MOLECULAR ANALYSES PLACE THE GENUS *KERAUNEA* OUTSIDE CONVOLVULACEAE

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Abstract. The genus *Keraunea* was recently described in the Convolvulaceae Juss. family. Two species are currently recognised, both from Brazil. Molecular sequence data using three commonly applied DNA markers (*matK*, *rbcL* and the *nuclear ribosomal Internal Transcribed Spacer*) show that neither species is correctly placed in Convolvulaceae but indicates that the type, *K. brasiliensis*, should be placed in Malpighiaceae despite several morphological anomalies. The second species, *K. capixaba*, should be placed in Ehretiaceae. Given the surprising nature of these results, further studies are recommended before formal reclassification of these two taxa is made.

Keywords: Brazil, Convolvulaceae, Ehretiaceae, Malpighiaceae, Neotropics, systematics

Keraunea Cheek & Sim.-Bianch. is a genus endemic to Brazil initially described in the family Convolvulaceae (Cheek and Simão-Bianchini, 2013). The genus includes two accepted species: *Keraunea brasiliensis* Cheek & Sim.-Bianch., the type species described from the Brazilian state of Bahía with a paratype from Minas Gerais (Cheek and Simão-Bianchini 2013), and *K. capixaba* Lombardi described from Espirito Santo (Lombardi, 2014). A few additional specimens have subsequently been ascribed to these two species, all of them from the same states where the species were first collected (see, e.g., records in GBIF: https://doi.org/10.15468/dl.e9wrys). In this article, we report the results of our study of images and herbarium specimens together with phylogenetic analyses of DNA sequence data sampled from type specimens of both species, which demonstrate the genus is misplaced in Convolvulaceae.

As part of our ongoing investigations of American Convolvulaceae (Wood, 2013; Wood et al., 2015; Muñoz-Rodríguez et al., 2019; Wood et al., 2020; Wood and Clegg, 2021), we came across high-resolution images of the type specimens of both *Keraunea brasiliensis* (K000979156) and *K. capixaba* (SP003725) available via JSTOR plants, as well as images of additional specimens available via the Reflora portal (http://reflora.jbrj.gov.br/reflora/herbarioVirtual). These specimens immediately attracted our attention because they did not resemble any American Convolvulaceae we have studied to date. The drawings and photographs in the original publications (Cheek and Simão-Bianchini, 2013, fig. 1; Lombardi 2014, fig. 1 and 2) are not an especially good fit with the morphology of Convolvulaceae, and there are some discrepancies between our observations of the types and the original descriptions and illustrations. Moreover, as indicated in the original publication (Cheek and Simão-Bianchini 2013), *Keraunea brasiliensis* resembles the Convolvulaceae genus *Neuropeltis* Wall., and that is the reason why *Keraunea* was originally placed in Convolvulaceae. However, *Neuropeltis* is restricted to the Palaeotropics, with a disjunct distribution in East Tropical Africa (ca. 9 species) and South East Asia and India (4 species). (Breteler, 2010; POWO 2020). Further, preliminary molecular analyses using DNA barcodes (see below) confirmed the position of *Neuropeltis* in Convolvulaceae but placed the *Keraunea* specimens outside this family (Fig. 1).

To further explore this question, we studied all *Keraunea brasiliensis* collections cited in the original publication: *L. Passos 5263* (isotype K000979156), *J. A. Lombardi 1819*, and *J. A. Lombardi 2107*. We studied these collections directly at the Kew herbarium or via high-resolution images in virtual herbaria. Similarly, we studied three *K. capixaba* collections listed in the original publication: *G. S. Siqueira 891* (isotype SP476897), *D. A. Folli 7117*, and *G. S. Siqueira 893*. To the best of our knowledge, the *Keraunea* species had not yet been sequenced when we began our study, or the sequences had not been made available (cf. Simões et al., 2022). Thus, in addition to our morphological studies, we also sampled and sequenced three of these collections to incorporate them in the Convolvulaceae phylogenies generated as part of our ongoing systematic studies of the family (Muñoz-Rodríguez et al., 2019).

