



Testing the species limits of the tarantulas (Araneae: Theraphosidae) endemic to California's Southern Coast Ranges, USA

JOSEPH S. WILSON,^{1*}† CLAYTON F. GUNNELL,² DAVID B. WAHL³ and JAMES P. PITTS² ¹Department of Biology, University of Nevada, Reno, NV, USA, ²Department of Biology, Utah State University, Logan, UT, USA and ³American Entomological Institute, Gainesville, FL, USA

Abstract. 1. The California floristic province is home to several threatened or endangered species and has been the focus of numerous conservation efforts. These conservation efforts have largely ignored the diverse and distinctive arthropod fauna found in this region.

2. We investigate the species boundaries of the four tarantula (Araneae: Theraphosidae) species endemic to California's Southern Coast Ranges through molecular phylogenetic analysis using a 680 bp region of the mitochondrial gene cytochrome oxidase subunit 1 from 51 individuals.

3. Our analysis resulted in a well-supported phylogeny showing three distinct clades. As a result, we recognise only one species in the Southern Coast Ranges (*Aphonopelma brunnium*, with *A. chamberlini* and *A. smithi* treated as junior synonyms; if the holotype of *A. rileyi* is located it will likely be a synonym as well). Two additional species were found in the foothills of the Sierra Nevada.

4. Although the tarantulas in California's Southern Coast Ranges are not as endemic as was previously thought, their position as top arthropod predators make them ideal sentinel species, suggesting they should be targeted by conservationists. Furthermore, our analyses illustrate the importance in using molecular tools to investigate biodiversity.

Key words. *Aphonopelma*, arthropod conservation, California floristic province, mygalomorph, phylogeography.

Introduction

The California floristic province is considered one of the few global biodiversity hot spots due to its high rate of endemism in both plant and vertebrate species (Mittermeier *et al.*, 2004). This region also houses a disproportionately high number of federally listed threatened or endangered species compared with the other parts of North America (Dobson *et al.*, 1997). Several of the species endemic to the California floristic province are found

only in California's Southern Coast Ranges, the group of mountain ranges running along the west side of the Central Valley from the San Francisco Bay in the north to the Transverse Ranges in the south (Fig. 1).

Although many of the endemic plants and animals in the Southern Coast Ranges have been targeted for conservation, little focus has been given to the arthropods of this region (IUCN, 2009). Redak (2000) suggested that multispecies habitat conservation plans must take into account arthropods, including insects and arachnids, if the goal of conserving biodiversity is to be met. Developing plans to conserve arthropod communities is difficult due, in part, to our lack of understanding of the extent of diversity in several groups – in North America only an estimated 56% of insect species and 27% of arachnids have been formally described (Redak, 2000).

*Correspondence: Joseph S. Wilson, Department of Biology, University of Nevada, Reno, NV 89557, USA. E-mail: joeswilson@gmail.com

†Current address: Department of Biology, Utah State University Tooele, 1021 West Vine Street, Tooele, UT 84074, USA

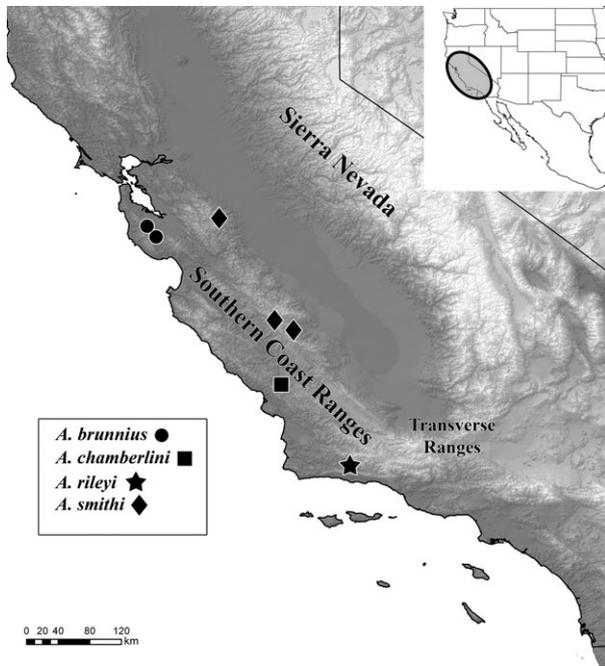


Fig. 1. Map of California showing the Southern Coast Ranges, the Sierra Nevada, and the Transverse Ranges. Known collection localities of the four *Aphonopelma* species described from this region are marked.

