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

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Communicating Editor: Alejandra Vasco

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 bommeridiids, 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 bommeride clade (pinnate leaf architecture, well-developed pseudodiusumus, and narrow, concolorous red-brown rhizome scales), 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 pseudodiusumus, and fractiferous petioles) are extensively homoplasious across cheilantheids. We identify three characters that unite the newly expanded bommeride clade: leaf indument of accicular trichomes, reticulate-cristate perispore morphology, and lateral initiation of the gametophyte meristem.

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

Pteridaceae is one of the most species-rich and ecologically diverse fern families (Schuettpelz et al. 2007). Cheilantheidae (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., Doropteris J.Sm., Notholaena R.Br., and Pellaea Link, were indeed polyphyletic. Subsequent molecular analyses of a broader sampling of cheilantheids (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), Calcipliopteris Yesilyurt & H.Schneid. (Yesilyurt and Schneider 2010), Gaga Pryer, F.W.Li & Windham (Li et al. 2012), Lyteuron (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 cheilantheid 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 Cheilantheidae. 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. deltoides 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 cheilantheid 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 bommerid clade, the earliest-diverging group of “core cheilantheids” (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 cheilanthsoids based on its simple (but often intricately pinnatifid), pentagonal leaf blades with acicular hairs, and unprotected sporangia scattered along the veins. Chelanthlas \textit{brandegeei}, at least superficially, is very distinct from \textit{Bommeria} with fully pinnate-pinnatifid, triangular leaf blades and a deeply lobed, well-differentiated marginal pseudindusium protecting the submarginally distributed sporangia.

Here we investigate the surprising phylogenetic placement of \textit{Chelanthlas \textit{brandegeei}} using three plastid markers (\textit{atpA}, \textit{rbcL}, and \textit{trnG-R}) in an analysis that includes all species previously hypothesized to be related to it, as well as all recognized taxa of \textit{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 \textit{C. brandegeei} is a member of the bommerid clade, sister to the five recognized species of \textit{Bommeria}. Because \textit{Bommeria} is a morphologically cohesive group, we have chosen to segregate the relatively distinct \textit{C. brandegeei} as a new monospecific genus, herein and henceforth named \textit{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 \textit{Baja \textit{brandegeei}}, the six taxa that TRYON (1960, 1972) and TRYON and TRYON (1982) considered most closely related to it (\textit{Chelanthlas \textit{fractifera}}, \textit{C. deltoidea}, \textit{C. capensis}, \textit{Notholaena aureolina}, \textit{N. jaliscana}, and \textit{N. ochracea}), all five species assigned to \textit{Bommeria} by Ranker and Haufler (1990), and the type species of seven other cheilanthsoid genera representing five of the major clades recognized by \textsc{Wendham et al.} (2009). Based on previous phylogenetic studies of cheilanthsid ferns (Schuettpelz et al. 2007; Eiserhardt et al. 2011; Yesilyurt et al. 2015), we chose \textit{Calciphilopteris ludens} (Wall. ex Hook.) Yesilyurt & H.Schneid., the apparent sister group to “core cheilanthsoids,” 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 \textit{rpl} gene (1309 bp) and complete \textit{atpA} gene with partial \textit{atpF} gene, \textit{atpF}-\textit{atpA} intergenic spacer, and partial \textit{atpA}-\textit{trnK} intergenic spacer (~1830 bp), as described in Schuettpelz and Pryer (2007); and \textit{trnG-R} intergenic spacer with partial \textit{trnG} gene and partial \textit{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 (\textit{atpA}, \textit{rbcL}, and \textit{trnG-R}), sequences were first aligned using MUSCLE (Edgar 2004) in Alineview 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 “genthreshfortopterm” 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 “genthreshfortopterm” 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; Manson-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 \textit{atp} \textit{rbcL}, and \textit{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 \textit{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 \textit{Baja \textit{brandegeei}} (D.C. Eaton) \textsc{Windham} & L.O.George, \textit{Bommeria ehrenbergiana} (Klotzsch) \textsc{Underw.}, \textit{B. elegans} (Davens.) \textsc{Ranker} & \textsc{Haufler}, \textit{B. hispida} (Mett. ex \textsc{Kuhn}) \textsc{Underw.}, \textit{B. petada} (Sw.) \textsc{E.Fourn.}, and \textit{B. subpalatacea} \textsc{Maxon} were carefully examined to compare sporophytic morphologies across the newly recircumscribed bommerid clade (see Additional Specimens Examined section of Taxonomic Treatment). We focused on those characters determined by \textsc{Haufler} (1979) and \textsc{Ranker} (1990) to be most useful in delimiting the genus \textit{Bommeria}, including leaf shape and dissection, leaf indument, and gametophyte symmetry. In addition, rhizome scale color, presence or absence of fructiferous petioles, extent of sporangial distribution, and pseudoidiosial morphology were characterized for all species. Representative photographs of many of these characters were taken using a Leica MZ 12.5 stereomicroscope at 8 x and 40 x magnification. Dry mounted slides of hairs and scales were photographed at 20 x magnification.

Number of spores per sporangium (32 vs. 64) and average spore diameter (μm) were recorded from nineteen herbarium specimens of \textit{Baja \textit{brandegeei}}, as well as a smaller number of specimens representing all \textit{Bommeria} species and taxa previously hypothesized to be closely related to \textit{Baja \textit{brandegeei}}. Voucher specimens for these sporule 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.

