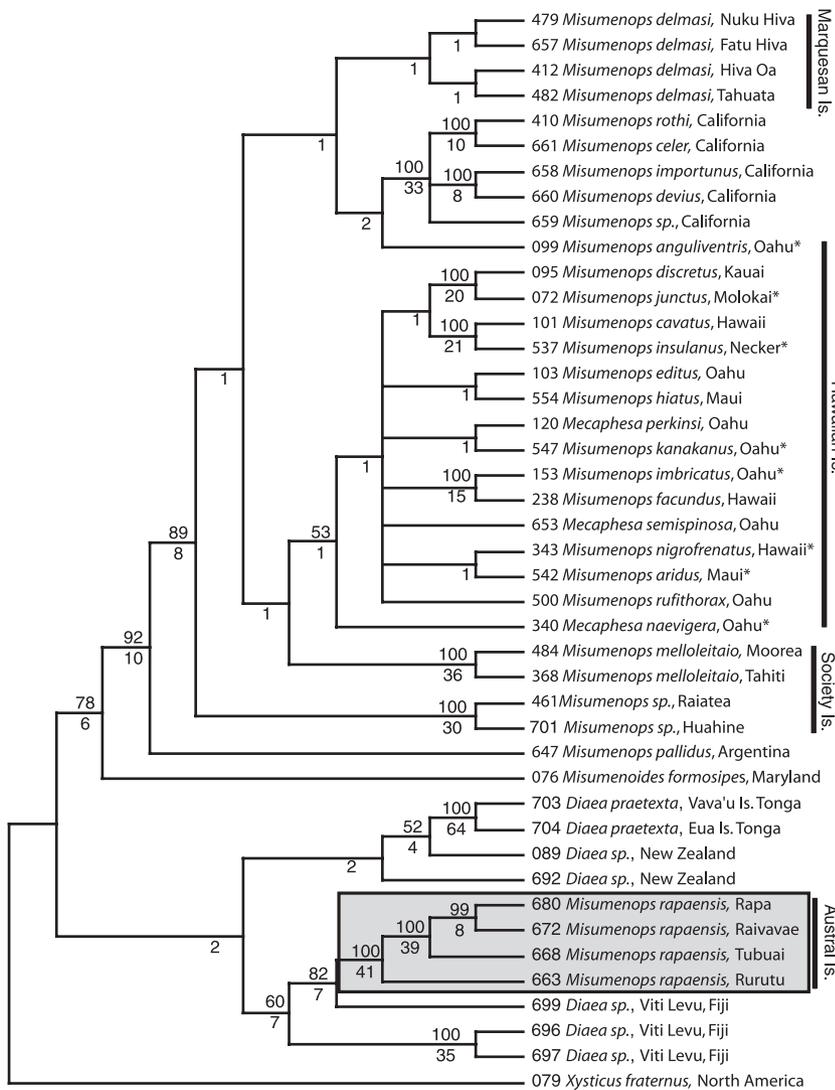
Figure 3 Strict consensus of 14 equally parsimonious trees retained from a parsimony search of combined mtDNA (1381 bp). Numbers above the branches refer to bootstrap support values from 1000 replicates. Numbers below the branches refer to decay index value. *Misumenops rapaensis* is outlined in the grey box; asterisks after Hawaiian taxa indicate species distributed on additional Hawaiian Islands (listed in Table 2).

(BS = 100, DI = 41). Instead of grouping with other sampled Polynesian *Misumenops* species, *M. rapaensis* was nested within a clade composed of other sampled *Diaea*, appearing most closely related to one Fijian specimen (BS = 82, DI = 7). In addition, the parsimony consensus united the following groups into one supported clade (BS = 92, DI = 10): all Hawaiian species (both *Misumenops* and *Mecaphesa*), the Marquesan and Society Island *Misumenops*, and North and South American *Misumenops*. Within this clade, the Hawaiian species, together with the Marquesan and Society Island and North American *Misumenops* are most closely related (BS = 89, DI = 8), and the Argentine *Misumenops pallidus* appears as sister to this group. North American *Misumenops* were monophyletic (BS = 100, DI = 33) and nested within this clade. The Marquesan *Misumenops delmasi* was united across four sampled islands, and the Society Islands' *Misumenops* were not monophyletic, instead appearing as two distinct lineages corresponding to the northern (Raiatea and Huahine) and southern (Moorea and Tahiti) island groups. Hawaiian *Mecaphesa* appeared as multiple lineages within a large

Hawaiian radiation including 12 of the 13 sampled Hawaiian *Misumenops*. The Hawaiian taxa were not monophyletic, as *Misumenops anguliventris* (Simon, 1900) appears more closely related to the North American *Misumenops*. However, relationships among the Hawaiian, Marquesan, Society Islands and North American *Misumenops* were poorly supported.

Based on the combined DNA data, MODELTEST selected the general time reversible model assuming a portion of invariable sites (I) following a gamma (Γ) distribution of rates (GTR+I+$\bar{\Gamma}$) (Rodriguez *et al.*, 1990; Yang *et al.*, 1994), with estimated parameters as follows: estimated base frequencies (A = 0.3367, C = 0.0919, G = 0.1041, T = 0.4673), rate parameter estimates ([A<>C] = 0.8876; [A<>G] = 26.3628; [A<>T] = 3.0079; [C<>G] = 4.1359; [C<>T] = 16.6406; [G<>T] = 1.0), proportion of invariable sites (I = 0.5302), and Γ shape parameter (α = 0.7119). Heuristic ML tree searches retained one likelihood tree (− ln L = 12099.34), presented in Fig. 4. Major topological features appearing in the parsimony consensus tree are found in the ML tree topology. Specifically, *M. rapaensis* was
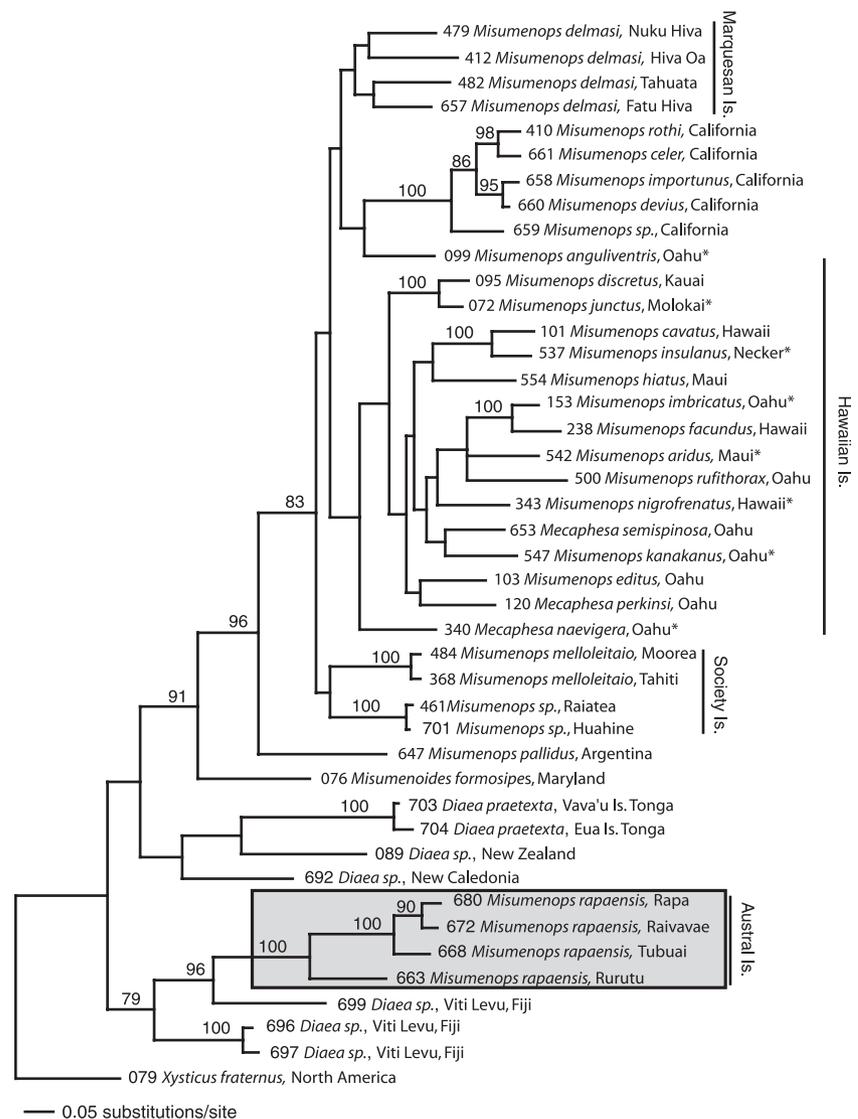
Figure 4 Phylogram of retained ML trees based on mtDNA (1381 bp). Numbers above branches indicate ML bootstrap replicate values from 100 replicates. Grey box and asterisks as in Fig. 3.

