

ORIGINAL
ARTICLE

Radiation following long-distance dispersal: the contributions of time, opportunity and diaspore morphology in *Sicyos* (Cucurbitaceae)

Patrizia Sebastian¹, Hanno Schaefer², Rafael Lira³, Ian R. H. Telford⁴ and Susanne S. Renner^{1*}

¹Systematic Botany and Mycology, University of Munich (LMU), Menzinger Strasse 67, 80638 Munich, Germany, ²Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA, ³Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, C.P. 54090, Mexico, ⁴School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

ABSTRACT

Aim To infer the most plausible explanations for the presence of 14 species of the Neotropical cucurbit genus *Sicyos* on the Hawaiian Islands, two on the Galápagos Islands, two in Australia, and one in New Zealand.

Location Neotropics, the Hawaiian and Galápagos archipelagos, Australia and New Zealand.

Methods We tested long-problematic generic boundaries in the tribe Sicyoeae and reconstructed the history of *Sicyos* using plastid and nuclear DNA sequences from 87 species (many with multiple accessions) representing the group's generic and geographic diversity. Maximum likelihood and Bayesian approaches were used to infer relationships, divergence times, biogeographic history and ancestral traits.

Results Thirteen smaller genera, including *Sechium*, are embedded in *Sicyos*, which when re-circumscribed as a monophyletic group comprises 75 species. The 14 Hawaiian species of *Sicyos* descended from a single ancestor that arrived c. 3 million years ago (Ma), Galápagos was reached twice at c. 4.5 and 1 Ma, the species in Australia descended from a Neotropical ancestor (c. 2 Ma), and New Zealand was reached from Australia. Time since arrival thus does not correlate with *Sicyos* species numbers on the two archipelagos.

Main conclusions A plausible mechanism for the four trans-Pacific dispersal events is adherence to birds of the tiny hard fruit with retrorsely barbed spines found in those lineages that underwent long-distance migrations. The Hawaiian clade has lost these spines, resulting in a lower dispersal ability compared with the Galápagos and Australian lineages, and perhaps favouring allopatric speciation.

Keywords

Australia, bird dispersal, diversification, Galápagos, Hawaiian radiation, Miocene, New Zealand, trans-Pacific dispersal.

*Correspondence: Susanne S. Renner, Systematic Botany and Mycology, University of Munich (LMU), Menzinger Strasse 67, 80638 Munich, Germany.
E-mail: renner@lrz.uni-muenchen.de

INTRODUCTION

The geographic origin and speed of diversification of flowering plant clades occurring on the archipelagos of the Pacific Ocean have attracted much recent attention (e.g. Wright *et al.*, 2000; Cronk *et al.*, 2005; Harbaugh & Baldwin, 2007; Clark *et al.*, 2008; Harbaugh *et al.*, 2009; Keppel *et al.*, 2009). Especially striking are radiations on the Hawaiian Islands, including the

Lobelioideae with 126 species, *Cyrtandra* (Gesneriaceae) with 59, *Melicope/Platydesma* (Rutaceae) with 52, and eight more genus-level clades each with ≥ 19 species (Baldwin & Wagner, 2010). Most Hawaiian lineages are younger than five million years (Myr) old (Lindqvist & Albert, 2002; Price & Clague, 2002; Clark *et al.*, 2009; Havran *et al.*, 2009; Willyard *et al.*, 2011), and, compared with other angiosperm rates so far reported, some of them have diversified at a higher rate

(Baldwin & Sanderson, 1998). The Galápagos Islands by contrast have produced few plant radiations, the largest among them the daisy genus *Scalesia* with 15 species going back to a common ancestor living 1.9–6.2 million years ago (Ma) (Schilling *et al.*, 1994) and *Varronia* with four species going back 1.12–4.5 Myr (Weeks *et al.*, 2010). The difference in the number and size of plant radiations on the two archipelagos could reflect the time available for diversification, ecological opportunity, and the propensity of particular clades to form isolated populations prone to interruption of gene flow. Other possible explanations include different extinction effects (e.g. resulting from different palaeoclimatic histories) or taxonomic bias (different species concepts applied on different archipelagos; Carine & Schaefer, 2010; Schaefer *et al.*, 2011).

Clades occurring on both the Hawaiian and Galápagos archipelagos should in principle allow the contribution of time and ecological opportunity to be disentangled from clade-specific propensities to form new species. The latter may correlate with dispersal ability, mating system, ease of hybridization, and speed of karyotype rearrangements (see also Price & Wagner, 2004). The indigenous floras of the Hawaiian and Galápagos archipelagos share only 24 genera, with 13 having endemic species on both archipelagos (Table 1). Among them

Table 1 Shared native angiosperm genera of the Hawaiian and Galápagos Islands. Genera in bold have endemic species on both archipelagos (data from Wiggins & Porter, 1971; Wagner *et al.*, 1990; Carr, 2006; Bungartz *et al.*, 2009).

Genus	Family	Hawaii		Galápagos	
		Endemic	Native	Endemic	Native
<i>Abutilon</i>	Malvaceae	3	1	1	0
<i>Acacia</i>	Mimosaceae	2	0	0	3
<i>Amaranthus</i>	Amaranthaceae	1	0	4	1
<i>Cordia/Varronia</i>	Boraginaceae	0	1	4	2
<i>Cuscuta</i>	Cuscutaceae	1	0	2	0
<i>Dodonaea</i>	Sapindaceae	0	1	1	0
<i>Chamaesyce</i>	Euphorbiaceae	15	0	8	0
<i>Gossypium</i>	Malvaceae	1	0	2	0
<i>Heliotropium</i>	Boraginaceae	0	2	1	3
<i>Ipomaea</i>	Convolvulaceae	1	4	2–3	3
<i>Lobelia</i>	Campanulaceae	13	0	0	1
<i>Lycium</i>	Solanaceae	0	1	1	0
<i>Peperomia</i>	Piperaceae	23	2	4	2
<i>Phyllanthus</i>	Euphorbiaceae	1	0	0	1
<i>Phytolacca</i>	Phytolaccaceae	1	0	0	1
<i>Pilea</i>	Urticaceae	0	1	1	1
<i>Pisonia</i>	Nyctaginaceae	2	3	1	0
<i>Plantago</i>	Plantaginaceae	3	0	1	0
<i>Plumbago</i>	Plumbaginaceae	0	1	0	2
<i>Portulaca</i>	Portulacaceae	3	1	1	0
<i>Psychotria</i>	Rubiaceae	11	0	2	0
<i>Sesuvium</i>	Aizoaceae	0	1	1	1
<i>Sicyos</i>	Cucurbitaceae	14	0	2	0
<i>Solanum</i>	Solanaceae	3	1	1	1
<i>Waltheria</i>	Sterculiaceae	0	1	0	1

is *Sicyos*, the focal clade of this study. *Sicyos* is a genus in the Cucurbitaceae that has 14 endemic species on the Hawaiian Islands (Wagner & Shannon, 1999), two species on the Galápagos Islands (Sebastian *et al.*, 2010a), two in Australia, one in New Zealand, and between 41 and 56 species in the Americas, depending on the taxonomic concept applied: several small genera have been included in *Sicyos* or segregated from it based mostly on fruit characters. Species of *Sicyos* are climbing or trailing annual or perennial vines that often occur in disturbed habitats. All *Sicyos* species are monoecious, with male and female flowers on each individual; the flowers are diurnal and depend on wasps and short-tongued bees for pollination (LaBerge & Hurd, 1965; Fig. 1a) because automatic selfing is precluded by their unisexuality. Fruit and seed morphology in the *Sicyos* alliance is exceptionally variable, and traits such as fleshy or hard fruits, with smooth surfaces or surfaces bearing barbed or hooked spines (Fig. 1e–i), are likely to influence dispersal.

