Origin of the Rapa endemic genus *Apostates*: Revisiting major disjunctions and evolutionary conservatism in the *Bahia* alliance (Compositae: Bahieae)

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Abstract Molecular phylogenetic analyses of nuclear and chloroplast DNA sequences indicate that the rediscovered *Apostates*, known only from Rapa in the Austral Islands of southeastern Polynesia, represents an example of extreme long-distance dispersal (>6500 km) from southwestern North America and one of at least four disjunctions of comparable magnitude in the primarily New World *Bahia* alliance (tribe Bahieae). Each of the disjunctions appears to have resulted from north-to-south dispersal since the mid-Miocene; three are associated with such marked morphological and ecological change that some of the southern taxa (including *Apostates*) have been treated in distinct genera of uncertain relationship. Phyllotaxy within the *Bahia* alliance, however, evidently has been even more conservative evolutionarily than reflected by previous taxonomies, with alternate-leaved and opposite-leaved clades in *Bahia* sensu Ellison each encompassing representatives of other genera that share the same leaf arrangements. A revised taxonomic treatment of the *Bahia* alliance is proposed to recognize morphologically distinctive, monophyletic genera, including the critically endangered *Apostates*.

Keywords amphitropical disjunctions; Austral Islands; biogeography; French Polynesia; islands; IUCN Red List; long-distance dispersal; molecular phylogenetics

■ INTRODUCTION

Diverse examples of extreme long-distance angiosperm dispersal out of temperate or semi-arid western North America to southern South America and to the high islands of the Hawaiian archipelago are well documented (reviewed by Wen & Ickert-Bond, 2009; Baldwin & Wagner, 2010). Convincing instances of trans-Pacific dispersal across the tropics from western North America to temperate Australasia also have been resolved, e.g., in *Lepidium* L. (Cruciferae; Dierschke & al., 2009) and *Microseris* D.Don (Compositae; Vijverberg & al., 1999, 2000), not to mention the far more numerous examples of dispersal between the Northern Hemisphere (primarily Eurasia) and Australasia involving the New Zealand montane flora (Raven, 1973; Winkworth & al., 2005). Less compelling evidence for primarily temperate North American plant groups in southeastern Polynesia probably reflects not only the low potential for transport across the intervening oceanic expanse but, especially, the low likelihood of suitable habitat in the mostly warm-tropical islands of the region. Origins of the southeastern Polynesian flora are not fully understood, however, and endemic taxa of uncertain relationships include some that may represent novel source areas and unusual biogeographic patterns.

Among the most promising areas for discovery of unusual biogeographic connections in southeastern Polynesia is Rapa (or Rapa Iti). Rapa is the highest, wettest, and coolest of the Austral Islands (Meyer, 2014), in the southernmost reaches of French Polynesia (Fig. 1; 27°37′S, 144°20′W, ~400 km south of the Tropic of Capricorn), not to be confused with Rapa Nui or Easter Island, at the southeasternmost edge of Polynesia. Although Rapa is a small (40.5 km²) and low (≤650 m elevation) island by comparison with islands of northern and southwestern Polynesia (e.g., Hawai'i and New Zealand), in the context of southeastern Polynesia, the Rapa flora is exceptionally rich in endemics (Florence, 1987; Meyer & al., 2014), with 20 endemic taxa of pteridophytes and more than 54 of angiosperms (Funk & Wood, 2014), including the endemic genera *Apostates* Lander (Compositae), *Pacifigeron* G.L.Nesom (Compositae), and *Metatrophis* F.Br. (Urticaceae), and appears to reflect a diversity of source areas. The Rapa fauna is also diverse for such a small island (Gillespie & al., 2012b), with a radiation of 67 species of flightless weevils (*Miocalles*; Paulay, 1985) and 100 species of endemic land snails in Tornatellidinae/Achatinellidae

and Endodontidae (Solem, 1983; Gargominy & Fontaine, 2014). Although the strongest floristic affinities of Rapa appear to be with the other Austral islands and, to a lesser degree, the other archipelagos of southeastern Polynesia (Meyer & al., 2014), putative source areas for the Rapa flora include temperate climatic regions of Australasia, e.g., *Veronica* L./*Hebe* Comm. ex Juss. (Plantaginaceae; Wagstaff & al., 2002), *Corokia* A.Cunn. (Argophyllaceae; Kårehed & al., 1999), and *Astelia* Banks & Sol. ex R.Br. (Asteliaceae; Birch & al., 2012), and the higher reaches of the Hawaiian Islands (see below), in keeping with the latitudinal setting of Rapa, where winters are so cold that breadfruit has not been successfully cultivated and coconut barely survives. Accordingly, Van Balgooy (1971: 112) regarded Rapa as an "anomalous district" in the southeastern Polynesia floristic region.

Arguably the least understood and most biogeographically intriguing taxon in the Rapa flora has been the endemic, monotypic genus *Apostates* (Compositae). Based on the only known reproductive collection of this broad-leaved, discoid-headed shrub, made in 1921 (*A.M. Stokes 186* (BISH, UC); Fig. 2D), Brown (1935) described it in the diverse Australasian genus *Olearia* Moench (~180 species; tribe Astereae), as *O. rapae* F.Br. *Olearia* has since been shown to be polyphyletic (Cross & al., 2002) and Lander (1989), who examined material of *O. rapae* during his studies of Australian *Olearia*, recognized that *O. rapae* did not belong in *Olearia* or any other described genus of tribe Astereae. Lander placed *O. rapae* in the new genus *Apostates* (Greek: deserter, renegade, runaway; named for the geographically and systematically isolated position of

the taxon), which he suggested might represent an extremely ancient (Cretaceous or early Cenozoic) lineage within Compositae. Nesom (1994) excluded *Apostates* from tribe Astereae and brought it to the attention of Karis (1998), who noted carbonized cypselae and other characteristics of the Heliantheae alliance (tribe Heliantheae s.l.). Based on morphology, Karis (1998: 134) concluded that "*Apostates* probably has its closest relatives in North America or Mexico" and that "the most likely part of [Heliantheae s.l.] to scrutinize with respect to sister group relationship is the subtribe Chaenactidinae of the Helenieae."

Here, we investigate the relationships and biogeographic origin of *Apostates* in the broader context of disjunct distributions and putatively conserved morphological characteristics in the clade to which it belongs. Wood (2010) found *Apostates* on a sea cliff at the northern edge of Rapa in 2002 (Fig. 1), 68 years after it was last collected (during the Mangarevan Expedition of 1934; Cooke, 1935), and Baldwin & al. (2002) proposed a molecular phylogenetic framework for helenioid Heliantheae that allowed us to address the following questions using nuclear ribosomal DNA (nrDNA) transcribed spacers (ITS, ETS) and four chloroplast DNA (cpDNA) regions (3'*ndhF*, 5'*trnK* intron, *rpl16* intron, *psbA-trnH* spacer): (1) Does *Apostates* have a New World origin, as suggested by Karis (1998), and can a continental source area be resolved? (2) Does the clade to which *Apostates* belongs include other examples of long-distance dispersal? (3) Does morphological variation in that clade allow for any insights about evolutionary change or conservatism in *Apostates* and other members of the group? (4) Do the findings have implications for taxonomy of *Apostates* and its relatives?
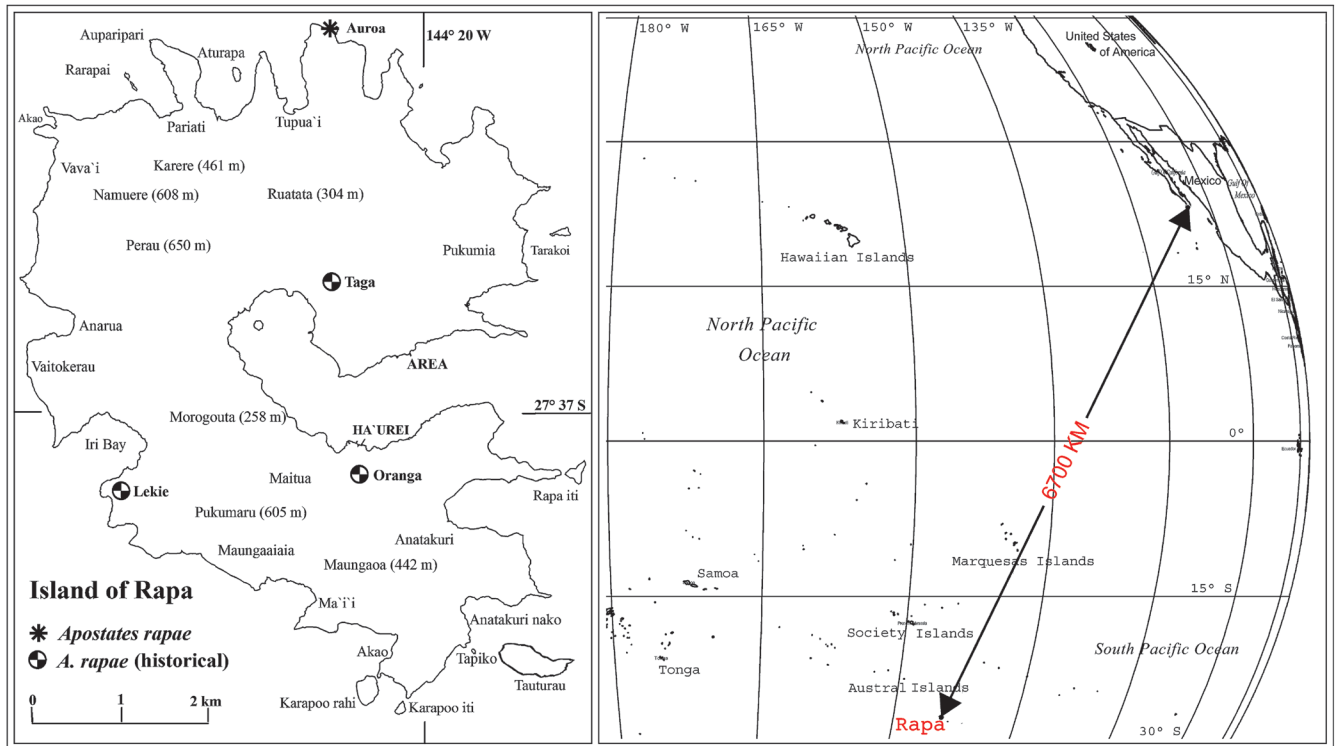

Fig. 1. Recent and historical locations of *Apostates rapae* on Rapa, Austral Islands **(left),** and Rapa in relation to North America and other Pacific islands **(right).**

Fig. 2. Diversity in the *Bahia* alliance. **A,** *Bahia neomexicana* (= *Picradeniopsis multiflora*, as treated here), scale bar = 10 mm (image by Michael Charters); **B,** *Bahia absinthifolia* (= *Picradeniopsis absinthifolia*, as treated here), scale bar = 10 mm (image by Christopher L. Christie); **C,** *Bahia ambrosioides*, scale bar = 10 mm (image by Stan Shebs); **D,** Isotype (at UC) of *Apostates rapae*; **E,** *Apostates rapae* (vegetative), scale bar = 10 mm (image by K.R. Wood); **F,** *Hymenothrix wrightii*, scale bar = 10 mm (image by Max Licher); **G,** *Amauriopsis dissecta* (= *Hymenothrix dissecta*, as treated here), scale bar = 60 mm (image by Rich Spellenberg); **H,** *Palafoxia arida*, scale bar = 10 mm (image by B.G. Baldwin).