strongly supported as monophyletic (BS = 100), appearing more closely related to Polynesian and Melanesian *Diaea* than to other Polynesian *Misumenops*. The ML tree contained a clade composed of all sampled Hawaiian, Marquesan and Society Island taxa in addition to the North American *Misumenops* (BS = 83). Within this clade, thomisids from the Marquesas and the Society Islands form monophyletic groups restricted to either archipelago. However, bootstrap resampling did not support these groupings. As in the MPTs, the Hawaiian taxa were not monophyletic, with *M. anguliventris* appearing more closely related to the North American *Misumenops*. Three independent Bayesian tree searches of the *16S-ND1 + COI* data set each reached stationarity well before 500,000 generations, with MCMC chains converging on narrow ranges of log likelihood values (from − ln *L* 12188.515 to 12134.526). Thus, the first 500 sampled trees were discarded as the 'burn-in'. Consensus trees computed for the remaining 2501 trees (for each run) were identical in topology and resulted in similar clade

posterior probability (PP) values. The topology of the Bayesian consensus tree (Fig. 5) is very similar to the trees resulting from the parsimony and ML analyses in that nearly all nodes strongly supported in the Bayesian tree (PP ≥ 0.90) are also recovered in the parsimony and ML trees. Similar to the ML tree, the Bayesian consensus also supported monophyly of the Society Islands' *Misumenops*.

Tree searches conducted with the additional *COI* sequences obtained from *M. rapaensis* excluded distantly related taxa such that these analyses were limited to specimens of *M. rapaensis* and the sampled Fijian *Diaea* spp. These analyses also excluded the first 82 bp (of the 820 bp *COI* fragment used in combined analyses above), because of missing data occurring in extreme 5′ section of these additional sequences. The resulting character matrix consisted of 738 bp, including 171 variable characters, 134 of which were parsimony informative. Heuristic parsimony searches yielded 36 MPTs 294 steps in length (CI = 0.721, RI = 0.859, RC = 0.619). A strict consensus of all MPTs retained appears in Fig. 6a. The consensus
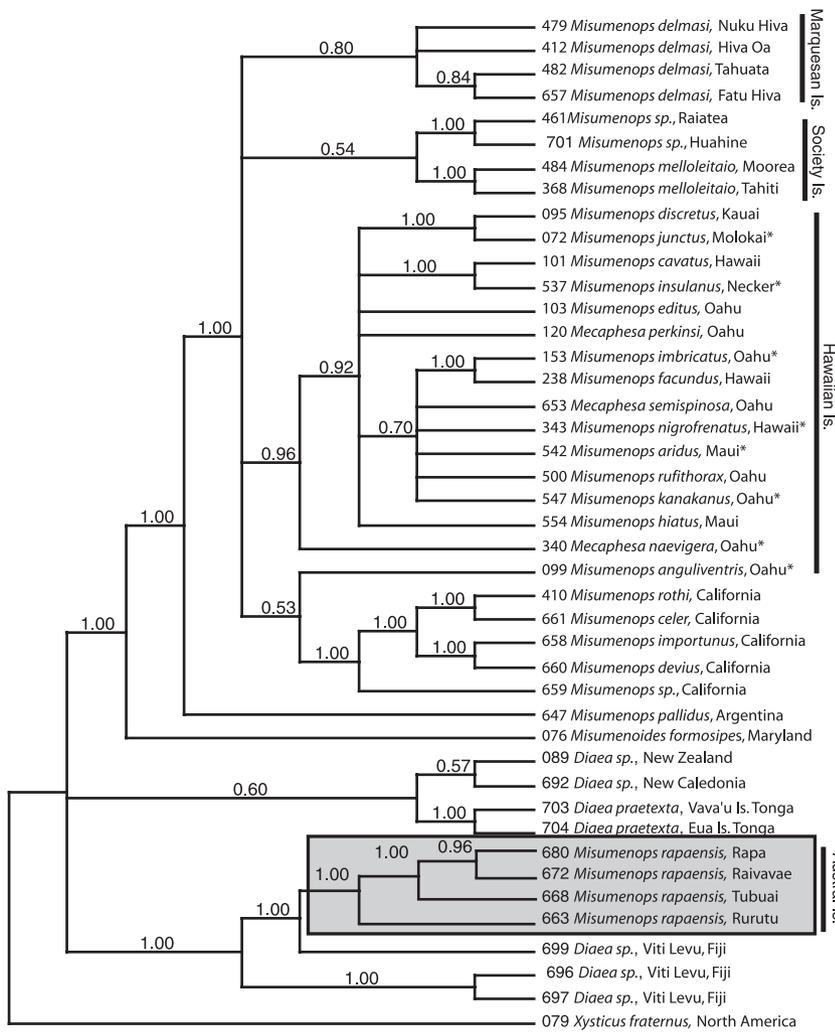
Figure 5 Post-burn-in consensus of trees sampled by Bayesian analysis of mtDNA, with clade posterior probability values indicated above branches. Grey box and asterisks as in Fig. 3.

tree shows all sampled populations of *M. rapaensis* as a strongly supported monophyletic group (BS = 100, DI = 21). Specimens collected from the islands of Rurutu and Tubuai were monophyletic in each of these islands, with these two clades being strongly supported (Rurutu: BS = 100, DI = 11; Tubuai: BS = 99, DI = 8). However, specimens collected from the islands Raivavae and Rapa were paraphyletic with respect to each other. Raivavae and Rapa are the two youngest islands, and together, haplotypes sampled from these two islands (Raivavae and Rapa) formed a well-supported clade (BS = 97, DI = 6). The clade corresponding to haplotypes sampled from Tubuai, the next oldest island, was sister to the Raivavae + Rapa clade. This group [Tubuai (Raivavae + Rapa)] was most closely related to the clade corresponding to the oldest included island, Rurutu.

For the *COI* data set, MODELTEST selected the TVM+I+Γ model of nucleotide substitution [TVM = transversion model], with estimated parameters as follows: estimated base frequencies (A = 0.28, C = 0.12, G = 0.16, T = 0.44), rate parameter estimates ([A<>C] = 1.70; [A<>G] & [C<>T] = 31.69; [A<>T] =4.59; [C<>G] = 2.73; [G<>T] = 1.00), proportion

