Leucheria Lag. includes *Polyachyrus* Lag. (Asteraceae; Nassauvieae)

[1]**Mark A. Hershkovitz**
Isla Negra, Chile

***Abstract*- Phylogenetic analysis of sequences from the nuclear ribosomal DNA internal transcribed spacer (ITS), plastome *rpl32-trnL*(UAA) intergenic spacer (*rpl32-trnL*), and plastome *trnL*(UAA) intron plus *trnL*(UAA)-*trnF*(GAA) intergenic spacer (*trnL-trnF*) demonstrates that the genus *Polyachyrus* Lag. is phylogenetically nested among species of *Leucheria* Lag. The data demonstrate that *Leucheria* and the monotypic *Oxyphyllum* Phil. share a unique common ancestor, but the present data cannot establish whether or not *Oxyphyllum* is sister to *Leucheria*. It appears as one of multiple unresolved lineages emerging from the *Leucheria* crown. The sister of this crown is a clade comprising *Marticorenia* Crisci and *Moscharia* Ruiz & Pav, with *Spinoliva* (Hook. & Arn.) G.Sancho, Luebert & Katinas being sister to all of these. The results demonstrate that secondary inflorescence heads of *Polyachyrus* and some *Leucheria* species are homologous rather than convergent, and that the ancestor of *Leucheria* occupied a warm, arid lowland rather than, as previously asserted, a cool, moist alpine/steppe habitat.**

***Index Terms*: *Leucheria*, *Polyachyrus*, *Oxyphyllum*, Asteraceae, Nassauvieae**

I. INTRODUCTION

Leucheria Lag. (Asteraceae; Nassauvieae) is a temperate South American genus comprising ca. 29 species (Katinas et al., 2022). Its monophyly has been presumed based on molecular phylogenetic analysis of Jara-Arancio et al. (2017), e.g., by Pérez et al. (2020) and Katinas et al. (2022; but see Katinas et al., 2008). Jara-Arancio et al. (2017) reported that the genus comprises two clades, one comprising acaulescent alpine/steppe species, and the other comprising caulescent species occupying diverse habitats.

Jara-Arancio et al. (2017) reported that the sister-group of *Leucheria* is a clade comprising the genera *Marticorenia* Crisci and *Moscharia* Ruiz & Pav. Sancho et al.'s (2018) molecular phylogenetic analysis of *Proustia* Lag. sensu lato sampled a single species of *Leucheria* and reported that these formed a well-supported but unresolved clade comprising this species and single sampled species of the genera *Oxyphyllum* Phil. (monotypic) and *Polyachyrus* Lag. This clade was, in turn, sister to a sample of *Moscharia*. They did not sample *Marticorenia*. Luebert et al. (2009) reported similar but more precise results, with *Polyachyrus* sister to two sampled species of *Leucheria*, and *Oxyphyllum* and *Moscharia* as the successive outgroups. This is somewhat in agreement with Katinas et al. (2008; Katinas & Forte, 2020; contra Katinas & Crisci, 2000), who proposed a sister relation between *Polyachyrus* and *Leucheria* based on molecular data and reproductive morphology. Jara-Arancio et al. (2017) did not sample from *Oxyphyllum* or *Polyachyrus*.

While sweeping the porch in Isla Negra, Chile, I accidently discovered that *Leucheria* is paraphyletic. Its clade includes *Polyachyrus* as sister to Jara-Arancio et al.'s (2017) Subclade II of the caulescent Clade B. *Oxyphyllum* seems most likely sister to this clade, but this remains to be resolved. These results are presented here, while a more detailed analysis of phylogeny and evolution in this clade will be available shortly.

II. MATERIALS AND METHODS

DNA sequences of species of the relevant taxa were downloaded from GenBank. These included sequences of the nuclear ribosomal DNA internal transcribed spacer region (ITS) and plastome (cpDNA) sequences of the *rpl32-trnL*(UAA) intergenic spacer (*rpl32-trnL*) and the *trnL*(UAA) intron plus *trnL*(UAA)-*trnF*(GAA) intergenic spacer (*trnL-trnF*). For *Leucheria*, *Marticorenia*, and *Moscharia*, the sequences are those listed in Jara-Arancio et al. (2017) plus three reported by Lavandero et al. (2020). For *Polyachyrus fuscus* (Meyen) Walp., for ITS, *trnL-trnF*, and *rpl32-trnL*, I used, respectively, GenBank accessions EF530263.1, EF530309.1, and MG553855.1; for *Oxyphyllum ulicinum* Phil., EU729344.1, EU729339.1, and MG553854.1; and for an additional outgroup, *Spinoliva* (Hook. & Arn.) G.Sancho, Luebert & Katinas subsp. *baccharoides* (D.Don ex Hook. & Arn.) G.Sancho (see Sancho et al., 2018), MG553793.1, MG553721.1, and MG553872.1.

Not all sequences reported by Jara-Arancio et al. (2017) were included in the present analysis. First I included taxa for which all three sequences were available and reduced the dataset to include only samples whose cpDNA sequences were unique. *Moscharia* was excluded because *rpl32-trnL* data are lacking and the contribution of available *trnL-trnF* data to total cpDNA informative variation was relatively small (see below). However, I performed separate analyses of ITS and *trnL-trnF* that included *Moscharia*. I have analyzed taxonomically more complete datasets separately, which will be posted separately, but, for the present purposes, I found that the taxon deletions did not affect the results emphasized here.

I also excluded taxa for which I considered at least one of the sequences to be "problematic" for one or another reason to be detailed in the later publication. *Leucheria rosea* Poepp. ex Less. was excluded, because the ITS and cpDNA sequences pertain to disparate clades, as indicated in the supplemental data of Jara-Arancio et al. (2017) and confirmed here. The present analysis included only the 3' portion (ITS2) of the *Leucheria suaveolens* (d'Urv.) Speg. ITS sequence, because the upstream portion of the published sequence is random noise.