The *Sicyos* clade, including the segregate genera, is especially diverse in Mexico, where several new species have been discovered in the recent past (Lira, 1994; Lira & Rodríguez-Arévalo, 1999; Rodríguez-Arévalo & Lira, 2001; Rodríguez-Arévalo, 2003; Rodríguez-Arévalo *et al.*, 2004, 2005). *Sicyos* is the name-giving taxon of the Sicyoeae, a tribe with 265 species in perhaps a dozen genera (Schaefer & Renner, 2011a,b). Family-wide molecular phylogenies relying on plastid and recently also nuclear data suggest that Sicyoeae are monophyletic (Kocyan *et al.*, 2007; Schaefer *et al.*, 2009; Schaefer & Renner, 2011b). However, none sampled more than a few species of *Sicyos*.

Here we use *Sicyos* to study whether time since arrival, ecological opportunity, or different fruit morphologies more plausibly explain the different species numbers produced in regions reached by long-distance dispersal, namely Hawaii (14 species), Galápagos (2), Australia (2) and New Zealand (1). A single medium-sized clade having produced species in all these areas provides a rare opportunity to disentangle the relative effects of age, traits and ecological opportunity on diversification.

MATERIALS AND METHODS

Taxon sampling, DNA sequencing, alignment and phylogenetic analysis

We used 112 accessions representing 87 species of Sicyoeae, including the type species of all relevant generic names so as to be able to decide the taxonomic fate of the previously segregated genera *Anomalosicyos* Gentry (7 species, Central to South America), *Cladocarpa* (H. St John) H. St John (20 species, Hawaii), *Costarica* L.D. Gómez (1 species, Costa Rica), *Microsechium* Naudin (2–4 species, Mexico and Guatemala), *Parasicyos* Dieterle (2 species, Guatemala), *Pterosicyos* Brandegee (1 species, Mexico and Guatemala), *Sarx* H. St John (2 species, Hawaii), *Sechiopsis* Naudin (5 species, Mexico and Guatemala), *Sechium* P. Browne (5 species, Mexico),

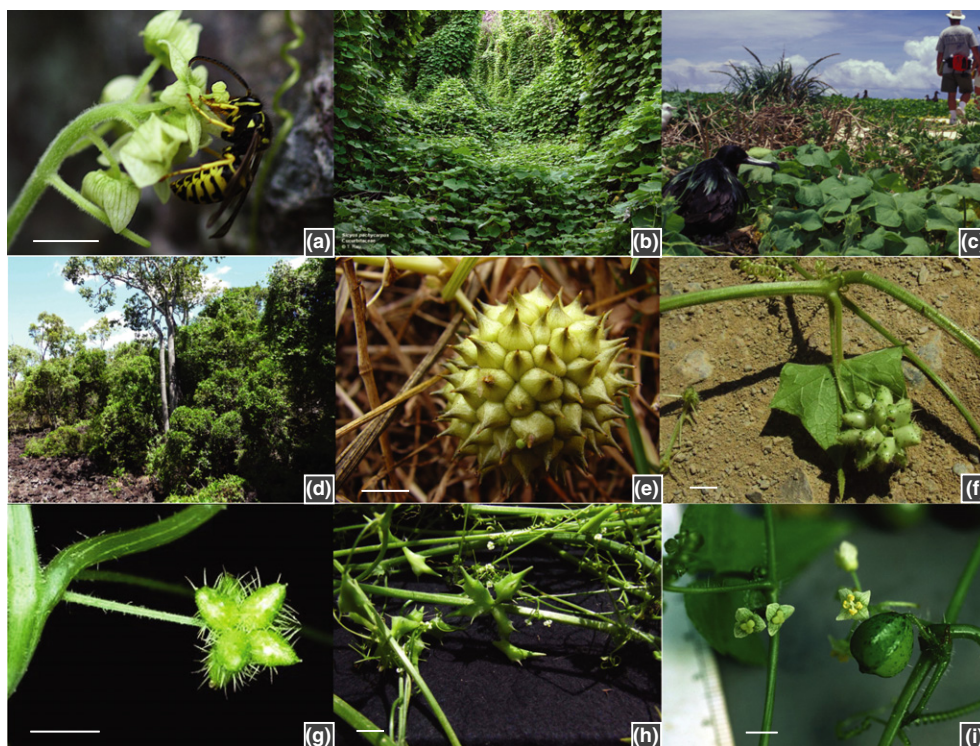


Figure 1 Habitats, flowers, and armed or unarmed fruits of *Sicyos* species from Hawaii, Australia and the continental mainland: (a) *S. angulatus* visited by *Vespa germanica* (USA), (b) *S. pachycarpus* (Hawaii), (c) *S. maximowiczii* growing in a colony of great frigatebird (*Fregata minor*), (d) *S. undara* (Australia), (e) *S. pachycarpus* (Hawaii), (f) *S. weberbaueri* (Peru), (g) *S. australis* (Australia), (h) *S. acari-eanthus* (Peru), (i) *Microsechium ruderale* (Guatemala). Scale bar = 1 cm. Photographs by: Forest & Kim Starr (a, e), T. Rau (b; Carr, 2006), H. Schaefer (b), P. Sebastian (d), M. Weigend (f, h), A. Lyne (g; APII) and M. Nee (i).

Sicyocarya (A. Gray) H. St John (25 species, Hawaii), *Sicyocaulis* Wiggins (1 species, Galápagos Islands), *Sicyosperma* A. Gray (1 species, Mexico and Arizona) and *Skottsbergiana* H. St John (2 species, Hawaii). No previous taxonomic fusions or segregations were based on molecular data. We were able to sample all species known from the Galápagos Islands, Australia and New Zealand, and 13 of the 14 known from the Hawaiian Islands. The missing Hawaiian species, *Sicyos semitonsus*, is close to *S. herbstii*, *S. hispidus* and *S. maximowiczii*, judging from the shared hairy fruit protuberances, but may actually be a hybrid (Telford, 1990; Starr & Martz, 1999). The type specimen of *Costarica hamata* was unavailable for sequencing, and instead we used material collected at the type locality on the slopes of the Irazú Volcano in Costa Rica. Appendix S1 in the Supporting Information lists all included species with their authors, geographic origin of the sequenced sample, voucher deposition and GenBank accession numbers. A total of 420 chloroplast and 98 nuclear sequences were newly generated for this study and have been submitted to GenBank (accession numbers JN560179–JN560696).

Genomic DNA was isolated from herbarium specimens or from silica-dried leaves, using the NucleoSpin plant kit (Machery-Nagel, Düren, Germany). Polymerase chain reaction (PCR) protocols and primers were the same as in Sebastian *et al.* (2010b). The plastid DNA regions sequenced were the

trnL intron, the adjacent *trnL*–*trnF* intergenic spacer, the *rpl20*–*rps12* intergenic spacer, the *trnS*–*trnG* intergenic spacer, the *psbA*–*trnH* intergenic spacer and the *rbcL* gene; the nuclear region sequenced was the complete internal transcribed spacer (ITS) region of the ribosomal DNA. For amplification of the *psbA*–*trnH* intergenic spacer, we used the primers listed in Volz & Renner (2009). The PCR products were purified with the PCR Wizard clean-up kit (Promega GmbH, Mannheim, Germany) or ExoSap (Fermentas, St Leon-Rot, Germany). Cycle sequencing was performed with the BigDye Terminator cycle sequencing kit on an ABI Prism 3100 Avant automated sequencer (Applied Biosystems, Foster City, CA). Sequencing primers were the same as those used for DNA amplification. The ITS region yielded single bands and unambiguous base calls, and we therefore refrained from cloning. Sequence assembly of forward and reverse strands was carried out with SEQUENCHER 4.7 (Gene Codes, Ann Arbor, MI), and sequences were aligned by eye using MACCLADE 4.08 (Maddison & Maddison, 2003).

