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Baja: A New Monospecific Genus Segregated from *Cheilanthes* s. l. (Pteridaceae)

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Abstract—The phylogenetic position of *Cheilanthes brandegeei*, a fern endemic to the Baja California Peninsula of Mexico, was investigated using three plastid markers (*atpA*, *rbcL*, *trnG-R*) and comparative morphology. Here we present robust evidence for the recognition of *C. brandegeei* as a member of the bommeriids, the sister clade to all other cheilanthoid ferns, and evidence that it is sister to all *Bommeria* species within that clade. Because of its distinctive morphology within the bommeriid clade (pinnate leaf architecture, well-developed pseudoindusium, and narrow, concolorous red-brown rhizome scales), here we propose the new genus ***Baja*** to accommodate it. Our results place ***Baja brandegeei*** together with other taxa that have a distribution in the Baja California Peninsula and mainland Mexico, rather than with hypothesized congeners in South America and Africa. Morphological characters traditionally used to classify this species as a *Cheilanthes* (patterns of sporangial distribution, presence of a well-developed pseudoindusium, and fractiferous petioles) are extensively homoplasious across cheilanthoids. We identify three characters that unite the newly expanded bommeriid clade: leaf indument of acicular trichomes, reticulate-cristate perispore morphology, and lateral initiation of the gametophyte meristem.

Keywords—Baja California, *Bommeria*, bommeriid ferns, cheilanthoid ferns, gametophyte development, plastid phylogeny.

Pteridaceae is one of the most species-rich and ecologically diverse fern families (Schuettpelz et al. 2007). Cheilanthoideae (sensu PPG I 2016) comprises nearly half the family, including more than 400 species adapted to seasonally-xeric habitats worldwide. Genera in this group have been notoriously difficult to circumscribe based on morphology alone, and these difficulties are often attributed to extensive convergent evolution in arid environments (Tryon and Tryon 1973, 1982). Early molecular studies (Gastony and Rollo 1995, 1998) confirmed that several large genera of cheilanthoid ferns, including *Cheilanthes* Sw., *Doryopteris* J.Sm., *Notholaena* R.Br., and *Pellaea* Link, were indeed polyphyletic. Subsequent molecular analyses of a broader sampling of cheilanthoids (Kirkpatrick 2007; Windham et al. 2009; Eiserhardt et al. 2011; Yesilyurt et al. 2015) have established a reliable phylogenetic framework for studying cheilanthoid diversification, identifying well supported monophyletic subgroups that have been segregated as new or recircumscribed genera; e.g. *Adiantopsis* Fée (Link-Pérez et al. 2011), *Calciphilopteris* Yesilyurt & H.Schneid. (Yesilyurt and Schneider 2010), *Gaga* Pryer, F.W.Li & Windham (Li et al. 2012), *Lytoneuron* (Klotzsch) Yesilyurt (Yesilyurt et al. 2015), *Myriopteris* Fée (Grusz and Windham 2013), and *Ormopteris* J.Sm. (Yesilyurt et al. 2015). Molecular data have also pinpointed several enigmatic species that have been placed within one genus due to some degree of morphological similarity, but whose genetic signature better supports their inclusion in another (e.g. the recent transfer of *Adiantum senae* Baker into *Adiantopsis* by Schuettpelz et al. 2014).

The focus of our study is one such species, currently known as *Cheilanthes brandegeei* D.C.Eaton. *Cheilanthes* has been shown to be polyphyletic by every molecular study with an adequate sampling of cheilanthoid ferns (e.g. Gastony and Rollo 1995, 1998; Kirkpatrick 2007; Eiserhardt et al. 2011; Yesilyurt et al. 2015), with species assigned to this genus found in nearly every major clade of the subfamily Cheilanthoideae. The situation has been improved somewhat by recent transfers of several species groups to *Adiantopsis* (Link-Pérez et al. 2011), *Gaga* (Li et al. 2012), and *Myriopteris* (Grusz and Windham 2013), but currently *Cheilanthes* remains an artificial and relatively uninformative taxonomic concept.

Cheilanthes brandegeei is a small, rock-dwelling fern endemic to the Baja California Peninsula of Mexico (Rebman 2018). It was the namesake of the "*C. brandegeei* group," one of eleven informal species groups of American *Cheilanthes* recognized by Tryon and Tryon (1982). This group included four other species, the Andean endemic *C. fractifera* R.M.Tryon, plus three primarily Mexican taxa *C. aurantiaca* (Cav.) T.Moore, *C. aurea* Baker, and *C. palmeri* D.C.Eaton, and was defined by having fractiferous petioles with large, thin scales on the petiole bases. The leaves of two of the species, *C. brandegeei* and *C. fractifera*, are characterized as sparsely pubescent, whereas the other three exhibit sparse to dense deposits of yellow or orange flavonoids ("farina") on their abaxial leaf surfaces. Recently, the farinose species were transferred to *Notholaena* and are currently named *N. ochracea* (Hook.) Yatsk. & Arbeláez, *N. aureolina* Yatsk. & Arbeláez, and *N. jaliscana* Yatsk. & Arbeláez, respectively (Yatskievych and Arbeláez 2008).

Tryon (1972) hypothesized that the wide geographic separation of *Cheilanthes brandegeei* (Baja California) from its presumed closest relative *C. fractifera* (Peruvian Andes) was a classic example of speciation after long-distance migration. Tryon (1960) had also speculated that *C. brandegeei* might be closely related to the South African/Namibian species *C. deltoidea* Kunze and *C. capensis* (Thunb.) Sw., based on their superficially similar leaf morphologies and fractiferous petioles. The geographic separation among these species was once again interpreted as an example of long-distance dispersal followed by speciation and cited by Moran and Smith (2001) as an indicator of floristic affinity between African and Neotropical pteridophytes.

Recent molecular analyses (Eiserhardt et al. 2011; Windham et al. in prep.) reveal that the non-farinose species considered by Tryon (1960, 1972) to be most closely related to *C. brandegeei* are deeply nested within the large hemionitid clade (Windham et al. 2009). It was somewhat surprising, then, when our ongoing molecular surveys of cheilanthoid ferns supported the earlier suggestion by Cranfill (Cranfill unpub. data, cited in Mickel and Smith 2004) that *C. brandegeei* might be a member of the bommeriid clade, the earliest-diverging group of "core cheilanthoids" (Windham et al. 2009). The other five species in this clade have all been assigned to the genus *Bommeria*

E.Fourn. (Haufler 1979; Ranker 1990; Ranker and Haufler 1990), which is easily distinguished from most other cheilanthoids based on its simple (but often intricately pinnatifid), pentagonal leaf blades with acicular hairs, and unprotected sporangia scattered along the veins. *Cheilanthes brandegeei*, at least superficially, is very distinct from *Bommeria* with fully pinnate-pinnatifid, triangular leaf blades and a deeply lobed, well-differentiated marginal pseudoindusium protecting the submarginally distributed sporangia.

Here we investigate the surprising phylogenetic placement of *Cheilanthes brandegeei* using three plastid markers (*atpA*, *rbcL*, *trnG-R*) in an analysis that includes all species previously hypothesized to be related to it, as well as all recognized taxa of *Bommeria*. We also critically reexamine morphological characters of both the sporophyte and gametophyte that may be useful in explaining relationships within this group. We confirm that *C. brandegeei* is a member of the bommeriid clade, sister to the five recognized species of *Bommeria*. Because *Bommeria* is a morphologically cohesive group, we have chosen to segregate the relatively distinct *C. brandegeei* as a new monospecific genus, herein and henceforth named *Baja* (see Taxonomic Treatment).

Materials and Methods

Taxon Sampling—Material for DNA extraction was obtained from twenty-one specimens, including two individuals of our target species *Baja brandegeei*, the six taxa that Tryon (1960, 1972) and Tryon and Tryon (1982) considered most closely related to it (*Cheilanthes fractifera, C. deltoidea, C. capensis, Notholaena aureolina, N. jaliscana,* and *N. ochracea*), all five species assigned to *Bommeria* by Ranker and Haufler (1990), and the type species of seven other cheilanthoid genera representing five of the major clades recognized by Windham et al. (2009). Based on previous phylogenetic studies of cheilanthoid ferns (Schuettpelz et al. 2007; Eiserhardt et al. 2011; Yesilyurt et al. 2015), we chose *Calciphilopteris ludens* (Wall. ex Hook.) Yesilyurt & H.Schneid., the apparent sister group to "core cheilanthoids," as our outgroup. Vouchers and GenBank accession numbers are indicated in Appendix 1.