Spiders in the genus *Aphonopelma* (Araneae: Theraphosidae), commonly referred to as tarantulas, are among the most widely recognized, yet taxonomically poorly known arthropods in North America. In California's Southern Coast Ranges, four *Aphonopelma* species have been recognised: *Aphonopelma brunnius* Chamberlin, 1940; *A. chamberlini* Smith, 1995; *A. rileyi* (Marx), 1888; and *A. smithi* Smith, 1995. It should be noted that the status of *A. rileyi* remains questionable, because the holotype is missing (Smith, 1995; Prentice, 1997) and is currently treated as a *nomia dubia*. Each of these species is known from only a few localities and might be considered narrowly endemic species (Smith, 1995; Fig. 1). The status, however, of each of these species is uncertain due to the extreme morphological similarity between *Aphonopelma* species due in part to homoplasious female characters (Bond & Hedin, 2006). Furthermore, each of these species was described from one or two specimens, so intra-specific variation is unknown (Prentice, 1997). Lastly, the species are not all described from the same sex. Because three of the species are only known from male specimens (*A. brunnius*, *A. chamberlini*, and *A. smithi*) and the other (*A. rileyi*) is only known from a female specimen, it is possible that some of these species are the opposite sex of another described species.

A high level of endemism in *Aphonopelma* is not totally unexpected. Recent molecular analyses of the eastern species, *A. hentzi*, revealed previously unrecognised diversity and cryptic species (Hamilton *et al.*, 2011). Although tarantula diversity has not been fully investigated in the

west, particularly using molecular tools, California's rich geological past has led to interesting patterns of diversification in other taxa inhabiting the California Floristic Province (Calsbeek *et al.*, 2003). Recent molecular analyses of other mygalomorph spiders (trapdoor spiders), for example, show that highly endemic species, as well as genetically isolated populations within these species, exist in the California Coast Ranges (Bond *et al.*, 2001, 2006). In some cases, populations isolated by as little as 3 km have distinct mtDNA haplotypes, suggesting limited gene flow (Bond *et al.*, 2006). Species-level genetic divergence was even found between distant populations that showed no morphological differentiation (Bond *et al.*, 2001). Although tarantulas may have greater dispersal abilities than trapdoor spiders, it is possible that molecular analyses of the tarantulas of the Southern Coast Ranges, like the trapdoor spiders, would show some degree of endemism.

In this study we use molecular tools to investigate three questions, (i) how many tarantula species inhabit the Southern Coast Ranges of California, (ii) are these species narrowly endemic as has been suggested by previous authors or is there some overlap in their range, and (iii) are these species restricted to the coast ranges or do they also occur in the Sierra Nevada foothills.

Materials and methods

Taxon sampling

Aphonopelma specimens were collected from sites in the Southern Coast Ranges from 2000 to 2009 by DBW and JPP. Collection sites were selected in part to include type localities of the four historical species (Fig. 2). Specimens were also collected from sites in the western foothills of the Sierra Nevada and Transverse Ranges (Fig. 2). Most tarantulas were captured alive and taken to the American Entomological Institute, Gainesville, FL.

Molecular methods

DNA was extracted from an autotomised leg using the High Pure PCR Template Preparation Kit (Roche Pharmaceuticals, Indianapolis, IN, USA). A portion of the mitochondrial gene cytochrome oxidase I (COI) was amplified using the primers described by Petersen *et al.* (2007). Sequences were analysed with an ABI Prism 3730 Genetic Analyzer. PCR products were sequenced in both directions and sequence contigs assembled using Sequencher 4.0 (Gene Code Corp., Ann Arbor, MI, USA). DNA sequences were aligned using Clustal W (Thompson *et al.*, 1994) and alignments were visually inspected and corrected in MacClade 4.07 (Maddison & Maddison, 2008). All COI sequences were deposited in GenBank (Table 1). Genetic distances between major clades were calculated as pairwise percentages by determining the number of