The aligned plastid DNA matrix comprised 4527 nucleotides, and the aligned ITS matrix 872 nucleotides. In eight cases, we combined plastid and nuclear sequences from different samples (Appendix S1). Maximum likelihood (ML) analyses and ML bootstrap searches (using 500 replicates) were carried out using RAXML 7.2.8 (Stamatakis, 2006). RAXML

searches relied on the GTR + Γ model, with model parameters estimated over the duration of specified runs. Analyses of the separate plastid and nuclear datasets (gene trees not shown) with one exception yielded congruent tree topologies, with differences restricted to tip nodes with low statistical support (bootstrap < 75%); the sole difference concerned *Microsechium gonzalo-palomae* (see Results).

Molecular clock analyses and diversification rates

To obtain age ranges for the nodes of biogeographic interest we used Bayesian time estimation and a relaxed clock uncorrelated-rates model as implemented in BEAST 1.6.1 (Drummond & Rambaut, 2007). Species with nearly identical sequences were excluded from the dating analysis to reduce stochastic error and rate heterogeneity, yielding an alignment of 81 species, including the early-diverging Sicyoeae *Luffa aegyptiaca*, *Nothoalsomitra suberosa* and *Trichosanthes ovigera* for rooting purposes (Schaefer & Renner, 2011b). The pollen *Hexacolpites echinatus* from the Oligocene (33.9 to 23 Ma) of Cameroon (Salard-Cheboldaef, 1978) is the oldest known hexacolpate echinate Sicyoeae-type pollen and was used as a calibration point. The most conservative assignment of this pollen is to the split between *Linnaeosicyos* with 4-colporate reticulate pollen (Schaefer *et al.*, 2008a) and the remaining New World Sicyoeae with 4–16 colpate/colporate and mostly echinate pollen. To cover the uncertainty in the pollen age, we applied a normally distributed prior probability distribution of 28.5 Ma \pm 6 Myr to this node, as there is little justification for weighting the probability towards the minimum bound of the stratum in which the pollen was found (Ho & Phillips, 2009). The root of the Sicyoeae was constrained to 37 Ma \pm 3 Myr (again with a normal prior distribution) based on the age found for this node in the family-wide analysis by Schaefer *et al.* (2009). All BEAST runs used a Yule tree prior and the GTR + Γ model with six rate categories; Monte Carlo Markov chains (MCMC) were run for 20 million generations, sampling every 1000th generation. Mixing of the chains and convergence were checked using TRACER 1.5 (Rambaut & Drummond, 2007); of the 20,001 posterior trees, the first 5000 were discarded as burn-in based on inspection of the TRACER files. Final trees were edited in FIGTREE 1.3.1 (Rambaut, 2006).

We modelled diversification as a time-homogeneous birth/death process, with a net diversification rate λ and a relative extinction rate $\kappa = 0$ or $\kappa = 0.9$ (Magallón & Sanderson, 2001). Rates were calculated using the rate.estimate algorithm implemented in the R package GEIGER 1.3.1 (Harmon *et al.*, 2008).

Ancestral area reconstruction

To infer the biogeographic history of Sicyoeae we used Bayesian MCMC searches in BEAST and the continuous-time Markov chain (CTMC) biogeographic reconstruction approach proposed by Lemey *et al.* (2009). The advantage of this approach is that it incorporates branch length information

as well as uncertainty in the tree topology. Priors for migration rates used a Γ distribution for the relative rate parameter (shape parameter = 1.0) and an exponential distribution (mean = 1.0) for the geosite model parameter as recommended by Lemey *et al.* (2009). The CTMC phylogeographic model assumes that ancestral ranges are limited to single regions, making it particularly relevant for clades in which dispersal plays a larger role than vicariance, as is the case for oceanic island archipelagos. The geographic regions coded were: (1) North American plate, (2) Caribbean plate, (3) South American plate, (4) Hawaii, (5) Galápagos, and (6) Australia/New Zealand.

Evolution of habitat occupation and fruit armature

To assess whether habitat diversity in a region is correlated with diversification we categorized habitats into (1) shrublands and coastal vegetation, (2) tropical deciduous forest, (3) tropical evergreen forest, (4) tropical wet montane or cloud forest, (5) *Pinus–Quercus* forest, and (6) dry montane forest, and then coded each species for its preferred habitat(s). Data on habitat preferences came from specimen labels and taxonomic and floristic treatments (Macbride, 1960; Wiggins & Porter, 1971; Wagner *et al.*, 1990; Jeffrey & Trujillo, 1992). Preferences were plotted on a ML phylogeny for the same 81 taxa as used for the molecular clock dating.

To infer ancestral states of fruit armature in *Sicyos*, we used ML as implemented in MESQUITE 2.7.4 (Maddison & Maddison, 2009), employing the Markov k-state one-parameter model (Lewis, 2001). The coded character states were: (1) armed, (2) unarmed, (3) winged, and (4) variable within-species (this was relevant for *Sicyos edulis*; Lira *et al.*, 1999). Transition parameters were estimated on the 81-taxon ML phylogeny.

RESULTS

Phylogenetic relationships of the Sicyoeae

The ML phylogeny for the Sicyoeae (Fig. 2) shows that almost all species of *Anomalosicyos*, *Cladocarpa*, *Costarica*, *Microsechium* (only the type species, *M. ruderale*), *Parasicyos*, *Pterosicyos*, *Sarx*, *Sechiopsis*, *Sechium*, *Sicyocarya*, *Sicyocaulis*, *Skottsbergiliana* and *Sicyosperma* are embedded among species of *Sicyos*, a clade that itself has 100% bootstrap support. In addition, all the segregate genera that had more than one species (*Anomalosicyos*, *Microsechium*, *Parasicyos*, *Sechiopsis*, *Sechium*) turn out to be polyphyletic, and *Frantzia*, which traditionally was seen as close to *Sechium*, instead constitutes a genetically distant lineage (Fig. 2). From now on, we focus on the monophyletic genus *Sicyos* as circumscribed in Fig. 2, that is, including all the former segregates. The Hawaiian species of *Sicyos* form a robustly supported monophyletic group, and this is also supported by a 6-bp deletion in their *trnL* intron. The single New Zealand species groups with the two Australian species. By contrast, the two species on the Galápagos