This work applies the taxonomic identifications given in the sequence documents. Most of these are from Jara-Arancio et al. (2017). Katinas et al. (2022) radically modified the species concepts in *Leucheria* such that several of the names applied here are reduced to synonymy. However, DNA sequences corresponding to Katinas et al.'s species are divergent and, more importantly, appear polyphyletic, sometimes grossly so, in Jara-Arancio et al. (2017) and in the present work. Mainly for this reason, the names used here, corresponding to earlier taxonomies, are retained.

The sequences were aligned manually and the alignment trimmed to reduce 5' and 3' ambiguity in some of the sequences. The alignment of all three loci is substantially different from that used by Jara-Arancio et al. (2017), as will be described in the forthcoming work. For purposes of phylogenetic analysis, informative length-variable regions consequent to phylogenetic sequence insertion or deletion (indels) were scored separately in matrices following each locus region. Up to four unordered indel states plus "N" (for ambiguous alignments) were allowed for a given indel region, and these were scored as conservatively as possible in order to minimize inherent bias.

Phylogenetic analysis applied maximum parsimony (MP) and maximum likelihood (ML) methods as implemented in PAUP version 4 (Swofford, 2003). MP tree construction and bootstrap analysis (1000 replicates) were undertaken using the default algorithm and parameters, except that the bootstrap analysis was performed using random addition sequence (10 replicates), holding 10 trees at each addition step, with maxtrees fixed at 100. These parameters yield anywhere between one and 100 trees per replicate and thus somewhere between 10^5–10^6 trees from which the bootstrap proportions are calculated. ML analysis used the 6-parameter general time-reversible substitution model with correction for estimated base frequencies and gamma rate correction. All parameters were estimated using an MP tree.

III. RESULTS

The complete data set yielded 258 parsimony-informative characters, of which 224 were substitution characters and 34 informative indel characters. ITS alone yielded 151, 146 substitution and 5 indel. The cpDNA data yielded the balance of 107 characters, 78 substitution and 29 indels. Within the cpDNA data, *trnL-trnF* accounted for, respectively, 21 and 5, while *rpl32*-trnL accounted for 57 and 24. Thus, per sequence length, the ITS is ca. six times more variable than the combined cpDNA loci. At the same time, the *rpl32-trnL* region is ca. three times more variable than *trnL-trnF* and much more variable in length than the other two loci.

Figure 1 shows a cladogram summarizing the strict MP and MP bootstrap consensuses from analysis of the combined ITS and cpDNA data, both with and without indel characters. Resolution of all consensuses is congruent, although, as shown, one terminal branch is resolved (in both bootstrap and strict MP consensuses) only using indel data. *Polyachyrus* appears in all consensuses as sister to Subclade II with 71–75% bootstrap support. The sister relation of Subclade I is less well-supported by the bootstrap. Monophyly of Subclade III and Clade A is strongly supported. The relation of these clades and *Oxyphyllum* is unresolved, but their monophyly relative to the clade comprising *Marticorenia* and *Spinoliva* is well supported.

Figure 2 shows a cladogram summarizing the strict MP and MP bootstrap consensuses plus the strict ML consensus of the ITS data analysis, both with and without indel data. This tree is congruent with the consensus of 25 trees saved during the ML analysis. The ML tree and MP consensus place *Polyachyrus* as sister to Subclade I, and these together as sister to Subclade II. But these relations and *all* successively deeper relations, including outgroup relations, received less than 50% MP bootstrap support. Figure 2 also shows three additional branches present *only* in the ML tree. Branches supported in the MP bootstrap of the ITS are mostly congruent with those supported in the bootstrap of all data. An exception is a Subclade III branch supported with 56-58% support in the ITS bootstrap but conflicting with better supported nodes in the combined data bootstrap.

Lack of ITS bootstrap support for the relations of *Polyachyrus* and the outgroups was peculiar. Analysis of the bootstrap partition tables revealed the cause. In some of the bootstrap trees, *Oxyphyllum* and *Polyachyrus* were both attracted to the Subclade I branch, sometimes taking with them *Spinoliva* or even all of the outgroups. Such trees at the very least showed *Oxyphyllum* nested within *Leucheria* and at most turned the *Leucheria* phylogeny inside-out. These peculiar MP results evidently were consequent to extreme base frequency differences among *Leucheria* clades. GC frequencies among aligned ITS variable (including informative) sites are: 67% (Subclade I), 61–65% (Subclade II), 58–62% (Subclade III), and 52–56% (Clade A). The *Polyachyrus* variable sites are 64% GC, within the Clade II range. Meanwhile, GC content at these sites in the outgroup sequences are 72% (*Oxyphyllum*), 64% (*Marticorenia*), and a whopping 77% (*Spinoliva*). Thus, at informative sites, the outgroups converge on Subclade I and, besides, if one sequence is attracted to Subclade I, the others will tend to follow based on overall sequence similarity.

Meanwhile, in other MP bootstrap trees, *Oxyphyllum* was sister to Clade A, the marked difference in GC content notwithstanding. This seems to be an essentially random result. An ML tree (Fig. 3; from among the 25 with equal likelihood) shows an extremely short branch length separating *Oxyphyllum* from the *Leucheria* crown. Naturally, some bootstrap samples will tend to oversample similarities between *Oxyphyllum* and particular *Leucheria* clades, especially Clade A given its long branch length. Figure 3 also may explain the attraction, unsupported by the bootstrap, of *Polyachyrus* to Subclade I rather than Subclade II in the MP and ML consensuses. Again, the subtending branch is very short, suggesting that *Polyachyrus* could go either way.

As noted, I excluded *Moscharia* from analysis of the complete dataset because there is no *rpl32-trnL* sequence available. However, I performed a separate bootstrap analysis of the ITS data that included *Moscharia*. This yielded a bootstrap consensus identical to that with *Moscharia* excluded, but with 100% support for a sister relation between *Moscharia* and *Marticorenia*.