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[7] Supplementary files at: https://figshare.com/projects/Ipomoea_Project_-_Oxford_University_-_Keraunea_Data/153432.

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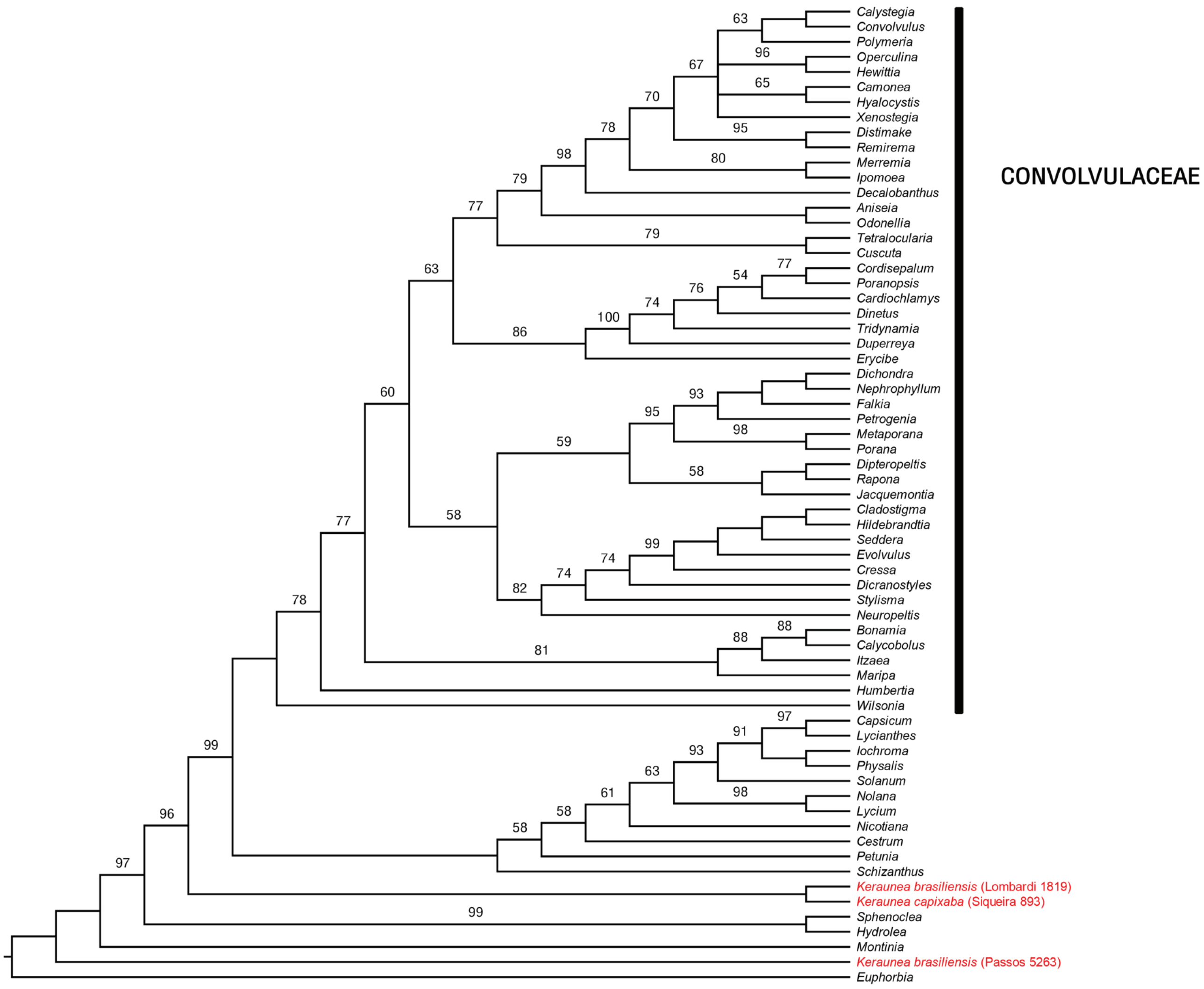

FIGURE 1. Maximum Likelihood phylogeny showing the position of the three specimens newly sequenced in this study (in red) outside Convolvulaceae. Phylogeny inferred using the chloroplast *rbcL+matK* regions; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. The black bar indicates the position of Convolvulaceae.