of invariable sites (I = 0.60), and Γ shape parameter (α = 0.56). Heuristic ML tree searches retained two trees identical in likelihood score ($-\ln L$ = 2513.90). These two trees only differed in the arrangement of haplotypes sampled from Raivavae and Rapa that were nearly identical in sequence. One of the two ML trees is presented in Fig. 6b. Again, *M. rapaensis* was monophyletic (BS = 93) and relationships among *M. rapaensis* from the different islands agreed with relationships presented in the parsimony consensus tree. Bayesian analyses of the *COI* data set were conducted using the GTR+I+Γ model of nucleotide substitution (six substitution rates) rather than the TVM+I+Γ model (five rates) selected by MODELTEST, as the TVM+I+Γ model cannot be implemented in MR. BAYES 3.0. The three runs reached stationarity well before 500,000 generations, and for each run consensus trees were generating from the remaining 2501 trees. The three Bayesian consensus trees were topologically identical to each other and were nearly identical to the parsimony and ML trees (Fig. 6a,b), the only difference being the placement of one individual from Raivavae (675) amongst two others from Raivavae and Rapa (see Fig. 6a).
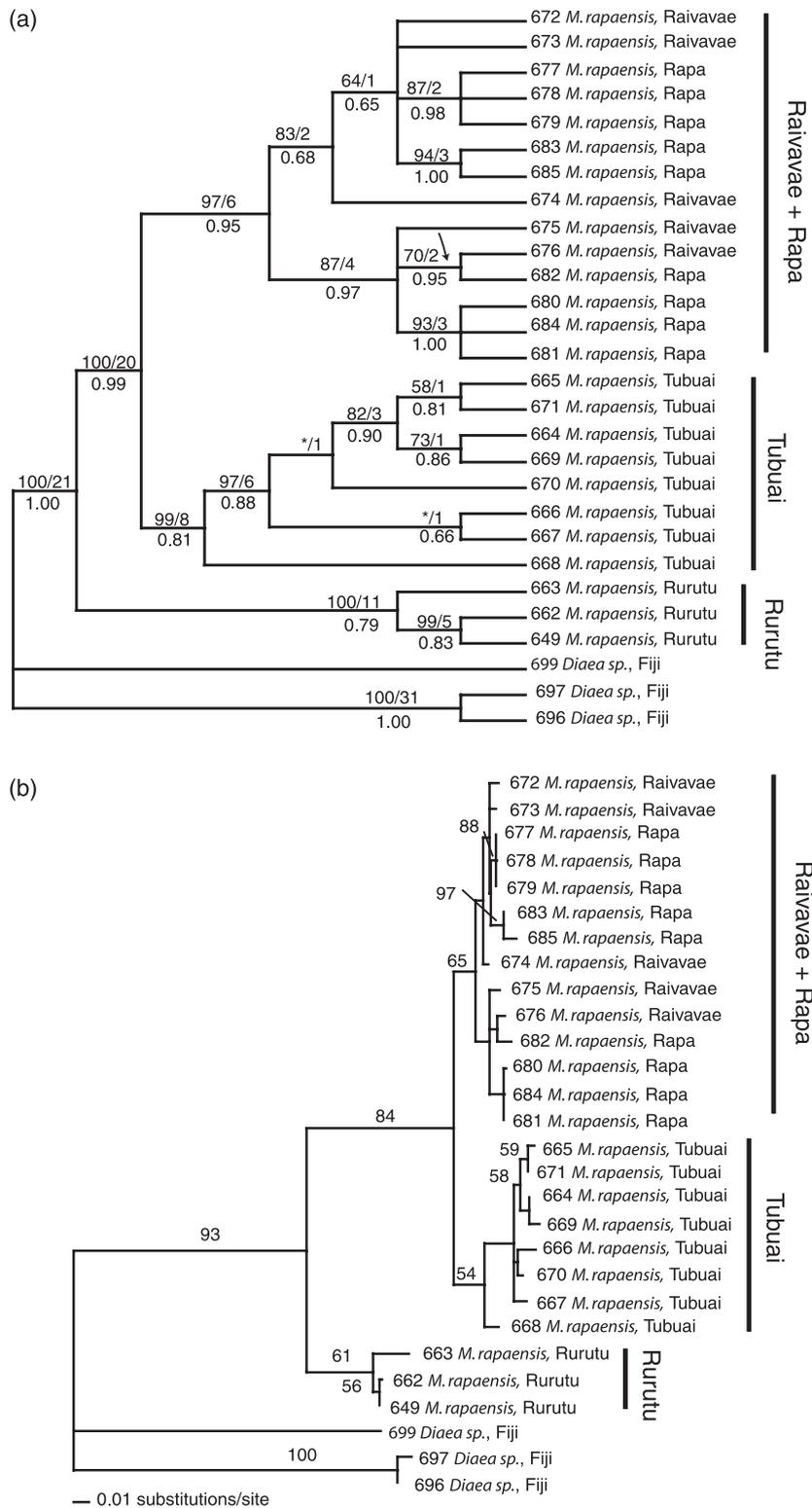
Figure 6 (a) Strict consensus of 36 equal length trees retained from a parsimony tree search based on additional *COI* data (738 bp). Numbers above branches on the left refer to parsimony bootstrap values from 1000 replicates (asterisks indicate < 50% bootstrap support). Numbers to the right of parsimony bootstrap values refer to decay indices. Numbers below the branch indicated clade posterior probability values. Arrow indicates a topological difference in the Bayesian consensus tree (675 is sister to 676 + 682, PP = 0.54). (b) Phylogram of one of two retained ML trees from analysis of *COI* data, numbers above branches refer to bootstrap values from 100 replicates.

DISCUSSION

Austral Islands' *Misumenops rapaensis*: intra-archipelago relationships

To date, the widespread distribution of *M. rapaensis* across the Austral Islands has not been satisfactorily explained. Berland (1942) concluded that across the different islands on which it occurs, *M. rapaensis* represented a single morphologically uniform species. However, our results indicate that between some islands of the archipelago populations of *M. rapaensis* are genetically quite distinct. Individuals collected from Rurutu and Tubuai formed well-supported monophyletic groups corresponding to each of these islands, while individuals from Raivavae and Rapa together comprised another separate monophyletic group. Moreover, the maximal ML-corrected genetic distance within *M. rapaensis* of the combined mitochondrial DNA (mtDNA) was as much as 11.3% (between individuals from Rurutu and Tubuai; Table 3). For the mitochondrial *COI* data alone, maximal uncorrected genetic distance across *M. rapaensis* was 8.9% (ML-corrected distance = 17.2%). Thus, across the Austral archipelago, *M. rapaensis* appears to consist of multiple genetically distinct lineages.

Ledoux & Halle (1995) suggested that the widespread distribution of *M. rapaensis* across the Austral Islands might imply the occurrence of occasional inter-island migration. Considering the substantial genetic distance exhibited between the specimens sampled from Rurutu and Tubuai, the occurrence of inter-island gene flow between these two islands seems unlikely. Successful colonization of isolated oceanic islands is an improbable event, even for particularly dispersive taxa, a view reinforced by the prevalence of endemic species restricted to single islands (Paulay, 1994). Consequently, the substantial genetic distances observed between Rurutu and Tubuai is not entirely unexpected in the light of the oceanic distance that separates these two islands (*c.* 250 km). Though based on a small number of individuals sampled from each island, the reciprocal monophyly of individuals sampled from Rurutu and from Tubuai within the phylogeny (Fig. 6a,b) suggests that the lineages restricted to either of these two islands descended from a single colonization event. Scaling the level of genetic distance exhibited between these two islands to Brower's (1994) rate of arthropod mitochondrial pairwise sequence divergence (2.3% Myr^{-1}) would suggest that the lineages restricted to Rurutu and Tubuai diverged roughly between 4.9 and 7.5 Ma.

In contrast to the oldest islands of Rurutu and Tubuai, the younger two islands, Raivavae and Rapa, exhibited much less genetic differentiation. Moreover, specimens sampled from these two younger islands, while together forming a monophyletic group, were paraphyletic with certain haplotypes distributed on Rapa being more closely related to those occurring on Raivavae. Paraphyly of Raivavae and Rapa implies the possibility of occasional gene flow between these two islands. However, the occurrence of inter-island gene flow between these two islands would be particularly surprising

given that they represent the two that are separated by the greatest distance (*c.* 500 km, roughly twice that between Rurutu and Tubuai). Paraphyly of these two islands may alternatively be explained as a consequence of incomplete lineage sorting following a recent colonization from Raivavae to Rapa, if the amount of time elapsed since colonization is insufficient for fixation of retained polymorphisms (Pamilo & Nei, 1988; Moore, 1995; Maddison, 1997).

Despite their reciprocal monophyly, *M. rapaensis* from the islands of Tubuai and from Raivavae + Rapa are much more genetically similar to each other than either group is to *M. rapaensis* from Rurutu (maximum *COI* divergence across Tubuai, Raivavae and Rapa ranges from 5.8% (corrected) to 8.8% (ML-corrected)). Thus, the split between the Tubuai clade and the clade comprising individuals from Raivavae and Rapa occurred more recently (*c.* 2.5–3.8 Ma) than the rough approximation of 4.9–7.5 Ma estimated for the divergence of *M. rapaensis* from Rurutu and Tubuai. It therefore appears that *M. rapaensis* initially colonized the Austral Archipelago several million years subsequent to the formation of Rurutu (12.68 Ma) and Tubuai (10.40 Ma) but possibly before the emergence of Raivavae (6.76 Ma) and Rapa (5.02 Ma). The estimated genetic divergence between individuals from Tubuai, Raivavae and Rapa further suggests that from the initial point of colonization (probably Rurutu or Tubuai), *M. rapaensis* did not reach Raivavae or Rapa until the emergence of both islands.