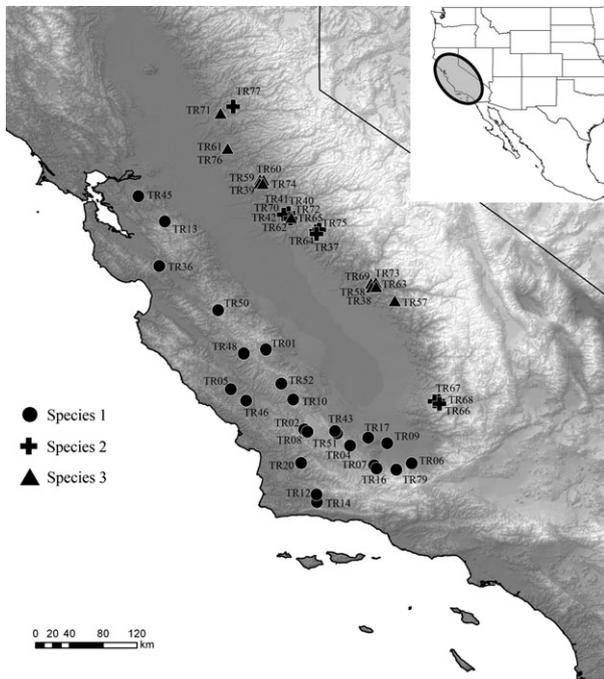


Fig. 2. Map of California showing the collection localities for all specimens used in the phylogenetic portion of this study. Symbols correspond to different genetically distinguished species based on the phylogenetic species concept (Queiroz, 1998). Voucher numbers are given and correspond to Table 1.

differences (point mutations and insertions or deletions) divided by the number of base pairs of the longer of the two sequences.

Phylogenetic analysis

The molecular data set was subjected to Bayesian analysis using MrBayes v3.1.2 (Ronquist & Huelsenbeck, 2003). Appropriate models of nucleotide substitution were determined in MrModeltest version 2.3 (Nylander, 2004). Bayesian analyses included four independent runs with three heated chains and one cold chain in each run. The Markov chain Monte Carlo chains were set for 3 000 000 generations and sampled every 100 generations; chains were run until the average standard deviation of the split frequencies dropped below 0.01. A burn-in of 10% was removed after convergence and diagnostic plots were assessed using Tracer 1.5 (Rambaut & Drummond, 2007). Several out-groups were included in the analysis. *A. iodius* (Chamberlin & Ivie), a species from the Great Basin, and *A. hentzi* from Oklahoma were included.

No fossils are available to calibrate a molecular clock for the *Aphonopelma* of central California so it remains unclear if the diversification of these three species is a result of Pleistocene climate change or Neogene mountain

building. Using our COI sequence data and a global arthropod molecular clock estimate of 2.3% sequence divergence between lineages per million years (Brower, 1994; Ayoub & Reichert, 2004) we roughly estimated the divergence time between species.

Results

Taxon sampling

A total of 280 tarantulas were collected and 51 were included in the molecular analyses. Because the descriptions of the type localities are vague for some species, collections were made as close to the recorded type locality as possible for each species. Much of the suitable habitat near the type locality for *A. brunnius* had been developed and no specimens were found in the patches of remaining habitat. Collections were made approximately 55 km south of the type locality at a site in the same mountain range as the original *A. brunnius* specimens were collected. The description of the type locality for *A. rileyi* is vague, simply being 'Santa Barbara Mountains'. Because of this ambiguous description, we collected multiple specimens from the mountains near Santa Barbara.

Molecular and phylogenetic results

Genetic distances were low between individuals collected from the Southern Coast Ranges (0–0.6%) suggesting only one species is present in this area. Genetic distances between individuals collected from the Sierra Nevada foothills and those from the Southern Coast Ranges were high (5.8–9.3%), suggesting that the Sierra Nevada foothill populations may be distinct from the Southern Coast Range populations. Also, distances were high between some Sierra Nevada populations (7.6–7.7%) suggesting two species may be present in the foothills of the Sierra Nevada.

Bayesian analysis of the combined molecular data produced a well-supported consensus tree that clearly shows three distinct species (Fig. 3). The populations from the Southern Coast Ranges all form a single clade with little phylogenetic structuring between populations, suggesting all of the populations represent one species. The populations from the Sierra Nevada foothills form two distinct clades separated by relatively long-branch lengths and are likely two discrete species.