MATERIALS AND METHODS

We sequenced two *Keraunea brasiliensis* specimens (the isotype *Passos 5263* and the paratype *Lombardi 1819*) and one *K. capixaba* specimen (the paratype *G. S. Siqueira 893*). We sequenced three DNA markers: the *nuclear ribosomal Internal Transcribed Spacer* (*nrITS*) (*Passos 5263* and *Lombardi 1819*), and the chloroplast *matK* (all specimens) and *rbcL* regions (*Passos 5263*). We extracted total genomic DNA using the Qiagen DNEasy extraction kit, and used primers AB101 and AB102 for *nrITS* amplification (Douzery et al., 1999); 413f-1 and 1227r-3 for *matK* amplification (Heckenhauer, Barfuss, and Samuel, 2016); and rbcL-1F and rbcL-1460R for *rbcL* amplification (Fay et al., 1998; Olmstead et al., 1992). In all cases, we used a reagent volume of 15 *μ*l (7.3 *μ*l H_2O, 3 *μ*l buffer, 0.7 *μ*l $MgCl_2$, 0.3 *μ*l of each primer, 0.5 *μ*l dNTPs, 1 *μ*l BSA, 0.4 *μ*l Taq polymerase, 1.5 *μ*l sample DNA) for PCR amplification and standard PCR conditions (5' at 80˚C; 30 cycles of 1' at 95˚C, 1' at 50˚C, and 4' at 65˚C and a final stage of 4' at 65˚C). We cleaned the PCR reactions using the GeneJET PCR purification kit. We sequenced the samples using Sanger sequencing at Source Biosciences in Cambridge, United Kingdom, with the same primers used in the PCR. Furthermore, in light of our results we repeated both DNA extractions and amplifications in a different laboratory, with identical results. *nrITS* samples generated in this study are available on GenBank (OP034980, OP034981); *rbcL* and *matK* sequences are available as supplementary material.

To place the *Keraunea* samples in a phylogenetic context, we first queried all our sequences against the NCBI database using BLAST (Madden, 2002) and inferred an *rbcL+matK* phylogeny (TVM+F+G4) including representatives of all genera in Convolvulaceae as well as several other genera in Solanales. In light of our results (see below), we also inferred a *matK* Angiosperm phylogeny using DNA sequence data previously published from across the Angiosperm diversity (Baldwin et al., 1995; Hilu et al., 2003). All phylogenies inferred in this study followed the same methodology, detailed next, with substitution models indicated in each case. We aligned the sequences using MAFFT v.7.310 (Katoh and Standley, 2013, 2016) and used Geneious v.9.1.8 to remove all columns in the alignments with 90% or more gaps. We then inferred a Maximum Likelihood phylogeny using IQ-Tree (Nguyen et al., 2015) with automatic model selection using ModelFinder (Kalyaanamoorthy et al., 2017) and 1,000 bootstrap replicates (-czb -bb 1000 -alrt 1000). The substitution model was selected based on the Bayesian Information Criterion. In the resulting phylogenies we collapsed all nodes with less than 50% bootstrap support (-minsup 0.5).

Results and Discussion

Both BLAST and phylogenetic analysis indicate the two *Keraunea brasiliensis* specimens and the one *K. capixaba* specimen sequenced do not belong in Convolvulaceae (Fig. 2). Furthermore, the Angiosperm phylogenies including most orders in Angiosperms (TVM+F+I+G4) indicate that the two *Keraunea* species are not closely related to each other: *K. brasiliensis* is nested within Malpighiaceae Juss. (order Malpighiales) and *K. capixaba* is nested within Ehretiaceae Mart. (order Boraginales). In other words, the genus *Keraunea* is polyphyletic with its two constituent species apparently belonging to Malpighiaceae and Ehretiaceae rather than Convolvulaceae as originally classified. The sequences we obtained were of high quality and showed no evidence of contamination, as would be expected since the labs where the DNA was processed had not sequenced any material of these families. We subsequently inferred densely-sampled phylogenies of the two families where these specimens were nested, Malpighiaceae and Ehretiaceae, and the results for each specimen are described below.