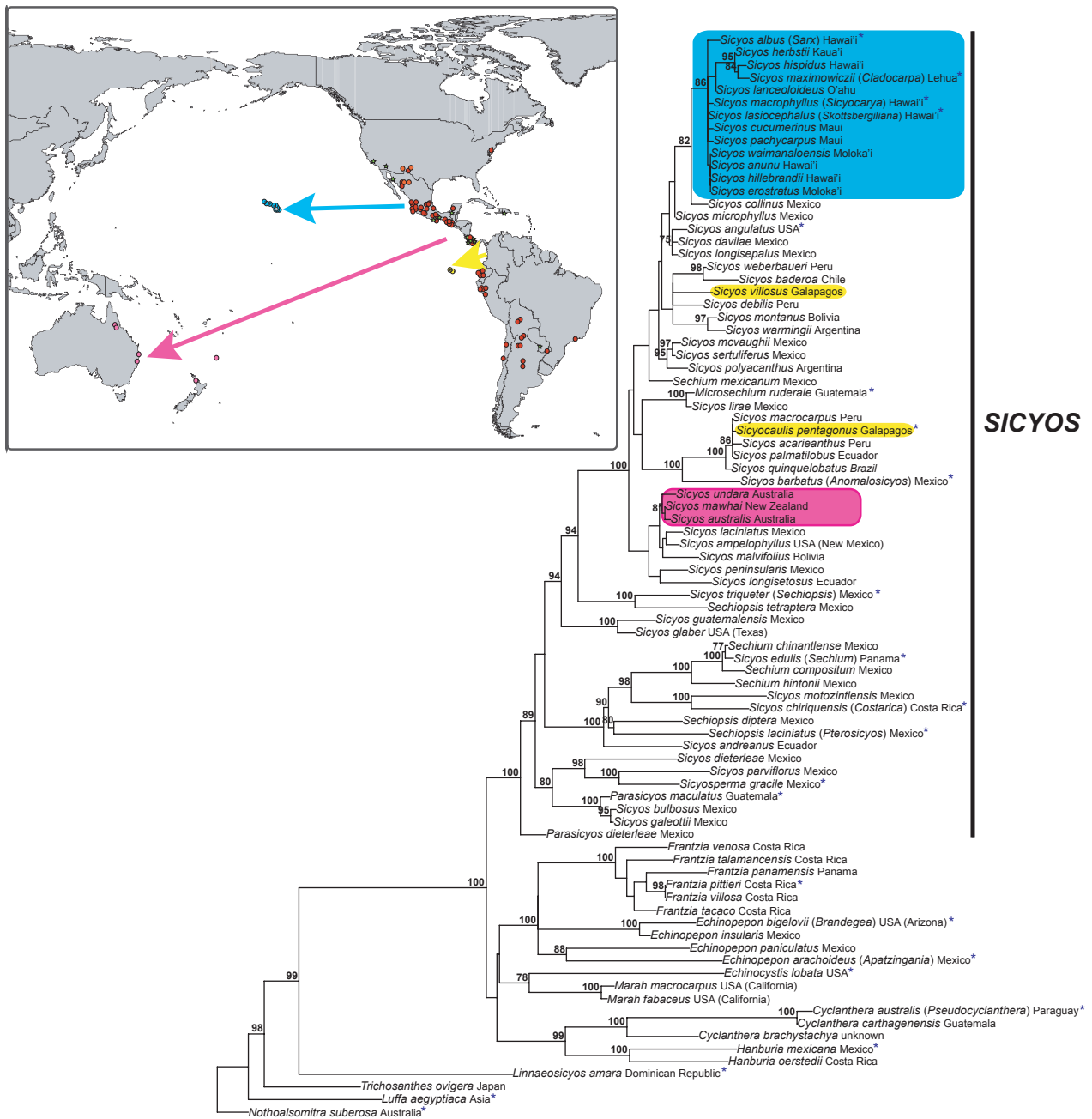


Figure 2 Maximum likelihood phylogram for 86 species of Sicyoeae (excluding *Microsechium gonzalo-palomae*; see Results) based on 5399 aligned nucleotides of plastid and nuclear sequences analysed under a GTR + Γ model. The tree is rooted on *Nothoalsomitra*. Values at nodes give likelihood bootstrap support $\geq 75\%$ based on 500 replicates. Boxes around clades and arrows in the inset mark the four long-distance dispersals to: Hawaii (blue), Galápagos (yellow) and Australia/New Zealand (pink). Stars indicate type species of currently or formerly accepted genera. Inset: Geographic origins of the sequenced plant material. Circles, *Sicyos*; stars, other Sicyoeae.

archipelago result from independent dispersals to the islands (Fig. 2).

The Mexican species *Microsechium gonzalo-palomae* is the only species placed differently in the plastid and nuclear (ITS) gene trees: based on its plastid sequences it clusters with the *Frantzia* clade, but based on its nuclear sequences it belongs in *Sicyos*. Two ITS sequences from duplicates of one of the two

existing herbarium collections of this species showed 10 nucleotide differences but nevertheless clustered together, suggesting multiple coexisting ITS copies, such as would be expected following hybridization. We excluded this species from our further combined analyses, as investigating the nature of this species or hybrid population will require fieldwork to collect more material.

Divergence times, direction of dispersal and diversification rates

Sicyos originated in North America (probably Mexico, see inset in Fig. 2) during the early Miocene, 23.6–15.1 Ma (Fig. 3). The common ancestor of the Hawaiian radiation is inferred to have diverged from a North American (Mexican) lineage 5.5–1.9 Ma and to have given rise to the extant Hawaiian species around 3 (4.1–1.3) Ma (Fig. 3). The Galápagos species *Sicyos villosus* is part of a clade occurring in Ecuador, Peru, Chile, Bolivia, Argentina and southern Brazil from which it diverged about 4.5 (6.4–2.8) Ma. The other Galápagos species, *Sicyocaulis pentagonus*, is nested in a separate clade among species from Ecuador, Peru and Brazil from which it diverged 1 (1.5–0.08) Ma, so the ancestral areas of both Galápagos species were probably in South America, possibly in adjacent mainland Ecuador (Fig. 3). The Australia/New Zealand clade is sister to species from the south-western United States, Mexico and Bolivia, and diverged from a North American ancestor 5.6–1.7 Ma. The Australian *Sicyos undara* is about 1 (3.6–0.5) Myr old, and its close relatives, *S. australis* and *S. mawhai*, the latter endemic to New Zealand, are about 0.7 (1.6–0.1) Myr old. The two new species, *S. mawhai* and *S. undara*, differ from *S. australis* in fruit morphology, number of flowers per inflorescence, and flower size and peduncle length (Telford *et al.*, 2012).

The net diversification rate (λ) of the *Sicyos* crown group in the Hawaiian Islands is $\lambda = 0.47\text{--}1.45$ species Myr^{-1} , assuming no extinction ($\kappa = 0$), or $\lambda = 0.18\text{--}0.58$ species Myr^{-1} if extinction rates are high ($\kappa = 0.9$; Table 2, which also summarizes the characteristics of the four trans-Pacific disjunctions). In the Australian/New Zealand clade, the diversification rate is $\lambda = 0.11\text{--}0.81$ species Myr^{-1} ($\kappa = 0$) or $\lambda = 0.03\text{--}0.24$ species Myr^{-1} ($\kappa = 0.9$). Of course, it is zero for the two single-species Galápagos lineages.

Habitat diversity and fruit morphology

Habitat preferences in *Sicyos* are variable even within very young clades and notably so in the Hawaiian clade (Fig. 1 and Appendix S2). We did not code disturbed versus undisturbed habitats; however, *Sicyos* species often grow in disturbed sites. Some of the widespread species, such as *Sicyos angulatus* and *S. polyacanthus*, occur in a wide range of habitats in their native ranges and are locally invasive in the Old World. The Hawaiian species are found in coastal areas, in arid or moist shrublands, or in openings in rain forest up to 2000 m elevation. *Sicyocaulis pentagonus* on the Galápagos is known only from a few collections in moist forests of the *Scalesia* zone between 130–200 and 400–550 m. The other Galápagos endemic, *Sicyos villosus*, is known from a single collection made by Charles Darwin on Floreana, which lacks habitat details. Habitats on Floreana, which has a maximum elevation of 640 m a.s.l., could have been coastal vegetation, arid shrublands, and/or moist *Scalesia* forest.

Of the two Australian species, *Sicyos australis* is widespread from northern Queensland to Tasmania, where it occurs in deciduous vine thickets, eucalypt forest, and in montane and near-coastal habitats; it has also been collected on New Zealand's North Island, Lord Howe (now extinct) and Norfolk Islands. The second Australian species, *S. undara*, is known only from the Undara Volcanic National Park in Queensland, where it grows in clay loam in boulder gullies of collapsed lava tubes in tropical deciduous forest. The New Zealand endemic, *S. mawhai*, is restricted to islands adjacent to the North Island and the Kermadec Islands, where it occurs in scrubs or forest margins of near-coastal sites.

Ancestral state reconstruction suggests that fruits armed with spines or hooks and winged fruits evolved several times (Appendix S3). Both Galápagos species as well as the Australian and New Zealand species have spiny fruits and are derived from relatives with such fruits (Fig. 1g and Appendix S3). By contrast, the Hawaiian clade lost the spines and instead has smooth fruits (Fig. 1e) or fruits with stubby, hairy protuberances (*Sicyos maximowiczii*, *S. hispidus*, *S. herbstii* and *S. semitonus*).