In light of the high genetic divergence between *M. rapaensis* from Rurutu and other island populations, Berland's (1942) description of *M. rapaensis* as a morphologically uniform species needs to be re-evaluated. For example, sister species of *Orsonwelles* spiders endemic to Hawaiian island of Kauai exhibit conspicuous differences in genitalic and somatic morphology, though having diverged as recently as 0.72 Ma (Hormiga, 2002; Hormiga *et al.*, 2003). An absence of morphological divergence across *M. rapaensis*, if indeed populations from Rurutu and Tubuai split between 4.9 and 7.5 Ma, would by comparison seem remarkable. Although Berland (1942) based his conclusion of morphological uniformity on examination of *M. rapaensis* from all four islands, he was only able to examine a single male from Raivavae, only females from Tubuai and a single juvenile from Rurutu. Ledoux & Halle (1995), in revising the species, only examined materials from Rapa. However, Ledoux & Halle (1995) did report a large variation in female body size (8.0–15.5 mm) from these specimens. Specimens of *M. rapaensis* examined in this study appeared to be morphologically similar and were consistent with the species descriptions of both Berland (1934, 1942) and Ledoux & Halle (1995). Nevertheless, we cannot at present rule out that there may be some morphological differences between genetically divergent island populations of *M. rapaensis*. Spider taxonomists most frequently rely on differences in genitalic morphology to recognize species, because for spiders genitalia appear to evolve rapidly (Huber, 2004) and for many closely related spider species reliable diagnostic features are only

provided by genitalic morphology (Hormiga *et al.*, 2003). Thus, observable differences in genitalic morphology might be expected between the most genetically divergent island populations of *M. rapaensis* (i.e. between Rurutu and all other island populations). Because males of *M. rapaensis* from Rurutu have not yet been described and we were unable to obtain males from this island for this study, additional collections may be necessary to rigorously assess the extent of morphological divergence of *M. rapaensis* across the Austral Islands.

Sequential colonization of islands

The progression rule – a pattern of lineage formation reflecting successive colonization of islands in order of their formation (Wagner & Funk, 1995) – has been illustrated by phylogenetic hypotheses of some Hawaiian taxa (e.g., Shaw, 1996; Hormiga *et al.*, 2003), and is also exhibited by taxa occurring in other hot-spot archipelagos such as the Galapagos (Sequeira *et al.*, 2000) and Canary Islands (Juan *et al.*, 1995, 2000). Colonization in the direction of younger islands is generally explained as a consequence of the increased success of establishment on younger islands where ecological opportunity is likely to be more readily available (Gillespie & Roderick, 2002). As illustrated in Fig. 2(inset), when applied to the Austral Archipelago for islands considered in this study, the progression rule would predict a pattern of phylogenetic relationships indicating the colonization of islands occurring in the following order: Rurutu, Tubuai, Raivavae then Rapa. A topology of the phylogenetic pattern consistent with this prediction is (Rurutu (Tubuai (Raivavae))), with older islands appearing in successively more basal positions relative to younger islands.

The topology for *M. rapaensis* across the Austral Islands (e.g. Fig. 6b) implies an area cladogram consistent with 10 equally parsimonious colonization patterns, including strict sequential colonization from older to younger islands, progressively dispersing from west to east. However, optimization of ancestral states onto the area cladogram, illustrating the various colonization scenarios (Fig. 7), indicates an ambiguity at the basal ingroup node. Specifically, the area cladogram cannot resolve whether the initial point of colonization was Rurutu, Tubuai or Raivavae. Unambiguous optimization of Rurutu, the oldest and westernmost island, at the basal node would require a doublet, or two successive lineages from Rurutu, at the base of the phylogeny. Thus, because the sampled individuals from Rurutu were monophyletic, a strict cladistic interpretation of the mitochondrial *COI* tree cannot rule out initial colonization of *M. rapaensis* to Tubuai or Raivavae instead of Rurutu. Nevertheless, the limited genetic divergence exhibited by the populations restricted to Tubuai, Raivavae and Rapa corroborates a recent colonization of Raivavae from Tubuai. The area cladogram also unambiguously implies that Rapa, the youngest and easternmost island, was colonized by *M. rapaensis* last. Taken together, the evidence suggests *M. rapaensis* initially colonized either Rurutu or Tubuai, and then from Tubuai colonized Raivavae and then Rapa.

It should be noted that the presented phylogenies, and the conclusions drawn from them, should be considered with a degree of caution as they were derived solely from mtDNA. Because mitochondrial genomes are inherited as a single unit, phylogenies generated from mitochondrial sequences alone essentially represent a single line of evidence for historical relationships. Moreover, because the mitochondrion is strictly maternally inherited, phylogenies based on mtDNA are limiting in that they can only reflect matrilineal history (Avise, 2000). For this reason, if inter-island colonization occurred frequently by males of *M. rapaensis*, but not by females, such events would not be recovered in our mitochondrial phylogenies. Analyses of nuclear DNA sequences may therefore be required for comprehensive inference of colonization patterns, as they may differ from those obtained from mitochondrial data alone (e.g. see Shaw, 2002).
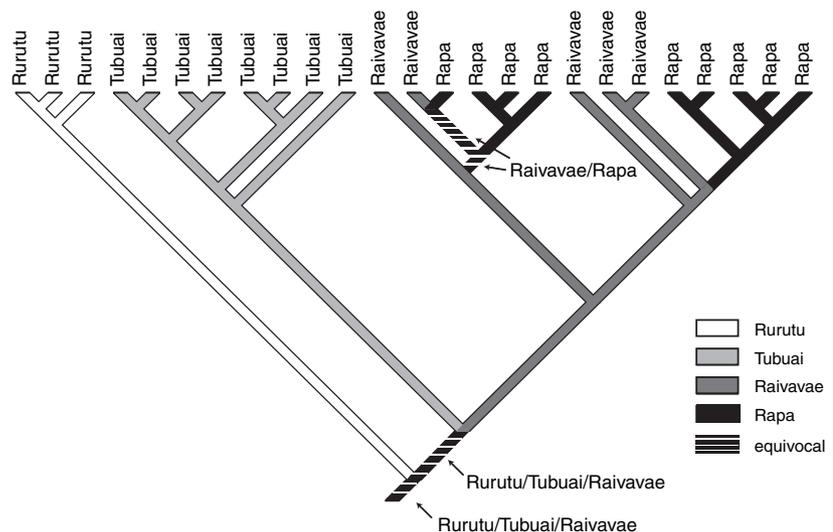
Figure 7 Area cladogram for *Misumenops rapaensis* depicting alternative colonization scenarios (using topology of Fig. 6b). Striped branches indicate equivocal states between islands, labelled with alternative optimizations.

Multiple origins of Polynesian Thomisidae

A prevailing view concerning the biogeographical origins of Polynesian biota is that the vast majority of taxa have colonized remote islands of the Central Pacific from Australasia using intermediate islands as stepping stones (Gressitt, 1956; Miller, 1996). Based on morphological studies, Lehtinen (1993) argued that thomisid spiders colonized the Central Pacific from two opposing directions, one being from the New World, giving rise to the *Misumenops* and *Mecaphesa* spiders of Hawaii, the Society Islands and the Marquesas, and the other direction being from Melanesia, giving rise to the widespread *Diaea* found in Tonga, Samoa and Fiji. However, Lehtinen (1993) could not determine the biogeographical affinities of *M. rapaensis* from the Austral Islands. In this study we have identified two distinct clades of thomisid spiders occurring across the terrestrial islands of the Central Pacific. Specifically, thomisids found in the Hawaiian, Society and Marquesan archipelagos together form a strongly supported clade with North and South American *Misumenops* while the Austral Islands' thomisids are far more closely related to *Diaea* spp. sampled from western Polynesian and Melanesian islands. Such a result implies that different lineages of thomisid spiders have independently colonized this remote region, possibly from different directions.