DNA Extraction, Amplification, and Sequencing—Genomic DNA was isolated from fresh, silica-dried, and/or herbarium material using either the DNeasy plant mini kit (Qiagen, Valencia, California) or the E.Z.N.A. SP plant DNA kit (Omega Bio-tek, Norcross, Georgia), following modifications described in Schuettpelz and Pryer (2007). Three plastid markers were amplified and sequenced: partial *rbcL* gene (1309 bp) and complete *atpA* gene with partial *atpF* gene, *atpF-atpA* intergenic spacer, and partial *atpA-trnR* intergenic spacer (~1830 bp), as described in Schuettpelz and Pryer (2007); and *trnG-R* intergenic spacer with partial *trnG* gene and partial *trnR* gene (~1100 bp) as described in Schuettpelz et al. (2015). DNA sequence chromatograms were manually edited and assembled using Sequencher 5.0.1 (Gene Codes Corporation 2011). A total of 28 sequences were newly acquired for this study and are deposited in GenBank (Appendix 1).

Phylogenetic Analysis—For each of the three plastid marker datasets (*atpA*, *rbcL*, and *trnG-R*), sequences were first aligned using MUSCLE (Edgar 2004) in Aliview 1.19 (Larsson 2014), and then manually adjusted based on similarity comparisons. Ambiguously aligned regions caused by insertions/deletions were excluded from further analysis. Alignment lengths, number of characters included in analyses, as well as percentages of missing data, variable sites, and phylogenetically informative sites are summarized in Table 1.

Prior to evolutionary model selection, each dataset was partitioned by coding/non-coding and by codon positions. The best model per partition was then selected within three substitution schemes (six model sets: JC, F81, K80, HKY, SYM, GTR) and four among-site rate variations (equal, + I, + G, + I + G) using a neighbor-joining tree and Bayesian information criterion (BIC) in PAUP* 4.0a159 (Swofford 2003). The best fitting models for each dataset are provided in Table 1.

Maximum likelihood analyses were carried out using Garli 2.0 (Zwickl 2006), with "genthreshfortopoterm" set to 1,000,000. The tree with the best likelihood score among four replicates was selected as the best ML tree; bootstrap support for ML (MLBS) was calculated from 1000 replicates, with "genthreshfortopoterm" set to 20,000. The Bayesian/MCMC analyses were carried out in MrBayes v. 3.2.3 (Ronquist et al. 2012) with two independent MCMC runs, each with four chains and 1,000,000 generations. The convergence of parameters was examined and confirmed using Tracer v. 1.6 (Rambaut et al. 2014). Trees were sampled every 1000 generations, and the first 25% of trees were discarded as burn-in.

Tree topologies generated from each individual plastid region were visually inspected and compared for conflicts using bootstrap values ≥ 80% or Bayesian posterior probabilities ≥ 99% (Hillis and Bull 1993; Mason-Gamer and Kellogg 1996). Because no topological incongruencies were observed among the three datasets, they were combined into a single dataset and subject to best model/partition selection in PAUP* 4.0a159 (Swofford 2003), ML analyses in Garli 2.0 (Zwickl 2006), and Bayesian/MCMC analyses in MrBayes v. 3.2.3 (Ronquist et al. 2012) as described above. The portions of the *atpA*, *rbcL*, and *trnG-R* genes analyzed in this study comprised 1811, 1309, and 974 bp, respectively; the concatenated data set included 4094 characters and 28 new sequences (Table 1). Phylogenetic trees were rooted using the outgroup *Calciphilopteris ludens*. All data sets and phylogenetic trees are deposited in the Dryad Digital Repository (George et al. 2019).

Morphology of Sporophytes, Spores, and Gametophytes—Herbarium specimens of *Baja brandegeei* (D.C. Eaton) Windham & L.O.George, *Bommeria ehrenbergiana* (Klotzsch) Underw., *B. elegans* (Davenp.) Ranker & Haufler, *B. hispida* (Mett. ex Kuhn) Underw., *B. pedata* (Sw.) E.Fourn., and *B. subpaleacea* Maxon were carefully examined to compare sporophytic morphologies across the newly recircumscribed bommeriid clade (see Additional Specimens Examined section of Taxonomic Treatment). We focused on those characters determined by Haufler (1979) and Ranker (1990) to be most useful in delimiting the genus *Bommeria*, including leaf shape and dissection, leaf indument, and gametophyte symmetry. In addition, rhizome scale color, presence or absence of fractiferous petioles, extent of sporangial distribution, and pseudoindusial morphology were characterized for all species. Representative photographs of many of these characters were taken using a Leica MZ 12.5 stereomicroscope at 8 × and 40 × magnification. Dry mounted slides of hairs and scales were photographed at 20 × magnification.

Number of spores per sporangium (32 vs. 64) and average spore diameter (μm) were recorded from nineteen herbarium specimens of *Baja brandegeei*, as well as a smaller number of specimens representing all *Bommeria* species and taxa previously hypothesized to be closely related to *Baja brandegeei*. Voucher specimens for these spore studies are listed in the Additional Specimens Examined section of the Taxonomic Treatment. These analyses were conducted by removing 1–5 mature, intact sporangia from select herbarium specimens, opening individual sporangia in small drops of glycerol on a glass slide, and manually counting spores per

Table 1. Sequence characteristics and best-fit sequence evolution models. Multiple models are presented in order of codon position partitions.

Plastid marker	# Taxa	Alignment length (bp)	Characters included (bp)	Missing data (bp / %)	Variable sites (bp / %)	Informative sites (bp / %)	Best-fit model (partitioned)
atpA	21	1847	1811	2229 / 5.9	383 / 21.1	210 / 11.6	GTR + G (first codon position); HKY + I (second codon position); GTR + G (third codon position and non-coding regions)
rbcL	21	1309	1309	97 / 0.4	245 / 18.7	141 /10.8	GTR + I (first codon position); K80 + I (second codon position); HKY + G (third codon position)
trnG-R	21	1261	974	915 / 4.5	448 / 46.0	248 / 25.5	HKY + G
combined	21	4417	4094	3241 / 3.8	1076 / 26.3	635 / 15.5	GTR + I (first codon position); HKY + I (second codon position); GTR + G (third codon position and non-coding regions)

sporangium on a Leica MZ 12.5 stereomicroscope at 50 × magnification and then measuring spores using an ocular micrometer mounted on a Meiji MT5310L phase contrast compound microscope. Perispore morphology, a character outside the scope of this study but considered an important synapomorphy of *Bommeria* by Ranker (1989), was compared among *Baja brandegeei* and all *Bommeria* species using data from Tryon and Lugardon (1991) and Ranker (1989); terminology follows Ranker (1989) (Table 2).

Gametophytes of *Baja brandegeei*, *Cheilanthes fractifera*, *Bommeria elegans*, *B. ehrenbergiana*, *B. pedata*, and *B. subpaleacea* were cultured from spores obtained from herbarium specimens or from refrigerated spores of specimens collected in the field (vouchers indicated in Additional Specimens Examined section of Taxonomic Treatment). Unsterilized spores were sown directly onto Hevly's medium (pH 7; Hevly 1963) in 60 mm diameter petri plates. These plates were sealed with Parafilm and positioned right-side up with 12 h of fluorescent light per day at approximately 23°C. Observations of developing gametophytes were made on a weekly basis over a period of 12 mo. Four plates, with healthy populations of four-month-old *Baja brandegeei* female gametophytes, were subject to a second sowing of spores to assess whether the presence of mature gametophytes influenced the sexuality of newly germinating gametophytes.

Results

Phylogeny—Our phylogenetic tree (Fig. 1) is robustly supported (BS ≥ 80%, PP ≥ 0.99) across most branches. This is the first analysis to include all known species of the bommeriid clade sensu Windham et al. (2009), and we confirm that this group is sister to all the other major clades of cheilanthoids (BS 86%, PP 1.0). *Baja brandegeei* is strongly recovered as a member of the bommeriid clade (BS 100%, PP 1.0) and is not closely related to its hypothesized South American and African relatives *Cheilanthes fractifera, C. capensis,* and *C. deltoidea*, which are strongly supported (BS 100%, PP 1.0) as members of the hemionitid clade and closely related to the South American type species of *Cheilanthes* (*C. micropteris* Sw.). The three other members of the "*Chelianthes brandegeei* group" of Tryon and Tryon (1982), formerly *C. aurantiaca*, *C. aurea,* and *C. palmeri* (labelled *Notholaena ochracea*, *N. aureolina*, and *N. jaliscana,* respectively, in Fig. 1), form a well-supported group (BS 93%, PP 1.0) within the notholaenid clade closely related to the type species of *Notholaena* (*N. trichomanoides* (L.) Desv.) and thus are far removed from *Baja brandegeei*.