Passos 5263, the isotype of Keraunea Brasiliensis

All three regions (*matK*, *rbcL* and *nrITS*) amplified for *Passos 5263*, the isotype of *Keraunea brasiliensis*, indicate it is nested within the family Malpighiaceae (Fig. 2). To further explore its position within the family, we inferred three species-level Malpighiaceae phylogenies—*matK* (TVM+F+G4), *matK*+*rbcL* (TVM+F+I+G4), and *nrITS* (TIM2+F+I+G)—with GenBank data and including representatives of all genera accepted in the most recent review of the family (Davis and Anderson, 2010) (Supplementary File 1). We used specimens of several genera as outgroups following Davis and Chase (2004), Wurdack and Davis (2009) and Cai et al. (2019): *Bergia* L. (Elatinaceae), *Elatine* L. (Elatinaceae), *Bhesa* Buch.-Ham. ex Arn. (Centroplacaceae), and *Euphorbia maculata* L. (Euphorbiaceae), with *E. maculata* used to root the phylogenies. The *matK* phylogeny places *Passos 5263* in a clade with *Mascagnia affinis* W.R. Anderson & C. Davis, *M. cordifolia* (A. Juss.) Griseb., and *M. dissimilis* C.V. Morton & Moldenke, all three species also present in Brazil[8] (Fig. 3a) and corresponding to the core/true *Mascagnia* rather than the many recent segregates of this former polyphyletic genus (Anderson and Davis, 2005a, 2005b, 2007, 2012, 2013). This clade of three species is also retrieved, with higher support, in Davis and Anderson (2010), a phylogeny based on *matK* and *rbcL* plus two additional regions not sequenced in our study, chloroplast *ndhF* and nuclear *PHYC*.

The *nrITS* phylogeny (Fig. 3b) places *Passos 5263* in a clade with three *Mascagnia* species widely distributed in South America: *M. australis* C.E. Anderson, *M. divaricata* (Kunth) Nied. and *M. sepium* (A. Juss.) Griseb. Again, *M. australis* and *M. divaricata* are within the same *Mascagnia* clade in Davis and Anderson (2010), whereas *M. sepium* was not included in that study but is also taxonomically recognised as a member of core/true *Mascagnia*.

In summary, our molecular results strongly suggest *Passos 5263* is a Malpighiaceae, most likely a *Mascagnia*, and would therefore justify transferring the species *Keraunea brasiliensis*—and therefore the genus *Keraunea pro parte*—to this family. However, these molecular results are particularly surprising because *K. brasiliensis* does not exhibit the canonical "Malpighiaceae morphology". Members of Malpighiaceae usually present simple, opposite leaves with T-shaped, unicellular trichomes and often inter-petiolar stipules, oil glands present on the sepals and/or extra-floral glands on the petiole or leaf blade, and five free, usually clawed petals (Davis, Anderson, and Donoghue, 2001; Anderson, 2004). In contrast, leaves in *Passos 5263* seem to be alternate, and oil glands cannot be readily observed on this specimen's sepals. Moreover, this specimen seems to have a sympetalous perianth, the branching of the inflorescence is alternate, and the fruit is very peculiar if Malpighiaceae. In addition, although the molecular results reported here are robust, considering the strong morphological differences between *K. brasiliensis* and the members of Malpighiaceae we hesitate to formally propose this taxonomic change. We think further study is advisable before *Keraunea brasiliensis* can be re-classified. An additional trait to explore is the three carpellate ovary with a single locule per ovule as is found in Malpighiaceae. Finally, we have not seen the holotype (deposited at Sao Paulo herbarium (SP) and not yet digitised) and it may be different in whole or in part from the isotype at Kew. In conclusion, it seems clear that *Keraunea brasiliensis* is not a Convolvulaceae and future studies should be able to determine its generic placement within Malpighiaceae.