DISCUSSION

Here we use a medium-sized clade (the genus *Sicyos*, which comprises 75 species in its new monophyletic circumscription) in order to study whether ecological opportunity or time available for diversification more plausibly explain the strikingly different species numbers in four regions reached by long-distance dispersal. Our dense species sampling allowed identification of the geographic origins of the disjunct species on Hawaii, the Galápagos, Australia and New Zealand. The distances from North America to Hawaii (3800 km) and from the South American mainland (Ecuador) to Galápagos (930 km) should favour plant arrival on the Galápagos, but hardly make it so frequent as to retard speciation. Indeed, based on our biogeographic reconstruction, Hawaii and Australia/New Zealand were reached a single time, while Galápagos was reached twice. The finding that more distant archipelagos have fewer arrivals and larger radiations fits with findings from archipelagic birds (Ricklefs & Bermingham, 2007).

We estimate that the genus *Sicyos* is about 19 Myr old, the Hawaiian radiation occurred 3 Ma, the Australian species are 2 Myr old, the New Zealand species 0.7 Myr old, and the two Galápagos species *Sicyos villosus* and *Sicyocaulis pentagonus* are 4.5 and 1 Myr old, respectively (for error margins see Table 2 and Fig. 3). Time *per se* therefore cannot explain the different species numbers in the four areas reached by long-distance dispersal. Instead, the species build-up on the Hawaiian Islands clearly exceeded that in the other regions, although the Hawaiian diversification rate of *Sicyos* is not exceptional compared with other plant radiations (Valente *et al.*, 2010). Morphologically, the Hawaiian *Sicyos* species are distinct from each other (Wagner & Shannon, 1999), although their genetic divergence is low (Fig. 2), a combination also found in other

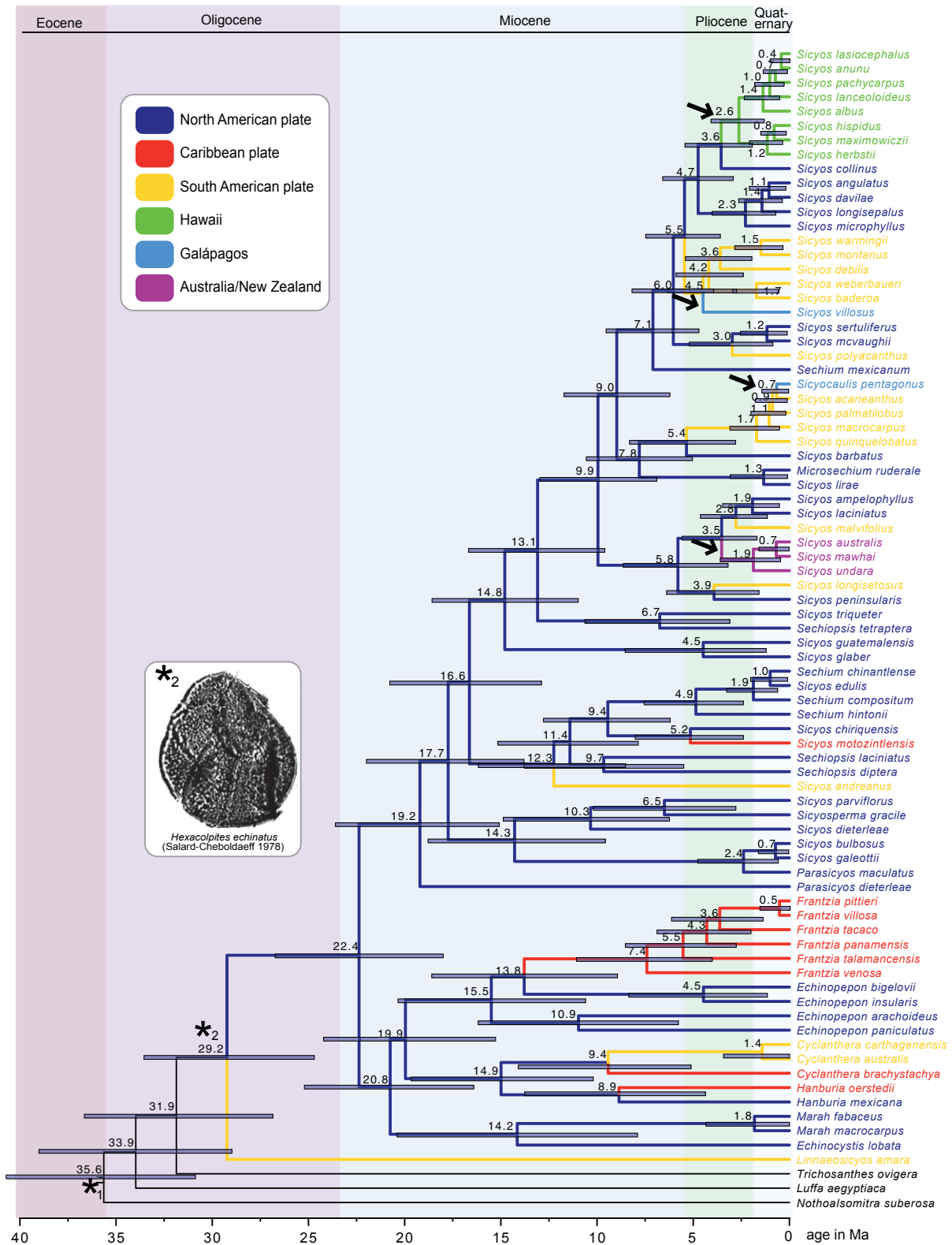


Figure 3 Chronogram and ancestral area reconstruction for *Sicyos* and related Sicyoeae obtained under a Bayesian relaxed clock and a continuous-time Markov chain biogeographic reconstruction applied to the data set used for Fig. 2 but excluding five Hawaiian species with almost identical sequences. Bars at nodes indicate the 95% confidence intervals around the estimated times. Numbers above branches give the node age, stars mark the calibration nodes, and arrows the four long-distance dispersals discussed in the text. Branch colour indicates character states for ancestral areas with the highest posterior probability (all ≥ 0.92 , except for a few outgroups), with the coding explained in the inset.

Table 2 Characteristics of the four *Sicyos* disjunctions compared here.

Characteristic	Hawaii	Australia/New Zealand	Galápagos 1 (<i>Sicyos villosus</i>)	Galápagos 2 (<i>Sicyocaulis pentagonus</i>)
Number of extant species	14	3	1	1
Distance from likely region of origin [km]	3800	6000	930	930
Relative habitat diversity	High	High	Low	Low
Dispersal ability (diaspore morphology)	Low	High	High	High
Stem age [Ma]	5.5–1.9	5.6–1.7	6.4–2.8	1.5–0.08
Crown age [Ma]	4.1–1.3	3.6–0.5	NA	NA
Diversification rate ($k = 0$) [species Myr ⁻¹]	0.47–1.45	0.11–0.81	0	0
Diversification rate ($k = 0.9$) [species Myr ⁻¹]	0.18–0.58	0.03–0.24	0	0

NA, not applicable.

Hawaiian radiations (Baldwin & Robichaux, 1995; Lindqvist *et al.*, 2003).