Within the bommeriid clade, the two accessions of *Baja brandegeei* are identical to one another and robustly supported as sister to all five species of *Bommeria* (BS 87%, PP 1.0; Fig. 1). Among *Bommeria* species, *B. ehrenbergiana* and *B. subpaleacea* are resolved as sister taxa, and *B. elegans* is, in turn, sister to this pair (BS 89%, PP 1.0). Relationships among this group, *B hispida,* and *B. pedata* are not resolved.

Morphology of Sporophytes, Spores, and Gametophytes—Our comparative investigation of morphological characters across *Baja brandegeei* and all *Bommeria* species is summarized in Table 2.

Sporophytes–The rhizome scales of *Baja brandegeei* are concolorous and distinctly orange to reddish brown, whereas those of most *Bommeria* species are light-brown with a darker central axis; *Bommeria hispida* is the exception with concolorous, light-brown scales. Fractiferous petioles (with multiple, well-defined transverse abscission zones near the base) are ubiquitous in *Baja brandegeei*, but are also common in *Bommeria pedata*, *B. elegans*, and *B. ehrenbergiana*. Leaf blade shape and dissection of *Baja brandegeei* are distinct from that observed in all species of *Bommeria* (Table 2). The leaves of *Baja brandegeei* are triangular and fully pinnate (nearly bipinnate) whereas those of *Bommeria* are pentagonal and technically simple. This means that although the leaves of *Bommeria* species are often elaborately lobed (pinnatifid to bipinnatifid), there is always a small wing of leaf tissue connecting the terminal segment of the leaf to the proximal pinnae and thus the leaf blades are never fully pinnate. In *Baja brandegeei*, the basal basiscopic pinnules of the proximal pinnae are only slightly larger than adjacent pinnules. In *Bommeria*, the basal basiscopic pinnules of the proximal pinnae lobes are enlarged relative to adjacent pinnules, contributing to the pentagonal outline of the leaf (Table 2).

All five *Bommeria* species exhibit distinctive acicular hairs on their leaf blade surfaces, and this is also true of *Baja brandegeei* (Table 2). Although the body of these hairs is unicellular, they arise from a bulbous cluster of cells partially embedded in the leaf surface that often remains attached when the hair is removed. The length and density of the hairs varies depending on the species and blade surface examined, but they are always present (Fig. 2B, D, F). Though sparse in some species, all bommeriids have scales on their abaxial leaf surfaces, ranging in width from biseriate in *Bommeria elegans* to scales > 10 cells wide in *B. hispida.* The linear leaf scales of *Baja brandegeei* most closely resemble those of *Bommeria ehrenbergiana*, *B. elegans*, and *B. pedata.*

The sporangia of *Baja brandegeei* are distributed submarginally near the vein tips and are fully covered by a lobed and well-differentiated pseudoindusium formed by the reflexed leaf margin (Fig. 2A). This contrasts with the unprotected sporangia of most *Bommeria* species that are distributed abaxially along the veins for at least half the distance from the leaf margin to the midrib (Fig. 2C). *Bommeria ehrenbergiana* is unusual in this regard, with sporangia distributed along the veins to occasionally being submarginal, and leaf margins that are slightly recurved at irregular intervals to form an undifferentiated pseudoindusium (Fig. 2E).

Spores–All specimens of *Baja brandegeei* examined produced 64 relatively small (< 55 μm) spores per sporangium, as did four of the five species of *Bommeria*. The exception within *Bommeria* was *B. pedata*, which yielded 32 large spores (Table 2; Fig. 1). Of the previously hypothesized relatives of *Baja brandegeei*, only two (*Cheilanthes capensis* and *C. deltoidea*) exhibited 64 small spores per sporangium (Fig. 1). The others produced 32 small (*C. fractifera*), 32 large (*Notholaena aureolina* and *N. jaliscana*), or 64 large spores (*N. ochracea*).

All species of the newly expanded bommeriid clade have reticulate-cristate perispores composed of a finely interwoven network of strands with varying degrees of strand fusion. The spores of *Baja brandegeei* display a degree of strand fusion most like that of *Bommeria ehrenbergiana* and *B. pedata* (see photos in Tryon and Lugardon 1991).

Gametophytes–Early gametophyte developmental events were qualitatively similar among *Bommeria* species and *Baja brandegeei* but varied slightly in developmental timing. Spores of all species began germinating within 18 d of sowing (5 d for *Baja brandegeei*). In all bommeriids, subsequent cell division proceeded to form a spathulate prothallial plate, and a multicellular meristem was initiated from marginal cells near the base of the prothallial plate (beginning at day 21 for *B. brandegeei*). In contrast, beginning at day 32, meristems were initiated in an apical position in *Cheilanthes fractifera* gametophytes (as in most hemionitid ferns), forming a symmetrical cordate thallus (Fig. 3). The lateral position of the multicellular meristem in *Baja brandegeei* and all *Bommeria* species resulted initially in a markedly asymmetrical thallus. Continued

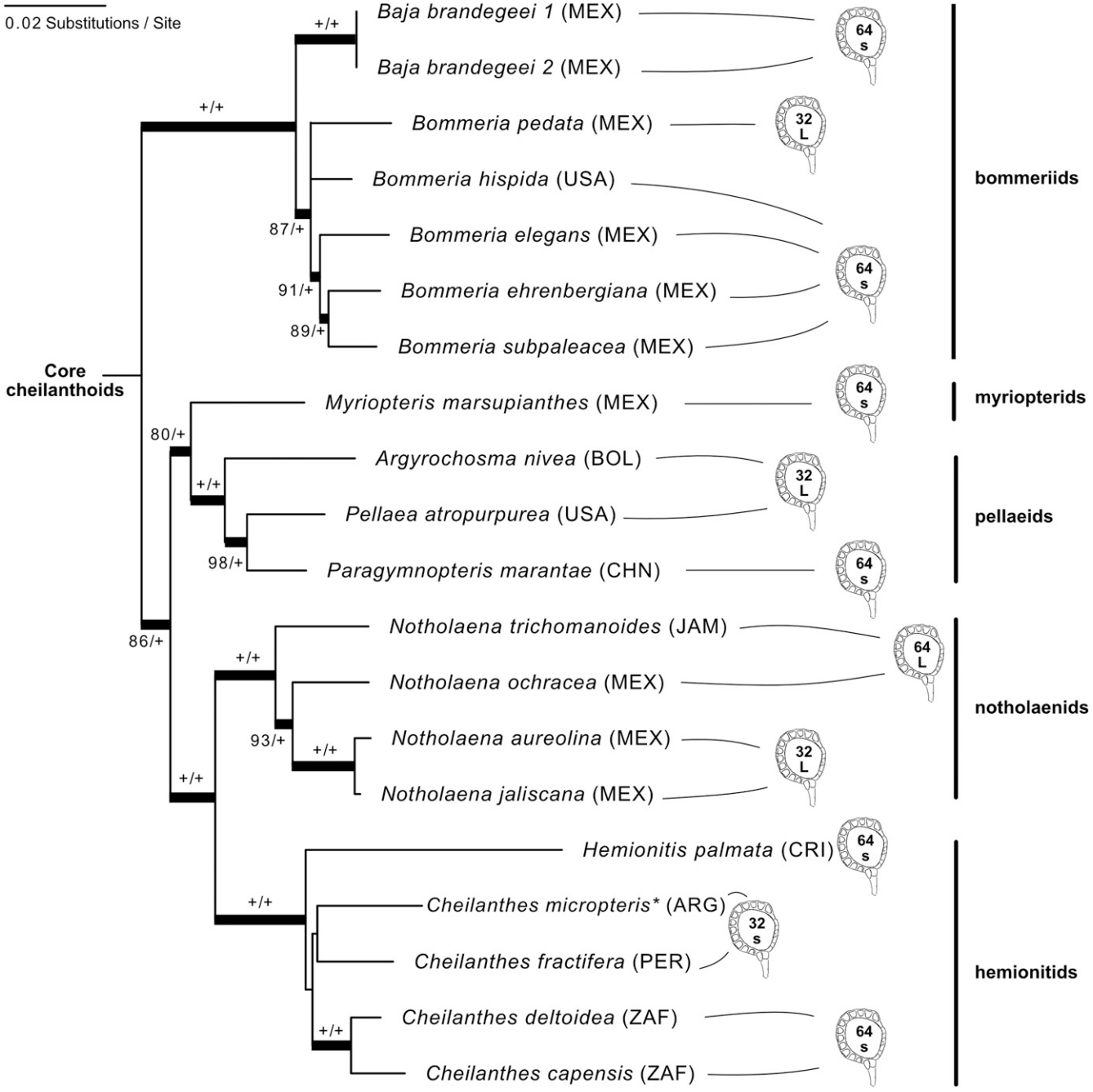

FIG. 1. Phylogeny of cheilanthoid ferns resulting from maximum likelihood analysis of the combined plastid *atpA*, *rbcL*, and *trnG-R* dataset. Maximum likelihood bootstrap percentages (BS ≥ 70) and Bayesian posterior probabilities (PP ≥ 0.99) are provided along the branches (BS/PP; values equal to 100 or 1.0 are indicated with a + sign); thickened branches correspond to BS ≥ 80% and PP ≥ 0.99. Geographical provenance of each voucher used to construct the phylogeny is shown as a 3-letter country code following the species name (ARG = Argentina, BOL = Bolivia, CHN = China, CRI = Costa Rica, JAM = Jamaica, MEX = Mexico, PER = Peru, USA = United States, ZAF = South Africa). Type species of *Cheilanthes* is indicated by an asterisk (*C. micropteris*). Number of spores per sporangium and their relative sizes (s = small, L = large, cf. Discussion) are indicated inside a sporangium sketch for each taxon. Major cheilanthoid clades discussed in text are indicated on tree; clade names follow Windham et al. (2009). *Calciphilopteris ludens* (not shown) is the outgroup.

growth and cell division in *B. brandegeei* gametophytes compensated for this initial asymmetry and resulted in a mature thallus up to 1 cm in diameter, with a well-developed archegonial cushion and two nearly symmetrical semicircular wings.