Based on these molecular and phylogenetic results, the four species described from the Southern Coast Ranges are not distinct. Therefore, based on the phylogenetic species concept (de Queiroz, 1998), *A. chamberlini* and *A. smithi* are junior synonyms of *A. brunnius* (**syn. n.**); if the holotype of *A. rileyi* is located and sufficient characters are recognisable, it will also likely be a junior synonym of *A. brunnius*.

Table 1. Descriptive information for all taxa used in the phylogenetic portion of this study including voucher ID number, collection locality, and GenBank accession numbers.

ID no.	Location	Species	COI accession no.
TR01	Fresno Co., Gatos Creek Park	Species 1	JX244852
TR02	San Luis Obispo Co., Pozo Road site	Species 1	JX244846
TR04	Kern Co.: near Crocker Springs	Species 1	JX244843
TR05	Monterey Co.: Temblor Range site on Highway 58	Species 1	JX244844
TR06	San Luis Obispo Co.: Carrizo Plain	Species 1	JX244809
TR07	Kern Co.: Grocer Grade summit	Species 1	JX244808
TR08	San Luis Obispo Co.: Hwy. 58 & Pozo Rd.	Species 1	JX244859
TR09	Kern Co.: Buena Vista Aquatic Recreation Area	Species 1	JX244849
TR10	San Luis Obispo Co.: Palo Prieta Canyon	Species 1	JX244841
TR12	Santa Barbara Co.: Sedgwick Reserve	Species 1	JX244855
TR13	Alameda Co.: Mines Road	Species 1	JX244842
TR14	Santa Barbara Co.: nr. Los Olivos	Species 1	JX244847
TR16	Kern Co.: Grocer Grade summit	Species 1	JX244850
TR17	Kern Co.: Elk Hills (male)	Species 1	JX244839
TR20	Santa Barbara Co.: Cuyama Valley, Site B	Species 1	JX244845
TR29	Nevada: Ash Meadows	<i>A. iodius</i>	JX244811
TR36	Santa Clara Co.: Chesboro Reservoir	Species 1	JX244857
TR37	Mariposa Co.: 4.1mi W-NW Mariposa	Species 2	JX244833
TR38	Fresno Co.: Pittman Hills Road, site 4	Species 3	JX244815
TR39	Calaveras Co.: 5.8 W-SW Angels camp	Species 3	JX244825
TR40	Tuolumne Co.: Don Pedro Lake, Hwy. 132 site 1	Species 2	JX244837
TR41	Tuolumne Co.: Don Pedro Lake, Hwy. 132 site 2	Species 2	JX244826
TR42	Mariposa Co.: Lake McClure, Merced Falls Road	Species 2	JX244838
TR43	Kern Co.: Temblor Mts., Hwy. 58 summit	Species 1	JX244854
TR44	Oklahoma	<i>A. hentzi</i>	JX244810
TR45	Contra Costa Co.: Mt. Diablo State Park, Site A	Species 1	JX244853
TR46	San Luis Obispo Co.: Nacimiento Lake Road, site 1	Species 1	JX244851
TR48	Monterey Co.: Hwy 198 – Peachtree Valley	Species 1	JX244860
TR50	San Benito Co.: Panoche Road	Species 1	JX244856
TR51	Kern Co.: Temblor Mts., Pee-Wee Park	Species 1	JX244858
TR52	Monterey Co.: Cholame Road	Species 1	JX244840
TR57	Fresno Co.: 8.4 miles SE Squaw Valley	Species 3	JX244824
TR58	Fresno Co.: Pittman Hills Road, site 4	Species 3	JX244821
TR59	Calaveras Co.: 5.8 mi. W-SW Angels Camp	Species 3	JX244816
TR60	Calaveras Co.: 5.8 mi. W-SW Angels Camp	Species 3	JX244820
TR61	Amador Co.: 3.4 mi. NW Ione	Species 3	JX244822
TR62	Mariposa Co.: Merced Falls Rd. (ca. 4.3 miles south of intersection w/Hwy. 132)	Species 2	JX244834
TR63	Fresno Co.: Pittman Hills Road, site 4	Species 3	JX244814
TR64	Mariposa Co.: 4.1 mi. W-NW Mariposa	Species 2	JX244827
TR65	Tuolumne Co.: nr. intersection of Hwy. 132 and Merced Falls Rd.	Species 2	JX244828
TR66	Kern Co.: Granite Rd., 2.2 mi. south of intersection with Hwy. 155	Species 2	JX244830
TR67	Kern Co.: Granite Rd., 2.2 mi. south of intersection with Hwy. 155	Species 2	JX244829
TR68	Kern Co.: Granite Rd., 2.2 mi. south of intersection with Hwy. 155	Species 2	JX244835
TR69	Fresno Co.: Pittman Hills Road, site 4	Species 3	JX244813
TR70	Mariposa Co.: Merced Falls Rd. (ca. 4.3 miles south of intersection w/Hwy. 132)	Species 3	JX244818
TR71	El Dorado Co.: Salmon Falls Rd., 7 miles NE Folsom	Species 3	JX244819
TR72	Tuolumne Co.: nr. intersection of Hwy. 132 and Merced Falls Rd.	Species 2	JX244836
TR73	Fresno Co.: Pittman Hills Road, site 4	Species 3	JX244812
TR74	Calaveras Co.: 5.8 mi. W-SW Angels Camp	Species 3	JX244823
TR75	Mariposa Co.: 4.1 mi. W-NW Mariposa	Species 2	JX244832
TR76	Amador Co.: 3.4 mi. NW Ione	Species 3	JX244817
TR77	El Dorado Co.: Dave Moore Nature Area, 1.1 mi. NW Coloma	Species 2	JX244831
TR79	Kern Co.: Wind Wolves Preserve	Species 1	JX244848