As time for speciation can be discounted as a strong explanation for the numbers of species in the four areas reached following long-distance dispersal, it might be extrinsic factors that make the Hawaiian Islands especially conducive to *Sicyos* speciation. Available area *per se* may influence diversification in island archipelagos (Ricklefs & Bermingham, 2007; Price & Wagner, 2011). The land area of the Hawaiian archipelago (16,300 km²) is more than twice that of the Galápagos (8000 km²). This could explain the larger species number on Hawaii compared with the Galápagos but certainly not that only three species evolved in Australia and New Zealand. However, extrapolation from land surface to number of suitable habitats is difficult (see also Price & Wagner, 2011). The Hawaiian archipelago harbours many types of plant formations (Mueller-Dombois & Fosberg, 1998), and species of *Sicyos* occupy most of them (Appendix S2). Especially relevant may be the extreme breadth of rainfall regimes on Hawaii. High islands, such as Kaua'i and Hawai'i, receive on their windward slopes as much as 12 m annual precipitation, whereas their leeward slopes experience warm-season droughts and as little as 250 mm annual precipitation, in common with some of the low islands. The Hawaiian soils derived from volcanism have accordingly experienced very different weathering (Cuddihy, 1989).

The Galápagos archipelago by comparison has fewer climate and vegetation types. Aridification there set in *c.* 3 Ma, while before that conditions were warmer and moister (Wara *et al.*, 2005; Federov *et al.*, 2006), potentially supporting rain forest vegetation. Today, the climate of the Galápagos Islands is characterized by highly variable convective rainfall during the hot season and by a prolonged cool season (June to December), with only little orographic rainfall on the higher windward sides of the islands and frequent droughts at lower elevations with arid-adapted vegetation types (Mueller-Dombois & Fosberg, 1998). The overall more arid climate on Galápagos compared with Hawaii, combined with fewer habitat types on smaller islands, may explain the absence of any large plant radiations on Galápagos. Among the 13 angiosperm genera with endemic species in both archipelagos

(Table 1) the Hawaiian genera usually have more species, and radiations of more than four species are almost entirely restricted to Hawaii.

An even broader range of climatic and edaphic conditions in the Australian region than in the Hawaiian Islands, however, did not result in a radiation of *Sicyos*, although further collecting and sequencing efforts may well reveal additional Australian species. The limited diversification of Australian *Sicyos* resembles the situation in the remaining Cucurbitaceae on that continent. These go back to some 20 independent arrivals from the Malesian region that occurred at different times over the past 35 Myr, with none currently having more than four living descendant species (Schaefer *et al.*, 2008b, 2009). The largest cucurbit radiations in Australia are *Austrobryonia*, with four species in the arid and semi-arid regions of the continent (Schaefer *et al.*, 2008b), and *Cucumis*, with two radiations of two/three species in tropical savanna habitats (Sebastian *et al.*, 2010b; Telford *et al.*, 2011). The reasons for the limited cucurbit diversification in Australia remain unclear.

In New Zealand, Cucurbitaceae had no endemic species before the discovery of *Sicyos mawhai*. This is surprising because Cucurbitaceae are successful transoceanic dispersers (Schaefer *et al.*, 2009; Duchon & Renner, 2010; Schaefer & Renner, 2010), and the distance of 2100 km between Australia and New Zealand has been overcome by many other disjunctly distributed Australia/New Zealand clades (Pole, 1994). Nor is *Sicyos* the only angiosperm genus disjunctly distributed between the Americas and the Australian/New Zealand region: Californian species of *Lepidium* (Brassicaceae) are phylogenetically closest to Australian/New Zealand species, which has been explained by transoceanic dispersals (Mummenhoff *et al.*, 2004).

Seabirds can act as dispersal agents across the Pacific Ocean (Falla, 1960; Carlquist, 1967) because at least some of them, such as storm petrels, shearwaters and frigate birds, nest on the ground or in burrows in coastal vegetation where they may contact fruiting plants [Marks & Leasure, 1992; Starr & Martz, 1999; our Fig. 1c shows a great frigatebird (*Fregata minor*) nesting among *Sicyos maximowiczii* on Laysan Island, Hawaii]. Some petrel populations migrate between Mexico, Central and

South America, the Galápagos and Hawaii, and one race of the white-faced storm-petrel (*Pelagodroma marina*) migrates across the Pacific between New Zealand and the Humboldt Current (off the coast of Peru), then west past the Galápagos Islands (Tomkins, 1982). Species of *Sicyos* have fleshy fruits (fresh up to c. 10 cm long) or hard fruits (5–10 mm long) that are smooth or barbed with hooked spines (Fig. 1 and Appendix S3). As the spiny *Sicyos* fruits are presented in multi-seeded infructescences, one contact with a bird can lead to several seeds being transported. Fruit morphology has been evolutionarily labile, and even fairly large wings have arisen several times (Appendix S3), the latter surprisingly not linked to any long-distance dispersal events. All lineages or species involved in long-distance dispersal to Hawaii, the Galápagos, Australia or New Zealand have spiny fruits. The spines, however, are readily lost; in *Sicyos edulis*, natural populations can contain individuals with spiny or smooth fruits (Lira *et al.*, 1999). Spines were also lost in the Hawaiian clade, where fruits are unarmed or in four species retain stubby outgrowths (Telford, 1990). Loss or reduction of dispersal ability is well documented in other insular plant and animal species (Carlquist, 1965, 1966a,b, 1974), the prime example being *Bidens*, which on the Hawaiian Islands lost the barbed awns responsible for long-distance dispersal in the mainland species (Carlquist, 1966a, 1967). Selection for loss of dispersibility should be strong because the majority of propagules that are dispersed away from islands will be lost at sea. In Hawaiian *Sicyos*, such limited dispersal ability could have promoted the isolation of populations and thus allopatric speciation in the diverse habitats and species build-up.

CONCLUSIONS

Sicyos, a clade of 75 species once the names in the segregate genera are transferred to the genus *Sicyos*, includes four trans-Pacific disjunctions. Small-scale habitat diversity and morphological adaptations (loss of spines leading to reduced dispersal ability) are the most plausible factors that could account for the significantly higher and more rapid accumulation of species on the Hawaiian Islands compared with the Galápagos, Australia or New Zealand.

ACKNOWLEDGEMENTS

For material we thank W. Wagner (United States National Herbarium, Washington, DC), B. Hammel (Missouri Botanical Garden) and M. Nee (New York Botanical Garden). We also thank C. Hughes, W. Wagner and an anonymous referee for helpful comments on our manuscript.

REFERENCES

- Baldwin, B.G. & Robichaux, R.H. (1995) Historical biogeography and ecology of the Hawaiian silversword alliance (Asteraceae): new molecular phylogenetic perspectives. *Hawaiian biogeography: evolution on a hot spot archipelago* (ed. by W.L. Wagner and V.A. Funk), pp. 259–287. Smithsonian Institution Press, Washington, DC.
- 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 USA*, **95**, 9402–9406.
- Baldwin, B.G. & Wagner, W.L. (2010) Hawaiian angiosperm radiations of North American origin. *Annals of Botany*, **105**, 849–879.
- Bungartz, F., Herrera, H.W., Jaramillo, P., Tirado, N., Jiménez-Uzcatégui, G., Ruiz, D., Guézou, A. & Ziemmeck, F. (2009) *Charles Darwin Foundation Galápagos species checklist*. Charles Darwin Foundation, Puerto Ayora, Galápagos. Available at: <http://www.darwinfoundation.org/datazone/checklists/> (accessed 10 July 2011).
- Carine, M.A. & Schaefer, H. (2010) The Azores diversity enigma: why are there so few Azorean endemic flowering plants and why are they so widespread? *Journal of Biogeography*, **37**, 77–89.
- Carlquist, S. (1965) *Island life*. Natural History Press, New York.
- Carlquist, S. (1966a) The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. *Evolution*, **20**, 433–455.
- Carlquist, S. (1966b) The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. *Brittonia*, **20**, 30–48.
- Carlquist, S. (1967) The biota of long-distance dispersal. V. Plant dispersal to Pacific islands. *Bulletin of the Torrey Botanical Club*, **94**, 129–162.
- Carlquist, S. (1974) *Island biology*. Columbia University Press, New York.
- Carr, G. (2006) *Hawaiian native plant genera*. University of Hawaii Botany Department, Manoa, Hawaii. Available at: <http://www.botany.hawaii.edu/faculty/carr/natives.htm> (accessed 10 July 2011).
- Clark, J.R., Ree, R.H., Alfaro, M.E., King, M.G., Wagner, W.L. & Roalson, E.H. (2008) A comparative study in ancestral range reconstruction methods: retracing the uncertain histories of insular lineages. *Systematic Biology*, **57**, 693–707.
- Clark, J.R., Wagner, W.L. & Roalson, E.H. (2009) Patterns of diversification and ancestral range reconstruction in the southeast Asian–Pacific angiosperm lineage *Cyrtandra* (Gesneriaceae). *Molecular Phylogenetics and Evolution*, **53**, 982–994.
- Cronk, Q.C.B., Kiehn, M., Wagner, W.L. & Smith, J.F. (2005) Evolution of *Cyrtandra* (Gesneriaceae) in the Pacific Ocean: the origin of a supertramp clade. *American Journal of Botany*, **92**, 1017–1024.
- Cuddihy, L.W. (1989) Vegetation zones of the Hawaiian Islands. *Conservation biology in Hawai'i* (ed. by C.P. Stone and D.B. Stone), pp. 27–37. University of Hawaii Press, Honolulu.
- Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.