Our results are consistent with Lehtinen's (1993) claim that thomisid spiders found in the Hawaiian, Society and Marquesan islands have a New World origin, as taxa from these three archipelagos appear closely related to North and South American *Misumenops* spiders. However, the recovered phylogenies show the North American *Misumenops* nested within a clade containing the Hawaiian, Marquesan and Society Island taxa, and the South American *M. pallidus* placed as sister to this large clade. The nested position of North American *Misumenops* is unexpected because it suggests a possible colonization of North America from eastern Polynesia. Colonization of oceanic islands is usually considered a unidirectional occurrence, although evidence does exist which supports instances of colonization from large islands such as Madagascar to continental Africa (Raxworthy *et al.*, 2002). Nevertheless, the nested position of the North American *Misumenops* in our trees is not well supported and the branch subtending the North American *Misumenops* is long (see Fig. 4). This result, in conjunction with the overall length heterogeneity of terminal branches, may explain the unexpected phylogenetic placement of this group. Given the unsampled diversity of *Misumenops* species known to occur in North and South America, Africa, Europe and Asia, inclusion of additional *Misumenops* species should be pursued as a strategy to break up such long branches and improve resolution between the eastern Polynesian taxa and their continental relatives.

A review of recent phylogenetic studies concerning Hawaiian taxa suggests that a close affinity between thomisid spiders of the eastern Polynesian islands (i.e. the Hawaiian, Society and Marquesan islands) and those of North and South America would not be entirely surprising. For example, the classic exception to the long-assumed western Pacific source for Hawaiian taxa is the silversword alliance (Asteraceae) (Carr, 1987) which is most closely related to the tarweeds of California in North America (Carlquist, 1970), a result confirmed by recent molecular work (Baldwin & Wessa, 2000; Carlquist *et al.*, 2003). Additional molecular studies of different Pacific plant groups indicate that the woody Hawaiian violets (*Viola*, Violaceae) (Ballard & Sytsma, 2000), Hawaiian mints (Lamiaceae) (Lindqvist & Albert, 2002), *Sanicula* (Apiaceae) (Vargas *et al.*, 1998), geraniums (Pax *et al.*, 1997), *Gunnera* (Wanntorp *et al.*, 2002), *Gossypium* (Dejoode & Wendel, 1992) and *Rubus* (Howarth *et al.*, 1997) all originated in the Americas. Moreover, molecular evidence has recently shown that the Hawaiian plant genus *Bidens* is sister to a radiation from the Marquesas, and together this clade is derived from continental America (Ganders *et al.*, 2000). Similarly, *Ilex anomala* (a plant occurring in the Hawaiian and Society islands) is most closely related to American species (Cuénoud *et al.*, 2000). Based on morphological characters, James (2004) found that the Hawaiian honeycreepers fall within the largely American cardueline finches. The nearly extinct radiation of Hawaiian geese is derived from the Canada goose (*Branta canadensis*) (Paxinos *et al.*, 2002). Hawaiian long-jawed spiders in the genus *Tetragnatha* are most closely related to those in the Americas, while those *Tetragnatha* found in the Society and Marquesan islands appear to have arisen from independent sources (Gillespie, 2002). Such examples suggest that although a number of Central Pacific lineages are derived from Australasia, a substantial portion of the biota of the Hawaiian (and possibly the Society and Marquesan) islands comprises lineages originating from the New World. Given the extreme isolation of the Hawaiian Islands, which in fact are almost as close to the nearest continent (North America 4000 km away) as to its nearest island group (Marquesas 3200 km), colonists of the Hawaiian Islands originating from North America may have been as frequent as those originating from island groups to the southwest.

Rather than grouping with other Polynesian *Misumenops*, the Austral Islands' *M. rapaensis* was consistently placed together in a clade with Fijian *Diaea*, with strong support for this grouping. That *M. rapaensis* falls with *Diaea* suggests that this species has been misclassified. This result is not unexpected considering that previous taxonomic treatments cast some doubt on its assignment to the genus *Misumenops*. Berland (1934) originally placed the species in *Misumenops* based on the size of its lateral anterior eyes, but considered *Misumenops* to be poorly defined, and further noted that *M. rapaensis* was remarkably large compared with other *Misumenops* species. Ledoux & Halle (1995), in revising the species, referred to it as '*Misumenops*' *rapaensis*, implying that *M. rapaensis* is not congeneric with the type species of *Misumenops*. However, Ledoux & Halle (1995) left *M. rapaensis* in *Misumenops* because of difficulty in determining its correct generic assignment. Clarification of relationships among the Melanesian and Polynesian *Diaea* will require

greater taxonomic sampling, particularly in areas such as Samoa, the Solomon Islands and Vanuatu where *Diaea* occurs but could not be included in this study (Platnick, 2005). Nevertheless, our results suggest that *M. rapaensis* falls within this group, and colonized the Austral Islands from the west, possibly directly from Fiji. Accordingly, our data provide evidence for Lehtinen's (1993) hypothesis that thomisid spiders colonized the Central Pacific from both east and west.

Narrow distributional boundary: where east meets west?

Phylogenetic analyses of our mitochondrial data set detected a narrow and well-defined distributional boundary separating the two clades of Polynesian thomisid spiders. The well-supported eastern clade comprising the Society Islands, the Marquesas, the Hawaiian Islands and North American *Misumenops*, spans a distance of *c.* 4500 km within the Central Pacific from Tahiti to the northern Hawaiian Islands (see Fig. 8). Abutting the southwestern edge of this distribution, separated by only 500 km of ocean at their closest points (between Tahiti and Rurutu islands), is the western clade (strictly defined as including Fijian *Diaea* and *M. rapaensis*). This western clade is similarly distributed over an expansive distance of ocean (1500 km across the Austral Islands extending 3000 km to Fiji) yet does not extend further east or northward to the Society Islands. Biogeographical relationships both within and between archipelagos contained in either clade suggest that thomisid spiders colonized islands greater than 500 km apart on multiple occasions. Thus it is surprising to find that the eastern and western clades do not overlap. A number of hypotheses could account for this narrow boundary.

Thomisid spiders presumably colonize oceanic islands by ballooning, an aerial dispersal mechanisms whereby air currents loft spiderlings when they produce silk strands (Foelix, 1996). One explanation for the distributional boundary separating the Society and Austral islands may be that past wind currents have been unsuitable for dispersal of thomisid spiders between these two archipelagos. However, the close phylogenetic relationships found between *Metrosideros* plants occurring in both the Austral and Society islands (Wright *et al.*, 2001), and among *Inseliellum* flies of the Austral, Society and Marquesan islands (Craig *et al.*, 2001), implies that past climatic conditions have allowed the establishment of other wind-dispersed taxa between archipelagos found on either side of this boundary. South of the equator, the prevailing southeast trade winds impede movement of aerial plankton from the Marquesan and Society islands to the Austral Islands, but might allow dispersal to the Society Islands from the Austral Islands directly southeast (Fig. 8). Wright *et al.* (2000) proposed that powerful westerly winds in the Southern Hemisphere during periods of maximum glaciation, in association with weakened trade winds, may have increased the range of wind-dispersed organisms eastward throughout the Pacific. Such wind currents would potentially obstruct dispersal of thomisid spiders from the Society Islands to the Australs, but might facilitate colonization events from the Australs to either the Society or Marquesan islands.

If indeed wind-dispersed thomisid spiders could breach the oceanic boundary separating the Austral and Society islands, ecological factors following colonization may instead explain the distributional limits of either clade. For example, the ability of any group to become successfully established in these islands may depend on the order of their arrival, such that the prior establishment (historical precedence) of thomisids in the
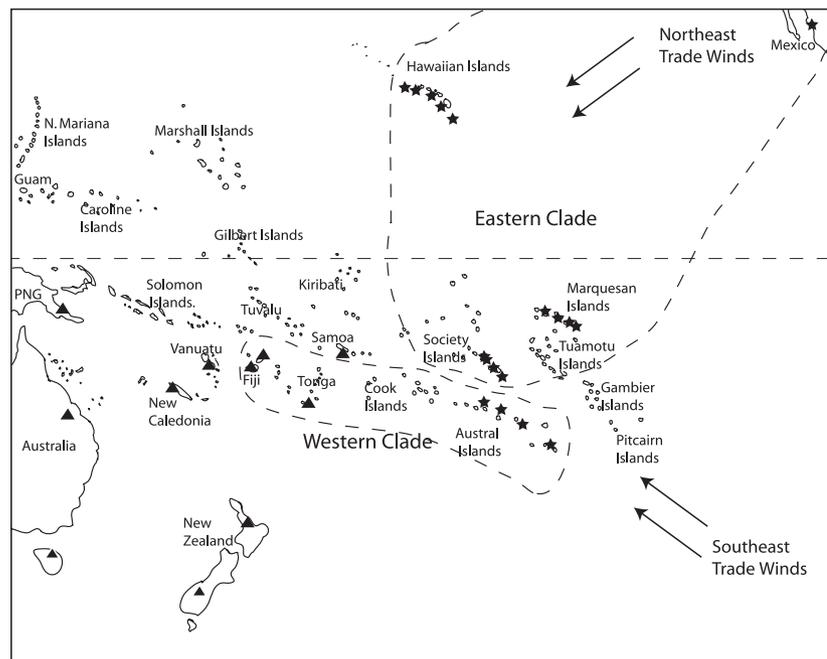
Figure 8 Distribution of eastern and western thomisid spider clades across the Pacific. Symbols indicate the distribution of the genera *Misumenops* (star) and *Diaea* (triangle).