■ MATERIALS AND METHODS

Taxon sampling. — Initial phylogenetic analyses of ITS sequences of helenioid Heliantheae studied by Baldwin & al. (2002) with inclusion of a sequence from *Apostates rapae* collected during the 2002 botanical expedition of Rapa (Wood & Perlman, 2002; Wood, 2010) indicated that our study should focus on the "*Bahia* clade" (hereafter, the *Bahia* alliance) of tribe Bahieae sensu Baldwin & al. (2002). The ITS findings indicating that our focus should be on *Bahia* and relatives were reinforced by a broader-scale analysis of cpDNA sequences of the Heliantheae alliance by Jose L. Panero (pers. comm.), who kindly informed B.G. Baldwin of his finding and subsequently included *Apostates* within Bahieae in his treatment of the tribe for *The families and genera of vascular plants* (Panero, 2007). Based on results of those initial analyses, representatives of *Achyropappus* Kunth, *Amauriopsis* Rydb., *Apostates*, *Bahia* Lag. (including *Cephalobembix* Rydb. and *Picradeniopsis* Rydb. ex Britton), *Florestina* Cass., *Holoschkuhria* H.Rob., *Hymenothrix* A.Gray, *Nothoschkuhria* B.G.Baldwin, *Palafoxia* Lag., *Platyschkuhria* Rydb., and *Schkuhria* Roth were chosen as the ingroup, with *Chaetymenia* Hook. & Arn. as the outgroup. Sampling of ingroup genera included the following taxa: all species of *Bahia* "series Oppositifoliae" sensu Ellison (1964) (including both species of *Picradeniopsis* sensu Strother, 2006) except *B. pringlei* Greenm. (unavailable), plus *B. neomexicana* (A.Gray) A.Gray, which Ellison (1964) treated in *Schkuhria* (as *S. multiflora* Hook. & Arn.); all species of *Amauriopsis* sensu Turner (2010) (= *Bahia* "series Alternifoliae" sensu Ellison, 1964) except *A. janakosana* B.L.Turner (unavailable); all species of *Achyropappus* sensu Turner (2012) except *A. depauperatus* (S.F.Blake) B.L.Turner (unavailable); the sole species of *Apostates*, *Holoschkuhria*, *Nothoschkuhria*, and *Platyschkuhria*; all species of *Hymenothrix* sensu Turner (1962) except *H. greenmanii* (Heiser) B.L.Turner (unavailable); all species of *Schkuhria* sensu Heiser (1945) and Turner (1995) except *S. greenmanii* Heiser (= *Hymenothrix greenmanii*, see above); and two species each of *Florestina* (~8 species; Turner 1963) and *Palafoxia* (~12 species; Turner & Morris, 1976). Other genera of Bahieae were resolved by Baldwin & al. (2002) to be members of other clades of the tribe, outside the study group. Voucher information is provided in Appendix 1.

DNA extraction and sequencing. — Total DNA was extracted from fresh, frozen, silica-dried, or press-dried (herbarium specimen) leaf material using the method of Doyle & Doyle (1987), modified by adding a phenol extraction, RNase digestion, and two ethanol precipitations of DNA, or using the DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.), following the manufacturer's procedure except for a longer (1–2 h rather than 10 min) incubation step for cell lysis. Polymerase chain reaction (PCR) amplifications of the 18S-26S nuclear ribosomal (nrDNA) internal transcribed spacer (ITS) region followed methods of Baldwin & Wessa (2000) except for use of AccuPower PCR Premix (K-2016; Bioneer, Chunbuk, Korea). The internal ETS primer ETS-Hel-1 was used with primer 18S-ETS (Baldwin & Markos, 1998) for ETS amplification and sequencing of the 3′ end of the nrDNA external

transcribed spacer (ETS), upstream of the 18S gene, using the same cycling conditions as for the ITS region except for a higher annealing temperature of 60°C. Primer pairs used for amplifying and sequencing the four chloroplast DNA (cpDNA) regions were as follows: 1587MADIA and 607R (Panero & Crozier, 2003) for the 3′ end of *ndhF* and the *ndhF-ycf1* intergenic spacer, trnK-3914F (Johnson & Soltis, 1994) and 884R (Panero & Crozier, 2003) for the 5′*trnK* intron and 5′ end of *matK*, F71 (Jordan & al., 1996) and R1516 (Kelchner & Clark, 1997) for the *rpl16* intron, and psbAF and trnHR (McGlaughlin & Friar, 2011) for the *psbA-trnH* intergenic spacer. PCR amplification of the four cpDNA genes involved an initial denaturation at 95°C for 4 min followed by 36 cycles of denaturation at 95°C for 1 min, primer annealing at 48°C for 45 s (+2 s/cycle), and primer extension at 72°C for 1 min (+9 min in final cycle). Both DNA strands were sequenced for each sample. Exonuclease I and shrimp alkaline phosphatase were used to remove excess nucleotides from PCR products using the PCR Product Pre-Sequencing Kit (70995, United States Biochemical Corp., Cleveland, Ohio, U.S.A.). Sanger sequencing of PCR products was conducted at the UC Berkeley DNA Sequencing Facility (Barker Hall) with the same primers used for PCR (except ITS5 was used instead of ITS-I for sequencing of the ITS region). GenBank accession numbers for sequences are provided in Appendix 1.

Analyses of phylogeny, biogeography, and morphological character evolution. — DNA sequences were aligned initially using MAFFT v.7.017 (Katoh & Standley, 2013), with default parameters as implemented in Geneious v.6.1.4 (Biomatters); resulting alignments were adjusted manually according to Simmons's (2004) similarity criterion. Sequence matrices and trees from this study are in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S18918). Congruence of signal among the four cpDNA regions and two nuclear ribosomal transcribed spacer regions was explored by comparison of bootstrap values and posterior probabilities for clades resolved from separate phylogenetic analyses of different gene regions (see below). Based on results from that comparison, the four cpDNA regions and two nrDNA regions were concatenated into a combined cpDNA matrix and a combined nrDNA matrix. All samples from which sequence data were obtained were represented in the concatenated matrices except for the sole representative of *Bahia pedata* A.Gray, which was excluded from the nrDNA matrix based on evident strong incongruence between ETS and ITS data for that specimen (see Electr. Suppl.: Figs. S1, S2). Sequences that were identical or potentially identical (with resolution of polymorphic or uncertain sites) within each matrix were merged prior to phylogenetic analysis. In addition, the alignment of *matK*, *ndhF*, and *rbcL* sequences of Compositae and other angiosperms analyzed by Barreda & al. (2015) was augmented with sequences of those three genes for nine taxa of Bahieae (*Amauriopsis dissecta* (A.Gray) Rydb., *Bahia absinthifolia* Benth., *Chaetymenia peduncularis* Hook. & Arn., *Florestina pedata* (Cav.) Cass., *Palafoxia arida* B.L.Turner & M.I. Morris, *Peucephyllum schottii* A.Gray) and its sister tribe Chaenactideae (*Dimeresia howellii* A.Gray, *Chaenactis douglasii* (Hook.) Hook. & Arn., *C. santolinoides* Greene) from

GenBank (Electr. Suppl.: Appendix S1) to allow for a fossil-calibrated analysis of divergence times in the *Bahia* alliance.

For the fine-scale phylogenetic analyses of the *Bahia* alliance, best-fit nucleotide substitution models for each data partition within the sequence matrices were assessed using PartitionFinder v.1.1.1 (Lanfear & al., 2012) under the Bayesian information criterion (BIC). Based on results from Partition-Finder, combined spacers (ETS, ITS-1, ITS-2) and the 5.8S gene were treated as separate data partitions in the nrDNA analyses and the combined cpDNA regions constituted a single partition. Phylogenetic analyses using maximum likelihood (ML) were conducted using RAxML v.7.2.7 (Pfeiffer & Stamatakis, 2010), with the GTR+G model and 1000-replicate rapid bootstrapping (Stamatakis & al., 2008), as implemented by the CIPRES science gateway (Miller & al., 2011). Phylogenetic analyses using Bayesian inference (BI) were conducted using MrBayes v.3.2.6 (Ronquist & al., 2012) and, for divergence time estimation of the nrDNA dataset, BEAST v.1.8.2 (Drummond & al., 2012), both as implemented by the CIPRES science gateway. The GTR+G model was specified for both the cpDNA data and the nrDNA spacer partition; for the 5.8S gene partition, the specified model was K80+I for the MrBayes nrDNA analysis and TrNef+I for the BEAST nrDNA analysis, which also implemented a Yule process model of speciation, random starting tree, and four independent Markov chain Monte Carlo (MCMC) runs of 10 million generations each, sampling one tree from the posterior distribution every 1000 generations. Two runs, each with three heated chains and one cold chain, were conducted for the MrBayes analyses, with the same number of generations and same sampling frequency as in the BEAST analysis. Tracer v.1.5 in the BEAST package was used to assess stationarity of tree likelihoods and convergence of the posterior distribution, based on effective sample size (ESS) scores of >200 in the final distribution for all parameters and graphical information for each BEAST run. For MrBayes analyses, stationarity was assessed by monitoring the average standard deviation of split frequencies, which dropped below 0.01 within the first million generations of each run. A highly conservative 25% burn-in was chosen for all BI analyses and, for the BEAST analysis, was removed using LogCombiner v.1.7.5 in the BEAST package. For the BEAST analysis, the maximum clade credibility (MCC) tree was found from the posterior distribution using TreeAnnotator v.1.7.5, also in the BEAST package. Divergence times were estimated in BEAST under a lognormal relaxed clock using (1) a secondary calibration (mean of 15.939 Ma, SD = 3.729, with normal distribution), derived from analysis of the expanded Barreda & al. (2015) dataset (see below), for the node representing all ingroup taxa except *Schkuhria* and (2) the mean ITS-1+ITS-2 substitution rate (0.004125 substitutions/site/million years [s/s/my], SD = 0.001808 s/s/my, with normal distribution) estimated from node-calibrated phylogenetic studies of herbaceous angiosperms (Kay & al., 2006). Divergence times were not estimated using cpDNA because of a lack of robust substitution-rate data to supplement the secondary nodal calibration. Use of primary calibrations in the above phylogenetic analyses was precluded by lack of fossils for the Heliantheae alliance that could be reliably assigned to particular tree nodes or stems.

To obtain the secondary calibration noted above, divergence times were estimated in a broad-scale analysis of the expanded Barreda & al. (2015) dataset by using the same three fossil calibrations and other priors used in that earlier study. The three calibrations, each with lognormal prior distributions, were as follows: 47.5 Ma for most recent common ancestor (MRCA) of Compositae minus Barnedesioideae and Famatinanthoideae; 72.1 Ma for the MRCA of *Barnedesia* Mutis ex L.f.+*Dasyphyllum* Kunth, and 125.0 Ma for the MRCA of eudicots. A birth-death speciation model, GTR+G+I substitution model, and random starting tree were also chosen, following Barreda & al. (2015). Four independent MCMC analyses of 400 million generations each were conducted using BEAST v.1.8.2, with sampling of one tree from the posterior distribution every 40,000 generations (burn-in 25%).

Historical biogeography was estimated using BioGeoBEARS (Matske, 2014) by comparing the dispersal-extinction-cladogenesis (DEC) ML model (Ree & Smith, 2007, 2008) and a Bayesian analysis of biogeography similar to Landis & al.'s (2013) BayArea method, both with and without founder-event ("jump") speciation ("J") and/or a geographic distance parameter ("X"). The models DEC, DEC+J, DEC+X, DEC+JX, BAYAREALIKE, BAYAREALIKE+J, BAYAREALIKE+X, and BAYAREALIKE+JX were compared statistically using the Akaike information criterion, with (AICc) and without (AIC) correction for finite sample sizes, and the BIC. Biogeographic distribution was treated at the level of continental or island occurrence: North America, South America, or Rapa. Distances between areas were measured using the DaftLogic distance calculator (https://www.daftlogic.com/projects-google-maps-distance-calculator.htm) from the approximate mid-point in the union of the ranges of taxa of the *Bahia* alliance within each area (U.S./Mexican border at El Paso, Texas/Ciudad Juarez, Chihuahua for North America; common border of Bolivia, Chile, and Peru for South America). Evolution of two morphological characters relevant to past taxonomies of the *Bahia* alliance (phyllotaxy and capitulum type) was estimated by the ancestral state reconstruction method in Mesquite v.3.02 (Maddison & Maddison, 2015) using maximum parsimony (MP) and ML. Phyllotaxy was scored as a two-state character (leaves basal and/or cauline and alternate versus leaves cauline and opposite or proximally opposite and distally alternate), as was capitulum type (heads radiate versus heads discoid). Coding of phyllotaxy conforms to Ellison's (1964) conception of *Bahia* "series Alternifolieae", with cauline leaves strictly alternate, and series "Oppositifoliae", with leaves opposite at least proximally.