Gametophytes of *Baja brandegeei* that were grown from an initial sowing of spores on 60 mm diameter plates of Hevly's medium (at densities of 1–100 spores per plate) developed only archegonia. Archegonia were first observed at 66 d and appeared to be continuously produced over the course of the observation period. Antheridia did not develop on these gametophytes for the entire 12-mo study period. When additional spores were subsequently sown onto plates with mature archegoniate gametophytes of *B. brandegeei*, the gametophytes that developed from these spores were exclusively male (antheridia began to form 36 d after sowing). The thalli of male gametophytes were small (< 2 mm in diameter) and relatively undifferentiated at sexual maturity.

TABLE 2. Morphological comparisons across bommeriid ferns, including *Baja brandegeei* and all five species of *Bommeria*. All leaf illustrations modified from Mickel and Smith (2004) except for *Baja* and *Bommeria hispida* drawn by Susan Fawcett. Perispore morphology data from Ranker (1989), Tryon and Lugardon (1991).

Taxon	*Baja brandegeei*	*Bommeria ehrenbergiana*	*Bommeria elegans*	*Bommeria hispida*	*Bommeria pedata*	*Bommeria subpaleacea*
Leaf illustrations						
Rhizome scale color	Red-brown	Light-brown/ darker central axis	Light-brown/ darker central axis	Light-brown	Light-brown/ darker central axis	Light-brown/ darker central axis
Petiole base with multiple abscission zones (fractiferous)	Present	Present	Present	Absent	Present	Absent
Leaf blade shape	Triangular	Pentagonal	Pentagonal	Pentagonal	Pentagonal	Pentagonal
Leaf blade dissection	Pinnate	Simple	Simple	Simple	Simple	Simple
Proximal pinnae dissection	Bipinnatifid	Pinnatifid to bipinnatifid	Pinnatifid	Bipinnatifid	Bipinnatifid	Pinnatifid to bipinnatifid
Basal basiscopic pinnule of proximal pinnae	Not prominent	Prominent	Prominent	Prominent	Prominent	Prominent
Terminal segment (distal to proximal pinnae) dissection	Pinnate-bipinnatifid	Pinnatifid to bipinnatifid	Simple	Bipinnatifid	Bipinnatifid	Pinnatifid to bipinnatifid
Leaf blade hairs	Acicular	Acicular	Acicular	Acicular & coiled	Acicular	Acicular
Sporangial distribution	Submarginal near vein tips	Along veins to occasionally submarginal	Along veins	Along veins	Along veins	Along veins
Pseudoindusium	Lobed/ well-differentiated	Entire/ undifferentiated	Absent	Absent	Absent	Absent
Spore # per sporangium (spore size: small <55μm; large >55μm)	64 (small)	64 (small)	64 (small)	64 (small)	32 (large)	64 (small)
Perispore morphology	Reticulate	Reticulate	Cristate to nearly smooth	Cristate	Cristate	Cristate
Gametophyte meristem initiation	Lateral	Lateral	Lateral	Lateral	Lateral	Lateral

DISCUSSION

In this study, we explored the relationships of the enigmatic species formerly known as *Cheilanthes brandegeei* (herein called *Baja brandegeei*) using both molecular and morphological datasets. Our molecular phylogenetic tree (Fig. 1) is well supported and agrees in overall topology with the summary tree of cheilanthoid ferns published by Windham et al. (2009). The molecular evidence strongly supports the inclusion of *Baja brandegeei* in the bommeriid clade as sister to *Bommeria* (represented here by all five recognized species). This validates an earlier report by Mickel and Smith (2004) of unpublished *rbcL* data from Cranfill placing it in the bommeriid clade.

Our molecular phylogenetic tree (Fig. 1) confirms that *Baja brandegeei* is not closely related to any of the cheilanthoid ferns with which it has been previously associated on morphological grounds. The most morphologically similar species, *Cheilanthes fractifera*, a putative South American relative of *Baja brandegeei* (Tryon and Tryon 1982), together with the South African/Namibian *C. deltoidea* and *C. capensis*, cluster with the type species of *Cheilanthes* (*C. micropteris*) in the hemionitid clade. The other three members of Tryon and Tryon's (1982) "*C. brandegeei* group" form a strongly supported clade with *Notholaena trichomanoides*, the type species of *Notholaena*.

Phylogenetic placement of *Baja brandegeei* in the bommeriid clade also makes more sense biogeographically, given that all other bommeriid species are confined to the Mexican and Central American hotspot of cheilanthoid diversity (Tryon and Tryon 1973). *Bommeria hispida* actually occurs on the Baja Peninsula in the Sierra de la Giganta, a mountain range on the eastern side of Baja California Sur. Although these species co-occur on the Peninsula, they are segregated geographically and also by habitat. *Baja brandegeei* is found in the Central and Vizcaíno desert regions and rocky islands off the east and west coasts, but it is largely absent from La Giganta where *Bommeria hispida* occurs (Fig. 4). *Baja brandegeei* is primarily found at elevations below 1000 m, whereas *Bommeria hispida* is only found above 1000 m. All other *Bommeria* taxa are restricted to montane habitats in mainland Mexico and Central America. The triploid apomict *Bommeria pedata* is distributed from western and central Mexico into Guatemala, Honduras, Nicaragua, and Costa Rica; *B. elegans*, *B. subpaleacea*, and *B. ehrenbergiana* have more restricted ranges in mainland Mexico and are only known from elevations above 900 m (Haufler 1979; Ranker and Haufler 1990).

The primary diagnostic character of the "*Cheilanthes brandegeei* group" as recognized by Tryon and Tryon (1982) was