Society Islands may prohibit subsequent establishment of thomisids from the Austral Islands, and vice versa. Historical precedence may explain why colonization generally proceeds in direction of the younger islands within the Hawaiian archipelago (Wagner & Funk, 1995). Rather than wind currents, this pattern is attributed to the increased probability of successful establishment for a species that arrives early in the formation of a biotic community, allowing access to a greater breadth of ecological resources (Gillespie, 2004). Prior establishment is likely to offer biotic resistance (Chapman, 1931; Elton, 1958) from additional colonizing lineages that would utilize similar resources. In the context of distributional limits of other taxa, the current study suggests that the remote oceanic biota of the Pacific comprise lineages arriving from both the east and the west, but that distributional limits across the ocean may be a function of dispersal ability coupled with biotic resistance resulting from historical precedence. It is therefore likely that many taxa that have successfully colonized any of the islands of the Central Pacific have the potential for further colonization, with this potential seldom being realized because of the historical precedence of earlier colonists.

The ages of the Austral Islands generally exceed those of the current high islands of the Hawaiian Archipelago (Kauai, c. 5 Myr), ranging from the youngest island Marotiri at 4.3 Myr to Rimitara at 14.8 Myr (Fig. 2). It should be noted that islands of the Hawaiian chain have been continuously available for colonization for the last 30 Myr (Carson & Clague, 1995). However, geological reconstruction shows that islands formed earlier than Kauai were generally smaller and widely separated, suggesting that colonization from extra-Hawaiian sources largely occurred within the last 5 Myr (Price & Clague, 2002). The Austral Islands have been available for colonization far longer than the Society and Marquesan islands, which are among the geologically youngest within the Pacific, estimated to have initially emerged no earlier than 7 and 6 Ma respectively (Craig et al., 2001). It is thus also possible that the eastern and western clades of thomisid spiders do not currently overlap simply because their ranges have only recently approached proximity (thomisids could not have colonized the Society Islands earlier than 7 Ma) and an insufficient amount of time has elapsed for successful establishment between the Society and Austral islands.

Diversification across archipelagos

The present study offers a rare opportunity to compare levels of genetic divergence and species diversity of a particular taxonomic group across four Polynesian hot-spot archipelagos. Thomisid spiders are particularly diverse in the Hawaiian Islands, with 20 described endemic species in two genera (Platnick, 2005). In addition to being species rich with multiple species typically co-occurring at numerous localities, the Hawaiian species exhibit diversity in somatic and genitalic morphology and are also ecologically diverse. Interspecific variation in the cryptic coloration of several Hawaiian species matches the particular microhabitat type where they are found

(e.g. lichens, mosses and leaves) (Suman, 1970). Indeed, Lehtinen (1993) proposed that all 20 Hawaiian species be considered an adaptive radiation. In contrast to the diverse Hawaiian fauna, a single thomisid species has been described as endemic to each of the Society, Austral and Marquesan archipelagos, although a second morphologically recognizable species occurs in the Society Islands (J. Garb, unpublished data). Our results support a single colonization to each of these three archipelagos. The presented phylogenies further suggest that the total species diversity found within the Hawaiian archipelago evolved following no more than one or two colonization events. The imbalance in species diversity across the four archipelagos might suggest that thomisid spiders colonized the Hawaiian Archipelago far earlier than the Marquesas, Society Islands and Austral Islands. However, our data reveal little more genetic divergence exhibited across 16 Hawaiian species (maximum ML distance = 14.0%) compared with those occurring on the Marquesas (10.4%), Society (10.1%) or Austral islands (11.3%), which in each of these archipelagos represents one or two morphologically recognized species (see Table 3). This result suggests a distinct asymmetry in rates of morphological evolution and species accumulation following colonization of each of these archipelagos, with substantially greater amounts of morphological divergence evolving in the Hawaiian Islands.

Examining features common to the Austral, Society and Marquesan islands, or perhaps some conditions specific to the Hawaiian Archipelago may identify a possible explanation for such asymmetrical diversification across archipelagos. For example, the Hawaiian Archipelago is considered somewhat geologically anomalous relative to other Pacific archipelagos because of the substantially greater amount and persistence of magma genesis occurring at the Hawaiian hot spot, producing much larger islands (Dickinson, 1998). The larger sizes and elevations attained by the Hawaiian Islands result in their exposure to a diversity of climatic regimes, varying in precipitation and temperature, which has led to the formation of greater numbers of ecosystems within the Hawaiian Islands. Moreover, larger islands can contain greater numbers of species and have lower extinction rates (MacArthur & Wilson, 1967; Johnson et al., 2000a). The islands of the Austral, Society and Marquesan archipelagos are far smaller in size than the Hawaiian Islands, with the largest islands in each of these three archipelagos being at least an order of magnitude smaller than the largest of the Hawaiian Islands. Consequently, the smaller sizes of these islands may account for the lack of morphological diversification observed in their thomisid spiders compared with those occurring in the Hawaiian archipelago.

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REFERENCES

Avise, J.C. (2000) *Phylogeography: the history and formation of species.* Harvard University Press, Cambridge, MA.

Baker, R.H. & DeSalle, R. (1997) Multiple sources of character information and the phylogeny of Hawaiian drosophilids. *Systematic Biology*, **46,** 654–673.

Baldwin, B.G. & Sanderson, M.J. (1998) Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proceedings of the National Academy of Sciences of the United States of America*, **95,** 9402–9406.

Baldwin, B.G. & Wessa, B.L. (2000) Origin and relationships of the tarweed-silversword lineage (Compositae-Madiinae). *American Journal of Botany*, **87,** 1890–1908.

Ballard, H.E. & Sytsma, K.J. (2000) Evolution and biogeography of the woody Hawaiian violets (Viola, Violaceae): Arctic origins, herbaceous ancestry and bird dispersal. *Evolution*, **54,** 1521–1532.

Banks, N. (1895) A list of the spiders of Long Island; with descriptions of new species. *Journal of the New York Entomological Society*, **3,** 76–93.

Berland, L. (1934) Araignees de polynesie. *Annales de la Societe Entomologique de France*, **103,** 321–336.

Berland, L. (1942) Polynesian spiders. *Occasional Papers of Bernice P. Bishop Museum*, **17,** 1–24.

Bonneville, A., Le Suave, R., Audin, L., Clouard, V., Dosso, L., Gillot, P., Janney, P., Jordahl, K. & Maamaatuaiahutapu, K. (2002) Arago Seamount: the missing hotspot found in the Austral Islands. *Geology*, **30,** 1023–1026.

Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, **42,** 795–803.

Brower, A.V.Z. (1994) Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceeding of the National Academy of Sciences of the United States of America*, **91,** 6491–6495.

Buckley, T.R., Arensburger, P., Simon, C. & Chambers, G.K. (2002) Combined data, Bayesian phylogenetics, and the origin of the New Zealand cicada genera. *Systematic Biology*, **51,** 4–18.

Burns, K.J., Hackett, S.J. & Klein, N.K. (2002) Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evolution*, **56,** 1240–1252.

Caccone, A., Gibbs, J.P., Ketmaier, V., Suatoni, E. & Powell, J.R. (1999) Origin and evolutionary relationships of giant Galapagos tortoises. *Proceedings of the National Academy of Sciences of the United States of America*, **96,** 13223–13228.