■ **RESULTS**

Phylogenetic resolution, congruence, and incongruence. — Results of BI and ML phylogenetic analyses of the *Bahia* alliance were topologically congruent for all well-supported clades in comparisons across trees based on the same dataset (Figs. 3, 4). Most clades in the nrDNA dataset were well-supported by both BI posterior probabilities and ML bootstrap

values; only six were weakly supported based on both estimates of clade reliability, all within the well-supported group corresponding to *Amauriopsis*, *Hymenothrix*, and *Platyschkuhria* (Fig. 4). About half as many clades were well supported by either measure in the cpDNA trees, although robust support was widely distributed across the trees and allowed for a broad comparison of cpDNA and nrDNA evidence of relationships within the *Bahia* alliance (Fig. 3). Results of the

fossil-calibrated analysis of *matK*, *ndhF*, and *rbcL* sequences to obtain the secondary calibration used in the BEAST analysis of nrDNA data of the *Bahia* alliance are deposited in TreeBASE and not shown here.

Well-supported nrDNA and cpDNA clades (Fig. 3) were mostly congruent and reinforce support for four deep clades corresponding to the following sets of taxa: (1) *Schkuhria* s.str., i.e., minus *S. degenerica* (Kuntze) R.E.Fr. (= *Nothoschkuhria*
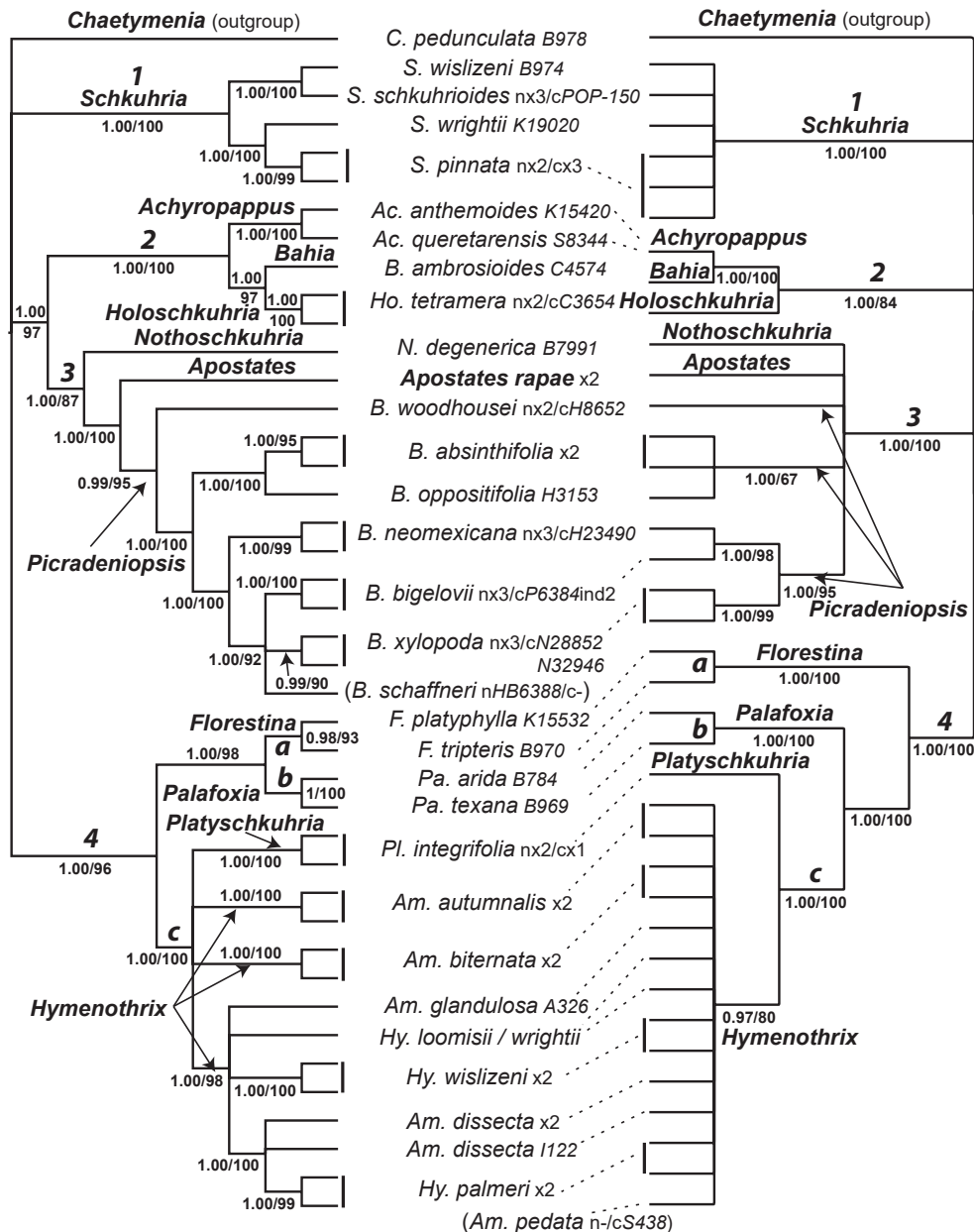

Fig. 3. Comparison of clades based on nuclear ribosomal DNA **(left)** and chloroplast DNA **(right)** of the *Bahia* alliance. Both trees are 95% majority-rule consensus trees from the Bayesian posterior distributions of MrBayes analyses. Clade credibility estimates shown along branches are posterior probabilities (left of slash or above branch) and maximum likelihood bootstrap values (right of slash or below branch). Main clades common to both trees are numbered or lettered (in italics) as presented in the Results. Genera indicated in bold along branches reflect the revised taxonomy adopted here. Taxon abbreviations: *Ac.*, *Achyropappus*; *Am.*, *Amauriopsis*; *B.*, *Bahia*; *C.*, *Chaetymenia*; *F.*, *Florestina*; *Ho.*, *Holoschkuhria*; *Hy.*, *Hymenothrix*; *N.*, *Nothoschkuhria*; *Pa.*, *Palafoxia*; *Pl.*, *Platyschkuhria*; *S.*, *Schkuhria*. See Appendix 1 for details on collections indicated after species names (n = nuclear ribosomal DNA; c = chloroplast DNA).

degenerica (Kuntze) B.G.Baldwin) and *S. multiflora* (= *Bahia neomexicana*); (2) *Achyropappus* sensu Turner (2012), *Bahia ambrosioides* Lag., and *Holoschkuhria*; (3) *Apostates*, North American taxa of *Bahia* "series Oppositifoliae" sensu Ellison (1964) plus *B. neomexicana*, and *Nothoschkuhria*; and (4) *Amauriopsis* sensu Turner (2010), *Florestina* sensu Turner (1963), *Hymenothrix* sensu Turner (1962), *Palafoxia* sensu Turner & Morris (1976), and *Platyschkuhria* sensu Ellison (1971).

Within the last clade, three well-supported subclades were resolved in both nrDNA and cpDNA trees: (a) *Florestina*; (b) *Palafoxia*; and (c) *Amauriopsis*, *Hymenothrix*, and *Platyschkuhria*. Among North American taxa of *Bahia* "series Oppositifoliae" plus *B. neomexicana*, both nrDNA and cpDNA trees congruently supported a clade corresponding to *Bahia absinthifolia* Benth. and *B. oppositifolia* (Nutt.) DC. and a clade corresponding to *B. bigelovii* A.Gray, *B. neomexicana*, *B. schaffneri* S.Watson (not sequenced for cpDNA), and *B. xylopoda* Greenm. Within *Schkuhria*, a well-supported clade

in the nrDNA trees that was resolved but not as strongly supported in the cpDNA trees included all sampled representatives of South American *S. pinnata* (Lam.) Kuntze ex Thell. and North American *S. wrightii* A.Gray, exclusive of North American *S. wislizeni* A.Gray and *S. schkuhrioides* Thell. In addition, three clades well supported only in the nrDNA trees but not strongly incongruent with cpDNA results based on posterior probabilities or bootstrap values include one corresponding to North American *Bahia* "series Oppositifoliae" plus *B. neomexicana*; the same clade plus *Apostates*; and *Amauriopsis dissecta* (A.Gray) Rydb. plus *Hymenothrix palmeri* A.Gray.

Evident incongruence between the nrDNA and cpDNA trees (Fig. 3) based on high posterior probabilities and bootstrap values for clades of overlapping but contrasting membership include relationships among *Achyropappus*, *Bahia ambrosioides*, and *Holoschkuhria*, with nrDNA supporting a clade of *B. ambrosioides* plus *Holoschkuhria* and cpDNA supporting *Achyropappus* plus *B. ambrosioides*; relationships among
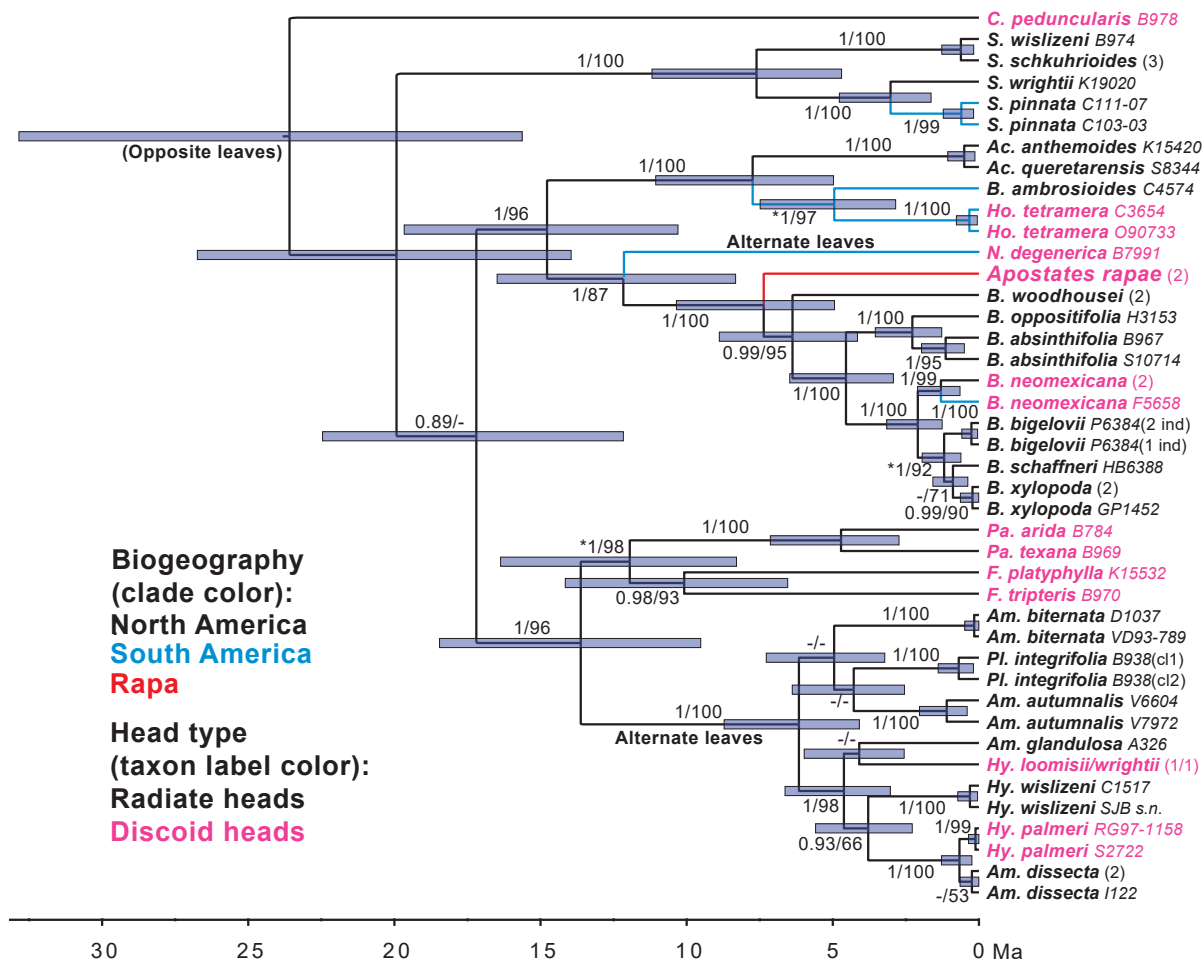