- Duchen, P. & Renner, S.S. (2010) The evolution of *Cayaponia* (Cucurbitaceae): repeated shifts from bat to bee pollination and long-distance dispersal to Africa 2–5 million years ago. *American Journal of Botany*, **97**, 1129–1141.
- Falla, R.A. (1960) Birds as dispersal agents. *Proceedings of the Royal Society B: Biological Sciences*, **152**, 655–659.
- Federov, A.V., Dekens, P.S., McCarthy, M., Ravelo, A.C., deMenocal, P.B., Barreiro, M., Pacanowski, R.C. & Philander, S.G. (2006) The Pliocene paradox (mechanisms for a permanent El Niño). *Science*, **312**, 1485–1489.
- Harbaugh, D.T. & Baldwin, B.G. (2007) Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): repeated dispersal throughout the Pacific. *American Journal of Botany*, **94**, 1028–1040.
- Harbaugh, D.T., Wagner, W.L., Allan, G.J. & Zimmer, E.A. (2009) The Hawaiian Archipelago is a stepping stone for dispersal in the Pacific: an example from the plant genus *Melicope* (Rutaceae). *Journal of Biogeography*, **36**, 230–241.
- Harmon, L.J., Weir, J.T., Brock, C., Glor, R.E. & Challenger, W. (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics*, **24**, 129–131.
- Havran, J.C., Sytsma, K.J. & Ballard, H.E., Jr (2009) Evolutionary relationships, inter-island biogeography and molecular evolution in the Hawaiian violets (*Viola*: Violaceae). *American Journal of Botany*, **96**, 2087–2099.
- Ho, S.Y.W. & Phillips, M.J. (2009) Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology*, **58**, 367–380.
- Jeffrey, C. & Trujillo, B. (1992) Cucurbitaceae. *Flora of Venezuela*, Vol. V, Part 1 (ed. by G. Morillo), pp. 11–202. Fondo Editorial Acta Científica Venezolana, Caracas.
- Keppel, G., Lowe, A.J. & Possingham, H.P. (2009) Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *Journal of Biogeography*, **36**, 1035–1054.
- Kocyan, A., Zhang, L.-B., Schaefer, H. & Renner, S.S. (2007) A multi-locus chloroplast phylogeny for the Cucurbitaceae and its implications for character evolution and classification. *Molecular Phylogenetics and Evolution*, **44**, 553–577.
- LaBerge, W.E. & Hurd, P.D. (1965) A new subgenus and species of matinal *Andrena* from the flowers of *Sicyos* (Cucurbitaceae) in Mexico. *Pan-Pacific Entomologist*, **41**, 186–193.
- Lemey, P., Rambaut, A., Drummond, A.J. & Suchard, M.A. (2009) Bayesian phylogeography finds its roots. *PLoS Computational Biology*, **5**, e1000520.
- Lewis, P.O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, **50**, 913–925.
- Lindqvist, C. & Albert, V.A. (2002) Origin of the Hawaiian endemic mints within North American *Stachys* (Lamiaceae). *American Journal of Botany*, **89**, 1709–1724.
- Lindqvist, C., Motley, T.J., Jeffrey, J.J. & Albert, V.A. (2003) Cladogenesis and reticulation in the Hawaiian endemic mints (Lamiaceae). *Cladistics*, **19**, 480–495.
- Lira, R. (1994) Especie nueva de *Microsechium* (Cucurbitaceae, tribu Sicyoeae, subtribu Sicyinae) del estado de Oaxaca, México. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Serie Botánica*, **65**, 73–81.
- Lira, R. & Rodríguez-Arévalo, I. (1999) Nuevas especies de los géneros *Cyclanthera* Schrad. y *Sicyos* L. (Sicyoeae, Cucurbitaceae) para la flora de México. *Acta Botanica Mexicana*, **48**, 11–19.
- Lira, R., Castrejón, J., Zamudio, S. & Rojas-Zenteno, C. (1999) Propuesta de ubicación taxonómica para los chayotes silvestres (*Sechium edule*, Cucurbitaceae) de México. *Acta Botánica Mexicana*, **49**, 47–61.
- Macbride, F.J. (1960) *Flora of Peru*, Botanical Series of the Field Museum of Natural History, Vol. XIII, Part V, No. 2. Chicago Natural History Museum Press, Chicago.
- Maddison, D.R. & Maddison, W.P. (2003) *MacClade*, version 4.0.8. Sinauer Associates, Sunderland, MA.
- Maddison, W.P. & Maddison, D.R. (2009) *MESQUITE: a modular system for evolutionary analysis*, version 2.72. Available at: <http://mesquiteproject.org/mesquite/mesquite.html> (accessed 10 July 2011).
- Magallón, S. & Sanderson, M.J. (2001) Absolute diversification rates in angiosperm clades. *Evolution*, **55**, 1762–1780.
- Marks, J.S. & Leasure, S.M. (1992) Breeding biology of Tristram's storm-petrel on Laysan Island. *Wilson Bulletin*, **104**, 719–731.
- Mueller-Dombois, D. & Fosberg, F.R. (1998) *Vegetation of the tropical Pacific islands*. Springer, Berlin.
- Mummenhoff, K., Linder, P., Friesen, N., Bowman, J.L., Lee, J.-Y. & Franzke, A. (2004) Molecular evidence for bicontinental hybridogenous genomic constitution in *Lepidium sensu stricto* (Brassicaceae) species from Australia and New Zealand. *American Journal of Botany*, **91**, 254–261.
- Pole, M. (1994) The New Zealand flora – entirely long-distance dispersal? *Journal of Biogeography*, **21**, 625–635.
- Price, J.P. & Clague, D.A. (2002) How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 2429–2435.
- Price, J.P. & Wagner, W.L. (2004) Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. *Evolution*, **58**, 2185–2200.
- Price, J.P. & Wagner, W.L. (2011) A phylogenetic basis for species–area relationships among three Pacific Island floras. *American Journal of Botany*, **98**, 449–459.
- Rambaut, A. (2006) *FigTree v. 1.3.1*. Available at: <http://tree.bio.ed.ac.uk/software/figtree/> (accessed August 2011).
- Rambaut, A. & Drummond, A.J. (2007) *Tracer 1.5*. Available at: <http://beast.bio.ed.ac.uk/Tracer> (accessed August 2011).
- Ricklefs, R.E. & Bermingham, E. (2007) The causes of evolutionary radiations in archipelagoes: passerine birds in the Lesser Antilles. *The American Naturalist*, **169**, 285–297.
- Rodríguez-Arévalo, I. (2003) A new species of *Sicyos* (Cucurbitaceae, Sicyoeae, Sicyinae) from Mexico and Guatemala. *Brittonia*, **55**, 69–72.