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[8] Adding the chloroplast *rbcL* region slightly improves phylogenetic resolution, but the only two *Mascagnia* (Bertero ex DC.) Bertero species (*M. adamsii* and *M. sepium*) that have data available for both *matK* and *rbcL* seem to be only distantly related to *Passos 5263*. See Supplementary File 3.

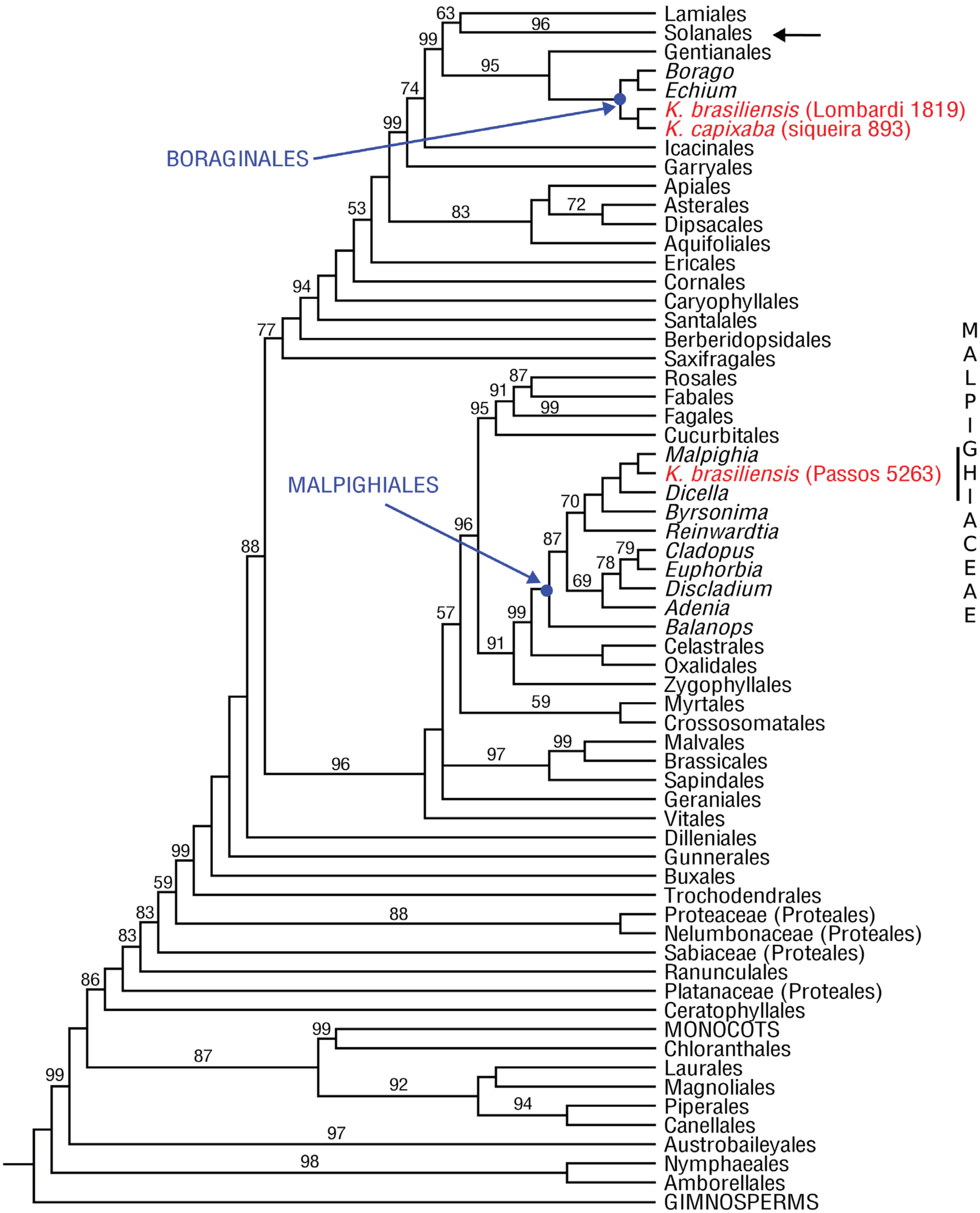

FIGURE 2. Summary Maximum Likelihood Angiosperm phylogeny showing the position of the three specimens newly sequenced in this study (in red). Phylogeny inferred using the chloroplast *matK* region; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. *Passos 5263* (*Keraunea brasiliensis*) is nested in Malpighiales; *Lombardi 1819* (*K. brasiliensis* Cheek & Sim.-Bianch.) and Siqueira 893 (*K. capixaba* Lombardi) are nested in Boraginales. The blue arrows indicate the position of Malpighiales and Boraginales; the black arrow indicates the position of Solanales, where the family Convolvulaceae belongs. See complete phylogeny in Supplementary File 2.

FIGURE 3. **A–B**. Summary Maximum Likelihood Malpighiaceae phylogenies showing the position of the *Passos 5263* specimen of *Keraunea brasiliensis* Cheek & Sim.-Bianch. (in red). Phylogenies inferred using A. the chloroplast *matK* region and B. the *nrITS* region; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. Passos 5263 (*Keraunea brasiliensis*) is nested in *Mascagnia* (Bertero ex DC.) Bertero in both phylogenies. See complete phylogenies in Supplementary File 3.

Lombardi 1819 and Siqueira 893 specimens

We also sequenced a paratype of *Keraunea brasiliensis—Lombardi 1819* (K) and one of *K. capixaba—Siqueira 893* (K). We sequenced *matK* and *nrITS* for *Lombardi 1819* and *matK* for *Siqueira 893*. We first checked our sequences against the GenBank database using BLAST and incorporated the *matK* sequences to the Angiosperm phylogenies