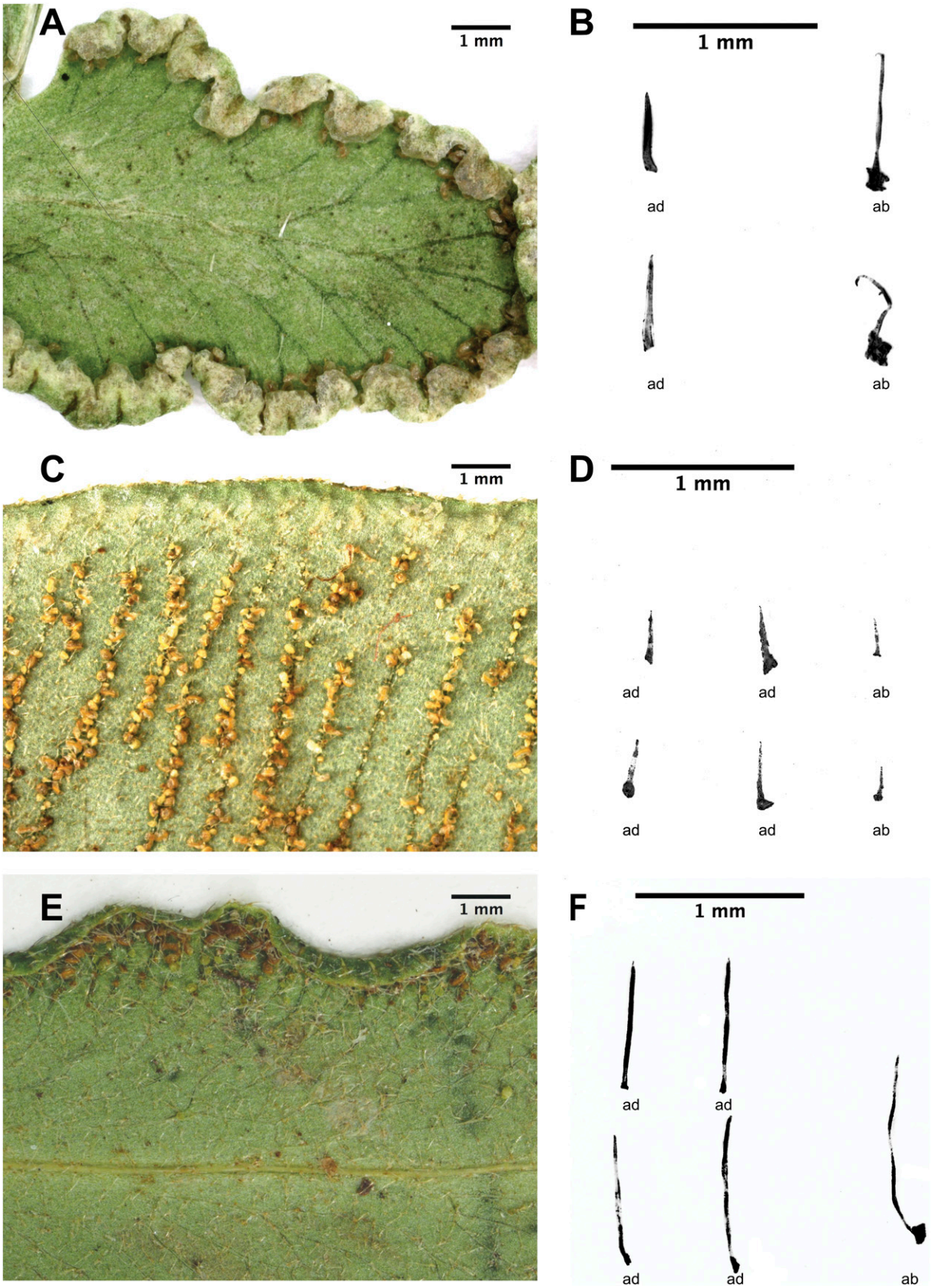

FIG. 2. Comparison of leaf margins, sporangial distribution, and leaf blade indument in *Baja brandegeei* and selected *Bommeria* species that encompass the variation found in that genus. A, C, E. Abaxial view of portion of leaf blade; B, D, F. Acicular leaf blade hairs (ad = adaxial hairs, ab = abaxial hairs). A. *Baja brandegeei* showing strongly recurved, deeply lobed margins forming well-differentiated pseudoindusium largely concealing submarginal sporangia. B. Hairs of *Baja brandegeei*. C. *Bommeria elegans* showing flat, undifferentiated margins (no pseudoindusium) and sporangia position following the veins for much of their length. D. Hairs of *Bommeria elegans*. E. *Bommeria ehrenbergiana* showing slightly and irregularly recurved margins forming an undifferentiated pseudoindusium not concealing the sporangia. F. Hairs of *Bommeria hispida*.

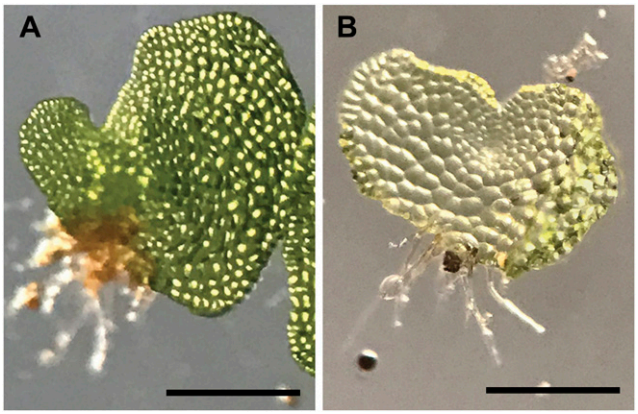

FIG. 3. Comparison of gametophyte meristem positions in A. *Baja brandegeei* (lateral) and B. *Cheilanthes fractifera* (apical). Scale bars = 1 mm.

fractiferous petioles, characterized by multiple, well-defined transverse abscission zones evenly spaced near the petiole base. The homoplastic nature of this character is undeniable considering our results, wherein former members of the "*C. brandegeei* group" are scattered across the entire cheilanthoid phylogenetic tree (Fig. 1). Within our restricted sampling, the fractiferous species *C. deltoidea* and *C. fractifera* were found to be most closely related to non-fractiferous *C. capensis* and *C. micropteris*, respectively (Fig. 1). We also note the occurrence of fractiferous petioles in three additional species in the bommeriid clade (Table 2). Leaf abscission is an important adaptation to conserving water in times of drought, and our data support Tryon's (1960) earlier reservations that fractiferous petioles may not be necessarily indicative of close relationships among xeric-adapted ferns.

Cheilanthoid ferns exhibit broad variation in sporangial distribution (extending along the veins vs. submarginal) and modification of leaf margins (plane vs. recurved). The latter character is further subdivided based on whether the recurved margin is differentiated into a prominent pseudoindusium or not. These characters tend to be strongly correlated, so much so that some authors (e.g. Pichi-Sermolli 1970) have segregated cheilanthoid ferns into separate families depending on whether the species have plane leaf margins with sporangia extending along the veins, or recurved leaf margins protecting the submarginal sporangia. One of the most surprising outcomes of this study is the discovery that *Baja brandegeei* (a typical representative of the latter group) is well supported as sister to *Bommeria* (a typical representative of the former group), which had previously been allied with *Hemionitis* L. It is suggested by our molecular phylogenetic tree (Fig. 1) that these characters are correlated and homoplastic. Plants with plane leaf margins and sporangia distributed along the veins occur in *Bommeria*, as well as in the distantly related *Hemionitis*. At the opposite end of the spectrum, recurved margins forming well-differentiated pseudoindusia are found in genera as distantly related as *Cheilanthes* s. s. (hemionitid clade), *Notholaena* (notholaenid clade), *Pellaea* (pellaeid clade), *Myriopteris* (myriopterid clade), and in *Baja* (bommeriid clade). The occasional appearance of submarginal sporangia protected by the irregular recurving of an undifferentiated leaf margin in *B. ehrenbergiana* (Fig. 2E) is an even more proximate example of convergent evolution. It is clear these features have been gained and lost many times during the long evolutionary history of cheilanthoid ferns.

A series of recent papers (Grusz et al. 2009; Beck et al. 2010; Sigel et al. 2011; Li et al. 2012; Schuettpelz et al. 2015) reminds us that the number of spores per sporangium and their relative sizes can provide critical insights into cheilanthoid relationships. Among polypod ferns (the clade of leptosporangiates including cheilanthoids), the plesiomorphic character state for sexual diploid species is 64 small spores per sporangium, with the actual spore size dependent on the particular clade (Sigel et al. 2011). Sexual polyploids generally produce 64 larger spores (see Barrington et al. 1986), whereas apomictic taxa yield 32 (usually even larger because the spores are unreduced; Haufler et al. 2016). Another apomorphic character state involves the production of 32 small spores per sporangium in sexual diploids due to the elimination of a mitotic cell division just prior to meiosis (Windham unpubl. data). Among cheilanthoid ferns this character state is quite rare compared to the others, having been reported in only two species of *Notholaena* (Rothfels et al. 2008) and in taxa closely related to the type species of *Cheilanthes* (Fig. 1). In fact, the production of 32 small spores per sporangium may provide a diagnostic synapomorphy for *Cheilanthes* s. s. (Li et al. 2012; Grusz and Windham 2013; Ponce and Scataglini 2018). Our observation of 64 small spores per sporangium from 19 collections scattered across the range of *Baja brandegeei* indicates it is a sexually reproducing species and is not closely related to *Cheilanthes* s. s. The spores are similar in number and size to those of the four sexual diploid species of *Bommeria* (Fig. 1; Gastony and Haufler 1976).

Members of the bommeriid clade, as newly circumscribed here, share three morphological synapomorphies: 1) leaves with unicellular, acicular hairs arising from a bulbous cluster of cells partially embedded in the leaf surface (Table 2; Fig. 2), 2) a reticulate-cristate perispore layer composed of finely interwoven strands, and 3) lateral initiation of gametophyte meristems. The particular hair type uniting members of the bommeriid clade has not been reported or observed in other cheilanthoid ferns, and it may be exclusive to this group. Somewhat similar hairs occur in *Myriopteris scabra* (C.Chr.) Grusz & Windham, but the latter differ in being conical in shape and heavily silicified. Of the species formerly thought to be related to *Baja brandegeei*, two (*Cheilanthes capensis* and *C. deltoidea*) have no indument on the blade surfaces, three (*Notholaena aureolina, N. jaliscana, and N. ochracea*) have farina-producing glands, and one (*Cheilanthes fractifera*) has multicellular hairs.