Fig. 4. Chronogram and maximum-clade-credibility (MCC) tree of the *Bahia* alliance based on Bayesian phylogenetic analysis of nuclear ribosomal external and internal transcribed spacer (ETS and ITS) regions. Branch lengths were scaled to time, in millions of years; node bars indicate the 95% highest posterior density (HPD) for ages. Biogeographic history of the *Bahia* alliance shown here along branches for the MCC tree conforms to nodal estimates obtained under the best-fit models (DEC+J and DEC+JX; Electr. Suppl.: Figs. 3, 4) using Akaike (AIC), corrected Akaike (AICc), or Bayesian (BIC) information criteria in BioGeoBEARS. Taxon abbreviations: *Ac.*, *Achyropappus*; *Am.*, *Amauriopsis*; *B.*, *Bahia*; *C.*, *Chaetymenia*; *F.*, *Florestina*; *Ho.*, *Holoschkuhria*; *Hy.*, *Hymenothrix*; *N.*, *Nothoschkuhria*; *Pa.*, *Palafoxia*; *Pl.*, *Platyschkuhria*; *S.*, *Schkuhria*. Clade credibility estimates shown along branches are posterior probabilities (left of slash) and maximum likelihood bootstrap values (right of slash); asterisks indicate incongruence with chloroplast DNA clades (see Fig. 3). See Appendix 1 for details on collections indicated after species names.

Florestina, *Palafoxia*, and the clade uniting *Amauriopsis*, *Hymenopappus*, and *Platyschkuhria*, with nrDNA supporting a clade of *Florestina* plus *Palafoxia* and cpDNA supporting *Palafoxia* plus *Amauriopsis*, *Hymenothrix*, and *Platyschkuhria*; and relationships among *Bahia bigelovii*, *B. neomexicana*, and *B. xylopoda*, with nrDNA supporting a clade of *B. bigelovii* plus *B. xylopoda* (plus *B. schaffneri*, not sampled for cpDNA), exclusive of *B. neomexicana*, and cpDNA supporting *B. bigelovii* plus *B. neomexicana*, exclusive of *B. xylopoda*.

Biogeographic model tests and estimates. — Historical biogeography within the *Bahia* alliance based on analyses of the nrDNA MCC tree in BioGeoBEARS was estimated similarly under those models that allowed for founder-event ("jump") speciation, which were uniformly of better fit than the otherwise same model not allowing for founder-event speciation. Comparisons based on the AICc and BIC indicated that the DEC+J model was the best fit; the AIC indicated that the DEC+JX model was best, but only slightly better than DEC+J (Table 1). Results under the two best-fit models are essentially the same (Electr. Suppl.: Figs. S3, S4) and those nodal estimates conform to biogeographic shifts shown on branches of the nrDNA chronogram in Fig. 4.

Morphological evolution. — Estimated evolution of phyllotaxy under both MP and ML criteria was the same, with an ancestral condition of leaves cauline and opposite at least at base and two origins of leaves cauline and alternate throughout or strictly basal—once on the branch uniting all taxa of *Amauriopsis*, *Hymenothrix*, and *Platyschkuhria* and once on the branch corresponding to *Nothoschkuhria* (Fig. 4). Evolution of head type was highly equivocal based on estimates using either the MP or ML criteria. If *Palafoxia* was scored as radiate, allowing for unsampled radiate species in that genus, then the MP mapping of head type was resolved as ancestrally radiate, with 6–7 origins of discoid heads across the *Bahia* alliance (results not shown; see Fig. 4 for head-types across taxa). No unequivocal estimates of discoid-to-radiate transformations were reconstructed under MP or ML criteria, irrespective of how head types were scored in *Palafoxia*.

■ DISCUSSION

***Apostates* belongs to the *Bahia* alliance. —** Our results uphold Karis's (1998) transfer of the endemic Rapa genus *Apostates* to Heliantheae s.l. and his suggestion based on morphology that *Apostates* might belong with North American or Mexican taxa of Chaenactidinae sensu Karis & Ryding (1994), which included all of the ingroup taxa studied here (plus other genera now treated in Bahieae and other primarily epaleate tribes of the Heliantheae alliance; see Baldwin & al., 2002). As noted above, our results also corroborate Panero's (2007) tribal placement of *Apostates* in Bahieae. Congruence between the nuclear and chloroplast trees indicate that *Apostates* is nested within the *Bahia* alliance, which represents all but ~10 genera in Bahieae and consists of four major clades (Fig. 3). Three of those clades (i.e., all but the clade corresponding to *Schkuhria* s.str.) each contain species of *Bahia* sensu Ellison (1964) and other genera;

Bahia in previous senses is not monophyletic. *Apostates* was strongly resolved by both nuclear and chloroplast DNA analyses to be part of the clade that includes all North American representatives of *Bahia* "series Oppositifoliae" sensu Ellison (1964) plus *B. neomexicana*, and South American *Nothoschkuhria*. The only other species of *Bahia* "series Oppositifoliae" and the type of *Bahia*, South American *B. ambrosioides*, belongs to the clade including North American *Achyropappus* and South American *Holoschkuhria*. All representatives of Ellison's (1964) *Bahia* "series Alternifolieae", justifiably removed from *Bahia* and treated as *Amauriopsis* by Turner (2012), following Panero (2007), belong to a clade with *Florestina*, *Hymenothrix*, *Palafoxia*, and *Platyschkuhria*.

***Apostates* represents long-distance dispersal from North America. —** The phylogenetic position of *Apostates* within a clade of otherwise New World taxa and the New World distributions of more distantly related members of tribe Bahieae (except the African genus *Hypericophyllum* Steetz) indicate that *Apostates* is an unusual example among southern Polynesian angiosperms of long-distance dispersal from the Americas. Results of the biogeographic analyses conducted here more specifically indicate a North American origin of *Apostates* (Fig. 4; Electr. Suppl.: Figs. S3, S4). Timing of divergence of the *Apostates* lineage was estimated based on nrDNA data at late Miocene to early Pliocene (7.36 Ma; 4.94–10.35 Ma 95% HPD), slightly before the oldest reported potassium-argon dates (4.8–4.1 Ma) for subaerially emplaced lava on Rapa (Diraison, 1991; see Meyer, 2014). From that perspective, *Apostates* appears to be a paleoendemic in the Rapa flora, although not as ancient as was considered by Lander (1989). [Note: Younger divergence times for *Apostates* and other members of the *Bahia* alliance cannot be ruled out based on results (published too recently for full consideration here) of Panero & Crozier (2016), who excluded *Tubulifloridites lilliei* type A pollen fossils used by Barreda & al. (2015) from analyses of divergence times in Asterales based on concerns about phylogenetic placement of those fossils (see Panero, 2016; Barreda & al., 2016)].

Other major disjunctions in the *Bahia* alliance. — Evolutionary change in morphology and ecology following long-distance dispersal is evident in *Apostates* and in some South

Table 1. Comparison of biogeographic models (in BioGeoBEARS) based on the Akaike (AIC), corrected Akaike (AICc), and Bayesian (BIC) information criteria and likelihood ratio test (see Materials and Methods for model descriptions). Highest values are shown in bold.

Model	LnL	AIC	AICc	BIC
DEC	−30.66	−57.32	−65.32	−68.80
DEC+J	**−27.90**	−49.80	**−61.80**	**−67.01**
DEC+X	−30.63	−55.26	−67.26	−72.47
DEC+JX	−28.13	**−48.26**	−64.26	−71.21
BAYAREA	−39.55	−75.10	−83.10	−86.58
BAYAREA+J	−28.42	−50.84	−62.84	−68.05
BAYAREA+X	−39.52	−73.04	−85.04	−90.25
BAYAREA+JX	−28.37	−48.74	−64.74	−71.69

American taxa of the *Bahia* alliance. *Apostates* differs from other members of the *Bahia* alliance in ways commonly associated with plant evolution on oceanic islands, as the only well-developed shrub within a predominantly herbaceous group (Carlquist, 1974; see Baldwin & al., 1998). Both *Apostates* and South American *Holoschkuhria*, the only taxon of the *Bahia* alliance known only from primary tropical forest, share characteristics that may reflect independent habitat shifts toward more mesic conditions, with leaves that are broad, thick, and entire, as opposed to thin and dissected (Givnish, 1978; Nobel, 2005).

Apostates represents the southern component of one of at least four major disjunctions between the Northern and Southern Hemispheres in the *Bahia* alliance, all of which evidently represent southward dispersal from western North America since the onset of mid-Miocene aridification there (Fig. 4; Pound & al., 2012). The disjunct southern taxa other than *Apostates* are all South American and occur in Mediterranean-like or dry high montane habitats except for *Holoschkuhria*, of Peruvian forests. The South American lineages and their estimated times of divergence from closest sampled relatives in North America include *Nothoschkuhria* (12.2 Ma; 8.3–16.5 Ma 95% HPD), *Bahia neomexicana* (1.3 Ma; 0.65–2.10 Ma), and *Bahia ambrosioides* plus *Holoschkuhria* (7.7 Ma; 5.0–11.1 Ma 95% HPD). Those disjunctions range in extent from ~3000 to ~6500 km, which at the upper end approaches the distance from southwestern North America (or central-western South America) to Rapa—and is nearly twice the distance from North America to Hawai'i.

Bahia ambrosioides and *Holoschkuhria* are unusually disparate taxa morphologically and ecologically by comparison with most examples of evolutionary divergence following dispersal from temperate North America to South America (reviewed by Wen & Ickert-Bond, 2009): *Bahia ambrosioides* Lag. is a subshrub with dissected leaves and radiate heads that occurs in open, often sandy, habitats in arid to Mediterranean-like regions of Chile's coast and coastal mountains (Ellison, 1964); monotypic *Holoschkuhria* (*H. tetramera* H.Rob.) is an herb with broad, entire leaves and discoid heads, known only from primary forest in northern Peru (Robinson, 2002) and an apparent example of a shift toward tropical ecology in the *Bahia* alliance, as noted above. Those two taxa have not been previously associated taxonomically below the tribal or subtribal level and the sister-group relationship between them resolved from nrDNA must be considered cautiously; the cpDNA results placed *B. ambrosioides* sister to North American *Achyropappus*, although both nrDNA and cpDNA trees resolved a robust clade including the three widely allopatric taxa *Achyropappus*, *B. ambrosioides*, and *Holoschkuhria* (Fig. 3).