<table>
<thead>
<tr>
<th>Plastid marker</th>
<th># Taxa</th>
<th>Alignment length (bp)</th>
<th>Characters included (bp)</th>
<th>Missing data (bp / %)</th>
<th>Variable sites (bp / %)</th>
<th>Informative sites (bp / %)</th>
<th>Best-fit model (partitioned)</th>
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<tr>
<td>\textit{atpA}</td>
<td>21</td>
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<td>1811</td>
<td>2229 / 5.9</td>
<td>383 / 21.1</td>
<td>210 / 11.6</td>
<td>GTR + G (first codon position); HKY + 1 (second codon position); GTR + G (third codon position and non-coding regions)</td>
</tr>
<tr>
<td>\textit{rbcL}</td>
<td>21</td>
<td>1309</td>
<td>1309</td>
<td>97 / 0.4</td>
<td>245 / 18.7</td>
<td>141 / 10.8</td>
<td>GTR + I (first codon position); K80 + 1 (second codon position); HKY + G (third codon position)</td>
</tr>
<tr>
<td>\textit{trnG-R}</td>
<td>21</td>
<td>1261</td>
<td>974</td>
<td>915 / 4.5</td>
<td>448 / 46.0</td>
<td>248 / 25.5</td>
<td>HKY + G</td>
</tr>
<tr>
<td>Combined</td>
<td>21</td>
<td>4417</td>
<td>4094</td>
<td>3241 / 3.8</td>
<td>1076 / 26.3</td>
<td>635 / 15.5</td>
<td>GTR + 1 (first codon position); HKY + 1 (second codon position); GTR + G (third codon position and non-coding regions)</td>
</tr>
</tbody>
</table>
sporophytes of most 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 Examinated 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 “Cheilanthes brandegeei group” of Tryon and Tryon (1982), formerly C. aurantiaca, C. aurea, and C. palmeri (labelled Notholaena ochracea, N. aurolina, 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 pinnales of the proximal pinnae are only slightly larger than adjacent pinnales. In Bommeria, the basal basiscopic pinnales of the proximal pinnae lobes are enlarged relative to adjacent pinnales, 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 pseudindusium 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 pseudindusium (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 aurolina 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
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.

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**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.
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.

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 Vizcaino 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’s (1982) “C. brandegeei group” form a strongly supported clade with Notholaena trichomanoides, the type species of Notholaena.
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*. 
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 cheilan-thoid 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.

Cheilanthes 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 pseudoinusium or not. These characters tend to be strongly correlated, so much so that some authors (e.g., Pichi-Sermolli 1970) have segregated cheilanthyoid 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 pseudoinusia are found in genera as distantly related as Cheilanthes s. s. (hemionitid clade), Notholaena (notholaenid clade), Pellaea (pellaenid clade), Myr-iopteris (myriopterid clade), and in Baja (bommeriid clade). The occasional appearance of submarginal sporangia protected by the irregular recurring 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 cheilanthyoid 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 cheilanthyoid relationships. Among polypod ferns (the clade of leptosporangiates including cheilanthyoids), 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; Hauffer 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 cheilanthyoid 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 Hauffer 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 cheilanthyoid 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 auriculina, N. jaliscana, and N. ochracea) have farinaproducing glands, and one (Cheilanthes fractifera) has multicellular hairs.

Perispore morphology has been of great value in understanding the relationships of cheilanthyoid 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 Hauffer 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.”
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 (Foir.) 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 Hauffer 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 Hauffer 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 (Schuettelz 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. pentalogical) 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, Brandegeee s.n. (lectotype designated here: YU (YU.014360!)), right side of sheet, consisting of one entire plant and three leaf fragments; isolecotypes: GH!, RSA!. In the original publication (Eaton 1890), Cheilanthes brandegeei was typified based on three Brandegeee 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 fructiferous (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 longer than adjacent pinnules; ultimate segments rounded; venation non-anastomosing, 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. Sorus completely covered by the recurved segment margins, the sporangia clustered near vein tips. **Sporaes** 64 per sporangium, trilcate, 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, aemispheric 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 ** 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 5462 (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, Brandegeee 225(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 pseudoinus. Drawings by Susan Fawcett based on A: Wiggins and Thomas 176 (SD); B, C, D: Rebman & Berian 28854 (SD); E: Moran 23952 (SD).

Acknowledgments

We thank the herbarium curators and staff at BRY, CAS, DS, DUKE, GH, IND, MEXU, MICH, MO, MSC, RSA, SD, UC, US, and YU for loans of their collections and sampling permission for our DNA studies. We also thank the curators and staff at VT for facilitating loans for illustration purposes. Special thanks to Jon Rehmman and Layla Aerne Hains at SD for their interest and assistance in acquiring fresh spores of Baja brandegeei and furnishing Baja California base maps. We also thank Christopher Haufler for providing spores of Bommeria subpalacea for comparative study. We acknowledge the generous talents of Susan Fawcett who created the line drawings of Baja brandegeei that were used in Fig. 5, and Nikolai M. Hay who produced the distribution map in Fig. 4 from our georeferenced data. This work was supported in part by an NSF Systematic Biology and Biodiversity Inventory award (DEB-0717398) to KMP and MDW.

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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