Perispore morphology has been of great value in understanding the relationships of cheilanthoid ferns (e.g. Tryon and Tryon 1973; Tryon and Lugardon 1991; Ranker 1989). Spore morphology and development in *Bommeria* and allied genera were studied thoroughly by Haufler and Gastony (1978b) and Ranker (1989). They observed that all *Bommeria* species had perispores composed of a finely interwoven network of strands with the degree of strand fusion producing the observed variation in spore surface features among species. They further noted that several *Bommeria* species went through a developmental sequence from reticulate to cristate as the strands continued to coalesce as spores matured. The observation of this developmental sequence from reticulate to cristate in *Hemionitis elegans* was pivotal in the decision to transfer this species into *Bommeria* (Ranker 1989). Tryon and Lugardon (1991), who first documented the spore morphology of *Baja brandegeei*, likewise described its reticulate-cristate spores as composed of a framework of "coalescent rodlets prolonged into more or less fused strands."

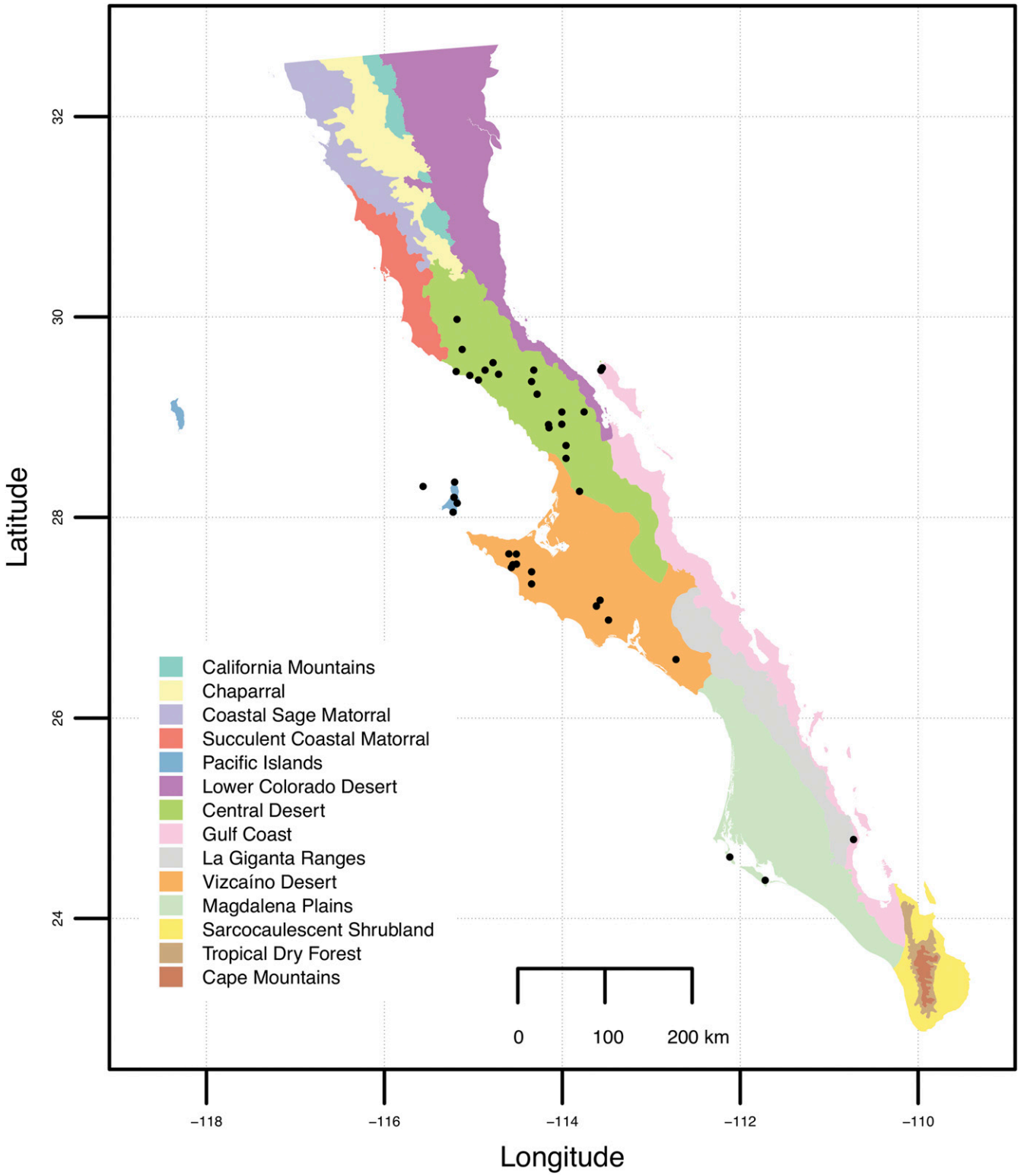

FIG. 4. Distribution of *Baja brandegeei* in the Baja California Peninsula of Mexico. Data points represent coordinates taken directly or georeferenced from location information on herbarium labels of 41 independent collections from 14 herbaria. Distribution information is based on specimens examined as well as databased herbarium specimens and represents a broad sampling of all accessible collections. Base map with ecoregions used with permission from Rebman (2018).

In the developing gametophyte, the initiation of a multicellular meristem in a lateral position, as opposed to the more typical apical position, occurs in all members of the bommeriid clade (Table 2). Gametophyte development in bommeriids is of the "*Ceratopteris*-type" in the classification system of Nayar and Kaur (1971), which is characterized by the absence of an apical cell and initiation of a multicellular meristem from marginal cells near the base of the prothallial plate. Meristem

development results in a marked asymmetry in the young gametophyte thallus in all bommeriid species, that may or may not persist as gametophyte development progresses. Recent studies of species from *Cheilanthes*, *Doryopteris*, *Gaga*, and *Myriopteris* have not identified lateral meristem initiation in these cheilanthoid genera (Gabriel y Galán and Prada 2010; Seral and Gabriel y Galán 2016). Gabriel y Galán (2011) reported that a "sub-lateral" meristem was formed in *Argyrochosma nivea* (Poir.) Windham, but that it soon appeared in an apical position because of the asymmetrical development of the lobes. Sexual development of gametophytes of *Baja brandegeei* closely follows the patterns in *Bommeria* observed by Haufler and Gastony (1978a). Initial development of archegoniate gametophytes and subsequent development of male gametophytes in the presence of mature archegoniate prothalli suggest the operation of an antheridiogen system like that found in *Bommeria* and detailed by Haufler and Welling (1994) as a system promoting outcrossing in natural populations.

Based on the data presented herein, *Baja brandegeei* can no longer be accommodated in *Cheilanthes*. A monophyletic genus including the type species of the latter (*C. micropteris*; Fig. 1) and *Baja brandegeei* would encompass all core cheilanthoids (ca. 500 species) and would have to be called *Hemionitis*, not *Cheilanthes*. Such a broad taxonomic construct would be both undefinable morphologically and uninformative, subverting two centuries of progress toward a better understanding of cheilanthoid evolution (Schuettpelz et al. 2018). Given the topology of our tree (Fig. 1), there remain two viable options: 1) transfer *Cheilanthes brandegeei* to *Bommeria* or 2) erect a new monospecific genus to accommodate this taxon. Although *Baja brandegeei* shares several morphological synapomorphies with other members of the bommeriid clade (the indument of unicellular acicular hairs being the most easily observed), it is readily separable by rhizome scale color, leaf shape and dissection, sporangial position, and the presence of a well-differentiated pseudoindusium (Table 2). It is further distinguished by occupying low elevation (< 1000 m), hot, desert habitats, in contrast to the five species of *Bommeria* that all occur in lower montane habitats at elevations > 1000 m. To acknowledge this morphological and ecological disparity, we describe the monospecific genus *Baja* to accommodate this distinctive taxon.

Taxonomic Treatment

Baja Windham & L.O.George, gen. nov. Type Species: *Baja brandegeei* (D.C.Eaton) Windham & L.O.George (= *Cheilanthes brandegeei* D.C.Eaton).

Most closely related to *Bommeria* E.Fourn. but differing in its concolorous, red-brown rhizome scales, triangular (vs. pentagonal) leaf blades, fully pinnate leaf dissection, and deeply lobed, well-differentiated pseudoindusium completely concealing the strictly submarginal sori. Differing from *Cheilanthes* Sw. sensu stricto in having 64 spores per sporangium (vs. 32 in sexual species), a leaf blade indument consisting of unicellular, acicular trichomes arising from a bulbous cluster of cells partially embedded in the leaf surface, and lateral initiation of gametophyte meristems.