aforementioned (Fig. 2). Interestingly, these two paratype specimens are nested in Boraginales and appear to be closely related to *Ehretia* P. Browne, *Halgania* Gaudich. and other genera in the family Ehretiaceae, recently segregated from Boraginaceae Juss. (Luebert et al., 2016). This was confirmed with a *matK* (TVM+F+G4) phylogeny of all accepted genera in Ehretiaceae (cf. Gottschling and Hilger 2004; Gottschling et al. 2014) and the other families in the order (Fig. 4a). In this *matK* phylogeny, both *Keraunea* specimens (*Lombardi 1819* and *Siqueira 893*) are most closely related to each other, and sister to a monophyletic genus *Ehretia*, with high support. The close relationship between *Lombardi 1819* and *Siqueira 893* is not surprising as these two specimens are remarkably similar morphologically.

A densely sampled *nrITS* phylogeny of Ehretiaceae (GTR+F+I+G4) places *Lombardi 1819* sister to monophyletic *Cortesia cuneifolia* Cav. (= *Ehretia cortesia* Gottschling), a genus recently segregated by Gottschling et al. (2014). This clade is sister to a monophyletic *Halgania* Gaudich., also with moderately high support (Fig. 4b). It is important to note that *Cortesia* Cav. and *Halgania* have not been sequenced for *matK* and therefore they are not included in the *matK* phylogeny.

The results of both *nrITS* and *matK* phylogenies presented here are congruent and show the two *Keraunea* collections *Lombardi 1819* and *Siqueira 893* are most closely related to *Cortesia, Halgania* and *Ehretia* P. Browne. Again, although our molecular results are robust, we think a comprehensive, complete study of *Keraunea* is needed before *Keraunea capixaba* and at least one of the *K. brasiliensis* paratypes can be re-classified. It seems clear that *K. capixaba* is also not a Convolvulaceae, and future studies should be able to confirm its placement in the right family, most likely Ehretiaceae.