In summary, when the bootstrap trees are threshed out and artifacts removed, the ITS sequences strongly support inclusion of *Polyachyrus* within *Leucheria* and its close relation at least with Subclades I and II as opposed to Subclade III and Clade A. The data weakly support a sister relation between *Oxyphyllum* and *Leucheria*, viz., as indicated in the MP and ML strict consensuses but with less than 50% MP bootstrap support. However, the data, again with artifacts discarded, at least indicate that *Oxyphyllum* and *Leucheria* form a clade, with *Marticorenia* + *Moscharia* and *Spinoliva* as the successive outgroups.

Figure 4 shows the MP bootstrap consensus for the cpDNA dataset including the 29 indel characters. The results for the MP bootstrap without indels, the MP strict consensuses, and the ML analysis are indicated. The cpDNA very strongly support a sister relation between *Polyachyrus* and Subclade II, and this support clearly is the source of the somewhat reduced support for this relation in the combined data MP bootstraps.

But this tree also shows *Oxyphyllum* included within *Leucheria*, in this case *neighboring* Subclade I. And the next lower node shows considerable MP bootstrap support for this inclusion, viz. 72%. However, this relation is supported only by the dataset including indel characters. It has < 50% support in the bootstrap analysis without indel characters, and it conflicts with relations indicated in the MP strict consensus and the single ML tree. These show a sister relation between Subclades I and II (as in the ITS analysis) with Subclade III, Clade A, and *Oxyphyllum* branches unresolved at the next deeper node.

It seems at least intriguing that both the ITS and cpDNA data show some evidence for the inclusion of *Oxyphyllum* within *Leucheria*, but this proves to be coincidence. The relation indicated in Fig. 4 owes to a different sort of artifact. In particular, the indel data includes that for several length-variable mononucleotide repeats (“microsatellites”). These were scored as unordered multistate characters according to repeat number. But these repeats are hypervariable. They may have phylogenetic signal at the lowest taxonomic levels, but not at deeper levels. It seems that *Oxyphyllum* was convergent with species of Subclades I and II in repeat number. And this is why this attraction disappears when the indel characters were excluded.

Ignoring the indel artifacts, as with the ITS data, the cpDNA data show *Oxyphyllum* in an essentially unresolved position within the *Leucheria* crown, with *Marticorenia* and *Spinoliva* as outgroups. However, unlike the ITS ML analysis, the cpDNA ML tree shows *Oxyphyllum* as part of a hard polytomy at the crown, viz. zero-length branches, with no evidence at all indicating that it is a sister group. The vegetative morphological distinctiveness of *Oxyphyllum* helps little in ascertaining its precise relation, since this is autoapomorphic. The main evidence for its phylogenetic exclusion from *Leucheria* is its patently shrubby habit, since all of the *Leucheria* lineages are herbaceous to, at best, suffrutescent (e.g., in *Polyachyrus*). In any case, as with ITS, I included *Moscharia* in a separate analysis of the *trnL-trnF* sequences. Again the data strongly supported a sister relation with *Marticorenia*, though with reduced support owing to the much lower amount of informative variation.

IV. DISCUSSION

The data analyzed here demonstrate unequivocally that *Polyachyrus* is nested within *Leucheria* and probably sister to *Leucheria* (caulescent) Clade B Subclade II of Jara-Arancio et al. (2017). The analysis also illuminates outgroup relations of *Leucheria*, demonstrating an extremely close relation with *Oxyphyllum* such that existing molecular evidence does not yet definitively exclude *Oxyphyllum* from the *Leucheria* crown. But the data do demonstrate that the outgroups of the crown include *Marticorenia* + *Moscharia* and *Spinoliva*. Previous molecular analyses (see above) that failed to find the relations demonstrated here either failed to sample all of the relevant outgroup taxa or sufficient species of *Leucheria*. Most notably, Luebert et al. (2009), based on analysis of (different) ITS and *trnL-trnF* sequences, illustrated a sister relation between *Polyachyrus* and two sampled *Leucheria* species, this clade in turn sister to *Oxyphyllum*. But the Bayesian posterior probabilities for these nodes were well below the canonical 95%

significance level [see Hershkovitz (2021) for discussion of bootstrap proportions and Bayesian posterior probabilities].

The present analysis used two data sources (nuclear and plastome), two datasets for each data source (with and without indel data), two optimization criteria (MP and ML), and two evaluation criteria (MP/ML resolution and MP bootstrap). The topologies obtained were substantially congruent. Incongruencies involving the central questions here, viz. intergeneric relations, were analyzed and explained. Analytical artifacts were identified, and accounting for these artifacts restored congruency. Incongruencies at other nodes were ignored here, but these can be resolved likewise. Indel data evidently added misleading homoplasy at deeper nodes, but similar incongruencies at shallower nodes might not be artifacts. Among closely related species, an indel might be the only sequence difference.

The analysis also uncovered marked ITS base compositional differences among the principal clades. This implies nonstationarity of the evolutionary process, which violates the principle assumption of standard and Bayesian ML analyses (see Hershkovitz, 2021). Hershkovitz (2021) argued that, in effect, there is no such a thing as a stationary evolutionary process, even when nonstationarity is not so conspicuous in a given data set. This is an axiom of the Principle of Evolutionary Idiosyncraticity consequent to evolution via Natural Drift (Maturana & Mpodozis, 2000; Mpodozis, 2022) consequent to autopoiesis (Maturana & Varela, 1972).

The present results greatly illuminate morphological and biogeographic evolution among the studied taxa. Most notably, Katinas et al. (2008) suggested that *Polyachyrus* and *Leucheria* were sister taxa, and later (Katinas & Forte, 2020; Katinas et al., 2022) cited Jara-Arancio et al.'s (2017) molecular analysis as the evidence for monophyly of *Leucheria*. Katinas emphasized that *Polyachyrus*, *Moscharia*, and several *Leucheria* Clade B species share secondary inflorescence heads viz. synflorescences or “pseudocephali,” while all but one other Clade B species manifest at least some anatomical evidence of pseudocephalic evolution. Meanwhile, the heads of all [sub(acaulescent)] Clade A species have “regular,” viz. monocephalic, inflorescences, like other Asteraceae generally. Because Katinas presumed that *Leucheria* was monophyletic, she reasoned that the pseudocephalic condition was ancestral in *Leucheria*, hence that monocephalia of Clade A species was secondary. It is not clear to me whether they believed that Clade A heads were truly monocephalic or, effectively, “pseudomonocephalic” via complete loss of the traits that would betray a pseudocephalic ancestry.