By contrast, the New World amphitropical disjunction in *B. neomexicana* (= *Schkuhria multiflora*), earlier noted by Heiser (1945) and confirmed here, conforms well to temperate herbaceous examples discussed by Raven (1963) and reviewed by Wen & Ickert-Bond (2009) of conspecific pairs that are morphologically similar and evidently reflect relatively recent long-distance dispersal from North America, mostly since the Pliocene and probably by birds. The comparably recent divergence between North American and South American clades in

Schkuhria (3.0 Ma; 1.6–4.8 Ma 95% HPD) does not represent amphitropical disjunction but, instead, a relatively minor range gap (~1500 km) from northern Central America to northern South America that may represent dispersal or vicariance. The evidently most ancient New World disjunction in the *Bahia* alliance, involving *Nothoschkuhria* (in dry highlands of Bolivia and northern Argentina) and its mostly southwestern North American sister group (i.e., *Bahia* "series Oppositifoliae" plus *B. neomexicana* and *Apostates*), is amphitropical and may represent a relatively early bird–dispersal event from North America to South America.

Comparable biogeographic patterns in the southern Polynesian flora. — Available molecular phylogenetic evidence indicates that the closest parallels to long-distance dispersal of the *Apostates* ancestor to southeastern Polynesia from North America likely reflect dispersal from tropical, rather than temperate, latitudes in the New World or indirect dispersal from the Americas via the Hawaiian Islands. Kimball & Crawford (2004) resolved a well-supported ITS clade uniting two other endemic Compositae genera of southeastern Polynesia, *Fitchia* Hook.f. and *Oparanthus* Sherff (tribe Coreopsideae), which in turn constituted a more inclusive clade with two monospecific Caribbean genera, *Narvalina* Cass. and *Selleophytum* Urb. A sister-group relationship between that Southeastern Pacific–Caribbean clade and *Petrobium* R.Br., one of the cabbage-tree genera of the mid-Atlantic island of St. Helena (Crawford & al., 2009), leaves uncertain the biogeographic history of the group, although dispersal from the Caribbean to the South Pacific seems most plausible. The most recent common ancestor of the *Fitchia-Oparanthus* clade within southeastern Polynesia has been suggested to have occupied Rapa based on unpublished nrDNA data from a diversity of taxa within both genera (see Wagner & Lorence, 2011).

Putative indirect dispersal from the New World to southeastern Polynesia via the Hawaiian Islands warrants more investigation; such a route is not evident from extant diversity in the *Bahia* alliance. In *Plantago* L. (Plantaginaceae), Dunbar-Co & al. (2008) resolved two endemic Rapa species, *P. rapensis* F.Br. and *P. rupicola* Pilg., as either the sister group of the Hawaiian clade, based on cpDNA, or of the Hawaiian clade plus western North American *P. macrocarpa* Cham. & Schltdl. based on nrDNA. They noted that the nrDNA results were congruent with dispersal from western North America, rather than from Rapa, to the Hawaiian Islands, in keeping with that well-established biogeographic pattern (see Baldwin & Wagner, 2010), but also noted that incongruence between cpDNA and nrDNA trees left open the possibility of dispersal from New Zealand to elsewhere in the South Pacific and then to the Hawaiian Islands, as resolved for various other Hawaiian angiosperms, e.g., *Metrosideros* Banks ex Gaertn. (Myrtaceae; Wright & al., 2001) and *Pittosporum* Banks ex Gaertn. (Pittosporaceae; Gemmill & al., 2002). Dispersal from the Hawaiian Islands to southern Polynesia, as appears plausible for *Plantago* and an endemic Polynesian genus in the Rapa flora of evident (tropical) American affinity, *Nesoluma* Baill. (Sapotaceae; Smedmark & Anderberg, 2007), has been suggested for various angiosperm clades of Australasian or

uncertain mainland affinity, such as *Melicope* J.R.Forst. & G.Forst. (Rutaceae; Harbaugh & al., 2009; Appelhans & al., 2014) and *Santalum* L. (Santalaceae; Harbaugh & Baldwin, 2007), based on molecular phylogenetic data and the potential for dispersal associated with north–south migratory bird routes in the central Pacific (see Gillespie & al., 2012a).

Intrinsic and extrinsic dispersal factors. — Fruits of *Apostates* and other members of the clades that include all examples of major disjunction in the *Bahia* alliance have some characteristics associated with external bird dispersal in Compositae (Carlquist, 1966), such as persistent pappus scales and antrorse hairs on the fruit body, at least on the four angles of the fruit or near its base. In accord with Baker's Rule (Baker, 1967), self-compatibility or pseudo-self-compatibility is a nearly ubiquitous characteristic of remote oceanic island angiosperms, including composites (Crawford & al., 2009), favoring colonization. Seed set from selfing has been documented in one of three species of *Bahia* "series Oppositifoliae" and two of three species of *Amauriopsis* (= *Bahia* "series Alternifoliae" sensu Ellison) studied experimentally by Ellison (1964). Those data are insufficient to draw conclusions about the likely ancestral state of *Apostates*, which has not been investigated for self-fertility.

We know of no bird migration route that would allow or would have allowed for direct dispersal from temperate America to southeastern Polynesia but cannot exclude the possibilities of dispersal by an accidental avian visitor or by a bird that no longer migrates along such a route, especially in light of the high diversity of birds estimated to have been lost from southern Polynesia as a result of anthropogenic factors (Duncan & al., 2013). Another possibility is that *Apostates* may represent arrival by an indirect route, which is easier to reconcile with modern bird migration patterns, followed by extinction elsewhere along that route (e.g., via the Hawaiian Islands, as discussed above). The Rapa flora includes other examples of extremely low likelihood plant dispersal events, even by comparison with direct dispersal from temperate North America; for example, presence on Rapa of an endemic subclade of the Glochidion clade in *Phyllanthus* L. (Phyllanthaceae) required independent dispersal to the island of an obligate, seed-predatory lineage of moths (in *Epicephala*) that are the only known effective pollinators (Hembry & al., 2013).

Evolutionary conservatism in the *Bahia* alliance? — Our results indicate that some morphological characters emphasized in previous taxonomies of the *Bahia* alliance have been either more conservative or less conservative evolutionarily than is reflected by generic circumscriptions. Both nrDNA and cpDNA trees presented here reinforce and extend Ellison's (1964) conclusion that phyllotaxy is an evolutionarily conservative character in *Bahia* (also see Ellison & al., 1962); taxa he treated in "series Alternifoliae" (recently treated in *Amauriopsis*), with leaves alternate throughout, and "series Oppositifoliae," with leaves opposite at least proximally, belong to distinct clades. Phyllotaxy is even more deeply conserved within the *Bahia* alliance and distinguishes deeper clades of the alliance, with alternate leaves shared by *Amauriopsis* (= *Bahia* "series Alternifoliae") plus all representatives of *Hymenothrix* and

Platyschkuhria and proximally opposite leaves shared by *Bahia* "series Oppositifoliae," plus *B. neomexicana* (= *Schkuhria multiflora*), and *Apostates*, despite striking divergence of the Rapa endemic in other vegetative characters (Fig. 2). Proximally opposite leaves are evidently the ancestral condition in the *Bahia* alliance, based on trait optimization on the cpDNA and nrDNA trees, with two shifts to alternate phyllotaxy, in the ancestors of *Nothoschkuhria* and at the base of the clade including *Amauriopsis*, *Hymenothrix*, and *Platyschkuhria* (see Fig. 4).

Presence or absence of ray florets appears to have been a source of confusion concerning relationships in the group and may have been given too much taxonomic weight. Non-monophyly of *Bahia* in previous senses to some extent reflects a generic concept based in part on the shared, ancestral characteristic of ray floret presence; other genera in the *Bahia* alliance—including *Apostates*—are characterized in part by discoid heads in most (*Hymenothrix*, *Palafoxia*) or all species, except for *Achyropappus*, *Amauriopsis*, *Platyschkuhria*, and the usually inconspicuously rayed *Schkuhria* (Fig. 4). Of those last four, primarily radiate genera, *Amauriopsis* was until recently (Baldwin & al., 2002; Panero, 2007; Turner, 2012) included in *Bahia* by most taxonomists and floristicians, and taxa of *Achyropappus* and *Platyschkuhria* have been treated in *Bahia* by some botanists, as well. The discoid species *B. neomexicana*, excluded from *Bahia* by Ellison (1964) and commonly placed in *Schkuhria* (as *S. multiflora*; see Heiser, 1945), is another apparent example of taxonomic confusion associated in part with absence of ray florets, as well as with presence of *Schkuhria*-like phyllary margins (Fig. 2A).

Taxonomic treatment. — Revision of generic boundaries in the *Bahia* alliance is necessary to achieve a taxonomy that reflects evidently monophyletic groups. *Florestina* and *Palafoxia* constitute well-characterized clades and results from the limited sampling conducted for this study are consistent with the morphological argument (Turner & Morris, 1976) that the two genera be maintained as distinct. *Platyschkuhria* is also distinctive and well-supported as a clade separate from *Amauriopsis* plus *Hymenothrix* based on cpDNA data. *Nothoschkuhria* was erected for *Schkuhria degenerica* (Roth) R.E.Fr. (Baldwin, 2015) based on evidence that it does not constitute a clade with *Schkuhria* s.str.

Amauriopsis (= *Bahia* "series Alternifoliae" sensu Ellison, 1964) and *Hymenothrix* are not as well characterized morphologically and results of this study, insofar as resolution is available, indicate that neither is monophyletic (Figs. 3, 4). Merger of *Amauriopsis* and *Hymenothrix* into a common, monophyletic genus characterized within the *Bahia* alliance in part by alternate leaves, obtuse to acute style-branch apices, often zygomorphic disc corollas (of outer florets), and pappus scales generally ≥10 or absent would simplify the taxonomy. *Hymenothrix* has priority for such a group (see Fig. 3).

Clades of the *Bahia* alliance represented by *Apostates*, North American *Bahia* "series Oppositifoliae" (including *Picradeniopsis*), and *Nothoschkuhria* and by *Achyropappus*, *B. ambrosioides*, and *Holoschkuhria* are arguably more heterogeneous and challenging to diagnose morphologically than the main alternate-leaved clade (i.e., *Hymenothrix* as recircumscribed

here). Treating the members of those heterogeneous clades in a common genus, *Bahia* (*B. ambrosioides* is the type), would result in a morphologically incongruous taxon. A more practical solution is to retain the distinctive *Apostates* as a genus and to recognize its primarily North American sister group as a separate genus, *Picradeniopsis* (see Fig. 3). Instead, recognizing *Cephalobembix* for the $x = 11$ clade of *B. bigelovii*, *B. neomexicana*, *B. pringlei* (not sampled here but highly similar to *B. xylopoda*), *B. schaffneri*, and *B. xylopoda* and recognizing *Picradeniopsis* for the $x = 12$ taxa (*B. absinthifolia*, *B. oppositifolia*, *B. woodhousei* (A.Gray) A.Gray) in the same sister-clade to *Apostates* is complicated in part by uncertainty about the phylogenetic relationships of *B. woodhousei* and whether or not a group comprising *B. absinthifolia*, *B. oppositifolia*, and *B. woodhousei* is monophyletic or paraphyletic. In *Picradeniopsis*, the names *P. oppositifolia* (Nutt.) Rydb. (= *Bahia oppositifolia*) and *P. woodhousei* (A.Gray) Rydb. (= *Bahia woodhousei*) are already available for the $x = 12$ taxa.

Under the above taxonomy, the genera *Achyropappus* sensu Turner (2012), *Apostates* (monotypic), *Bahia* (monotypic), and *Holoschkuhria* (monotypic) continue to be recognized.