Here, we have shown that *Keraunea brasiliensis* and *K. capixaba* comprise a mixture of specimens from different Angiosperm families not Convolvulaceae. We have refrained from proposing formal taxonomic changes as we think a comprehensive study of all material assigned to *Keraunea* is necessary, including the broader context of the respective families where the two species belong. It is unlikely that the mere addition of more molecular data will clarify the position of these two species, at least for their family designations, unless such a study is accompanied by a comprehensive taxonomic study of herbarium and living material. The results of our study highlight several important aspects of contemporary plant systematics. First, the inadequate role of gross morphology in placing some material in the correct family. Second, the ability of molecular sequence data to quickly place difficult specimens in the correct family. Third, the large fraction of taxa that still remain to be classified and fully understood.

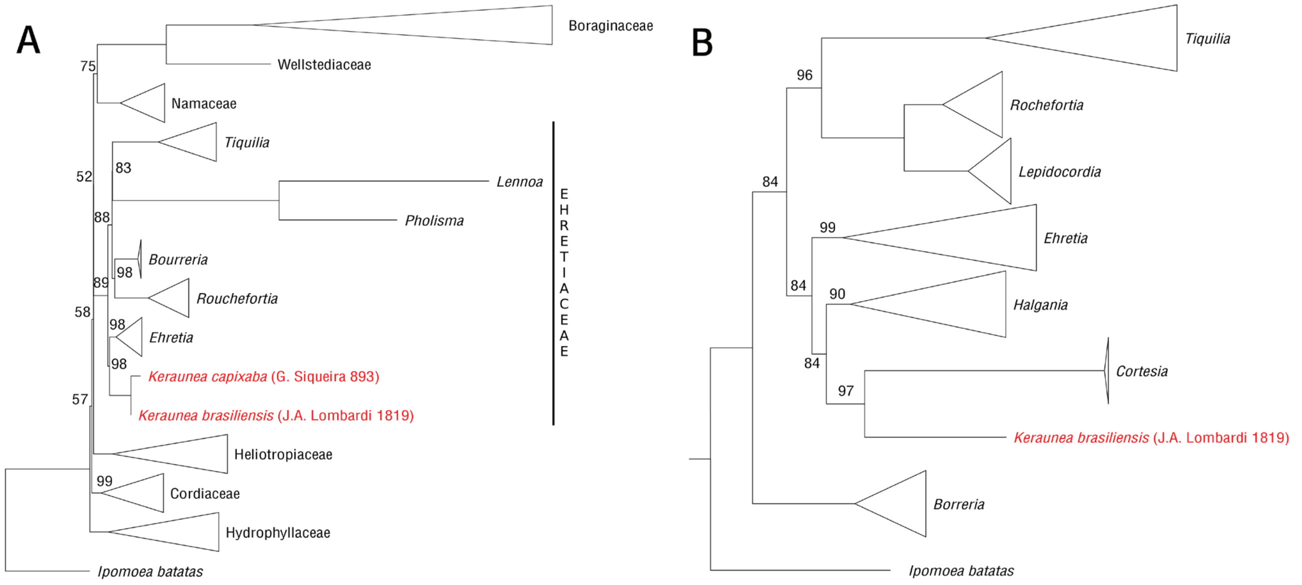

FIGURE 4. **A–B**. Summary Maximum Likelihood phylogenies showing the position of *Keraunea brasiliensis* Cheek & Sim.-Bianch. specimen *J.A. Lombardi 1819* and *K. capixaba* Lombardi specimen *G. Siqueira 893* in Ehretiaceae. A. Boraginales phylogeny inferred using the chloroplast *matK* region. B. Ehretiaceae phylogeny inferred using the *nrITS* regions. Triangles represent monophyletic family and/or genera with multiple specimens; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. In A., the two specimens newly sequenced in this study, *Lombardi 1819* and *Siqueira 893*, are most closely related to each other and sister to a monophyletic genus *Ehretia* P. Browne, with high support. In B., *Lombardi 1819* is most closely related to a monophyletic genus *Cortesia* Cav., which is not included in A. See complete phylogenies in Supplementary file 4.

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