Perhaps contributing to the classical generic distinction between *Polyachyrus* and *Leucheria* is the form of the pseudocephalus. In *Polyachyrus*, it is distinctively (oblong-)globose, whereas both pseudocephali and monocephali of *Leucheria* appear relatively “flat” and spreading. The corolla in both genera is zygomorphic (“ray flowers”). But in *Leucheria*, the lower lip is rather long, whereas in *Polyachyrus*, it is much shorter and almost resembles a “disk flower” in its proportions. Also, *Polyachyrus* species are more suffrutescent than *Leucheria* species.

The present data explain pseudocephalia in *Polyachyrus* as homologous to that in *Leucheria* Clade B. At the same time, pseudocephalia characterizes one of the outgroup genera, *Moscharia*, which is sister to *Marticorenia*, which I presume to be monocephalic. I also presume that *Oxyphyllum* is monocephalic. Thus, while Katinas' observations prove to be highly insightful and phylogenetically significant, the hypothesis that pseudocephalia is ancestral in this clade proves to be problematic. The inclusion of *Polyachyrus* in Clade B now renders more parsimonious 2–3 origins of pseudocephalia rather than a higher number of reversals to the ultimately ancestral monocephalic condition.

Jara-Arancio et al. (2017; including M.T.K. Arroyo) tentatively concluded that the acaulescent habit (viz. of Clade A species) represents the ancestral condition in *Leucheria*. Given that the acaulescent habit is associated with the cooler/wetter alpine/steppe habitats of all Clade A species, this hypothesis implies that the alpine/steppe habitat also is ancestral, and that the lowland and often drier habitat of ca. half of Clade B species is derived. However, these conclusions do not follow from their phylogenetic estimate: (1) both of their outgroup taxa are caulescent; (2) one of them is lowland; and (3) their tree shows as unresolved (viz. < 50% Bayesian posterior probability) the relations among Clade A and the three Clade B subclades.

Pérez et al. (2020; including Jara-Arancio and Arroyo) later indeed asserted that the high elevation colder habitat was ancestral in *Leucheria*. This they interpreted using ML ancestral state reconstruction over the phylogenetic tree of Jara-Arancio et al. (2017) with the unsampled taxa pruned. The tree they illustrated (Pérez et al., 2020: Fig. 2) is unrooted, but drawn so that Clade A appears to be the “basal” lineage. They failed to note that more than half of the nodes in their presumed phylogeny were supported at less than the canonical 95% posterior probability significance level in Jara-Arancio et al. (2017), and most of these much less than that.

Pérez et al. (2020) also reported that, according to Hershkovitz et al. (2006), the *Chaetanthera*-*Oriastrum* clade (Mutiseae) also had a high Andean origin. Hershkovitz et al. (2006; again including M.T.K Arroyo) made no such claim. Quite to the contrary, Hershkovitz et al. (2006; see also Hershkovitz, 2021) demonstrated that the exclusively alpine genus *Oriastrum* must have originated at much *lower* elevations, because the alpine habitat did not exist at its time of origin. The ascent of *Oriastrum* to alpine habitats was consequent to subsequent orogenic events. Meanwhile, *Chaetanthera* s. str. had a low elevation origin, with the alpine species being derived. Arroyo really needs to read her publications.

The present analysis sheds some light on the ancestral habitat of *Leucheria*. Among the outgroups, only the suffrutescent *Marticorenia* occurs at high elevations. Its sister, *Moscharia*, along with *Spinoliva*, occur in low elevation and relatively arid habitats. *Oxyphyllum* likewise is a low elevation arid habitat species. *Leucheria* Clade A comprises exclusively alpine/steppe species but, their monocephalic heads notwithstanding, their acaulescent form must be considered derived. Notably, the molecular data show this clade as comprising a crown of genetically closely related sequences subtended by a relatively long branch. Meanwhile, sequences of the caulescent Clade B species diverge much closer to the *Leucheria* crown. This divergence geometry resembles that of *Chaetanthera-Oriastrum*, except that this diversification seems to be much younger (see Pasini et al., 2016). This is consistent with the notion that both the habit and habitat of Clade A species is more recently derived.

Meanwhile, Clade B includes both high and low elevation species. The phylogenetic evidence provides no basis to conclude that the high elevation habitat is ancestral, given the outgroup habitats. Phylogenetic habitat reconstruction is required. Notably, addition of the low elevation *Polyachyrus* lineage to the equation should favor a low elevation origin for Subclade II, while Subclade I is low elevation. Subclade III itself includes two subclades, one with three low elevation species and the other larger but polymorphic. Phylogenetic resolution within the latter is poor, but there is no evidence that the high elevation condition is ancestral, and there is some evidence for high-low elevation species pairing. Overall, the evidence thus suggests that the ancestral habitat of Subclade III also is low elevation. Thus, the ancestral habitat in the *Leucheria-Oxyphyllum* clade is low elevation and probably also relatively warm and arid, with higher elevation, cooler, and more humid habitats being derived.

V. NEW COMBINATIONS IN *LEUCHERIA*

Given the evidence for phylogenetic nesting of *Polyachyrus* in *Leucheria*, species of the former should be transferred to the latter, as follows:

Leucheria annua (I.M.Johnst.) Hershk., comb. nov. BASIONYM: *Polyachyrus annuus* I.M.Johnst., Contr. Gray Herb. 85: 134. 1929.

Leucheria carduoides (Phil.) Hershk. comb. nov. BASIONYM: *Polyachyrus carduoides* Phil., Fl. Atacam. 28. 1860.

Leucheria cinerea (Ricardi & Weldt) Hershk., comb. nov. BASIONYM: *Polyachyrus cinereus* Ricardi & Weldt, Gayana, Bot. no. 26: 26. 1974.