Cambridge, F.O.P. (1900) Arachnida – Araneida and Opiliones. *Biologia Centrali-Americana, Zoology*, **2,** 89–192.

Carlquist, S. (1970) *Hawaii: a natural history: geology, climate, native flora and fauna above the shoreline.* Natural History Press, Garden City, NY.

Carlquist, S., Baldwin, B.G. & Carr, G.D. (2003) *Tarweeds and silverswords: evolution of the Madiinae (Asteraceae).* Missouri Botanical Garden Press, St Louis, MO.

Carr, G.D. (1987) Beggar's ticks and tarweeds: masters of adaptive radiation. *Trends in Ecology and Evolution*, **2,** 192–195.

Carson, H.L. & Clague, D.A. (1995) Geology and biogeography of the Hawaiian Islands. *Hawaiian biogeography: evolution in a hot spot archipelago* (ed. by W. Wagner and V. Funk), pp. 14–29. Smithsonian Institution Press, Washington, DC.

Carson, H.L. & Templeton, A.R. (1984) Genetic revolutions in relation to speciation phenomena the founding of new populations. *Annual Review of Ecology and Systematics*, **15,** 97–132.

Chapman, R.N. (1931) *Animal ecology.* McGraw-Hill, New York.

Chittka, L. (2001) Camouflage of predatory crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae/Hymenoptera: Apidae). *Entomologia Generalis*, **25,** 181–187.

Clague, D.A. & Dalrymple, G.B. (1987) The Hawaiian-Emperor volcanic chain. *Volcanism in Hawaii* (ed. by R.W. Decker, T.L. Wright and P.H. Stauffer), pp. 1–54. U.S. Geological Survey Professional Paper 1350, U.S. Government Printing Office, Washington, DC.

Clarke, J.F.G. (1971) The Lepidoptera of Rapa Island. *Smithsonian Contributions to Zoology*, **56,** 1–282.

Cooke, C.M., Jr (1934) Report of C. Montague Cooke Jr., malacologist and leader, Mangarevan expedition. *Bulletin of the Bernice P. Bishop Museum*, **133,** 36–56.

Craig, D.A., Currie, D.C. & Joy, D.A. (2001) Geographical history of the central-western Pacific black fly subgenus *Inseliellum* (Diptera: Simulium) based on a reconstructed phylogeny of the species, hot spot archipelagos and hydrogeological considerations. *Journal of Biogeography*, **28,** 1101–1127.

Cuénoud, P., Del Pero Martinez, M.A., Loizeau, P.-A., Spichiger, R., Andrews, S. & Manen, J.-F. (2000) Molecular phylogeny and biogeography of the genus *Ilex* L. (Aquifoliaceae). *Annals of Botany*, **85,** 111–122.

DeBry, R.W. & Olmstead, R.G. (2000) A simulation study of reduced tree-search effort in bootstrap resampling analysis. *Systematic Biology*, **49,** 171–179.

Dejoode, D.R. & Wendel, J.F. (1992) Genetic diversity and origin of the Hawaiian Islands cotton, *Gossypium tomentosum*. *American Journal of Botany*, **79,** 1311–1319.

Dickinson, W.R. (1998) Geomorphology and geodynamics of the Cook-Austral Island-Seamount chain in the South Pacific Ocean: implications for hotspots and plumes. *International Geology Review*, **40**, 1039–1075.

Duncan, R.A. & McDougall, I. (1974) Migration of volcanism with time in the Marquesas Islands, French Polynesia. *Earth and Planetary Science Letters*, **21**, 414–420.

Duncan, R.A. & McDougall, I. (1976) Linear volcanism in French Polynesia. *Journal of Volcanology and Geothermal Research*, **1**, 197–227.

Elton, C.S. (1958) *The ecology of invasion by plants and animals*. Chapman & Hall, London.

Felsenstein, J. (1985) Confidence limits on phylogenies an approach using the bootstrap. *Evolution*, **39**, 783–791.

Foelix, R. (1996) *The biology of spiders*, 2nd edn. Oxford University Press, Oxford.

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. *Molecular Marine Biology and Biotechnology*, **3**, 294–299.

Ganders, F.R., Berbee, M. & Pirseyedi, M. (2000) ITS base sequence phylogeny in *Bidens* (Asteraceae): evidence for the continental relatives of Hawaiian and Marquesan *Bidens*. *Systematic Botany*, **25**, 122–133.

Gillespie, R.G. (2002) Biogeography of spiders on remote oceanic islands of the Pacific: archipelagos as stepping stones? *Journal of Biogeography*, **29**, 655–662.

Gillespie, R.G. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science*, **303**, 356–359.

Gillespie, R.G. & Roderick, G.K. (2002) Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology*, **47**, 595–632.

Goodacre, S.L. & Wade, C.M. (2001) Patterns of genetic variation in Pacific island land snails: the distribution of cytochrome b lineages among Society Island *Partula*. *Biological Journal of the Linnean Society*, **73**, 131–138.

Grant, P.R. (1998) *Evolution on islands*. Oxford University Press, Oxford.

Grant, P.R. & Grant, B.R. (1996) Speciation and hybridisation in island birds. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, **351**, 765–772.

Gressitt, J.L. (1956) Some distributions patterns of Pacific island fauna. *Systematic Zoology*, **5**, 11–32.

Hedin, M.C. (1997) Speciational history in a diverse clade of habitat-specialized spiders (Araneae: Nesticidae: *Nesticus*): inferences from geographic-based sampling. *Evolution*, **51**, 1929–1945.

Hedin, M.C. & Maddison, W.P. (2001) A combined molecular approach to phylogeny of the jumping spider subfamily Dendryphantinae (Araneae: Salticidae). *Molecular Phylogenetics and Evolution*, **18**, 386–403.

Heiling, A.M., Heberstein, M.E. & Chittka, L. (2003) Crab spiders manipulate flower signals. *Nature*, **421**, 334.

Hormiga, G. (2002) *Orsonwelles*, a new genus of giant linyphiid spiders (Araneae) from the Hawaiian Islands. *Invertebrate Systematics*, **15**, 369–448.

Hormiga, G., Arnedo, M. & Gillespie, R.G. (2003) Speciation on a conveyor belt: sequential colonization of the Hawaiian Islands by *Orsonwelles* spiders (Araneae, Linyphiidae). *Systematic Biology*, **52**, 70–88.

Howarth, D.G., Gardner, D.E. & Morden, C.W. (1997) Phylogeny of *Rubus* subgenus *Idaeobatus* (Rosaceae) and its implication toward colonization of the Hawaiian Islands. *Systematic Botany*, **22**, 433–441.

Huber, B.A. (2004) The significance of copulatory structures in spider systematics. *Studien zur Theorie der Biologie, Band 5, Biosemiotik- Praktische Anwendung und Konsequenzen für die Einzeldisziplinen* (ed. by J. Schult), pp. 89–100. Verlag für Wissenschaft und Bildung, Berlin.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

James, H.F. (2004) The osteology and phylogeny of the Hawaiian finch radiation (Fringillidae: Drepanidini), including extinct taxa. *Zoological Journal of the Linnean Society*, **141**, 207–255.

Johnson, K.P., Adler, F.R. & Cherry, J.L. (2000a) Genetic and phylogenetic consequences of island biogeography. *Evolution*, **54**, 387–396.

Johnson, M.S., Murray, J. & Clarke, B. (2000b) Parallel evolution in Marquesan partulid land snails. *Biological Journal of the Linnean Society*, **69**, 577–598.

Jordan, S., Simon, C. & Polhemus, D. (2003) Molecular systematics and adaptive radiation of Hawaii's endemic damselfly genus *Megalagrion* (Odonata: Coenagrionidae). *Systematic Biology*, **52**, 89–109.

Joy, D.A. & Conn, J.E. (2001) Molecular and morphological phylogenetic analysis of an insular radiation in Pacific black flies (Simulium). *Systematic Biology*, **50**, 18–38.

Juan, C., Oromi, P. & Hewitt, G.M. (1995) Mitochondrial DNA phylogeny and sequential colonization of Canary Islands by darkling beetles of the genus *Pimelia* (Tenebrionidae). *Proceedings of the Royal Society of London Series B, Biological Sciences*, **261**, 173–180.