Baja brandegeei (D.C.Eaton) Windham & L.O.George, comb. nov., *Cheilanthes brandegeei* D.C.Eaton, Bull. Torrey Bot. Club 17: 215, pl. 104. 1890. Type: Mexico. Baja California Sur: Magdalena Bay, Magdalena Island, 21 Jan 1889, *Brandegee s.n.* (lectotype designated here: YU (YU.014360)!, right side of sheet, consisting of one entire plant and three leaf fragments; isolectotypes: GH!, RSA!). In the original publication (Eaton 1890), *Cheilanthes brandegeei* was typified based on three Brandegee specimens collected in January, March, and April of 1889. All three are represented in the D. C. Eaton collection deposited in the Yale Herbarium, and we have chosen YU.014360 as the lectotype. This specimen is the only one with a complete leaf attached to a rhizome and was clearly the subject of the species illustration published with the protologue.

Plants rupestral. **Rhizomes** short-creeping, horizontal, solenostelic, scaly; rhizome scales lanceolate, concolorous (orange to reddish brown), with entire margins. **Leaves** closely-spaced, scales on petiole bases slightly broader than rhizome scales; petioles castaneous, proximally fractiferous (with multiple abscission grooves perpendicular to axis) and terete with a single V-shaped vascular bundle, distally flattened to longitudinally grooved on adaxial surfaces; rachises castaneous and adaxially grooved proximally, narrowly winged distally, the lighter colored wings continuous with costae and blade segments; leaf blade triangular, nearly as wide as long, pinnate-bipinnatifid at base tapering to pinnatifid in ultimate distal segment; basal basiscopic pinnules of the proximal pinnae only slightly larger than adjacent pinnules; ultimate segments rounded; venation nonanastomosing, the veins ending in prominent submarginal hydathodes; adaxial indument of sparse acicular hairs; abaxial indument of acicular hairs and occasional narrow scales. Segment margins recurved, forming a prominently lobed, well-differentiated pseudoindusium discontinuous at sinuses of large leaflet lobes. Sori completely covered by the recurved segment margins, the sporangia clustered near vein tips. **Spores** 64 per sporangium, trilete, dark amber, with reticulate perispore composed of a finely interwoven network of strands. **Gametophytes** primarily but not exclusively unisexual: female gametophytes with multicellular meristem developing laterally, large (up to 1 cm width) at maturity with well-developed archegonial cushion and two nearly symmetrical wings with ruffled edges; male gametophytes smaller, ameristic or with multicellular meristem developing laterally. Illustrations—Fig. 5; Mickel and Smith (2004: 777, Fig. 75 M–O); Eaton (1890: pl. 104).

Distribution and Ecology—Endemic to the Baja California Peninsula, Mexico; distributed between the 30th and 24th parallels on the peninsula and on the Pacific Islands of Cedros, Magdalena, Margarita, and San Benito, as well as Ángel de la Guarda in the Gulf. This species is concentrated in the arid Vizcaíno and Central Deserts ecoregions (Fig. 4) and associated with rocky and shaded microhabitats from 30–975 m.

Etymology—The generic name *Baja* refers to the endemic distribution of the genus on the Baja California Peninsula of Mexico.

Additional Specimens Examined—(Superscript * indicates specimens used for spore measurements; superscript ^{G} indicates specimens used for gametophyte culture). **Mexico.** —Baja California: Cedros Island, Mar 1897, *Anthony 308* (DS, MO, UC, US); Loma Creston Prieto, on mesa 3.3 mi S of Rancho Santa Catarina on road to Punta Canoas, 27 Feb 1991, *Boyd & Ross 5426* (RSA, UC); coastal terraces NW of Punta Canoas, 16.5 mi S of Rancho Santa Catarina on road to Punta Canoas, 28 Feb 1991, *Boyd & Ross 5462* (RSA); Cedros Island, 2 Apr 1897, *Brandegee 2251*(SD, UC*); San

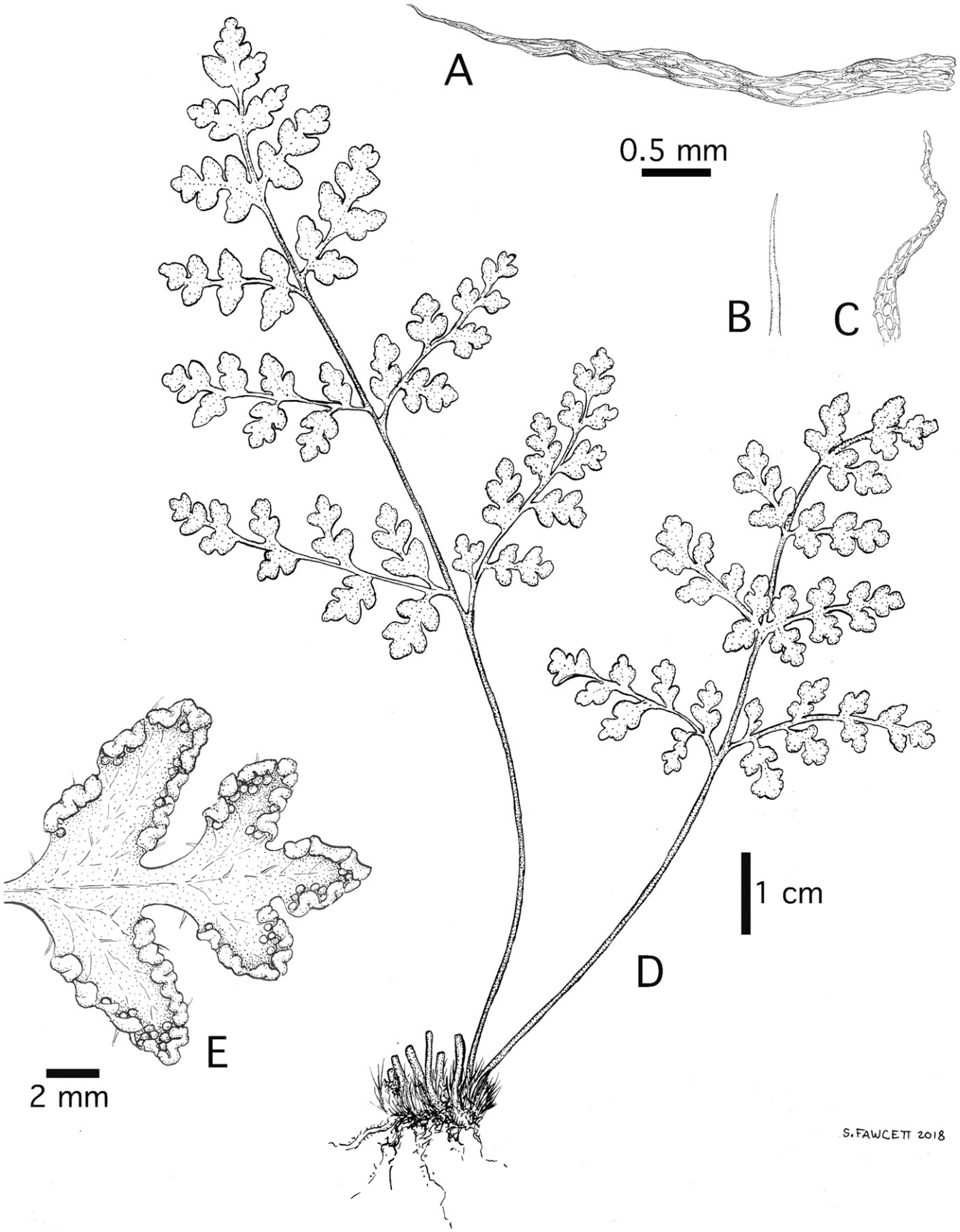

FIG. 5. *Baja brandegeei*. A. Rhizome scale. B. Acicular hair from abaxial leaf surface. C. Scale from abaxial leaf surface. D. Habit. E. Detail of sporangia and pseudoindusia. Drawings by Susan Fawcett based on A: *Wiggins and Thomas 176* (SD); B, C, D: *Rebman & Berian 28854* (SD); E: *Moran 23952* (SD).