Leucheria fusca (Walp.) Hershk., comb. nov. BASIONYM: *Polyachyrus fuscus* Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 288. 1843.

Leucheria duraniana Hershk., nom. nov. BASIONYM: *Polyachyrus gayi* J.Rémy, Fl. Chil. [Gay] 3(3): 372. 1848. HOLOTYPE: Chile, Coquimbo Prov. Oct. 1836, *C. Gay 173* (P: P00283285 {image!})

Polyachyrus gayi and *Leucheria gayana* both honor Claudio Gay. The difference is in their form: the former is substantive and the latter is adjectivial (Nicolson, 1974). Conventionally, the latter is purely honorific, while the former indicates a direct role of the honoree in recognition of the taxon. Nonetheless, the epithets essentially yield homonyms when applied in the same genus (Art. 53 of the ICN; Turland et al., 2018) and, in any case, otherwise likely are to be confused. The new name honors Dr. José Elias Durán Lima and his wife, Susana Yolanda Roa Ferreira, and family. For four years, we were close neighbors on a street in Santiago's Barrio República, where I had lived in a rented room in a house and otherwise survived by daily harvesting of food from garbage containers on the street, often lunches that students receive for free and throw away. Unexpectedly, the room became unavailable, and I could find no suitable and affordable alternative. This jeopardized my ongoing research. Dr. Durán and his family kindly invited me to stay in their summer home in Isla Negra, where I have spent the past six months. Here, I was able to continue my existing projects and initiate new ones, the present one in particular. Thus, Dr. Durán and his family played a critical role in the discovery of the relations of *Polyachyrus*, and it is fitting that they be so honored.

Leucheria poeppigii (Kunze ex Less.) Hershk. comb. nov. BASIONYM: *Polyachyrus poeppigii* Kunze ex Less., Linnaea 5(1): 5. 1830.

Leucheria sphaerocephala (D.Don) Hershk., comb. nov. BASIONYM: *Polyachyrus sphaerocephalus* D.Don, Trans. Linn. Soc. London 16(2): 230. 1830.

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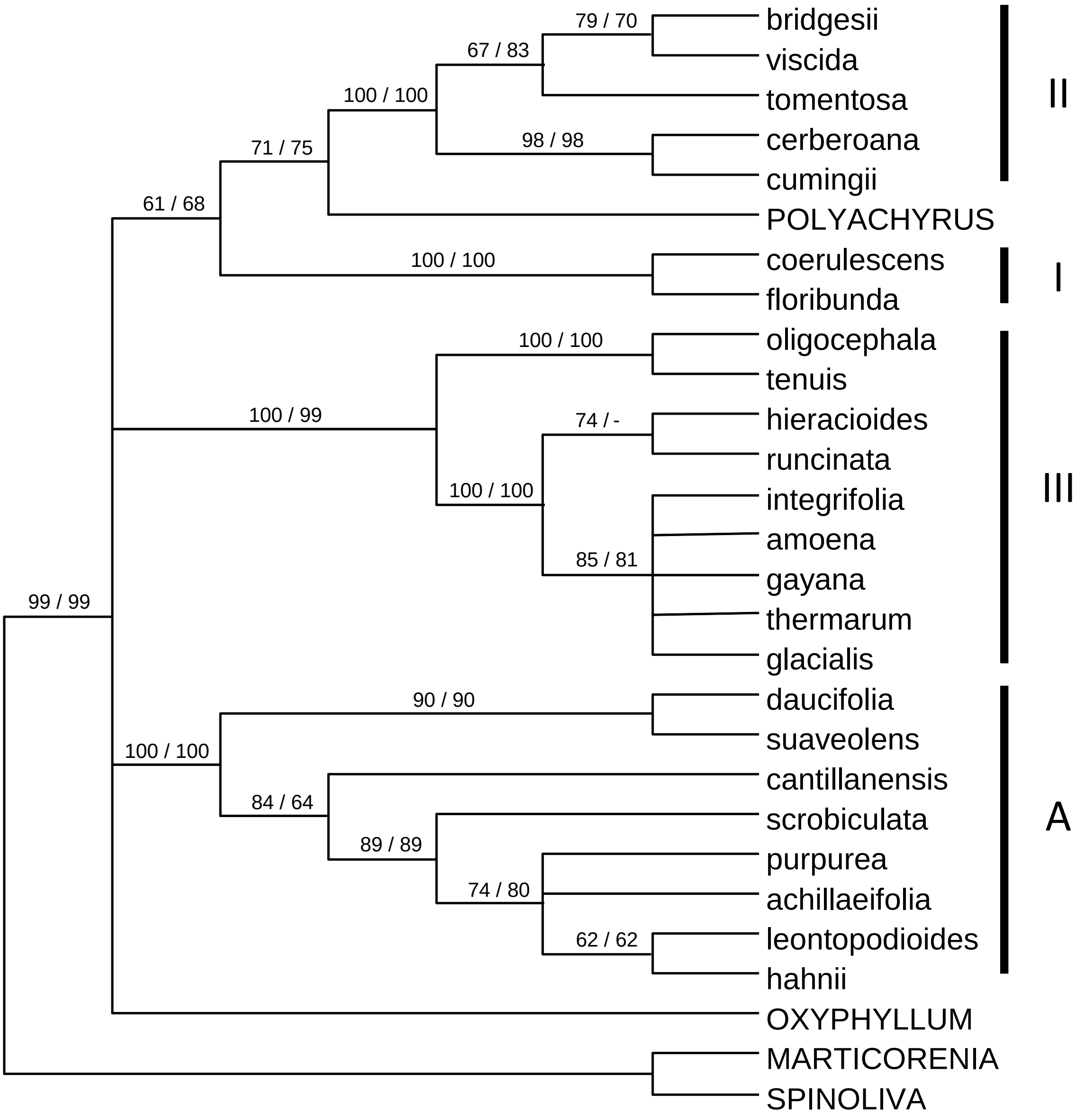

Fig. 1. MP bootstrap consensus for combined ITS and cpDNA data. Numbers above the branches correspond to bootstrap support with/without indel data. All branches occur also in the MP consensuses. Names in lower case correspond to *Leucheria* species epithets used for the same sequences in Jara-Arancio et al. (2017). Names in upper case correspond to samples of other genera. Labelled bars to the right correspond to *Leucheria* Clade A and (Clade B) Subclades I, II, and III of Jara-Arancio et al. (2017).