Key to genera of the *Bahia* alliance

1. Leaves alternate throughout, sometimes basal 2
1. Leaves opposite throughout, or distally alternate 4
2. Ray florets 0; disc corollas actinomorphic; pappus scales 8, alternate scales awned .... ***Nothoschkuhria***
2. Ray florets 0 or 3–25; all or outermost disc corollas often zygomorphic; pappus scales (0–)10–18, ± uniformly awned or awnless 3
3. Perennials; leaves often basal, blades usually entire (rarely trifid) .... ***Platyschkuhria***
3. Annuals, biennials, or, rarely, short-lived perennials; leaves cauline, blades ternately to triternately divided .... ***Hymenothrix***
4. Heads radiate with ray and disc corollas pinkish to purplish, or discoid with corollas white to pinkish or purplish; style branch apices acuminate; pappus scales 4–10 5
4. Heads radiate with ray corollas yellow or white and disc corollas yellow, or discoid with corollas yellowish or white to violet-pink; style branch apices obtuse or acute; pappus scales usually 8–18, rarely fewer or 0 6
5. Leaf blades entire or crenate to biternately dissected; heads discoid; disc corollas ± actinomorphic; style branches abaxially papillate distally .... ***Florestina***
5. Leaf blades entire; heads radiate or discoid; disc corollas ± actinomorphic or ± zygomorphic; style branches abaxially papillate throughout .... ***Palafoxia***
6. Leaf blades pinnately or bipinnately divided, lobes linear-filiform; phyllaries usually glandular-punctate; ray florets (0)1–4(5), often inconspicuous; disc florets ≤20 .... ***Schkuhria***
6. Leaf blades entire or lobed to ternately dissected, lobes linear to ovate; phyllaries not glandular-punctate, glands, if present, often sessile, not deeply impressed; ray florets 0 or 2–20; disc florets 15–120 7

7. Leaf blades entire, elliptic to widely ovate; heads discoid 8
7. Leaf blades usually ternately dissected, elliptic to cordate or deltate in outline, rarely lobed or entire, lanceolate; heads radiate or discoid 9
8. Shrubs; leaves resinous, punctate; corolla lobes 5 .... ***Apostates***
8. Herbs; leaves velutinous; corolla lobes 4 .. ***Holoschkuhria***
9. Annuals; heads radiate; phyllaries 4–5; ray florets 2–5; cypselae 3(–4)-sided .... ***Achyropappus***
9. Annuals or perennials; heads radiate or discoid; phyllaries 8–24 or, if 5–7, heads discoid or plants suffrutescent; ray florets 0 or 5–20; cypselae 4-sided 10
10. Suffrutescent perennials; ray florets 4–9, corollas white or cream-colored .... ***Bahia***
10. Suffrutescent or herbaceous perennials or annuals; ray florets 0 or 3–15, corollas yellow .... ***Picradeniopsis***

New combinations for the proposed taxonomic changes

Hymenothrix autumnalis (W.L.Ellison) B.G.Baldwin, **comb. nov.** ≡ *Bahia autumnalis* W.L.Ellison in Rhodora 66: 199. 1964 ≡ *Amauriopsis autumnalis* (W.L.Ellison) B.L.Turner in Phytoneuron 2010-10: 2. 2010 – Holotype: Mexico, Nuevo León, 31 mi S of Galeana on the Ascension road, 1 Oct 1960, *M.C. Johnston & J. Crutchfield 5856* (TEX barcode 00374146! [digital image]; isotype: MEXU barcode MEXU 00069068! [digital image]).

Hymenothrix biternata (A.Gray) B.G.Baldwin, **comb. nov.** ≡ *Bahia biternata* A.Gray in Smithsonian Contr. Knowl. 5(6) [Pl. Wright. 2]: 95–96. 1853 ≡ *Schkuhria biternata* (A.Gray) A.Gray in Proc. Amer. Acad. Arts 9: 199. 1874 ≡ *Eriophyllum biternatum* (A.Gray) Kuntze, Revis. Gen. Pl. 1: 337. 1891 ≡ *Villanova biternata* (A.Gray) Wooton & Standl. in Contr. U.S. Natl. Herb. 19: 725. 1915 ≡ *Amauriopsis biternata* (A.Gray) B.L.Turner in Phytoneuron 2010-10: 2. 2010 – Holotype: U.S.A., New Mexico, gravelly hills near Ojo de Gavilan, Aug 1851, *C. Wright 1256* (GH barcode 00263044! [digital image]; isotypes: GH barcode 00004042!, K(2) barcodes K001065695! & K001065696!, NY barcode 00162426!, PH barcode 00007419! [all as digital images]).

Hymenothrix dissecta (A.Gray) B.G.Baldwin, **comb. nov.** ≡ *Amauria? dissecta* A.Gray in Mem. Amer. Acad. Arts, n.s., 4(1) [Pl. Fendler.]: 104. 1849 ≡ *Villanova chrysanthemoides* A.Gray in Smithsonian Contr. Knowl. 5(6) [Pl. Wright. 2]: 96. 1853, non *V. dissecta* DC., Prodr. 6: 75. 1836 ≡ *Bahia chrysanthemoides* (A.Gray) A.Gray in Proc. Amer. Acad. Arts 19: 28. 1883 ("1884"), nom. illeg. ≡ *Bahia dissecta* (A.Gray) Britton in Trans. New York Acad. Sci. 8(3–4): 68. 1889 ≡ *Eriophyllum chrysanthemoides* (A.Gray) Kuntze, Revis. Gen. Pl. 1: 337. 1891, nom. illeg. ≡ *Villanova dissecta* (A.Gray) Rydb. in Bull. Torrey Bot. Club 37: 333. 1910, nom. illeg. ≡ *Amauriopsis dissecta* (A.Gray) Rydb. in Britton & al., N. Amer. Fl. 34(1): 37. 1914 – Holotype:

U.S.A., New Mexico, a few miles E of Mora River, Aug 1847, *A. Fendler 537* (GH barcode 00000807! [digital image]).

= *Bahia dissecta* var. *anisopappa* S.F.Blake in J. Wash. Acad. Sci. 25: 319. 1935 – Holotype: Mexico, Baja California, Sierra San Pedro Martir, below La Grulla, sandy soil along La Sanca Creek, 2040 m, 17 Sep 1930, *I.L. Wiggins & D. Demaree 4870* (US barcode 00124779! [digital image]; isotypes: CAS barcode 0001039!, LL barcode 00374147!, UC barcode UC 535826! [all except UC as digital images]).

Hymenothrix glandulopubescens (Waterf.) B.G.Baldwin, **comb. nov.** ≡ *Hymenopappus glandulopubescens* Waterf. in Rhodora 59: 97. 1957 – Holotype: Mexico, Durango, 11 mi W of Durango, grassy flats, 10 Aug 1956, *Waterfall 12576* (OKLA barcode 100109! [digital image]; isotypes: GH barcode 00009326!, TEX barcode 00374183! [all as digital images]).

= *Bahia glandulosa* Greenm. in Proc. Amer. Acad. Arts 39(5): 116–117. 1904, non *Hymenothrix glandulosa* S.Watson in Proc. Amer. Acad. Arts 23: 278. 1888 ≡ *Amauriopsis glandulosa* (Greenm.) B.L.Turner in Phytoneuron 2010-10: 3. 2010 – **Lectotype, designated here** (lectotype designation has been attributed erroneously to R. McVaugh, Fl. Novo-Galiciana 12: 110. 1984): Mexico, Durango, vicinity of the City of Durango, Apr–Nov 1896, *E. Palmer 492* (GH barcode 00004053! [digital image]; isolectotypes: F barcode v0049736F!, GH barcode 00004054!, K barcode K000502265!, MO barcodes MO-193588! & MO-193589!, UC barcode UC 135316!, US barcode 00124780!, VT barcode UVMVT027146! [all except UC as digital images]). Gray referred to two collections in the protologue (*E. Palmer 492*, indicated erroneously as "Parker" there, and *C.G. Pringle 308*) that must be regarded as syntypes of *Bahia glandulosa*; Ellison (1964) mistakenly referred to Palmer's collection as holotype and did not choose between the two sheets of that collection at GH (i.e., barcodes 00004053, 00004054), although he acknowledged that only one sheet can be holotype. McVaugh also referred to Palmer's collection at GH as the type (see above), without mentioning Pringle's collection or presence of two sheets of *Palmer 492* at GH.

Hymenothrix janakosana (B.L.Turner) B.G.Baldwin, **comb. nov.** ≡ *Amauriopsis janakosana* B.L.Turner in Phytoneuron 2010-10: 3–4, fig. 1. 2010 – Holotype: Mexico, Chihuahua, Municipio Ojinaga, NE flank of Sierra de Hechiceros, 950–1150 m, 2 Oct 1972, *F. Chiang, T. Wendt & M.C. Johnston 9665* (LL barcode 00055730! [image in protologue]).

Hymenothrix pedata (A.Gray) B.G.Baldwin, **comb. nov.** ≡ *Bahia pedata* A.Gray in Smithsonian Contr. Knowl. 3(5) [Pl. Wright. 1]: 123. 1852 ≡ *Schkuhria pedata* (A.Gray) A.Gray in Proc. Amer. Acad. Arts 9: 199. 1874 ≡ *Eriophyllum pedatum* (A.Gray) Kuntze, Revis. Gen. Pl. 1: 337. 1891 ≡ *Amauriopsis pedata* (A.Gray) B.L.Turner in Phytoneuron 2010-10: 4. 2010 – Holotype: U.S.A., between western Texas and El Paso, New Mexico (in protologue: "the record

of the locality lost"), May–Oct 1849, *C. Wright 387* (GH barcode 00004044! [digital image]; isotypes: GH(2) barcodes 00004045! & 00004046!, NY barcode 00162434!, US barcode 00124786! [all as digital images]).

Picradeniopsis absinthifolia (Benth.) B.G.Baldwin, **comb. nov.** ≡ *Bahia absinthifolia* Benth., Pl. Hartw.: 18. 1839 ≡ *Eriophyllum absinthifolium* (Benth.) Kuntze, Revis. Gen. Pl. 1: 336. 1891 – Holotype: Mexico, Aguascalientes, 1837, *Hartweg 128* (K barcode K000502262! [digital image]; isotypes: E barcode E00433061!, GH barcode 00261700!, LD barcode 1046146! [all as digital images]).

= *Bahia dealbata* A.Gray in Mem. Amer. Acad. Arts, n.s., 4(1) [Pl. Fendler.]: 99. 1849 ≡ *Bahia absinthifolia* var. *dealbata* (A.Gray) A.Gray in Smithsonian Contr. Knowl. 3(5): 121. 1852 ≡ *Picradeniopsis dealbata* (A.Gray) Wooton & Standl. in Contr. U.S. Natl. Herb. 16(4): 192. 1913 – **Lectotype (designated here):** Mexico, Chihuahua, valley between Mapimi and Guajuquilla, *Dr. Gregg s.n.* (GH barcode 00261701! [digital image]).

Based on McVaugh's (1970) discussion of Hartweg's itinerary in Mexico, K000502262 (*Hartweg 128*), from Aguascalientes, is the evident holotype of *Bahia absinthifolia*, as also concluded by Ellison (1964) and McVaugh (1984); another specimen at Kew indicated as *Hartweg 128* from Zacatecas (K000502264) may be an isotype. In the protologue of *B. dealbata*, Gray referred to two collections that must be regarded as syntypes; Ellison's (1964) mistaken reference to the collection from the valley between Mapimi and Guajuquilla (GH 00261701) as holotype and to the other collection indicated in the protologue, at "Cadenas" (GH 00261702), as paratype has been misinterpreted as a lectotypification (e.g., W.T. Kittridge, 2007, annotation on GH 00261701).

Picradeniopsis bigelovii (A.Gray) B.G.Baldwin, **comb. nov.** ≡ *Bahia bigelovii* A.Gray in Emory, Rep. U.S. Mex. Bound. Bot. 2(1): 96. 1859 ≡ *Schkuhria bigelovii* (A.Gray) A.Gray in Proc. Amer. Acad. Arts 9: 199. 1874 ≡ *Eriophyllum bigelovii* (A.Gray) Kuntze, Revis. Gen. Pl. 1: 337. 1891 – Holotype: U.S.A., W Texas, valley of the Limpio, Jul 1852, *Bigelow s.n.* (GH barcode 00004040! [digital image]; apparent isotype: NY barcode 00162425! [digital image]).