- Rodríguez-Arévalo, I. & Lira, R. (2001) Nueva especie del género *Sicyos* L. (Cucurbitaceae) para la República Mexicana. *Boletín de la Sociedad Botánica de México*, **68**, 81–84.
- Rodríguez-Arévalo, I., Lira, R. & Dávila, P. (2004) Two new species of *Sicyos* L. (Cucurbitaceae) from Guerrero and Oaxaca, Mexico. *Botanical Journal of the Linnean Society*, **145**, 373–378.
- Rodríguez-Arévalo, I., Lira, R. & Calzada, I. (2005) A new species of *Sicyos* L. (Cucurbitaceae) from Oaxaca, Mexico. *Brittonia*, **57**, 43–46.
- Salard-Cheboldaëff, M. (1978) Sur la palynoflore Maëstrichtienne et Tertiaire du bassin sédimentaire littoral du Cameroun. *Pollen et Spores*, **20**, 215–260.
- Schaefer, H. & Renner, S.S. (2010) A gift from the New World? The West African crop *Cucumeropsis mannii* and the American *Posadaea sphaerocarpa* (Cucurbitaceae) are the same species. *Systematic Botany*, **35**, 534–540.
- Schaefer, H. & Renner, S.S. (2011a) Cucurbitaceae. *Families and genera of vascular plants*, Vol. 10 (ed. by K. Kubitzki), pp. 112–174. Springer Verlag, Berlin.
- Schaefer, H. & Renner, S.S. (2011b) Phylogenetic relationships in the order Cucurbitales and a new classification of the gourd family (Cucurbitaceae). *Taxon*, **60**, 122–138.
- Schaefer, H., Kocyan, A. & Renner, S.S. (2008a) *Linnaeosicyos* (Cucurbitaceae), a new genus for the Caribbean sister group of the New World Sicyeae. *Systematic Botany*, **33**, 349–355.
- Schaefer, H., Telford, I.R.H. & Renner, S.S. (2008b) *Austrobryonia* (Cucurbitaceae), a new Australian endemic genus, is the closest living relative to the Eurasian and Mediterranean *Bryonia* and *Ecballium*. *Systematic Botany*, **33**, 125–132.
- Schaefer, H., Heibl, C. & Renner, S.S. (2009) Gourds afloat: a dated phylogeny reveals an Asian origin of the gourd family (Cucurbitaceae) and numerous oversea dispersal events. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 843–851.
- Schaefer, H., Moura, M., Maciel, M.G.B., Silva, L., Rumsey, F.J. & Carine, M.A. (2011) The Linnean shortfall in oceanic island biogeography: a case study in the Azores. *Journal of Biogeography*, **38**, 1345–1355.
- Schilling, E.E., Panero, J.L. & Eliasson, U.H. (1994) Evidence from chloroplast DNA restriction site analysis on the relationships of *Scalesia* (Asteraceae: Heliantheae). *American Journal of Botany*, **8**, 248–254.
- Sebastian, P., Schaefer, H. & Renner, S.S. (2010a) Darwin's Galápagos gourd: providing new insights 175 years after his visit. *Journal of Biogeography*, **37**, 975–980.
- Sebastian, P., Schaefer, H., Telford, I.R.H. & Renner, S.S. (2010b) Cucumber (*Cucumis sativus*) and melon (*C. melo*) have numerous wild relatives in Asia and Australia, and the sister species of melon is from Australia. *Proceedings of the National Academy of Sciences USA*, **107**, 14269–14273.
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.
- Starr, F. & Martz, K. (1999) *S.S. Midway Expedition – May 21, 1999–June 16, 1999*. Trip Report. United States Fish and Wildlife Service. Available at: <http://www.hear.org/starr/publications/ssmidway.pdf> (accessed August 2011).
- Telford, I.R.H. (1990) Cucurbitaceae. *Manual of the flowering plants of Hawai'i* (ed. by W.L. Wagner, D.R. Herbst and S.H. Sohmer), pp. 568–581. University of Hawaii Press & Bishop Museum Press, Honolulu.
- Telford, I.R.H., Sebastian, P., Bruhl, J.J. & Renner, S.S. (2011) *Cucumis* (Cucurbitaceae) in Australia and eastern Melanesia, including newly recognized species and the sister species to *C. melo*. *Systematic Botany*, **36**, 376–389.
- Telford, I.R.H., Sebastian, P., de Lange, P.J., Bruhl, J.J. & Renner, S.S. (2012) Morphological and molecular data reveal three rather than one species of *Sicyos* (Cucurbitaceae) in Australia, New Zealand and the Islands of the South West Pacific. *Australian Systematic Botany*, doi: 10.1071/SB11032.
- Tomkins, R.J. (1982) Migration of white-faced storm-petrels *Pelagodroma marina* in the South Pacific and the status of the Kermadec subspecies. *Emu*, **84**, 32–35.
- Valente, L.M., Savolainen, V. & Vargas, P. (2010) Unparalleled rates of species diversification in Europe. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1489–1496.
- Volz, S.M. & Renner, S.S. (2009) Phylogeography of the ancient Eurasian medicinal plant genus *Bryonia* (Cucurbitaceae) inferred from nuclear and chloroplast sequences. *Taxon*, **58**, 550–560.
- Wagner, W.L. & Shannon, R.K. (1999) Nomenclator of Hawaiian *Sicyos* (Cucurbitaceae). *Novon*, **9**, 441–447.
- Wagner, W.L., Herbst, D.R. & Sohmer, S.H. (1990) *Manual of the flowering plants of Hawai'i*. University of Hawaii Press & Bishop Museum Press, Honolulu.
- Wara, M.W., Ravelo, A.C. & Delaney, M.L. (2005) Permanent El Niño-like conditions during the Pliocene warm period. *Science*, **309**, 758.
- Weeks, A., Baird, K.E. & McMullen, C.K. (2010) Origin and evolution of endemic Galápagos *Varronia* species (Cordiaceae). *Molecular Phylogenetics and Evolution*, **57**, 948–954.
- Wiggins, I.L. & Porter, D.M. (1971) *Flora of the Galápagos Islands*. Stanford University Press, Stanford, CA.
- Willyard, A., Wallace, L.E., Wagner, W.L., Weller, S.G., Sakai, A.K. & Nepokroeff, M. (2011) Estimating the species tree for Hawaiian *Schiedea* (Caryophyllaceae) from multiple loci in the presence of reticulate evolution. *Molecular Phylogenetics and Evolution*, **60**, 29–48.
- Wright, S.D., Yong, C.G., Dawson, J.W., Whittaker, D.J. & Gardner, R.C. (2000) Riding the ice age El Niño? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences USA*, **97**, 4118–4123.

SUPPORTING INFORMATION

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

Appendix S1 List of Sicyoeae species with their authors, geographic origin of the sequenced sample, voucher deposition, and GenBank accession numbers for all sequences included in this study.

Appendix S2 Habitat types of Sicyoeae species plotted on an 86-species maximum likelihood phylogeny.

Appendix S3 Evolution of armed fruits and unarmed fruits in the Sicyoeae inferred on an 86-species maximum likelihood phylogeny under maximum likelihood optimization.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

Patrizia Sebastian is a PhD student in the laboratory of Susanne Renner at the University of Munich (LMU), where she is working on the evolution of *Cucumis*, *Sicyos* and other Cucurbitaceae.

The main research interests of the authors are the evolution, biogeography and systematics of plants.

Author contributions: P.S. and S.R. designed the research; P.S. collected and analysed the data; H.S., I.T. and R.L. selected and supplied plant materials; P.S., H.S. and S.R. wrote the paper.

Editor: José María Fernández-Palacios