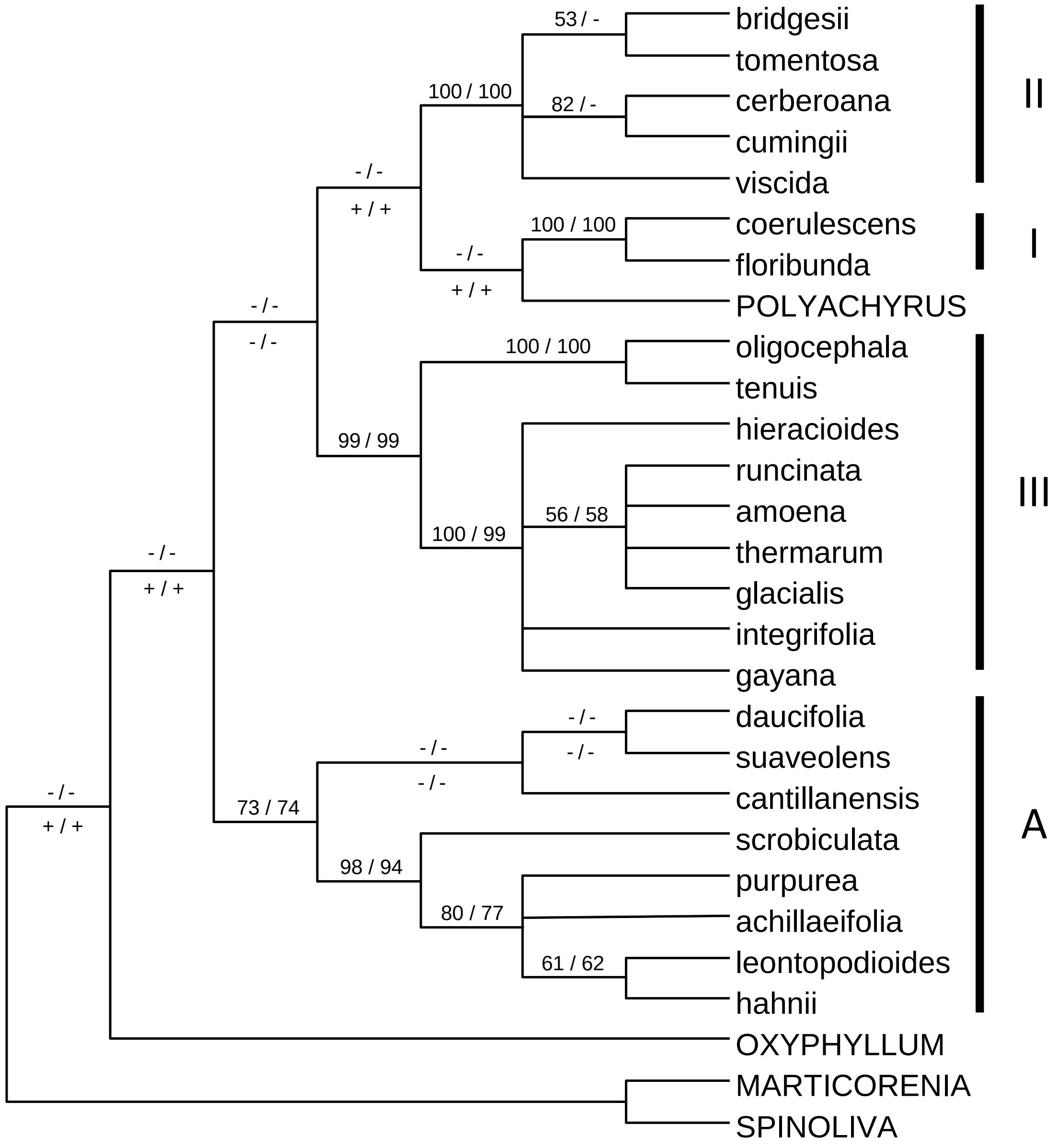

Fig. 2. Consensus of 25 ML trees for the ITS data. Numbers above the branches correspond to MP bootstrap support with/without indel data. Symbols below selected branches correspond to the presence of the branch in MP consensuses with/without indel data. All other branches were present in both consensuses. Names in lower case correspond to *Leucheria* species epithets used for the same sequences in Jara-Arancio et al. (2017). Names in upper case correspond to samples of other genera. Labelled bars to the right correspond to *Leucheria* Clade A and (Clade B) Subclades I, II, and III of Jara-Arancio et al. (2017).