Picradeniopsis multiflora (Hook. & Arn.) B.G.Baldwin, **comb. nov.** ≡ *Schkuhria multiflora* Hook. & Arn. in J. Bot. (Hooker) 3: 322. 1841 (replacement name for *Achyropappus schkuhrioides* D.Don ex Hook. & Arn. in J. Bot. (Hooker) 3: 322. 1841, nom. illeg., non *Achyropappus schkuhrioides* Link & Otto, Icon. Pl. Rar.: 59, pl. 30. 1829) ≡ *Bahia gilliesii* A.Gray in Proc. Amer. Acad. Arts 19: 28. 1884, non *Bahia multiflora* (Nutt.) Nutt. in Trans. Amer. Philos. Soc., n.s., 7: 373. 1841 – Holotype: Argentina, Mendoza, Chilicito, *Gillies 147* (K barcode K000502243! [digital image]); isotype: E barcode E00265077! [digital image]).

= *Schkuhria neomexicana* A.Gray in Mem. Amer. Acad. Arts, n.s. 4(1) [Pl. Fendler.]: 96. 1849 ("*Neo-Mexicana*") ≡ *Amblyopappus neomexicanus* (A.Gray) A.Gray in Torrey,

Pacif. Railr. Rep. 4(5): 106. 1857 ≡ *Bahia neomexicana* (A.Gray) A.Gray in Proc. Amer. Acad. Arts 19: 27–28. 1883 ("1884") ≡ *Achyropappus neomexicanus* (A.Gray) A.Gray ex Rydb., Fl. Colorado: 377. 1906 ≡ *Cephalobembix neomexicana* (A.Gray) Rydb. in Britton & al., N. Amer. Fl. 34(1): 46. 1914 – Holotype: U.S.A., New Mexico, Santa Fé, margin of fields, Jul–Aug 1847, *A. Fendler 458* (GH barcode 00011828! [digital image]; isotypes: E barcode E00433062!, GH barcode 00011829! [all as digital images]).

= *Schkuhria pusilla* Wedd., Chlor. Andina 1: 73, pl. 14b. 1856 ("1855") ≡ *Rothia pusilla* (Wedd.) Kuntze, Revis. Gen. Pl. 3(3): 170. 1898 ≡ *Schkuhria multiflora* var. *pusilla* (Wedd.) Cabrera in Anales Soc. Ci. Argent. 114: 192. 1932 – Holotype: Bolivia, near Potosi, *d'Orbigny 1403* (P n.v.).

= *Rothia intermedia* Kuntze, Revis. Gen. Pl. 3(3): 170. 1898 – **Lectotype (designated here):** Bolivia, Challapata, 3 Nov 1892, *O. Kuntze s.n.* (NY barcode 00232812! [digital image]; isotype: NY barcode 00232811! [digital image]).

= *Schkuhria pusilla* var. *aristata* R.E.Fr. in Nova Acta Regiae Soc. Sci. Upsal., ser. 4, 1(1): 85. 1905 ≡ *Schkuhria multiflora* var. *aristata* (R.E.Fr.) Cabrera in Anales Soc. Ci. Argent. 114: 193. 1932 – Holotype: Argentina, Provincia Jujuy, Moreno, ca. 3500 m, 12 Dec 1901, *R.E. Fries 812b* (S n.v.; isotype: CORD barcode CORD 00004735! [digital image]).

= *Schkuhria pusilla* var. *longipedicellata* Hauman in Anales Soc. Ci. Argent. 86: 328. 1918 ("*longepedicellata*") – Holotype: Argentina, Precordillera of San Juan, Carmen Alto, Feb 1897, *Bodenbender s.n.* (BR barcode 00000552823! [digital image]).

Lectotypification of *Rothia intermedia* is necessary because neither of the two sheets of Kuntze's type collection at NY was designated as the holotype.

Picradeniopsis pringlei (Greenm.) B.G.Baldwin, **comb. nov.** ≡ *Bahia pringlei* Greenm. in Proc. Amer. Acad. Arts 32: 309–310. 1897 – Holotype: Mexico, Hidalgo, valley near Tula, calcareous bluffs, 2070 m, 6 Aug 1896, *C.G. Pringle 6407* (GH barcode 00004055! [digital image]; isotypes AC barcode 00319337!, BR barcode 00000526170!, CAS barcode 0001036!, CM barcode 2259!, E barcode E00433060!, F barcode v0049737F!, GOET barcode GOET001078!, JE barcode JE00004603!, K barcode K000502260!, M barcode M-0030106!, MEXU(2) barcodes MEXU 01220331! & MEXU 01220332!, MIN barcode 1000405!, MO barcode MO-193590!, NDG barcode NDG61577!, NY barcode 00162441!, PH barcode 00007418!, S No. S08-622!, TEX barcode 00000403!, UC barcode UC 2026178!, US(2) barcodes 00124787! & 00931060!, VT barcode UVMVT027147! [all except UC as digital images]).

Picradeniopsis schaffneri (S.Watson) B.G. Baldwin, **comb. nov.** ≡ *Bahia schaffneri* S.Watson in Proc. Amer. Acad Arts 26: 142. 1891 ≡ Holotype: Mexico, San Luis Potosí, sandy plains near San Luis Potosí, 18 May 1889, *C.G. Pringle 3028* (GH barcode 00004056! [digital image]).

Picradeniopsis schaffneri var. *aristata* (Rydb.) B.G.Baldwin, **comb. nov.** ≡ *Bahia aristata* Rydb. in Britton & al., N. Amer. Fl. 34: 36. 1914 ≡ *Bahia schaffneri* var. *aristata* (Rydb.) W.L.Ellison in Rhodora 66: 284. 1964 – Holotype: Mexico, San Luis Potosí, hacienda of Angostura, alkaline plains, 11 Jul 1891, *C.G. Pringle 5127* (GH barcode 00004049! [digital image]).

Picradeniopsis xylopoda (Greenm.) B.G.Baldwin, **comb. nov.** ≡ *Bahia xylopoda* Greenm. in Proc. Amer. Acad. Arts 34: 577. 1899 – Holotype: Mexico, Hidalgo, bare hills above Pachuca, 2590 m, 30 Jul 1898, *C.G. Pringle 6931* (GH barcode 00004057! [digital image]; isotypes AC barcode 00319338!, BR barcode 00000526203!, C barcode C10007005!, CM barcode 2260!, E barcode E00433059!, F barcode v0049738F!, GOET barcode GOET001076!, JE barcode JE00004606!, K barcode K000502261!, M barcode M-0030108!, MEXU barcode MEXU 01220333!, MIN barcode 1000406!, MO barcode MO-193591!, NDG barcode NDG61580!, NY barcode 00162442!, PH barcode 00007415!, POM barcode RSA0000943!, RM barcode RM0000813!, S No. S08-621!, TEX barcode 00000404!, UC barcode UC 89925!, US(2) barcodes 00124788! & 00931061!, VT barcode UVMVT027149! [all except UC as digital images]).

= *Bahia ehrenbergii* Sch.Bip. ex Rydb. in Britton & al., N. Amer. Fl. 34: 35. 1914 – Holotype: Mexico, *Ehrenberg 362* (GH barcode 00004051! [digital image]).

Extreme endangerment of *Apostates*. — Based on the last botanical survey on Rapa (Wood & Perlman, 2002), *Apostates rapae* is known from only two individuals, which occur within meters of each other along the remote northern seacliffs of Rapa, east of Tupua'i Bay (Fig. 1). That site is known as Tegaere by local Rapan fisherman and can be approached by boat followed by a short swim to shore near the headland cliffs of Auroa Point. Specialized climbing line and gear were used by K.R. Wood to rappel down to the plants from a safe vantage above. The sea-cliff habitat of *A. rapae* is an open mesic shrubland dominated by native species <2 m in height, including the shrubs *Myoporum rapense* F.Br., *Scaevola taccada* var. *tuamotuensis* H.St.John, *Eugenia reinwardtiana* (Blume) DC., and *Osteomeles anthyllidifolia* (Sm.) Lindl., associated herbs including *Dianella intermedia* var. *punctata* F.Br., *Portulaca lutea* Sol. ex G.Forst., and *Lycium sandwicense* A.Gray, the sedge *Cyperus javanicus* Houtt., and grasses *Chrysopogon aciculatus* (Retz.) Trin. and *Ischaemum stokesii* F.Br., in addition to the ferns *Asplenium obtusatum* G.Forst. and *Polystichum rapense* E.D.Br.

The main threats to the habitat of *A. rapae* include fire, feral goats, and non-native invasive plants. Goats were observed eating native plants in this region and contribute to increased erosion and rockslides. Invasive non-native plant taxa include *Psidium cattleianum* Sabine, *Miscanthus floridulus* (Labill.) Warb.*, Scirpus nodosus* Rottb., *Sporobolus elongatus* R.Br., and *Eleusine indica* (L.) Gaertn. Another serious threat for *A. rapae* is reduced fitness (loss of vigor

and reproductive success) with loss of genetic diversity and vulnerability to stochastic events (e.g., landslide) with so few existing individuals. When evaluated using the International Union for Conservation of Nature (IUCN) criteria for endangerment (IUCN, 2012, see also http://www.iucnredlist.org/technical-documents/categories-and-criteria), *A. rapae* falls into the Critically Endangered (CR) category, which designates *A. rapae* as facing the highest risk of extinction; it meets the IUCN criteria in having a range of less than 100 km², an area of occupancy of less than 10 km², is known from a single location with a continuing decline inferred for the number of mature individuals, a continuing decline in the quality of habitat, and a population size less than 50 mature individuals. Our formal evaluation can be summarized by the following IUCN hierarchical alphanumeric coding system of criteria and subcriteria: (CR B1ab(i,ii,iii,v) + 2ab(i,ii,iii,v); D).

The evidence presented here that the critically endangered *Apostates* represents a unique biogeographic pattern in southeastern Polynesia and an exceptional example of long-distance dispersal across the tropical Pacific gives added justification to Lander's (1989) proposal of adopting Melville's (1979) "Fire Brigade" conservation approach of ex situ cultivation of *Apostates* as soon as live cuttings or seeds can be obtained. Phenological considerations indicate that efforts to obtain seed may be most successful late in the year: *A. rapae* was observed in flower only in September 1921, by Stokes; subsequent collections made by Anderson, Fosberg, and St. John in July 1934 were without flower or fruit, as were the more recent collections made by Wood in May 2002 with persistent capitulescence branches from the previous flowering season (Fig. 2E).

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Appendix 1. Voucher information for collections included in molecular phylogenetic analyses of the *Bahia* alliance. GenBank accession numbers are listed in the following order: ITS, ETS, 3′*ndhF*, 5′*trnK* intron, *rpl16* intron, and *psbA-trnH* spacer. An asterisk (*) indicates new sequences.