Juan, C., Emerson, B.C., Oromi, P. & Hewitt, G.M. (2000) Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends in Ecology and Evolution*, **15**, 104–109.

Keast, A. (1996) Pacific biogeography: patterns and processes. *The origin and evolution of Pacific Island biotas, New Guinea to eastern Polynesia: patterns and processes* (ed. by A. Keast and S.E. Miller), pp. 477–512. SPB Academic Publishing, Amsterdam.

Keating, B. (1987) Summary of radiometric ages from the Pacific. *Intergovernmental Oceanographic Commission, Technical Series, UNESCO*, **32**, 1–67.

Ledoux, J.-C. & Halle, N. (1995) Araignees de l'ile Rapa (iles Australes, Polynesie). *Revue Arachnologique*, **11**, 1–15.

Lehtinen, P.T. (1993) Polynesian Thomisidae – a meeting of old and new world groups. *Memoirs of the Queensland Museum*, **33,** 585–591.

Lindqvist, C. & Albert, V.A. (2002) Origin of the Hawaiian endemic mints within North American *Stachys* (Lamiaceae). *American Journal of Botany*, **89,** 1709–1724.

Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. & Rodrigues-Schettino, L. (1998) Contigency and determinism in replicated adaptive radiations of island lizards. *Science*, **279,** 2115–2118.

MacArthur, R. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Maddison, W.P. (1997) Gene trees in species trees. *Systematic Biology*, **46,** 523–536.

Miller, S.E. (1996) Biogeography of Pacific insects and other terrestrial invertebrates: a status report. *The origin and evolution of Pacific Island biotas, New Guinea to eastern Polynesia: patterns and processes* (ed. by A. Keast and S.E. Miller), pp. 463–475. SPB Academic Publishing, Amsterdam.

Mitchell, A.D. & Heenan, P.B. (2002) *Sophora* sect. Edwardsia (Fabaceae): further evidence from nrDNA sequence data of a recent and rapid radiation around the Southern Oceans. *Botanical Journal of the Linnean Society*, **140,** 435–441.

Moore, W.S. (1995) Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. *Evolution*, **49,** 718–726.

Munschy, M., Antoine, C., Guille, G. & Guillou, H. (1998) La croute oceanique et les points chauds de la Polynesie Francaise (Ocean Pacific Central). *Geologie de la France*, **3,** 5–13.

Ono, H. (1988) *A revisional study of the spider family Thomisidae of Japan*. National Science Museum, Tokyo.

Palumbi, S.R., Martin, A., Romano, S., McMillian, W.O., Stice, L. & Grabowski, G. (1991) *The simple fool's guide to PCR, Special Publication*. Department of Zoology, University of Hawaii, Honolulu, HI.

Pamilo, P. & Nei, M. (1988) Relationships between gene trees and species trees. *Molecular Biology and Evolution*, **5,** 568–583.

Paulay, G. (1985) Adaptive radiation on an isolated oceanic island: the Cryptorhynchinae Curculionidae of Rapa revisited. *Biological Journal of the Linnean Society*, **26,** 95–188.

Paulay, G. (1994) Biodiversity on oceanic islands: its origin and extinction. *American Zoologist*, **34,** 134–144.

Pax, D.L., Price, R.A. & Michaels, H.J. (1997) Phylogenetic position of the Hawaiian geraniums based on rbcL sequences. *American Journal of Botany*, **84,** 72–78.

Paxinos, E., James, H.F., Olson, S.L., Sorenson, M.D., Jackson, J. & Fleischer, R.C. (2002) mtDNA from fossils reveals a radiation of Hawaiian geese recently derived from the Canada goose (*Branta canadensis*). *Proceedings of the National Academy of Sciences of the United States of America*, **99,** 1399–1404.

Platnick, N.I. (2005) *The world spider catalog, version 3.5. Pages American Museum of Natural History* [WWW document].

URL http://research.amnh.org/entomology/spiders/catalog81-87/index.html [accessed on 5 November 2005].

Posada, D. & Crandall, K.A. (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14,** 817–818.

Price, J.P. & Clague, D.A. (2002) How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **269,** 2429–2435.

Raxworthy, C.J., Forstner, M.R.J. & Nussbaum, R.A. (2002) Chameleon radiation by oceanic dispersal. *Nature*, **415,** 784–787.

Rodriguez, F., Oliver, J.L., Marin, A. & Medina, J.R. (1990) The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology*, **142,** 458–501.

Sequeira, A.S., Lanteri, A.A., Scataglini, M.A., Confalonieri, V.A. & Farrell, B.D. (2000) Are flightless *Galapaganus* weevils older than the Galapagos Islands they inhabit? *Heredity*, **85,** 20–29.

Shaw, K.L. (1996) Sequential radiations and patterns of speciation in the Hawaiian cricket genus *Laupala* inferred from DNA sequences. *Evolution*, **50,** 237–255.

Shaw, K.L. (2002) Conflict between nuclear and mitochondrial DNA phylogenies of a recent species radiation: what mtDNA reveals and conceals about modes of speciation in Hawaiian crickets. *Proceedings of the National Academy of Sciences of the United States of America*, **99,** 16122–16127.

Simberloff, D.S. & Wilson, E.O. (1969) Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, **50,** 278–296.

Simon, E. (1900) Arachnida. *Fauna Hawaiiensis, or the zoology of the Sandwich Isles: being results of the explorations instituted by the Royal Society of London promoting natural knowledge and the British Association for the Advancement of Science, London*, **2,** 443–519.

Simon, C. (1987) Hawaiian evolutionary biology: an introduction. *Trends in Ecology and Evolution*, **2,** 175–178.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, **87,** 651–701.

Sorenson, M.D. (1999) *TreeRot*, Ver. 2. Boston University, Boston, MA.

Suman, T.W. (1970) Spiders of the family Thomisidae in Hawaii. *Pacific Insects*, **12,** 773–864.

Sundevall, J.C. (1833) *Conspectus Arachnidum*. Londini Gothorum, Lund.

Swofford, D.L. (2002) *PAUP*. Phylogenetic analysis using parsimony (*and other methods)*. Sinauer Associates, Sunderland, MA.

Thorell, T. (1869) On European spiders. Review of the European genera of spiders, preceded by some observations on zoological nomenclature. *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, **7,** 1–108.

Trewick, S.A. & Wallis, G.P. (2001) Bridging the 'beech-gap': New Zealand invertebrate phylogeography implicates Pleistocene glaciation and Pliocene isolation. *Evolution*, **55**, 2170–2180.

Vargas, P., Baldwin, B.G. & Constance, L. (1998) Nuclear ribosomal DNA evidence for a western North American origin of Hawaiian and South American species of *Sanicula* (Apiaceae). *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 235–240.

Wagner, W.L. & Funk, V.A. (eds) (1995) *Hawaiian biogeography: evolution on a hot spot archipelago*. Smithsonian Institution Press, Washington, DC.

Wanntorp, L., Wanntorp, H.-E. & Kaellersjoe, M. (2002) Phylogenetic relationships of *Gunnera* based on nuclear ribosomal DNA ITS region, rbcL and rps16 intron sequences. *Systematic Botany*, **27**, 512–521.

Wilson, J.T. (1963) A possible origin of the Hawaiian Islands. *Canadian Journal of Physics*, **41**, 863–870.

Wright, S.D., Yong, C.G., Dawson, J.W., Whittaker, D.J. & Gardner, R.C. (2000) Riding the ice age El Nino? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 4118–4123.

Wright, S.D., Yong, C.G., Wichman, S.R., Dawson, J.W. & Gardner, R.C. (2001) Stepping stones to Hawaii: a trans-equatorial dispersal pathway for *Metrosideros* (Myrtaceae) inferred from nrDNA (ITS + ETS). *Journal of Biogeography*, **28**, 769–774.

Yang, Z. & Kumar, S. (1996) Approximate methods for estimating the pattern of nucleotide substitution and the variation of substitution rates among sites. *Molecular Biology and Evolution*, **13**, 650–659.

Yang, Z., Goldman, N. & Friday, A. (1994) Comparison of models for nucleotide substitution used in maximum-likelihood phylogenetic estimation. *Molecular Biology and Evolution*, **11**, 316–324.

BIOSKETCHES

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