COI, cytochrome oxidase I.

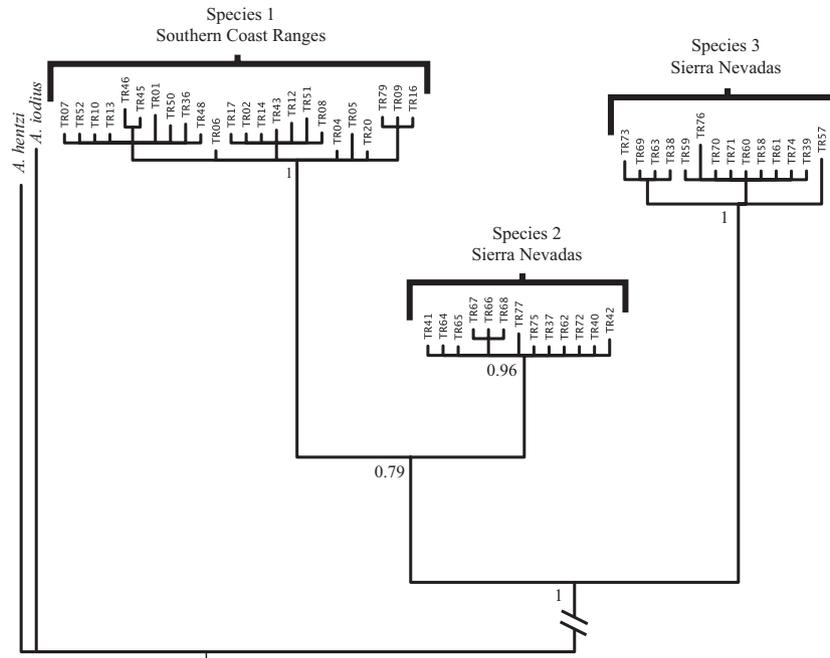


Fig. 3. Consensus tree of Bayesian analysis of the cytochrome oxidase I sequences. Numbers at each node represent posterior probabilities. Voucher numbers correspond to Fig. 2 and Table 1.

Discussion

The genetic data show that only one tarantula species inhabits the Southern Coast Ranges of California (*A. brunnius*) rather than the four species that have been described from this region. Our analyses also suggest that two additional species can be found in the foothills of the Sierra Nevada (Fig. 3). It remains unclear if these are undescribed or if they are known species previously only recognised from the Mojave and Great Basin deserts. Additional molecular analyses of tarantulas from areas surrounding the Central Valley of California will address this question.