Achyropappus anthemoides Kunth, MEXICO, Mexico State, 4.5 mi W of Santa Maria del Monte, *Keil 15420, Luckow* (UC), AF374894, KX260999*, KX261129*, KX261167*, KX261091*, KX261048*; ***Achyropappus queretarensis*** B.L.Turner, MEXICO, Hidalgo, 1 mi S of Maguey, *Spellenberg, Zimmerman, Zucker & Cunningham 8344* (UC), KX260963*, KX261000*, KX261130*, –, KX261092*, KX261049*; ***Amauriopsis autumnalis*** (W.L.Ellison) B.L.Turner [≡ ***Hymenothrix autumnalis*** (W.L.Ellison) B.G.Baldwin, as treated here], MEXICO, Coahuila, 8 km W of Saltillo, *Villarreal 6604, Carranza, Comparán, Lozano* (TEX), KX260964*, KX261001*, KX261131*, KX261168*, KX261093*, KX261050*; Nuevo Leon, 20 km NE of Doctor González, *Villarreal 7972, Carranza* (TEX), KX260965*, KX261002*, KX261132*, KX261169*, KX261094*, KX261051*; ***Amauriopsis biternata*** (A.Gray) B.L.Turner [≡ ***Hymenothrix biternata*** (A.Gray) B.G.Baldwin, as treated here], U.S.A., Arizona, Maricopa Co., *Doan 1037, Damrel* (ASU), KX260966*, KX261003*, KX261133*, KX261170*, KX261095*, KX261052*; Pinal Co., *Van Devender & Van Devender 93-789* (UC), KX260967*, KX261004*, KX261134*, KX261171*, KX261096*, KX261053*; ***Amauriopsis dissecta*** (A.Gray) Rydb. [≡ ***Hymenothrix dissecta*** (A.Gray) B.G.Baldwin, as treated here], U.S.A., Arizona, Coconino Co., *Scott 1205* (ASC), KX260968*, KX261005*, KX261135*, KX261172*, KX261097*, KX261054*, *Scott 1258* (ASC, UC), AF374889, KX261006*, KX261136*, KX261173*, KX261098*, KX261055*; Gila Co., *Imdorf 122, Rebman* (UC), KX260969*, KX261007*, KX261137*, KX261174*, –, KX261056*; ***Amauriopsis glandulosa*** (Greenm.) B.L.Turner [≡ ***Hymenothrix glandulopubescens*** (Waterf.) B.G.Baldwin, as treated here], MEXICO, Durango, Municipio Súchil, Rancho Temazcal, *Alvarado 326* (TEX), KX260970*, KX261008*, –, KX261175*, KX261099*, KX261057*; ***Amauriopsis pedata*** (A.Gray) B.L.Turner [≡ ***Hymenothrix pedata*** (A.Gray) B.G.Baldwin, as treated here], U.S.A., Texas, Presidio Co., *Scudday 438* (UC), KX260971*, KX261009*, KX261138*, KX261176*, KX261100*, KX261058*; ***Apostates rapae*** (F.Br.) Lander, FRENCH POLYNESIA, Rapa, Tupuaki Bay region, eastern cliffs (Auroa), *Wood 9789* (PTBG), KX260972*, KX261010*, KX261139*, KX261177*, KX261101*, KX261059*; same locality, *Wood 9790* (PTBG), KX260973*, KX261011*, KX261140*, KX261178*, KX261102*, KX261060*; ***Bahia absinthifolia*** Benth. [≡ ***Picradeniopsis absinthifolia*** (Benth.) B.G.Baldwin, as treated here], U.S.A., New Mexico, Eddy Co., *Baldwin 967, Bainbridge* (UC), AF374892, KX261012*, KX261141*, KX261179*, KX261103*, KX261061*; MEXICO, San Luis Potosi, Highway 49 at Kilometer 40 NW of San Luis Potosi, and then 2 km E of highway, *Spellenberg & Mahrt 10714* (UC), KX260974*, KX261013*, KX261142*, KX261180*, KX261104*, KX261062*; ***Bahia ambrosioides*** Lag., CHILE, Aconcagua Province, Aconcagua, *Cheese & Watson 4574* (UC), KX260975*, KX261014*, KX261143*, KX261181*, KX261105*, KX261063*; ***Bahia bigelovii*** A.Gray [≡ ***Picradeniopsis bigelovii*** (A.Gray) B.G.Baldwin, as treated here], U.S.A., Texas, Jeff Davis Co., *Powell 6384, Powell* (SRSC), individuals 1, 2, KX260976*, KX261015*, KX261144*, KX261182*, KX261106*, KX261064*; individual 3, KX260977*, KX261016*, –, –, –, –; ***Bahia neomexicana*** (A.Gray) A.Gray [≡ ***Picradeniopsis multiflora*** (Hook. & Arn.) B.G.Baldwin, as treated here], U.S.A., Arizona, Mohave Co., *Higgins 23490* (BRY), KX260978*, KX261017*, KX261145*, KX261183*, KX261107*, KX261065*; California, San Bernardino Co., *Boyd 5209* (UC), KX260979*, KX261018*, –, –, –, –; BOLIVIA, Departmento La Paz, Provincia Camacho, shore of Lake Titicaca, *Feuerer 5658* (TEX), KX260980*, KX261019*, –, –, –, –; ***Bahia oppositifolia*** (Nutt.) DC. [≡ ***Picradeniopsis oppositifolia*** (Nutt.) Rydb., as treated here], U.S.A., Wyoming, Fremont Co., *Hartman 3153* (UC), AF374893, KX261020*, KX261146*, KX261184*, KX261108*, KX261066*; ***Bahia schaffneri*** S.Watson var. ***schaffneri*** [≡ ***Picradeniopsis schaffneri*** (S.Watson) B.G.Baldwin var. ***schaffneri***, as treated here], MEXICO, San Luis Potosi, 16.5 mi N of Charcas, *Henrickson B6388* (UC), KX260981*, KX261021*, –, –, –, –; ***Bahia woodhousii*** (A.Gray) A.Gray [≡ ***Picradeniopsis woodhousei*** (A.Gray) Rydb., as treated here], U.S.A., New Mexico, De Baca Co., *Higgins 8652* (ASU), KX260982*, KX261022*, KX261147*, KX261185*, KX261109*, KX261067*; Texas, Randall Co., *Higgins 11316* (ASU), KX260983*, –, –, –, –, –; ***Bahia xylopoda*** Greenm. [≡ ***Picradeniopsis xylopoda*** (Greenm.) B.G.Baldwin, as treated here], MEXICO, Hidalgo, Municipio Pachuca, 6 km N of Pachuca, *Garcia P. 1452* (LL), KX260984*, KX261023*, –, –, –, –; Veracruz (near Puebla border), Municipio Perote, 9 km above and NW of Frijol Colorado, *Nee & Taylor 28852* (TEX), KX260985*, KX261024*, KX261148*, KX261186*, KX261110*, KX261068*; NW of Frijol Colorado, *Nee 32946* (UC), KX260986*, KX261025*, KX261149*, KX261187*, KX261111*, KX261069*; ***Chaetymenia peduncularis*** Hook. & Arn., MEXICO, Jalisco, road between Ameca and Atenguillo at Puente El Rialito, *Baldwin 978, Panero, Bainbridge, Francisco-Ortega* (UC), AF374900, KX261026*, KX261150*, KX261188*, –, KX261070*; ***Florestina platyphylla*** (B.L.Rob. & Greenm.) B.L.Rob & Greenm., MEXICO, Oaxaca, 7.3 mi NW of Totolapan, *Keil 15532, Luckow* (UC), AF374883, KX261027*, KX261151*, KX261189*, KX261112*, KX261071*; ***Florestina tripteris*** DC., MEXICO, Nuevo León, between Nuevo Laredo and Monterrey, *Baldwin 970, Panero, Bainbridge, Francisco-Ortega* (UC), AF374884, KX261028*, KX261152*, KX261190*, KX261113*, KX261072*; ***Holoschkuhria tetramera*** H.Rob., PERU, Departmento Amazonas, Provincia Luya, Distrito Camporrendondo, Jaipe, *Campos, Campos & Sembrera 3654* (MO), KX260987*, KX261029*, KX261153*, KX261191*, KX261114*, KX261073*; same locality, *Ollgaard & al. 90733* (US), KX260988*, KX261030*, –, –, –, –; ***Hymenothrix loomisii*** S.F.Blake, U.S.A., Arizona, Yavapai Co., *Baker 9647, Wright* (ASU), KX260989*, KX261031*, KX261154*, KX261192*, KX261115*, KX261074*; ***Hymenothrix palmeri*** A.Gray, MEXICO, Chihuahua, 6.1 mi E of Cumbres de Majalca, *Sundberg 2722, Lavin* (TEX), KX260990*, KX261032*, KX261155*, KX261193*, KX261116*, KX261075*; Sonora, Municipio Yecora, NW of Yecora cemetery, *Reina G. 97-1158, Van Devender, Trauba* (TEX), KX260991*, KX261033*, KX261156*, KX261194*, KX261117*, KX261076*; ***Hymenothrix wislizeni*** A.Gray, U.S.A., Arizona, Pima Co., Santa Catalina Mountains, Pima Canyon, *Bainbridge s.n.* (UC), AF374887, KX261034*, KX261157*, KX261195*, KX261118*, KX261077*; New Mexico, Luna Co., *Columbus 1517* (UC), KX260992*, KX261035*, KX261158*, KX261196*, KX261119*, KX261078*; ***Hymenothrix wrightii*** A.Gray, U.S.A., Arizona, Cochise Co., *Baldwin 964, Bainbridge* (UC), AF374888, KX261036*, KX261159*, KX261197*, KX261120*, KX261079*; ***Nothoschkuhria degenerica*** (Kuntze) B.G.Baldwin, BOLIVIA, Provincia Murillo, La Paz (Calacoto), 30 km down Rio La Paz and then rising W (via altiplano), *Beck 7991* (UC), KX260993*, KX261037*, –, –, –, KX261080*; ***Palafoxia arida*** B.L.Turner & M.I.Morris var. ***arida***, U.S.A., California, San Diego Co., *Baldwin 784, Kyhos, Martens* (JEPS), AF374881, KX261038*, KX261160*, KX261198*, KX261121*, KX261081*; ***Palafoxia texana*** DC. var. ***texana***, MEXICO, Nuevo León, between Nuevo Laredo and Monterrey, *Baldwin 969, Panero, Bainbridge, Francisco-Ortega* (UC), AF374882, KX261039*, KX261161*, KX261199*, KX261122*, KX261082*; ***Platyschkuhria integrifolia*** (A.Gray) Rydb. var. ***integrifolia***, U.S.A., Wyoming, Fremont Co., *Baldwin 938, Bainbridge* (UC), AF374890 (clone 1)/AF374891 (clone 2), KX261040*, KX261162* (individual 1)/KX261163* (individual 2), KX261200* (individual 1)/KX261201* (individual 2), KX261123* (individual 1)/KX261124* (individual 2), KX261083* (individual 1)/KX261084* (individual 2); ***Schkuhria pinnata*** (Lam.) Kuntze ex Thell., ARGENTINA, Provincia Santiago del Estero, Highway 157, 21 km S of San Pedro, *Clarke 103-03* (UCR) [= var. *abrotanoides* (Roth) Cabrera sensu Heiser (1945)], KX260994*, KX261041*, KX261164*, KX261202*, KX261125*, KX261085*; Provincia Jujuy, 10 km S of Tumbaya, *Clarke 111-07* (UCR) [= var. *octoarista* (DC.) Cabrera sensu Heiser (1945)], KX260995*, KX261042*, KX261165*, –, –, KX261086*; CHILE, Coquimbo, Provincia Elqui, 9 km E of Vicuña up the Elqui River, *Clarke 23-06* (UCR) [= var. *pinnata* sensu Heiser (1945)], –, –, –, –, –, KX261087*; ***Schkuhria schkuhrioides*** (Link & Otto) Thell., MEXICO, State of Mexico, 3 km SE of Huehuetoca, *Rzedowski 28,378* (DS), KX260996*, KX261043*, –, –, –, –; Municipio Teoloyucan, Teoloyucan, *Espinosa Garcia 608* (CAS), KX260997*, KX261044*, –, –, –, –; Municipio Zumpango, shore of Lake Zumpango, *Pérez O. P-150* (UC), KX260998*, KX261045*, KX261166*, –, KX261126*, KX261088*; ***Schkuhria wislizeni*** A.Gray, MEXICO, Durango, Kilometer 93 along Highway 40, *Baldwin 974, Panero, Bainbridge, Francisco-Ortega* (UC), AF374886, KX261046*, –, KX261203*, KX261127*, KX261089*; ***Schkuhria wrightii*** A.Gray, U.S.A., Arizona, Santa Cruz Co., *Keil 19020, Pinkava* (UC), AF374885, KX261047*, –, KX261204*, KX261128*, KX261090*.