Benitos Island, 4 Apr 1889, *Brandegee s.n.* (UC); Punta Prieta, n.d., *Brattstrom s.n.* (SD); Cedros Island, North Bay and hillsides inland from lighthouse, 3 Apr 1949, *Dawson 6119* (RSA); Valle de Agua Amarga, 15 mi W of Los Ángeles Bay, 16 Apr 1947, *Harbison s.n.* (DS, SD); Isla Ángel de la Guarda, N slope, ridge W of Cerro Ángel, alt. 700 m, 20 Apr 1966, *Moran 12906* (CAS, DS, MICH, RSA*, SD, UC, US*); arroyo 5.5 mi ESE of Los Morros, alt. 450 m, 29 Mar 1970, *Moran 17084* (SD*, UC); Isla Ángel de la Guarda, N slope, W base of peak, 6 km SE of Puerto Refugio, alt. 105 m, 17 Mar 1977, *Moran 23952* (SD*); Cedros Island, Cañón de la Mina, [28.35164, -115.21023], alt. 30 m, 13 Apr 1983, *Oberbauer et al. s.n.* (SD*); W of Kenten Hill, 4 July 1979, *Pray 3480* (RSA); Cañón Lazaro, 29.41639, -115.03944, 17 Apr 1997, *Rebman et al. 3980* (SD*[G]); Ensenada, NW end of Laguna El Caporal, W of Laguna Isolote and Laguna Chapala in small canyon on NW side of dried lake and on lower slopes of limestone cliffs, 29.2696, -114.59022, alt. 365 m, 23 Apr 2017, *Rebman et al. 33108* (SD*[G]); R. El Chileno, alt. 212 m, 18 April 2010, *Salazar & López 5262* (SD); Mesa de Cerrito Blanco ca. Cuesta San José, alt. 351 m, 13 Apr 2010, *Salazar et al. 5389* (SD*[G]); 9 mi E of Punta Prieta, 19 Feb 1982, *Shreve 6875* (MICH, MO, US); ca. 8 mi S of Rosarita, 26 Jan 1988, *Thorne et al. 5889* (BRY, RSA); 7.2 mi SW of Las Arrastras, along road to Rancho Laguna Chapala Seca, 15 Nov 1967, *Wiggins 20911* (DS); 2.5 mi S of Punta Prieta, 17 Oct 1959, *Wiggins 15080* (CAS, US); road to Bahía de los Ángeles, 9 mi E of Punta Prieta, 0.25 mi S of road at piles, 19 Feb 1935, *Wiggins 7649* (DS, MICH, US); inner end of Escondido Canyon 11.1 mi S of Punta Prieta, 23 Feb 1935, *Wiggins 7716* (UC); S of Rancho Mesquital, alt. 110 m, 30 Oct 1946, *Wiggins 11325* (DS, RSA, UC); 5 mi W of San Borja on road to Rosarito, 18 Feb 1962, *Wiggins 16738* (DS); Arroyo San José, 17 mi toward coast from Cerro Blanco, [29.42777, -114.71603], alt. 245 m, 9 Feb 1962, *Wiggins & Thomas 176* (SD); ca. 24 km NW by air from turn off of Highway 1 to Bahía de los Ángeles, 29.22917, -114.28306, alt. 615 m, 20 Mar 1910, *Wilder et al. 10–167* (SD). —Baja California Sur: Magdalena Island, 17 Jan 1889, *Brandegee s.n.* (GH, US); Magdalena Island, 21 Jan 1889, *Brandegee s.n.* (GH, RSA); steep Pacific slope canyon of Sierra Placeros, 3 Jul 1986, *Breedlove 62594* (CAS, MICH*); near mouth of Puerto Nuevo Canyon, Sierra de Placeros, 4 Mar 1992, *Breedlove 72761* (CAS); 35 mi SE of Bahía Tortugas, Pacific slope of Sierra de Placeros, 3 Jul 1985, *Breedlove 62331* (CAS); Picachos de Santa Clara, 11 May 1947, *Gentry 7701* (DS, RSA*, UC); Cerro Tordillo, Sistema de la Sierra Vizcaíno, 3 Dec 1947, *Gentry 7421* (MICH, RSA*[G], UC*); Sierra de la Giganta: N ridge of Cerro Mechudo, alt. 975 m, 3 Nov 1971, *Moran 18934* (GH, MICH, SD, UC, US*); N slope of SE peak, Picachos de Santa Clara, alt. 375 m, 3 Feb 1973, *Moran & Reveal 19679* (RSA*, SD*); N edge of mesa above Arroyo Malarrimo, alt. 180 m, 7 Feb 1973, *Moran 19897* (SD*, US); N slope of Cerro Azul, 9 Feb 1973, alt. 450 m, *Moran & Reveal 19978* (SD*, US); Sierra Santa Clara, N of Punta Abreojos, W of San Ignacio, 26.97842, -113.48098, alt. 105 m, 7 Oct 2014, *Rebman & Berian 28854* (SD); between Laguna San Ignacio and San Juanico, along old road to top of mesa, 26.58489, -112.72208, alt. 235 m, 20 Oct 2009, *Rebman & Delgadillo 18465* (SD).

Acknowledgments

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Author Contributions

Conceptualization: LOG, KMP, and MDW; Data Curation: LH and T-TK; Formal Analysis: T-TK; Funding Acquisition: KMP and MDW; Investigation: LOG; Project Administration: KMP; Supervision: MDW; Visualization: KMP; Writing, Original Draft Preparation: LOG, KMP, and MDW; Writing, Review, and Editing: LOG, KMP, T-TK, LH, and MDW.

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Appendix 1. Vouchers and GenBank accession numbers for taxa used in the molecular phylogenetic analysis. Taxon, authority, collection country, political division, *collector(s), collection number,* herbarium code, Fern DNA database number (fernlab.biology.duke.edu), GenBank accession numbers for *atpA*, *rbcL*, *trnG-R* (in that order). Superscript numbers 1 and 2 following *Baja brandegeei* below refer to replicates in Figure 1.

Ingroup: *Argyrochosma nivea* (Poir.) Windham var. *nivea*, Bolivia, Oruro, *Torrico & Castillo 622*, MO, #6236, HQ846396, HQ846445, HQ846493. *Baja brandegeei*[1] (D.C. Eaton) Windham & L.O.George, Mexico, Baja California Sur, *Breedlove 62594*, MICH, #4508, MK020101, MK020112, MK020120. *B. brandegeei*[2], Mexico, Baja California Sur, *Rebman 3980*, SD, #11977, MK020102, MK020113, MK020121. *Bommeria ehrenbergiana* (Klotzsch) Underw., Mexico, Hidalgo, *Yatskievych & Gastony 89-203*, IND, #644, MK020103, U19497, MK020122. *Bommeria elegans* (Davenp.) Ranker & Haufler, Mexico, Oaxaca, *Yatskievych & Gastony 89-258*, IND, #658, MK020104, U27729, MK020123. *Bommeria hispida* (Mett. ex Kuhn) Underw., USA, Arizona, *Schuettpelz 467*, DUKE, #3174, EU268725, EF452142, EU268671. *Bommeria pedata* (Sw.) E.Fourn., Mexico, Jalisco, *Beck 1156*, DUKE, #6940, MK020105, MK020114, MK020124. *Bommeria subpaleacea* Maxon, Mexico, Puebla, *Rojas-Martínez et al. 520*, MEXU, #11978, MK020106, MK020115, MK020125. *Cheilanthes capensis* (Thunb.) Sw., South Africa, Northern Cape, *Mothogoane 734*, US, #6175, MK020107, MK020116, MK020126. *Cheilanthes deltoidea* Kunze, South Africa, Cape Province, *Rodin 2187*, UC, #1126, MK020108, MK020117, MK020127. *Cheilanthes fractifera* R.M. Tryon, Peru, Lima, *Saunders 353*, UC, #6301, MK020109, MK020118, MK020128. *Cheilanthes micropteris* Sw., Argentina, Misiones, *Deginani 1363*, MO, #3709, MK020110, EF452145, EU268683. *Hemionitis palmata* L., Costa Rica, Heredia, *Rothfels et al. 08-184*, DUKE, #5137, EF452098, KC984525, EU268690. *Myriopteris marsupianthes* Fée, Mexico, Texcoco, *Jankiewicz 13*, UC, #6158, KF961739, KF961803, KF961864. *Notholaena aureolina* Yatsk. & Arbeláez, Mexico, Oaxaca, *Windham et al. 544*, DUKE, #4055, EU268729, EU268778, EU268675. *Notholaena jaliscana* Yatsk. & Arbeláez, Mexico, Nayarit, *Rothfels et al. 3118A*, DUKE, #6553, MK020111, MK020119, JQ855909. *Notholaena ochracea* (Hook.) Yatsk. & Arbeláez, Mexico, Morelos, *Yatskievych & Gastony 89-285*, IND, #4515, EU268728, EU268777, EU268674. *Notholaena trichomanoides* (L.) Desv. var. *subnuda* Jenman, Jamaica, Middlesex, *Ranker 860*, UT, #4054, EU268762, EU268807, EU268710. *Paragymnopteris marantae* (L.) K.H.Shing, China, Yunnan, *Yatskievych et al. 02-35*, MO, #3736, EU268763, EF452161, EU268711. *Pellaea atropurpurea* (L.) Link, USA, Cultivated - originally from Virginia, *Schuettpelz 312*, DUKE, #2957, JQ855925, EF452162, JQ855913.

Outgroup: *Calciphilopteris ludens* (Wall. ex Hook.) Yesilyurt & H.Schneid., Germany, Cultivated – origin unknown, *Schneider s. n.*, GOET, #3510, EU268741, EF452150, EU268688.