Although our analyses show that tarantulas in the Southern Coast Ranges are not as narrowly endemic as other taxa, tarantulas may be useful as indicators of overall ecosystem health. Arthropods are an important component of a diverse ecosystem and should be included in multispecies habitat conservation plans (Redak, 2000). Because of their position at the top of the food chain, predators are often suggested as reliable sentinel species (indicator species) (Sergio *et al.*, 2008). As tarantulas are top arthropod predators and often are locally abundant (J. P. Pitts & D. B. Wahl, pers. comm.), they should be of great interest to ecologists and conservation biologists and may be useful as sentinel species.

Our analyses also illustrate the importance of using molecular data to test patterns of biodiversity. In many cases, molecular evidence has uncovered cryptic species, which are of conservation concern (e.g. Hamilton *et al.*, 2011; Wilson *et al.*, 2012). Other analyses, however, have

found that morphologically based species diversity (like diversity estimates in tarantulas) can be overestimated, particularly when vague colour characters are used to distinguish species (e.g. Williams *et al.*, 2011).

The oversplitting of the tarantulas of the Southern Coast Ranges may have resulted from multiple factors. Morphological variants of a single species can erroneously be described as separate nominal species when few specimens are used to make the description (Funk & Omland, 2003). All four of the historical *Aphonopelma* species were described based on one or two specimens. Also, when taxa become popular among hobbyists they are often oversplit into as many different variants as possible (e.g. cactuses: Anderson, 2001). Collection location, colour, or both have often been used to distinguish supposed species of Californian tarantulas. Without knowledge of intra-specific variation, it is impossible to know if different colour variants represent different species, or if they are simply members of a morphologically variable species. Furthermore, colour can be a misleading diagnostic character for North American tarantulas as an individual spider may appear dramatically different before and after a moult (J. P. Pitts & D. B. Wahl, pers. comm.).

The varied geological history of California has led to interesting patterns of diversification in several taxa, particularly in the Central Valley and surrounding mountains (Feldman & Spicer, 2006). Several taxa exhibit a deep genetic split across the Transverse Ranges in Southern California that has been associated with uplift during the Miocene/Pliocene (~5 Ma) (Calsbeek *et al.*, 2003). Other data suggest that the genetic divergence seen across the

Transverse Ranges is a result of Pleistocene climatic cycles (~1.8–0.01 Ma) (Feldman & Spicer, 2006). Divergence time estimates for the split between the tarantula species restricted to the Southern Coast Ranges and those species inhabiting the Sierra Nevada foothills indicate that the split occurred approximately 2.5–4 Ma. This date corresponds to some estimates of major episodes of uplift in California (Wilson & Pitts, 2010). The split between the two species in the Sierra Nevada foothills is estimated to have occurred approximately 3 Ma. It remains unclear what geologic events may have led to this divergence. If other hypothesised molecular clocks are used to calculate divergence dates (i.e. 4% sequence divergence per million years; Hamilton *et al.*, 2011), the splits among species is estimated to have occurred in the late Pleistocene (1.4–2.3 Ma). More data are needed, however, before a clear understanding of the historical biogeography of these species can be obtained.

Although our analyses show that tarantulas in the Southern Coast Ranges are not as narrowly endemic as trapdoor spiders, tarantulas may be useful as indicators of overall ecosystem health. Arthropods are an important component of a diverse ecosystem and should be included in multispecies habitat conservation plans (Redak, 2000). Because of their position at the top of the food chain, we suggest that tarantulas can and should be used sentinel species (indicator species).

Acknowledgements

We would first like to thank Carol von Dohlen at Utah State University for the use of laboratory space and equipment. We also thank Tom Prentice for specimens.