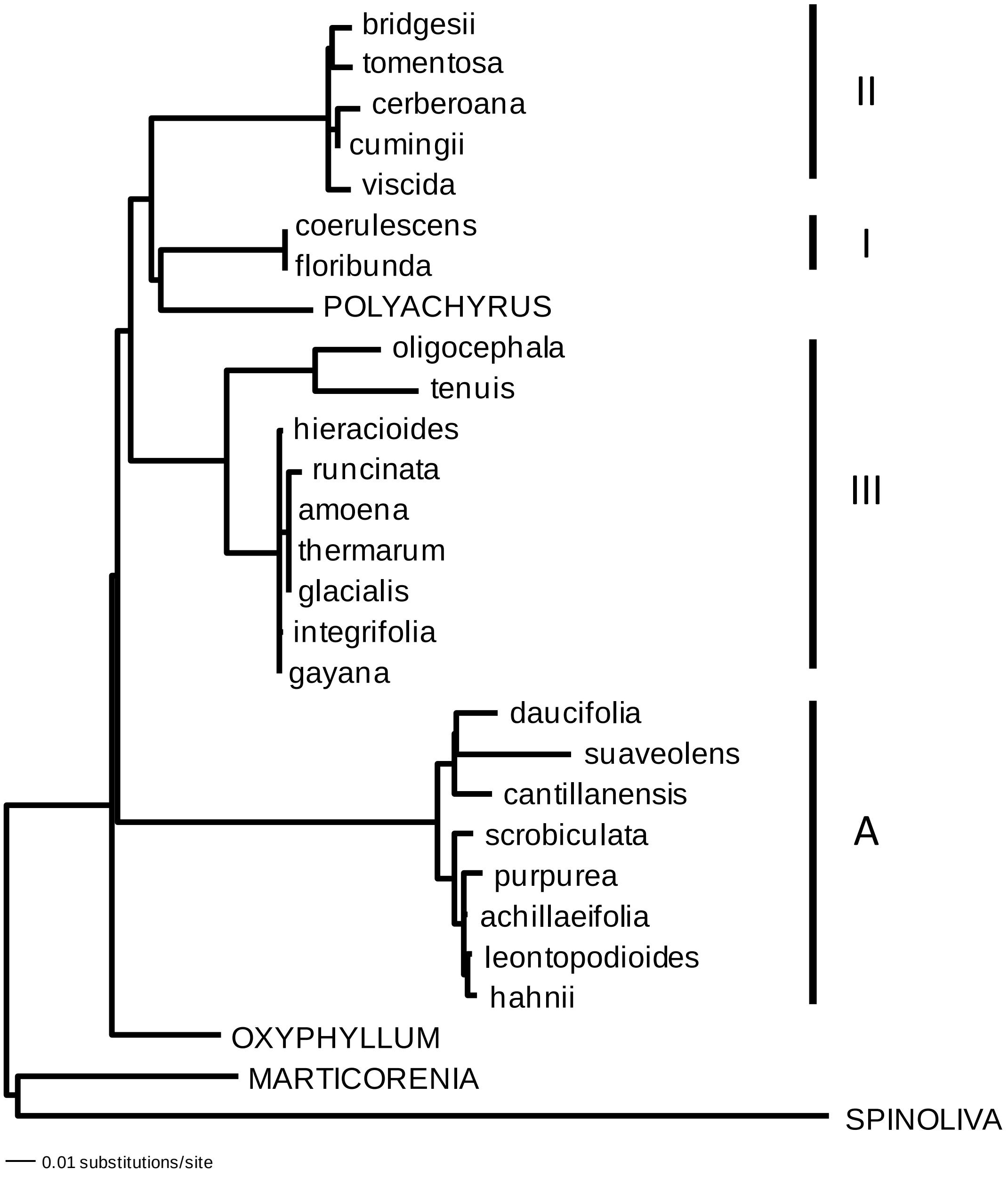

Fig. 3. Phylogram of one of 25 ML trees for the ITS data. Note the very short branches at the base of the tree and the very long branches of the Clade A stem and *Spinoliva*. Names in lower case correspond to *Leucheria* species epithets used for the same sequences in Jara-Arancio et al. (2017). Names in upper case correspond to samples of other genera. Labelled bars to the right correspond to *Leucheria* Clade A and (Clade B) Subclades I, II, and III of Jara-Arancio et al. (2017).