References

- Anderson, E.F. (2001) *The Cactus Family*. Timber Press, Portland, Oregon.
- Ayoub, N.A. & Reichert, S.E. (2004) Molecular evidence for Pleistocene glacial cycles driving diversification of a North American desert spider, *Agelenopsis aperta*. *Molecular Ecology*, **13**, 3453–3465.
- Bond, J.E., Beamer, D.A., Lamb, T. & Hedin, M. (2006) Combining genetic and geospatial analyses to infer population extinction in mygalomorph spiders endemic to the Los Angeles region. *Animal Conservation*, **9**, 145–157.
- Bond, J.E. & Hedin, M. (2006) A total evidence assessment of the phylogeny of North American euctenizine trapdoor spiders (Araneae, Mygalomorphae, Cyrtachenidae) using Bayesian inference. *Molecular Phylogenetics and Evolution*, **41**, 454–471.
- Bond, J.E., Hedin, M.C., Ramirez, M.G. & Opell, B.D. (2001) Deep molecular divergence in the absence of morphological and ecological change in the Californian coastal dune endemic trapdoor spider *Aptostichus simus*. *Molecular Ecology*, **10**, 899–910.
- Brower, A.V.Z. (1994) Phylogeny of *Heliconius* butterflies inferred from mitochondrial DNA sequences (Lepidoptera: Nymphalidae). *Molecular Phylogenetics and Evolution*, **3**, 159–174.
- Calsbeek, R., Thompson, J.N. & Richardson, J.E. (2003) Patterns of molecular evolution and diversification in a biodiversity hotspot: the California Floristic Province. *Molecular Ecology*, **12**, 1021–1029.
- Dobson, A.P., Rodriguez, J.P., Roberts, W.M. & Wilcove, D.S. (1997) Geographic distribution of endangered species in the United States. *Science*, **275**, 550–553.
- Feldman, C.R. & Spicer, G.S. (2006) Comparative phylogeography of woodland reptiles in California: repeated patterns of cladogenesis and population expansion. *Molecular Ecology*, **15**, 2201–2222.
- Funk, D.J. & Omland, K.E. (2003) Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review Ecology and Systematics*, **34**, 397–423.
- Hamilton, C.A., Formanowicz, D.R. & Bond, J.E. (2011) Species delimitation and phylogeography of *Aphonopelma hentzi* (Araneae, Mygalomorphae, Theraphosidae): Cryptic diversity in North American tarantulas. *PLoS ONE*, **6**, e26207.
- IUCN (2009) *IUCN Red List of Threatened Species*, Version 2009.2. IUCN, Gland, Switzerland.
- Maddison, D. & Maddison, W. (2008) *MacClade v. 4.07*. Sinauer Associates, Sunderland, Massachusetts.
- Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. & Da Fonseca, G.A.B. (2004) *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX, Mexico City.
- Nylander, J.A.A. (2004) *MrModeltest v2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- Petersen, S.D., Mason, T., Akber, S., West, R., White, B. & Wilson, P. (2007) Species identification of tarantulas using exuvia for international wildlife law enforcement. *Conservation Genetics*, **8**, 497–502.
- Prentice, T.R. (1997) Theraphosidae of the Mohave Desert west and north of the Colorado River (Araneae, Mygalomorphae, Theraphosidae). *Journal of Arachnology*, **25**, 137–176.
- de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation. A conceptual unification and terminological recommendations. *Endless Forms. Species and Speciation* (ed. by D.J. Howard and S.H. Berlocher), pp. 57–75. Oxford University Press, New York.
- Rambaut, A. & Drummond, A.J. (2007) Tracer v1.5. <<http://beast.bio.ed.ac.uk/Tracer>> 11th September 2012.
- Redak, R.A. (2000) Arthropods and multispecies habitat conservation plans: are we missing something? *Environmental Management*, **26**, 97–107.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K. & Hiraldo, F. (2008) Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annual Review of Ecology, Evolution and Systematics*, **39**, 1–19.
- Smith, A.M. (1995) *Tarantula Spiders: Tarantulas of the USA and Mexico*. Fitzgerald Publishers, London, UK.
- Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, **22**, 4673–4680.
- Williams, K.A., Manley, D.G., Pilgrim, E.M., von Dohlen, C.D. & Pitts, J.P. (2011) Multifaceted assessment of species validity

- in the *Dasymutilla bioculata* species group (Hymenoptera: Mutillidae). *Systematic Entomology*, **36**, 180–191.
- Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012) Historical biogeography of the arid-adapted velvet ant *Sphaerophthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography*, **39**, 336–352.
- Wilson, J.S. & Pitts, J.P. (2010) Illuminating the lack of consensus among descriptions of earth history data in the North

American deserts: a resource for biologists. *Progress in Physical Geography*, **34**, 419–441.

Accepted 9 August 2012

Editor: Calvin Dytham

Associate editor: Donald Quicke