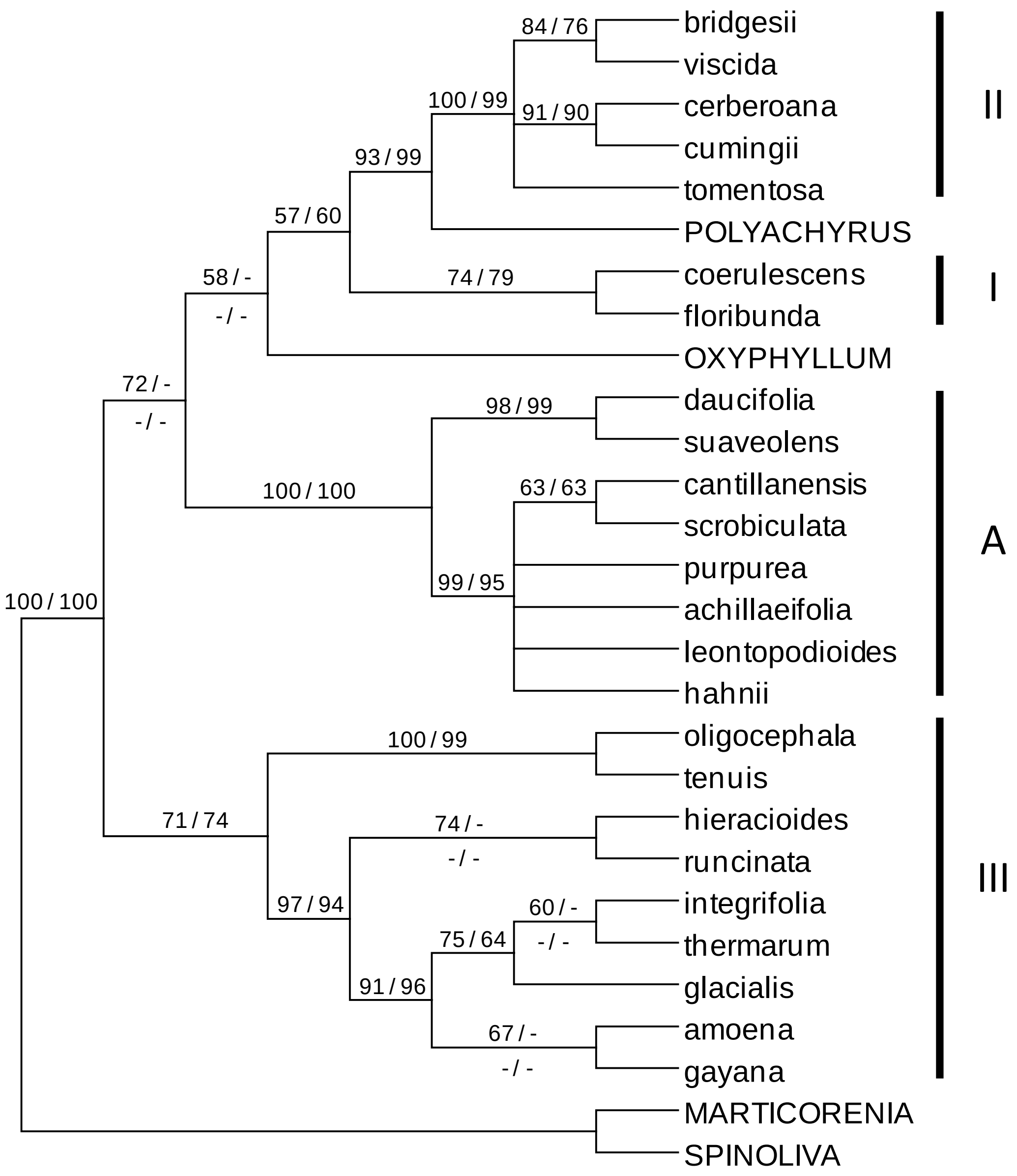

Fig. 4. MP bootstrap consensus for the cpDNA data with indels included. Numbers above the branches correspond to bootstrap support with/without indel data. Symbols below the branches correspond to the presence of the branch in ML/MP strict consensuses. Note that several branches are present only in the MP analysis with indel data included. Names in lower case correspond to *Leucheria* species epithets used for the same sequences in Jara-Arancio et al. (2017). Names in upper case correspond to samples of other genera. Labelled bars to the right correspond to *Leucheria* Clade A and (Clade B) Subclades I, II, and III of Jara-Arancio et al. (2017).

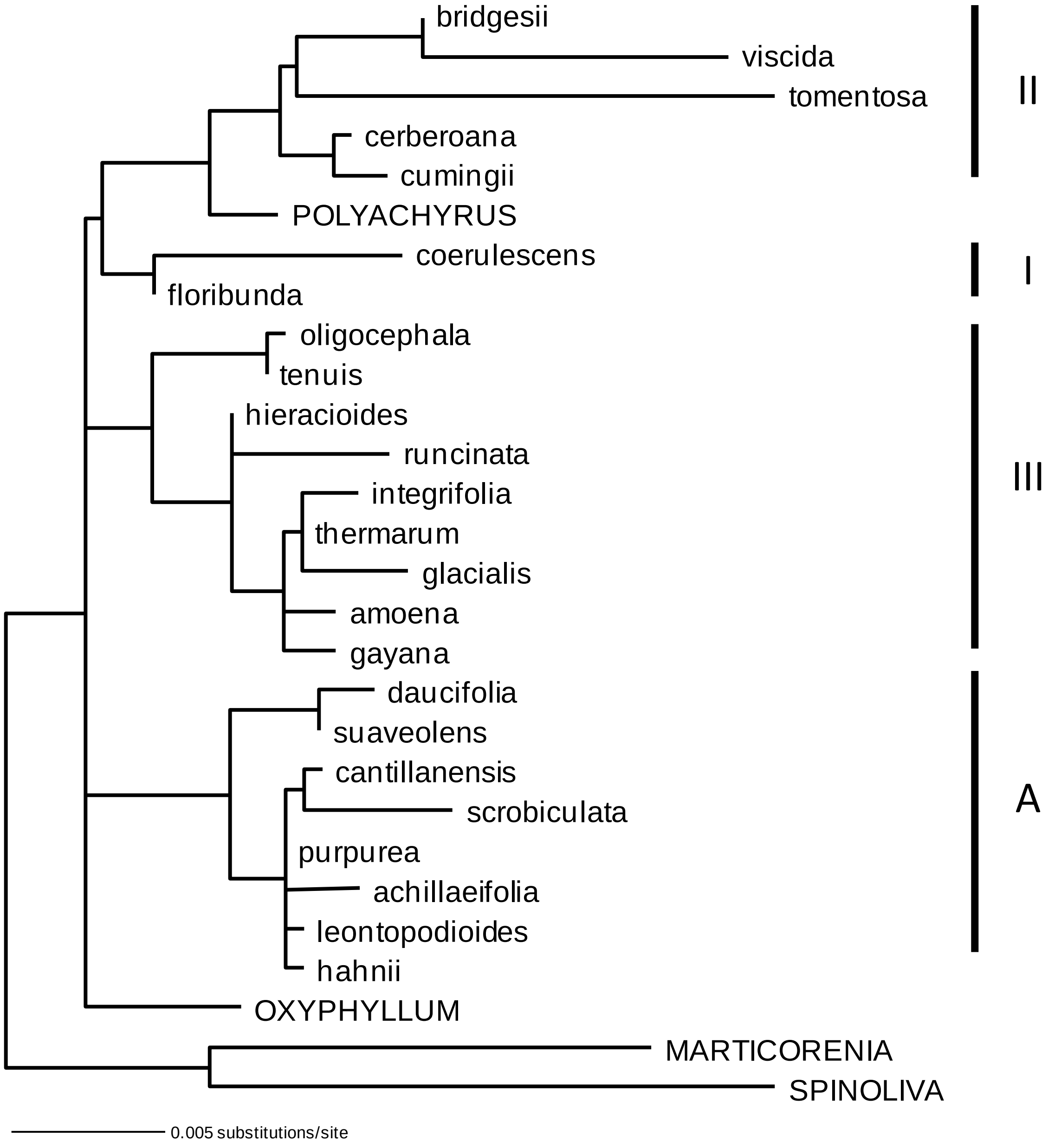

Fig. 5. Phylogram of the single ML tree for the cpDNA data. Note the zero-length branches at the base of the tree. Names in lower case correspond to *Leucheria* species epithets used for the same sequences in Jara-Arancio et al. (2017). Names in upper case correspond to samples of other genera. Labelled bars to the right correspond to *Leucheria* Clade A and (Clade B) Subclades I, II, and III of Jara-Arancio et al. (2017).